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**Zooplankton communities in small Waikato lakes and ponds:
are natural waters and farm dams the same?**

A thesis

submitted in partial fulfilment

of the requirements for the degree

of

Master of Science in Ecology and Biodiversity

[Faculty of Science and Engineering]

at

The University of Waikato

by

KELLY LE QUESNE



THE UNIVERSITY OF
WAIKATO
Te Whare Wānanga o Waikato

2019

Abstract

Ponds have been identified as biodiversity ‘hotspots’ that play an important role in supporting and maintaining biodiversity. In freshwater ecosystems, zooplankton are an essential trophic link between algae and fish, and some species act as biological indicators for aquatic system ‘health’. Most research pertaining to zooplankton biodiversity and community assemblages is skewed towards large lakes, reservoirs or urban ponds, while research on small ponds in rural environments is scarce. Consequently, the aim of my research was to examine and compare the biodiversity and community composition of zooplankton in natural ponds and dams in rural environments. To achieve this, 19 farm dams and 19 natural farm ponds in the Waikato region, New Zealand, were sampled for zooplankton in winter/spring (Aug-Sep 2018) and summer (Jan 2019). Environmental factors also were measured, including water temperature, dissolved oxygen, conductivity, water colour (gilvin), pH, chlorophyll-*a*, nutrient concentrations (total nitrogen and phosphorus), elevation, pond surface area and the number of waterbodies within a 2 km radius.

All ponds were eutrophic to hypertrophic, and genera typical of these environments, such as *Brachionus*, *Keratella* and *Polyarthra*, were common in both farm dams and natural ponds. Zooplankton species richness was similar among farm dams and natural ponds (20.7 and 22.4 species, respectively; t-test $p = 0.406$), although there was a lot of variation within each pond type. Temperature (stepwise linear regression $R^2 = 0.26$; $p = 0.025$) and pond surface area (stepwise linear regression $R^2 = 0.23$; $p = 0.016$) were significant predictors of species richness in natural ponds; however, no significant relationships could be found between the measured environmental variables and species richness for farm dams. Zooplankton community composition differed between farm dams and natural ponds (one-way ANOSIM $p = 0.014$). A SIMPER analysis indicated that crustaceans (e.g., *Chydorus* sp., *Acanthocyclops robustus* and *Simocephalus vetulus*) were generally more abundant in natural ponds than in farm dams, whereas rotifers (e.g., *Polyarthra dolichoptera* and *Keratella tecta*) were more abundant in farm dams than in natural ponds. A canonical correspondence analysis indicated that variation in zooplankton community composition among natural ponds was explained by dissolved oxygen concentration ($p = 0.002$) and conductivity levels ($p = 0.020$). In

contrast, the community composition of zooplankton in farm dams could not be explained by any of the measured environmental variables. Two genera (*Erignatha clastopis* and *Octotrocha speciosa*) and one species (*Cephalodella theodora*) were recorded that had not previously been identified in New Zealand. In total, three non-indigenous species were recorded in 7% of farm dams and 2% of natural ponds studied.

My findings suggest that zooplankton communities differ between farm dams and natural ponds. Farm dams are primarily composed of a relatively unstructured subset of small, eurytopic and opportunistic zooplankton species (e.g., of *Brachionus* and *Keratella*). On the other hand, natural pond assemblages consisted of larger zooplankton species that are better adapted to the local conditions (e.g., *Chydorus* sp. and *Simocephalus vetulus*). This suggests natural ponds have had a longer period of time for more slowly dispersing species to colonise, whereas farm dams contain species that are capable of dispersing at much faster rates. Further, my results highlight that when examining environmental determinants of zooplankton community composition in water bodies across the landscape, natural and constructed ponds should be separated, as they appear to be structured by different variables. The prevalence of non-indigenous species in farm dams appears low relative to lakes and urban ponds in New Zealand, likely due to limited movement between ponds by humans. This suggests that these waterbodies are not acting as ‘stepping stones’ for non-indigenous species across rural landscapes. Overall, my research highlights the diverse taxa found in small agricultural ponds, and improves our knowledge and understanding of zooplankton communities in small natural and constructed ponds. Further, these findings emphasize the need for management and conservation of small water bodies, as they play a significant role in maintaining and supporting zooplankton communities (including rare species).

Acknowledgements

A big thank you to my academic supervisor, Ian Duggan! Thank you for all of your expert advice and support for the past year and a half. I have learnt so much about zooplankton and their environments, and am very grateful for your patience and guidance (without it I am sure that I would still be staring down that microscope!). I have thoroughly enjoyed working with you.

A special thanks to the landowners and farm managers for allowing me to study their ponds. I couldn't have done it without you (literally)!

Cheers! To all of my field assistants – Anita Pearson, Scott Le Quesne, Ryan Le Quesne, Raewyn Le Quesne, Georgina Flowers, Ruth Barrow, Kit Squires, Heather Taitibe, Shaun Sanders and Laura Francis – I really appreciate you all lending a hand and making my fieldwork all the more enjoyable, whilst also learning a little about zooplankton yourselves!

I would also like to thank Melissa Collins, Anita Pearson, Ashley Wade, Colin Le Quesne and Brydget Tulloch for proof reading parts of my thesis – fresh eyes make all the difference. My gratitude also extends to Sophie Coenen, who provided expert advice and guidance on the use of Esri ArcMap GIS. A special thank you to Cheryl Ward for helping me with thesis formatting. It wouldn't be a research project without the technicians. Thank you to Bex Gibson, Lee Laboyrie and Warrick Powrie for the countless lab inductions and equipment trainings.

Thank you to Deniz Özkundakci from the Waikato Regional Council (WRC) for providing the WRC lakes database and supporting this project. Also a huge thank you to the University of Waikato Postgraduate Taught Scholarships and Research Masters scholarship, the WRC Study Award and the Waikato Graduate Women Education Trust Masters Study Award for financially supporting my postgraduate education and research.

Last but not least, thank you to the R block crew at the University of Waikato, flatmates, friends and family for all of the laughs, yarns and good times. Most importantly thank you for supporting me throughout my studies. You're awesome!

Once again, thanks to you all, Kelly.

P.s. I know you will all DEFINITELY read my thesis once it is completed 😊.

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Chapter 1

Introduction

1.1 Small water bodies in rural landscapes

On a global scale, there are approximately 304 million lakes and ponds (area between 0.0025 km² and 378,119 km²) covering approximately 4.2 million km² in area, across a broad biogeographical range, from high alpine areas to dry lowland floodplains (Downing *et al.*, 2006). Of these, the vast majority – almost 280 million water bodies – are less than 1 ha (Downing *et al.*, 2006; Downing, 2010). Constructed farm impoundments are common across rural landscapes and have been created by damming small portions of natural streams to collect water. Farm dams provide stock water and crop irrigation, and are used recreationally by waterfowl hunters (Brönmark & Hansson, 2002). Farm dams are rarely mapped and, as such, the exact numbers of small farm dams are unknown. Nevertheless, advances in global imagery over the past decade show that their surface area is significant, adding approximately 77,000 km² of standing water to the global pondscape (network of ponds) (Downing *et al.*, 2006). Consequently, small lakes and ponds, including constructed water bodies on farms, have been frequently overlooked in limnological studies due to the wide belief that these systems are of negligible importance (Brönmark & Hansson, 2002; Biggs *et al.*, 2005).

Globally and domestically, research and sampling effort on small lakes and ponds lags behind larger waterbodies (Wagner *et al.*, 2008). Further, definitions of what constitutes a pond are broad and arbitrary. De Meester *et al.* (2005) provides a very broad definition, where ponds are considered small and shallow water bodies; no upper size limit was provided by these authors, because they argued that delineation was too arbitrary, as shallow lakes and small ponds share many characteristics that make them hard to distinguish, and that they merely represent a gradient in ecological conditions (De Meester *et al.*, 2005; Søndergaard *et al.*, 2005). However, Hamerlík *et al.* (2013) argue that separating ponds and lakes at approximately 2 ha water surface area is relevant to ecological thresholds (e.g., benthic macroinvertebrate species-area relationships changed significantly at 2 ha surface area in central Europe). Simple size-based definitions are often used to define ponds

(Biggs *et al.*, 2005; Oertli *et al.*, 2009). For example, Biggs *et al.* (2005) define a pond as water bodies between 0.0001 ha and 2 ha in surface area, which may be permanent or seasonal, including both man-made and natural water bodies.

Recent research has demonstrated that small lentic habitats, and the network of ponds, provide an array of ecosystem services including carbon cycling, hydrological regulation, sedimentation control, and contribution to ecological and biodiversity values (Oertli *et al.*, 2009; Boix *et al.*, 2012; Mimouni *et al.*, 2018). Pond habitat heterogeneity and variation in environmental conditions means that these water bodies often support higher diversities of species compared to larger lakes. Ponds have been considered “biodiversity hotspots” for invertebrate species in Europe (Davies *et al.*, 2008) and Asia (Chen *et al.*, 2019), and often contain rare and/or threatened species. For example, 37 farm ponds in France contained 40% of the regions’ species pool of Odonata (dragonflies), including 7 rare and 26 common species (Ruggiero *et al.*, 2008). The biodiversity of artificial ponds is thought to equal that of natural ponds and can even enhance pondscape resilience by providing complementary habitats for colonisation (Deacon *et al.*, 2018). For example, Apinda Legnouo *et al.* (2014) surveyed only 18 artificial ponds and recorded 37 genera and 57 species of aquatic beetles and bugs. Additionally, Australian farm dams had a higher average macroinvertebrate species richness than nearby streams (Brainwood & Burgin, 2009). Casas *et al.* (2012) compared morphological and environmental factors of farm ponds and wetlands in Andalusia, Spain, and proposed that farm ponds likely play an important role in conserving and enhancing regional diversity levels, but highlight that further research on farm ponds is required.

Despite growing concerns for the conservation of ponds, most legislation and environmental protection policies, globally, are aimed at larger water bodies; as such, there is a lack of protection and conservation of small water bodies throughout the world. For example, in Australia, pond habitats are not covered by the national-scale Environment Protection and Biodiversity Conservation Act, 1999 (EPBC Act., 1999). Similarly, in the United States, the Clean Water Act does not encompass pond ecosystems (U.S. Environmental Protection Agency and U.S. Department of

the Army., 2015). The New Zealand Policy Statement for Freshwater Management (NZPS-FM) is a guide for local authorities to ensure that responsible management of freshwaters is carried out under the Resource Management Act 1991 (Ministry for the Environment, 2017); as stated by the NZPS-FM, a “freshwater management unit is the water body, multiple water bodies or any part of a water body determined by the regional council as the appropriate spatial scale for setting freshwater objectives and limits for freshwater accounting and management purposes” (Ministry for the Environment, 2017). Consequently, the management of freshwater bodies is at the discretion of regional councils, and large water bodies have received far more research and monitoring attention than ponds by these agencies. Furthermore, the legislations described above do not incorporate farm dams, potentially due to a lack of knowledge of the values or significance of this pond type. Increasing research effort pertaining to biodiversity values of farm dams and natural ponds could be used to encourage pond conservation, while also broadening our understanding of pond ecology. For example, my research will be contributing to the Waikato Regional Council (WRC) lake/pond database, for use in future environmental monitoring or environmental management. Contribution to the WRC lakes database is particularly important as natural ponds are under-represented, and farm ponds are unrepresented in this database. Furthermore, these water bodies are under-represented in New Zealand literature in general, and my research aims to fill that current knowledge gap.

1.2 Importance of zooplankton

Globally, invertebrates make up 99% of animal biodiversity (Lydeard *et al.*, 2004). The diversity of freshwater lakes, ponds and large rivers are dominated by zooplankton communities, with more than 70,000 species described globally (Brönmark & Hansson, 2002). Although typically small in size, the biodiversity of invertebrates is essential for supporting and maintaining ecosystem functioning. Based on their trophic position in food webs, zooplankton can play a significant role in sustaining higher trophic levels (i.e., fish) and controlling algal growth (Elser & Goldman, 1991; Jeppesen *et al.*, 2011). The significance of zooplankton in the food web was illustrated by a study of eight lakes in Brussels, Belgium, where the main factor causing an ecosystem shift from a turbid, algal dominated state to a clear-water state was an increased level of phytoplankton grazing by cladocerans

following removal of fish from the system (Peretyatko *et al.*, 2009). This is a common phenomenon, which has been demonstrated in many experimental and field studies (e.g., Theiss *et al.*, 1990; Sommer *et al.*, 2001; Symons *et al.*, 2012; Jurczak *et al.*, 2019). Based on their trophic position and sensitivity to the environment, zooplankton are highly recommended for ecological assessments and have been included in a variety of biotic indices to assess the health of aquatic ecosystems (Jeppesen *et al.*, 2011).

1.2.1 Biological indicators

Bioindicators are regularly used as a tool to assess water quality changes in streams, lakes and ponds. They provide integrated information regarding the physical, chemical and biological factors within the water body (Gannon & Stemberger, 1978; Duggan *et al.*, 2001a; Jeppesen *et al.*, 2011; Jurczak *et al.*, 2019). In some cases, cladocerans and copepods are used as indicators (Webber *et al.*, 2005). However, the use of microcrustaceans as indicators is commonly limited in freshwaters because of their low diversity relative to marine environments, thus rotifers are commonly considered better in freshwater systems (Duggan *et al.*, 2001b; Wallace, 2002). Rotifers are a diverse phylum with approximately 2000 species recognised globally (Segers, 2008), and more than 480 species have been recorded in New Zealand since 1859 (Shiel *et al.*, 2009). Predominantly filter- or suspension-feeders, rotifers have a unique sensitivity to changes in food type or density based on changes in environmental variables (e.g., nutrient concentrations) along trophic gradients (Siegfried *et al.*, 1989; Duggan *et al.*, 2001b; Duggan *et al.*, 2002). Jeppesen *et al.* (2000) drew attention to the sensitivity of rotifers to the environment following their study on 71 shallow Danish lakes, where they identified that zooplankton composition varied among lakes in association with variability in total phosphorus concentrations. These examples emphasize the important role of zooplankton communities in freshwater environments around the globe.

1.2.2 Algae and bacteria processing

Ponds are often subject to human pressures and intensive agriculture, which is a major driver of zooplankton biodiversity and water quality degradation (Brönmark & Hansson, 2002). Intensive agriculture and human activity have been the primary

causes of eutrophication in water bodies around the globe. Dodson *et al.* (2005) conducted a study on zooplankton community composition from 73 shallow lakes in south-eastern Wisconsin, USA, and found zooplankton species richness was lower in agricultural and urban environments compared to natural ('pristine') reference sites. However, experimental and field studies show that zooplankton can reduce the effect of water quality degradation via the control of algal blooms (Gerasimova & Pogozhev, 2002; Pogozhev & Gerasimova, 2005).

Cladocera have been observed to control algal biomass in lakes and ponds, and improve water quality. For example, Lampert *et al.* (1986) demonstrated that grazing by zooplankton sufficiently controls algae biomass in time-over-lapping enclosure experiments. Multiple studies show that herbivorous zooplankton can effectively control phytoplankton biomass and maintain a clear-water state, but highlight that differences in zooplankton communities influences the grazing pressure exerted on phytoplankton (e.g., Theiss *et al.*, 1990; Kagami *et al.*, 2002; Gerasimova *et al.*, 2018). Few studies examining these interactions have been undertaken in farm dams and ponds; Gerasimova *et al.* (2018) concluded that in agricultural ponds, *Daphnia longispina* was able to suppress algal blooms in the absence of planktivorous fish. All of these studies show similar patterns where, in the absence of planktivorous fish, larger zooplankton are able to regulate algal populations. Further, Eivers *et al.* (2018) indicated that zooplankton communities in wetland treatment ponds may help process algae and bacteria. In New Zealand constructed treatment wetlands, a high abundance of bdelloid rotifers, which are mostly bacterivorous, indicated that these species were likely to improve water quality via the reduction in bacterial contamination to receiving sites. These examples highlight the importance of understanding zooplankton community composition in natural ponds and farm dams. Improving our knowledge of species assemblages in farm dams may allow landowners to promote and manage zooplankton communities to improve water quality. Maintaining healthy waters and waterways is of high priority to the agricultural sector, domestically and internationally. My research can provide important information to farm owners, their advisors and interested industry participants, regarding the water quality parameters and pond health for both natural and constructed waters on their properties. Consequently, this could offer valuable insights into water and land

management that may be required. When collated, the data from this research will be made available to the farmers involved in the study, and others, giving them the opportunity to examine their own ponds and comparable benchmarks.

1.3 Zooplankton and constructed waters

Despite its ecological importance, zooplankton biodiversity remains under-represented in global pond research. Given the spatial extent of artificial water bodies globally, it is surprising that biotic and abiotic assessment of these water bodies remains understudied. Many aquatic ecology studies concentrate on fish or macroinvertebrates (e.g., Williams *et al.*, 2004; Davies *et al.*, 2008). Those that do include zooplankton surveys have typically focused on larger sized zooplankton (e.g., Cladocera and Copepoda) (Pace & Orcutt, 1981; Gerasimova *et al.*, 2018), and their interactions with environmental factors or other ecological processes (e.g., predation on smaller zooplankton or grazing on algae) (Duggan *et al.*, 2002; Dodson *et al.*, 2009), rather than the biodiversity values of communities. Similar to other limnological studies, most research pertaining to zooplankton biodiversity is skewed towards large natural lakes (Havens & Beaver, 2011), large reservoirs (Pinto-Coelho *et al.*, 2005; Goswami & Mankodi, 2012), or urban ponds (de Paggi Susana *et al.*, 2008; Mimouni *et al.*, 2015), and research on farm dams is scarce. In addition, few studies have considered whether observed trends in natural lakes apply to ‘artificial’ water bodies. For example, Merrix-Jones *et al.* (2013) conducted a global meta-analysis that focused on zooplankton communities in artificial and natural lakes. These authors concluded that species richness in artificial lakes was comparable to that of natural lakes, but that zooplankton communities differed between the lake types. In New Zealand, a comparison of 23 constructed lakes and 23 natural lakes found similar species richness between lake types, but also identified differences in zooplankton community composition (Parkes & Duggan, 2012). The above studies suggest that constructed farm dams may play a significant role in enhancing biodiversity by supporting different communities than natural ponds. My research will, locally and globally, improve and broaden our understanding of zooplankton composition in small natural and constructed ponds.

1.3.1 Constructed waters and non-indigenous species

One of the key threats to zooplankton biodiversity is the invasion by non-indigenous species. Non-native zooplankton species have invaded lakes across the globe. For example, from the early 1990s, there have been at least 6 records of cladocerans and 21 copepods invading North American freshwater and estuarine environments (Havel & Medley, 2006). The introduction of non-indigenous zooplankton can have significant impacts on native biodiversity values. For example, the Eurasian cladoceran *Bythotrephes longimanus* invaded the Great Lakes and 50 other water bodies within their vicinity; a rapid loss in zooplankton species richness has subsequently been observed, particularly of cladoceran taxa (Yan *et al.*, 2002). In New Zealand, over one-third of non-indigenous species in standing freshwater are zooplankton, and the invasion rate in constructed waters is disproportionately high (Banks & Duggan, 2009; Branford & Duggan, 2017; Duggan & Collier, 2018). The growing number of non-native zooplankton is indicative of their dominance as an invading taxonomic group.

High biodiversity levels are proposed to increase the resilience of ecosystems to environmental changes, anthropogenic impacts and invasions by non-native species (Kennedy *et al.*, 2002; Havel *et al.*, 2005; Daleo *et al.*, 2009). Artificial water bodies are relatively recent additions to the landscape and have had less time to accumulate species (Havel *et al.*, 2005), suggesting that these waters would be more susceptible to invasions owing to low biotic resistance. Parkes & Duggan (2012) argue that the absence of locally well-adapted zooplankton species and the presence of opportunistic species in constructed lakes is a significant factor contributing to the prevalence of non-native species. For example, Taylor & Duggan (2011) demonstrated in experimental ponds that in the absence of native calanoid copepods, the North American *Skistodiaptomus pallidus* was able to establish, indicating that biotic resistance could be important for reducing the establishment of non-native species. Likewise, Dzialowski (2010) found that the presence of key species, such as cladoceran *Daphnia magna*, provided resistance to the establishment of non-native *Daphnia lumholtzi* in experimental mesocosms. These findings suggest that the high frequency of non-indigenous species in constructed waters may be due to the absence of specific 'key' species in zooplankton communities.

At a regional level, ponds (natural and artificial) have been demonstrated to act as discrete habitat patches and ‘stepping stones’ to facilitate the movement of various species across the landscape (Hassall, 2014). Constructed water bodies are also considered to aid in, and sometimes increase, the rate of establishment and spread of non-indigenous species, by providing additional habitats (Kolar & Lodge, 2001; Havel *et al.*, 2005; Parkes & Duggan, 2012; Mimouni *et al.*, 2018). There are many examples globally of zooplankton preferentially invading constructed aquatic habitats. For example, *Eurytemora velox* (typically found in brackish areas of estuaries in the British Isles) was recorded in 23 constructed waters well inland of the coast, suggesting that artificial water bodies have facilitated the invasion of these euryhaline calanoid copepods into freshwaters across England (Duggan & Payne, 2017). Johnson *et al.* (2008), observed that the spiny water flea *Bythotrephes longimanus* invaded constructed water bodies at a faster rate compared to natural lakes in the Laurentian Great Lakes region. Another commonly cited zooplankton invasion is that of the cladoceran *Daphnia lumholtzi*. Originating from the tropics, this species invaded a Texan reservoir in 1990 and proceeded to spread and establish in a further 125 US lakes, primarily in constructed reservoirs (Havel & Hebert, 1993; Havel & Medley, 2006). Finally, Banks & Duggan (2009) concluded that a variety of constructed water bodies (e.g., farm ponds, ornamental ponds, reservoirs and retired mines) had aided the establishment and spread of non-indigenous calanoid copepods throughout the North Island, New Zealand.

The number of non-indigenous invertebrate species have increased in New Zealand lacustrine systems since the year 2000, with an estimated 34% being non-native zooplankton (Duggan & Collier, 2018). Of the eight non-native zooplankton species present in New Zealand, three are daphnids (*Daphnia galeata*, *D. obtusa* and *D. pulex*) and five are calanoid copepods (*Boeckella symmetrica*, *B. minuta*, *Calamoecia ampulla*, *Sinodiaptomus valkanovi* and *Skistodiaptomus pallidus*) (Duggan & Collier, 2018). Invaders, such as *D. galeata* and calanoid copepods, have become widely distributed across the North Island of New Zealand, and have been recorded in lake areas that are widely geographically separated. For example, *D. galeata* was first recorded in 1993 in Hamilton Lake, Waikato, but since then has become established in other Waikato lakes, as well as, Auckland and Rotorua water bodies (Duggan *et al.*, 2006). This relatively rapid spread may indicate that

constructed farm dams could be acting as ‘stepping stones’, facilitating the movement of non-indigenous species across the landscape. Improving our knowledge of the prevalence of non-native species in farm dams is important for understanding the extent in which these species have spread across the region.

1.3.2 Zooplankton in farm dams

It is important to reiterate that data on farm dam biodiversity is minimal, even though ponds are considered biodiversity ‘hotspots’, and biodiversity is integral to healthy ecosystem functioning. Internationally, research on zooplankton in farm dams is rare. One example, by Geddes (1986), examined zooplankton communities from four different farm dams in Adelaide, Australia, and found 28 different species. The author argued that farm dam zooplankton assemblages were predictable based on competition and predation. Zooplankton were sampled using a 10 m oblique tow of a 150 µm mesh plankton net. The author noted that their methods were likely to have underestimated the total number of species present, particularly smaller species and those restricted to deeper waters, and they highlighted that further research is required.

Knowledge of zooplankton biodiversity and community composition in New Zealand farm dams and ponds is also limited. Byars (1960) was the first to conduct a year-long study of zooplankton in a single New Zealand farm pond. Their investigation identified seasonal changes in zooplankton composition and that many species were shared with the Northern Hemisphere (e.g., Great Britain, North America and Japan). Another example examined the ecology of a single temporary farm pond near Auckland, which indicated that fauna in the pond was similar to that of nearby permanent natural and artificial ponds (Barclay, 1966). Recently, Eivers *et al.* (2018) compared zooplankton communities between drains, natural lakes and constructed treatment wetland ponds. With zooplankton compositions that differed from adjacent lakes and drains, the authors suggested that these ponds improved zooplankton biodiversity in agricultural peat lake catchments. It is evident that further research needs to be conducted on zooplankton in farm dams owing to the lack of current knowledge and the potential of these ponds to contribute to the regional species pool.

1.4 Aims and hypotheses

The main aim of this research project is to compare zooplankton biodiversity and community composition between small natural farm ponds and farm dams within the Waikato region, New Zealand. Another aim is to identify the environmental determinants structuring zooplankton diversity and composition within each pond group. I will also focus on the frequency of non-indigenous species in natural farm ponds and constructed farm dams, to determine whether the ponds act as stepping-stones for non-native species across landscapes. This research can be used to improve our current understanding of biodiversity values in farm dams and natural ponds, contributing to a current global, and local, knowledge gap. My hypotheses are that species richness will be similar between farm dams and natural ponds, but that community composition will differ between the two groups of ponds. Further, I expect non-indigenous species to be more common in farm dams than natural ponds.

Chapter 2

Methods

2.1 Site selection

A total of 152 natural ponds and farm dams was identified from across the Waikato region using a combination of Google Maps, Esri ArcMap GIS, historic maps from the University of Waikato, and the Waikato Regional Council's lakes/ponds database. The pool of sites contained a range of small natural lakes (>2 ha) and ponds such as oxbow formations and peat ponds (hereafter referred to as ponds), as well as constructed farm dams. Farm dams were classified as streams that had been dammed by humans. For this study, any ponds less than 0.06 ha (too small to identify using the maps and software mentioned above) or greater than 3.6 ha (equivalent to the largest farm dam available) were excluded.

A subset of 38 sites was selected for this study; 19 farm dams and 19 natural ponds (Figure 1). Initial selection of the ponds required a random stratified selection process. This was to create comparable datasets that were not affected by differences in size or climatic factors, and were representative of ponds throughout the Waikato region. The surface area (ha) of the ponds was measured using Esri ArcMap GIS tools and was categorised into two groups; ≥ 1 ha or < 1 ha. This was to ensure that the size range being studied was similar between farm dams and natural ponds. Sites were then categorised into three groups by location (northern, central, or southern Waikato) to ensure that latitudinal variation was similar. Using Microsoft Excel (version 15.0), a random number was generated for each of the sites and the 19 sites with the highest random numbers selected from each category.

Upon initial visitation, some sites were removed as they did not meet the original criteria set (e.g., some deemed natural ponds had recently been modified or dammed), or access to the site was denied by the farm owner. Where this occurred, the next site with the highest random number was selected.

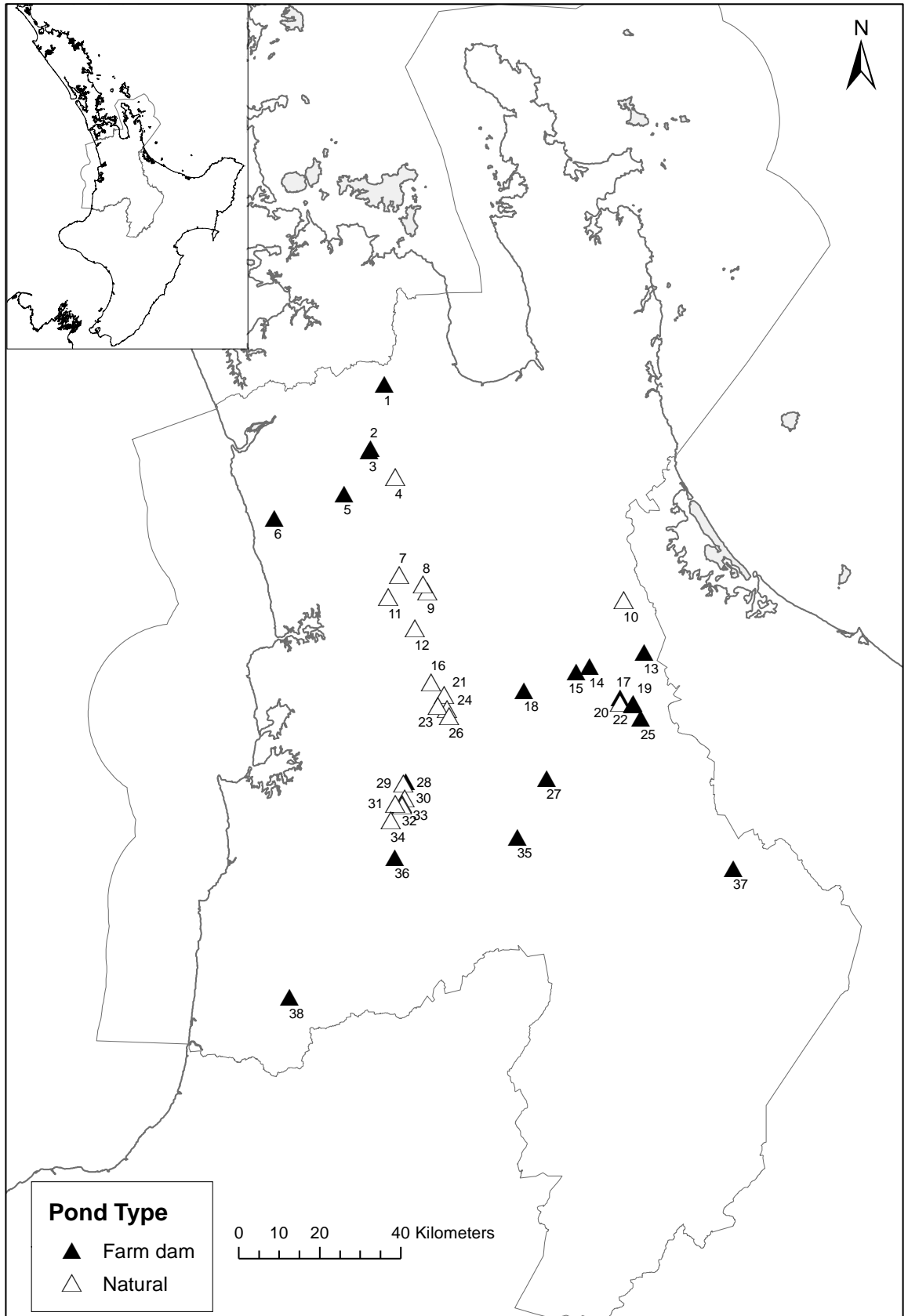


Figure 1. Farm dam and natural pond site locations for zooplankton sampling within the Waikato region, New Zealand.

2.2 Fieldwork sampling

2.2.1 Water quality sampling

Water samples for total phosphorus (TP) and total nitrogen (TN) were collected approximately 5 cm beneath the surface of each pond in 120 mL and 100 mL bottles, respectively. The total nitrogen bottles contained a sulphuric acid preservative to prevent denitrification. Each bottle was labelled and stored on ice until being transferred to the laboratory refrigerator. For chlorophyll-*a* analysis, a syringe was used to filter 50 mL of water at low vacuum through a 0.2 µm Whatman GF/C glass microfiber filter. If the water was turbid (e.g., if there was a high algal concentration), only 20 mL was filtered. Each filter paper was folded in half, wrapped in foil, labelled, and placed in a tube on ice until it could be stored in the laboratory freezer for later analysis (Paul, 2010). Dissolved oxygen, temperature and conductivity were measured *in situ* with a handheld Yellow Springs Instruments (YSI) Model 2030 meter. An additional 20 mL water sample was also collected from each pond to measure the yellow colour (gilvin) of the water.

2.2.2 Zooplankton sampling

Samples were collected from pond edges during August and September 2018 (winter sampling) and in January 2019 (summer sampling). Following the method described in Branford & Duggan (2017), zooplankton were collected near the water's surface (depth of 30-50 cm) by 10 fillings of a two litre clear plastic jug. The 20 L of pond water was then filtered through a 40 µm mesh plankton net, resulting in a concentrated zooplankton sample. This method was used as opposed to horizontal tows because it allowed for a quantitative measure of zooplankton abundance. Immediately following collection, the samples were preserved using 100% ethanol (final concentration 70%) and labelled. All of the zooplankton sampling equipment was placed in a salt water bath between sites to avoid cross-contamination of the samples, and to prevent the introduction of species into new water bodies.

2.3 Laboratory analyses

2.3.1 Water quality parameters

Both TN and TP were stored in the fridge (4°C) before analysis by Hill Laboratories, Hamilton. Total Kjeldahl Nitrogen (TKN) was digested using phenol/hypochlorite colorimetry with a Discrete Analyser (APHA 4500-Norg D. 4500 NH₃ F 22nd ed. 2012). Nitrate-N and nitrite-N were calculated from total oxidised nitrogen using an automated cadmium reduction with a flow injection analyser (APHA 4500-NO₃ I 22nd ed. 2012). TN was calculated by the addition of the TKN, nitrate-N, and nitrite-N values. TP digestion used ascorbic acid colorimetry with a Discrete Analyser (APHA 4500 – P B & E 22nd ed. 2012).

For the yellow colour (gilvin) analysis, a 20 mL water sample from each pond was filtered through an Advantec 0.45 µm mixed cellulose ester membrane filter to prepare the samples. Water colour was measured at 440 nm (as recommended by Cuthbert & del Giorgio (1992)) using a single beam Biochrom Libra S4 spectrophotometer (range = 352 – 1100 nm) which was calibrated using ultrapure water.

2.3.2 Chlorophyll-*a* extraction and analysis

A standard protocol for fluorometric determination of chlorophyll-*a* pigments was used as a proxy for algal biomass (Paul, 2010). Extraction and analysis were carried out in a dimly lit room to avoid degradation of the samples. Each filter paper was ground to a slurry with 90% MgCO₃-buffered acetone using an electric tissue grinder (DLAB D-160). The slurry was placed in a 4°C fridge for a minimum of 2 hours (no more than 24 hours). After steeping, the samples were shaken and centrifuged for 10 minutes at 1,461 G. Sample supernatant fluorescence was then measured before and after acidification using a Turner Designs 10-AU fluorometer. Phaeophytin degradation was corrected for by the addition of 150 µL of 0.1 N HCl. All readings were entered into a pre-programmed Microsoft Excel (version 15.0) spreadsheet to calculate total chlorophyll-*a* concentrations based on calibration curves derived from known chlorophyll-*a* concentrations.

2.3.3 Trophic level index

The Trophic Level Index (TLI) of Burns *et al.* (1999) was calculated for each farm dam and natural pond using total nitrogen (TLn), total phosphorus (TLp), and chlorophyll-*a* (TLc) values. In many of the ponds, a measurement of Secchi depth was not possible due to their shallow nature, as such, this variable was not used in the TLI calculations.

2.3.4 Zooplankton

A stereo dissecting microscope and compound microscope (Olympus SZ60 and Olympus BH-2) were used to count and identify zooplankton using magnifications of up to 400x. Initially, the samples were washed with tap water through a 40 µm sieve to remove ethanol from the sample. Any excess debris was rinsed thoroughly and removed from the sample. The samples were made up to a known volume (between 25 mL and 250 mL), and 5 mL aliquots were examined microscopically on a gridded (12 columns and five rows) perspex counting tray until, either, 300 individuals had been identified and counted, or, until the whole filtered sample had been searched if fewer individuals were present.

Copepods were identified by dissecting (using minuten pins) the 5th pair of pleopods from female cyclopoids and male calanoids. They were dissected under a stereo dissecting microscope, then covered by a cover slip, and examined under a compound microscope. Soft-bodied rotifers were identified by the examination of their trophi (jaws). To do so, rotifer specimens were placed on a slide with a coverslip and a small drop of sodium hypochlorite was used to dissolve the body, leaving behind the trophi. Where possible, all zooplankton were identified to species level using relevant taxonomic keys (e.g., Edmondson, 1959; Dumont, 1992; Shiel, 1995; Chapman *et al.*, 2011).

2.4 Statistical analyses

2.4.1 Environmental variables

Environmental variables were compared between farm dams and natural ponds. Each of the environmental variables was averaged between summer and winter to create a single data set. Following this, STATISTICA version 13.1 (Statsoft, Inc., Tulsa, USA) was used to test each environmental variable for normality (Shapiro-Wilks test) and homogeneity of variances (Levene's test). If the environmental data were normally distributed and had homogenous variances, a parametric t-test for independent samples (groups) was used to determine if there was a significant difference between farm dams and natural ponds. When necessary, data were \log_{10} transformed to improve normality. Where the data were still not normal or still had significant differences in variances, a non-parametric Mann-Whitney U test was performed.

2.4.2 Species richness

In most biological studies a complete census of any community is impossible, and often requires intensive sampling efforts (Chao & Chiu, 2016). The Chao-1 estimator (bias-corrected) can be used to estimate the species richness of each of the sampled sites (Coddington *et al.*, 1996; Chao & Chiu, 2016). The Chao-1 estimator focuses on rarer species abundances rather than dominant species, and generates the lower bound for species richness. It takes into account the species present once and the species present just twice within each site. This method has been shown to be a reliable indicator for estimating species richness in a variety of zooplankton studies (e.g., Coddington *et al.*, 1996; Schuler *et al.*, 2015; Zokan & Drake, 2015). Copepod nauplii were removed from the species list as these juveniles could not be confidently designated to a species.

$$S_{Chao1} = S_{obs} + f_1^2/(2f_2) \quad \text{If } f_2 > 0 \quad (1)$$

$$S_{Chao1} = S_{obs} + f_1(f_1 - 1)/2 \quad \text{If } f_2 = 0 \quad (2)$$

Where ' S_{Chao1} ' is the estimated species richness, ' S_{obs} ' is number of species observed, ' f_1 ' is the number of singletons (species found only once in the site), ' f_2 ' is the number of doubletons (species found just twice in the site). Equation 1 was

used for all calculations except when doubletons were zero, in which case, Equation 2 was used.

STATISTICA version 13.1 (Statsoft, Inc., Tulsa, USA) was used to test the estimated species richness' for normality (Shapiro-Wilks test; $p > 0.20$) and homogeneity of variances (Levene's test; $p = 0.48$). Following this, a t-test for independent samples (groups) was used to determine if there was a significant difference in estimated species richness between natural ponds and farm dams.

Chao-1 estimated species richness was compared with each environmental variable to determine if there was a relationship. Correlation coefficients (R^2) were generated using STATISTICA version 13.1 (Statsoft, Inc., Tulsa, USA). A stepwise linear regression was performed, using STATISTICA version 13.1 (Statsoft, Inc., Tulsa, USA), to determine which environmental variables predicted species richness in farm dams and natural ponds individually. A stepwise linear regression was performed as it identifies the most significant factor causing variation and proceeds to select factors that account for the remainder of the variation. In contrast, the relationships presented by correlation coefficients assume all variables are independent of each other. Environmental variables (where necessary) and species richness values were \log_{10} transformed to improve normality.

2.4.3 Zooplankton community composition

For the following analyses, nauplii were removed from the species list, as these juvenile copepods could not confidently be designated to a species (and likely comprised more than one species). Harpacticoid copepods that could be identified to species level are referred to in the full list of species. However, for the following statistical analyses, harpacticoid species were grouped together as a single taxon, 'harpacticoid copepods', as they were present in low numbers and young copepod stages could not be identified.

A non-metric multidimensional scaling (nMDS) plot was used to determine whether differences in community composition exist between farm dams and

natural ponds. A one-way ANOSIM was performed to test for significant differences in community composition between farm dams and natural ponds. Following this, a similarity percentages (SIMPER) analysis, based on the Bray-Curtis similarity matrix, was used to identify the contribution of each species to the observed dissimilarity between farm dams and natural ponds. These analyses were conducted using STATISTICA version 13.1 (Statsoft, Inc., Tulsa, USA). Species were removed (to reduce the influence of species that were sampled by chance) if they were not present in three or more sites and if the maximum number per litre was less than five. This resulted in a reduction in the total number of species from 107 (including rare species) to 52 species. Species data were transformed using $\log(x + 1)$ to down weight the contribution of abundant species.

Canonical correspondence analyses (CCA) were carried out separately on the natural and farm dam data sets, to infer which environmental variables most greatly explained the variation in community composition in each data set. The analyses were performed using Canoco for Windows version 4.5 (Centre for Biometry, Wageningen, The Netherlands). To reduce the influence of zooplankton sampled by chance, rare species were removed if they were not present in three or more sites and if the maximum number per litre was less than five. This resulted in a reduction in the total number of species from 107 (including rare species) to 42 species in natural ponds and 34 species in farm dams. Species data were transformed using $\log(x + 1)$ to down weight the contribution of abundant species. Environmental data were \log_{10} transformed (where necessary) to improve normality, and subsequently standardised to zero mean and unit variance to make differing scales of measurement comparable (ter Braak & Smilauer, 1998). To determine which environmental variables were statistically most significant for explaining the variation of zooplankton community composition in farm dams and natural ponds, Forward Selection and Monte Carlo permutation tests were performed using Canoco for Windows version 4.5 (Centre for Biometry, Wageningen, The Netherlands).

Chapter 3

Results

3.1 Environmental variables

Site selection was primarily based on pond surface area (ha) and location within the Waikato region (i.e., similar latitudinal spread). Effort was made to ensure that pond surface area was similar across the sampling sites, allowing valid comparisons to be made between the environmental variables and zooplankton communities of natural and constructed ponds. There was no significant difference between the surface area of farm dams and natural ponds ($p = 0.530$). However, there was a marginally significant difference in latitude between natural ponds and farm dams ($p = 0.042$) (Table 1). As shown in Figure 1, natural ponds were more localised, and typically followed larger rivers, whereas farm dams occurred throughout the landscape. Given that natural ponds were difficult to locate, and were formed by similar processes, it is unsurprising that the location of natural ponds in this study was marginally different to farm dams. However, the narrow latitudinal range examined (all ponds were within a latitude of 36-37°) make this factor unlikely to influence patterns in community composition.

Most environmental variables were similar between farm dams and natural ponds, including total nitrogen, total phosphorus, temperature, conductivity, chlorophyll-*a*, elevation and the number of water bodies within a 2 km radius of the sites (Table 1). However, water colour (gilvin) and Trophic Level Index (TLI) were statistically higher in natural ponds compared to farm dams. Dissolved oxygen concentration and pH were significantly lower in natural ponds compared to farm dams (Table 1).

Table 1. Descriptive statistics of environmental variables for 19 farm dams and 19 natural ponds in the Waikato region. Significant p -values are in bold. A single asterisk (*) indicate that non-parametric Mann-Whitney U tests were used; all other variables used parametric t-tests for independent variables (groups).

	Farm dam			Natural			p -value
	Mean	Minimum	Maximum	Mean	Minimum	Maximum	
Total nitrogen (g m^{-3})	2.3	0.7	6.4	4.6	1.2	28.8	0.060
Total phosphorus (g m^{-3})	0.2	0.0	0.5	0.2	0.0	0.6	0.152
Yellow colour (absorbance at 440 nm)	0.075	0.008	0.861	0.093	0.024	0.225	0.002
Temperature ($^{\circ}\text{C}$)	18.4	13.8	20.9	17.6	15.6	21.3	0.133
Dissolved oxygen (mg L^{-1})*	8.8	5.4	11.9	5.6	1.1	17.4	<0.001
Conductivity ($\mu\text{S cm}^{-1}$)	120.5	56.4	170.5	136.3	78.5	236.9	0.221
pH	7.3	6.7	8.4	6.7	5.8	8.7	0.002
Chlorophyll- a ($\mu\text{g L}^{-1}$)	23.2	2.5	104.3	40.3	7.8	215.8	0.220
Trophic Level Index	5.6	4.2	6.7	6.2	4.8	7.8	0.027
Surface area (ha)*	1.1	0.1	3.6	1.3	0.1	3.4	0.530
No. water bodies within 2 km radius*	5.58	1	15	5.11	2	9	0.672
Latitude ($^{\circ}\text{S}$)*	37.7	37.1	38.6	37.9	37.3	38.9	0.042
Elevation (m)	96.4	13.0	234.0	40.1	9.0	89.0	0.717

3.2 Zooplankton species diversity

In total, 107 zooplankton taxa were recorded throughout the study; 90 rotifers, 6 copepods, 10 cladocerans and ostracods. Of those, 91 taxa were found in farm dams and 83 species in natural ponds (Table 2). The observed average species richness of the natural ponds was slightly higher (22.4) than in farm dams (20.7), however, the difference was not statistically significant (t-test; $p = 0.406$). The number of species that occurred in only one farm dam or one natural pond (i.e., singletons) were relatively similar between farm dams and natural ponds (26 and 30 respectively) (Table 2). In natural ponds, 65% of species occurred in two or more ponds. In contrast, farm dams had a higher proportion with 73% of species occurring in two or more ponds. Two genera (*Erignatha clastopis* and *Octotrocha speciosa*) and one species (*Cephalodella theodora*) were recorded that had not previously been identified in New Zealand (Table 2) (Shiel *et al.*, 2009). A single individual of *E. clastopis* was found once in a farm dam. Both *C. theodora* and *O. speciosa* were recorded in the same natural pond, with only single individuals found of each. All other species recorded had been identified in New Zealand prior to this study. Non-native species occurred in a greater number of farm dams than natural ponds, but were overall uncommon. In total, three non-indigenous species were recorded; *Daphnia galeata* (recorded in two farm dams), *D. pulex* (recorded in one natural pond) and *Boeckella minuta* (recorded in one farm dam) (Table 2; Figure 2).

Species richness for farm dams and natural ponds was extrapolated using the Chao-1 species richness estimator (Table 3). Both pond types showed high variation in species richness, but no significant difference was found between farm dams and natural ponds (t-test; $p = 0.601$). Individual farm dams ranged in estimated species richness' from 14.0 to 70.0 (the highest richness among all ponds) and natural ponds ranged between 8.0 (the lowest richness) and 56.3 (the second highest richness).

Table 2. List of zooplankton species recorded in Waikato farm dams and natural ponds during this study. Species and numbers in bold refer to species present in only one farm dam or one natural pond. Site location numbers refer to Figure 1. Unidentified juvenile harpacticoid copepods and copepod nauplii are not listed.

Species	Natural	Farm dam
Rotifers		
<i>Anuraeopsis fissa</i> (Gosse, 1851)	4,7,10,30,31,33	5,14,15,19,37
<i>Ascomorpha ecaudis</i> (Perty, 1850)	12	3
<i>Ascomorpha saltans</i> Bartsch, 1870	20	22,25
<i>Aspelta angusta</i> Harring & Myers, 1928	24	3,14,22,36
<i>Asplanchna brightwelli</i> Gosse, 1850	7,8,12,21,23,33,34	17,19,35,27,37
<i>Asplanchna girodi</i> de Guerne, 1888		5,28
<i>Asplanchna priodonta</i> Gosse, 1850	12	
Bdelloid spp.	4,7,8,9,10,11,12,16,20,21,23,24,26,29,30,31,32,33,34	1,2,3,5,6,13,14,15,17,18,19,22,25,27,28,35,36,37,38
<i>Brachionus angularis</i> Gosse, 1851	7,8,20,23,29,30,32	2,19,22,27,37
<i>Brachionus budapestinensis</i> (Daday, 1885)	7,8,23	5,17,22
<i>Brachionus calyciflorus</i> Pallas, 1766	7,8,20,23,24,31,33	2,5,15,17,19,22,27,37
<i>Brachionus caudatus</i> Barrois & Daday, 1885		3,18
<i>Brachionus lyratus</i> Shephard, 1911		1
<i>Brachionus quadridentatus</i> Hermann, 1783	4,7,20,21,23,26,29	1,2,5,17,18,19,25,27,36,37
<i>Brachionus urceolaris</i> Müller, 1773		5,17,38
<i>Cephalodella catellina</i> (Müller, 1786)	21	17,27
<i>Cephalodella c.f. intuta</i> Myers, 1924	26	1,2,3,36
<i>Cephalodella forficula</i> (Ehrenberg, 1832)	9	5,19,28

Table 2 continued. List of zooplankton species recorded in Waikato farm dams and natural ponds during this study. Species and numbers in bold refer to species present in only one farm dams or one natural pond. Site location number refer to Figure 1. Unidentified juvenile harpacticoid copepods and copepod nauplii are not listed.

Species	Natural	Farm dam
Rotifers		
<i>Cephalodella gibba</i> (Ehrenberg, 1832)	8,30,32	5,13,14,36
<i>Cephalodella gracilis</i> (Ehrenberg, 1832)		2,36
<i>Cephalodella tenuiseta</i> (Burn, 1890)		28
<i>Cephalodella theodora</i> Koch-Althaus, 1961	20	
<i>Cephalodella ventripes</i> (Dixon-Nuttall, 1901))	8,20,21,23,29,31,32,33	17,25,27,37,38
<i>Collotheca</i> sp.		37
<i>Colurella adriatica</i> Ehrenberg, 1831		13
<i>Colurella uncinata</i> (Müller, 1773)	8,23	25,28
<i>Conochilus coenobasis</i> (Skorikov, 1914)		15
<i>Dicranophoroides caudatus</i> (Ehrenberg, 1834)	7,11,20,29,32,33	19,28,35
<i>Dicranophorus epicharis</i> Harring & Myers, 1928	8,20,24,26,31,32	2,3,13,14,19,27,28,37
<i>Encentrum</i> sp.	4	
<i>Epiphanes macroura</i> (Barrois & Daday, 1894)	4,30	2
<i>Erignatha clastopis</i> (Gosse, 1886)		37
<i>Euchlanis dilatata</i> Ehrenberg, 1832	26	1
<i>Euchlanis meneta</i> Myers, 1930	23	
<i>Euchlanis pyriformis</i> Gosse, 1851	9,23,26	37
<i>Filinia longiseta</i> (Ehrenberg, 1834)	7,9,10,20,29,30,33	3,5,17,19,22,35

Table 2 continued. List of zooplankton species recorded in Waikato farm dams and natural ponds during this study. Species and numbers in bold refer to species present in only one farm dams or one natural pond. Site location number refer to Figure 1. Unidentified juvenile harpacticoid copepods and copepod nauplii are not listed.

Species	Natural	Farm dam
Rotifers		
<i>Filinia novaezealandiae</i> Shiel & Sanoamuang, 1993	7,8,11,16,23,31,33	2,3,5,13,27,37
<i>Gastropus hyptopus</i> (Ehrenberg, 1838)	20,30	
<i>Gastropus minor</i> (Rousselet, 1892)	10	15
<i>Itura aurita</i> Wulfert, 1935	4	13
<i>Itura myersi</i> Wulfert, 1935	7,8,11,20,21,23,30	3,13,14,27,28,35,36,37,38
<i>Keratella cochlearis</i> (Gosse, 1851)		3,5,6,14,25
<i>Keratella procurva</i> Thorpe, 1891	9,24,28,33	28
<i>Keratella slacki</i> (Berzins, 1963)	7,8,9,10,11,16,20,24,29,30	1,3,5,14,17,18,19,22,27,36,37,38
<i>Keratella tecta</i> (Gosse, 1851)	8,9,10,33	1,3,5,6,14,15,19,25,36,38
<i>Keratella tropica</i> (Apstein, 1907)	8,23,26,29,30	1,5,6,14,15,19,22,25,27
<i>Lecane bulla</i> (Gosse, 1851)	4,7,8,10,21,23,24,26,32,33	1,3,6,13,14,19,22,25,27,28,35,36,37,38
<i>Lecane closterocerca</i> (Schmarda, 1859)	4,8,9,29,30,33	2,13,14,22,27,28,37
<i>Lecane hamata</i> (Stokes, 1896)	4,8,10,21,23	2,35
<i>Lecane luna</i> (Müller, 1776)	30,32	
<i>Lecane lunaris</i> (Ehrenberg, 1832)	7,8,9,11,12,16,24,26,32,33	2,6,13,14,17,19,25,28,35,36
<i>Lecane ohioensis</i> (Herrick, 1885)	33	13,27,28,37
<i>Lepadella acuminata</i> (Ehrenberg, 1834)	8,29	15,25
<i>Lepadella ovalis</i> (Müller, 1786)	4,7,8,21,24	3,5,25,27,28,36,37

Table 2 continued. List of zooplankton species recorded in Waikato farm dams and natural ponds during this study. Species and numbers in bold refer to species present in only one farm dams or one natural pond. Site location number refer to Figure 1. Unidentified juvenile harpacticoid copepods and copepod nauplii are not listed.

Species	Natural	Farm dam
Rotifers		
<i>Lepadella rhomboides</i> (Gosse, 1886)	4	
<i>Lindia torulosa</i> Dujardin, 1841	24	1,27,37
<i>Lophocharis salpina</i> (Ehrenberg, 1834)	4,8	
<i>Monommata</i> sp.	30	13,27,37
<i>Mytilinia mucronata</i> (Müller, 1773)	4,8,26,30	5
<i>Mytilinia ventralis</i> (Ehrenberg, 1832)		36,38
<i>Notommata cyrtopus</i> Gosse, 1886	4	13,19,27,35,37
<i>Notommata pseudocerberus</i> de Beauchamp, 1908		13
<i>Octotrocha speciosa</i> Thorpe, 1893	20	
<i>Platyias quadricornis</i> (Ehrenberg, 1832)	4,7,8,11,21,23,29	2,28
<i>Pleurotrocha petromyzon</i> (Ehrenberg, 1830)		27,36
<i>Polyarthra dolichoptera</i> Idelson, 1925	4,7,8,9,11,12,16,20,23,26,29,30,31,32,33,34	1,2,3,5,6,14,15,17,18,19,22,25,27,28,35,37,38
<i>Pompholyx complanata</i> Gosse, 1851	8	1,6,19,22
<i>Proales</i> sp.	23,24,30	14,25,27,28,37
<i>Squatinella mutica</i> (Ehrenberg, 1832)	8,12,26,29,30,33	
<i>Synchaeta grandis</i> Zacharias, 1893		5
<i>Synchaeta longipes</i> (Gosse, 1887)		1,36,37
<i>Synchaeta oblonga</i> Ehrenberg, 1832	7,30	3,6,14,27,37,38

Table 2 continued. List of zooplankton species recorded in Waikato farm dams and natural ponds during this study. Species and numbers in bold refer to species present in only one farm dams or one natural pond. Site location number refer to Figure 1. Unidentified juvenile harpacticoid copepods and copepod nauplii are not listed.

Species	Natural	Farm dam
Rotifers		
<i>Synchaeta pectinata</i> Ehrenberg, 1832	7,11,30,33	3,6,18,28,35,38
<i>Synchaeta stylata</i> Wierzejski, 1893	20	14
<i>Taphrocampa selenura</i> Gosse, 1887		13
<i>Testudinella mucronata</i> (Gosse, 1886)		5
<i>Testudinella patina</i> (Hermann, 1783)	7,8,10,16,21,26,32	2,13,17,19
<i>Trichocerca bidens</i> (Lucks, 1912)		1
<i>Trichocerca brachyura</i> (Gosse, 1851)	4,7,10,20,21,26	3,15,22
<i>Trichocerca elongata</i> (Gosse, 1886)	4,7,8,11,23,29,33	6,35
<i>Trichocerca longiseta</i> (Schrank, 1802)	24	36
<i>Trichocerca porcellus</i> (Gosse, 1851)	32	
<i>Trichocerca pusilla</i> (Jennings, 1903)	20	2,28,37
<i>Trichocerca rattus</i> (Müller, 1776)		13
<i>Trichocerca similis</i> (Wierzejski, 1893)	6,11,12,20,24,30,31,32,33,34	3,13,14,17,18,19,27,28,35,37
<i>Trichocerca tenuior</i> (Goss, 1886)	11	2,19,25,28
<i>Trichocerca tigris</i> (Müller, 1786)	4,23,30	27,35,38
<i>Trichocerca vernalis</i> (Hauer, 1936)	7,32	6
<i>Trichotria tectractis</i> (Ehrenberg, 1830)	8,9,12,24,2,32	13,14,22,35
Unknown sp.	11	

Table 2 continued. List of zooplankton species recorded in Waikato farm dams and natural ponds during this study. Species and numbers in bold refer to species present in only one farm dams or one natural pond. Site location number refer to Figure 1. Unidentified juvenile harpacticoid copepods and copepod nauplii are not listed.

Species	Natural	Farm dam
Calanoid copepods		
<i>Boeckella delicata</i> Percival, 1937	4,32	14,18,27,28
<i>Boeckella minuta</i> Sars, 1896		3
Cyclopoid copepods		
<i>Acanthocyclops robustus</i> (Sars, 1863)	4,7,8,9,10,11,12,16,20,21,23,24,26,29,30,31,32,33,34	1,2,3,5,6,13,14,15,17,18,19,22,25,27,28,36,37,38
<i>Paracyclops fimbriatus</i> (Fischer, 1853)		6
Harpacticoid copepods		
<i>Attheyella rotoruensis</i> Lewis, 1972	16	
<i>Elaphoidella bidens</i> (Schmeil, 1894)	23	1
Cladocerans		
<i>Alona</i> sp.	7,8,9,11,12,16,23,24,26,29,30,31,32,33	1,3,5,6,13,14,15,17,18,19,22,25,27,28,35,36,37,38
<i>Bosmina meridionalis</i> Sars, 1904	7,8,9,11,16,23,24,30,31,32,33	1,5,6,15,28
<i>Ceriodaphnia dubia</i> Richard, 1894	11,24	
<i>Chydorus</i> sp.	4,7,8,9,10,11,12,16,21,23,24,26,29,30,31,32,33,34	1,2,3,5,6,13,14,15,17,18,19,22,25,27,28,35,36,37,38
<i>Daphnia galeata</i> Sars, 1863		1,18

Table 2 continued. List of zooplankton species recorded in Waikato farm dams and natural ponds during this study. Species and numbers in bold refer to species present in only one farm dams or one natural pond. Site location number refer to Figure 1. Unidentified juvenile harpacticoid copepods and copepod nauplii are not listed.

Species	Natural	Farm dam
Cladocerans		
<i>Daphnia pulex</i> Leydig, 1860	34	
<i>Daphnia thomsoni</i> Sars, 1894		27,28
<i>Ilyocryptus sordidus</i> (Lievin, 1848)	11,12,16,20,23,24,29,30,32,33	2,14,15,27
<i>Pseudomoina lemnae</i> (King, 1853)	11	
<i>Simocephalus vetulus</i> Schoedler, 1858	4,7,8,10,21,23,24,26,29,30	2,3,13,14,15,19,25,35,36,37,38
Other crustaceans		
Ostracods	4,7,8,9,11,12,16,21,23,24,26,29,30,31,32,33,34	1,2,3,5,6,13,14,15,17,19,22,25,27,28,35,36,38

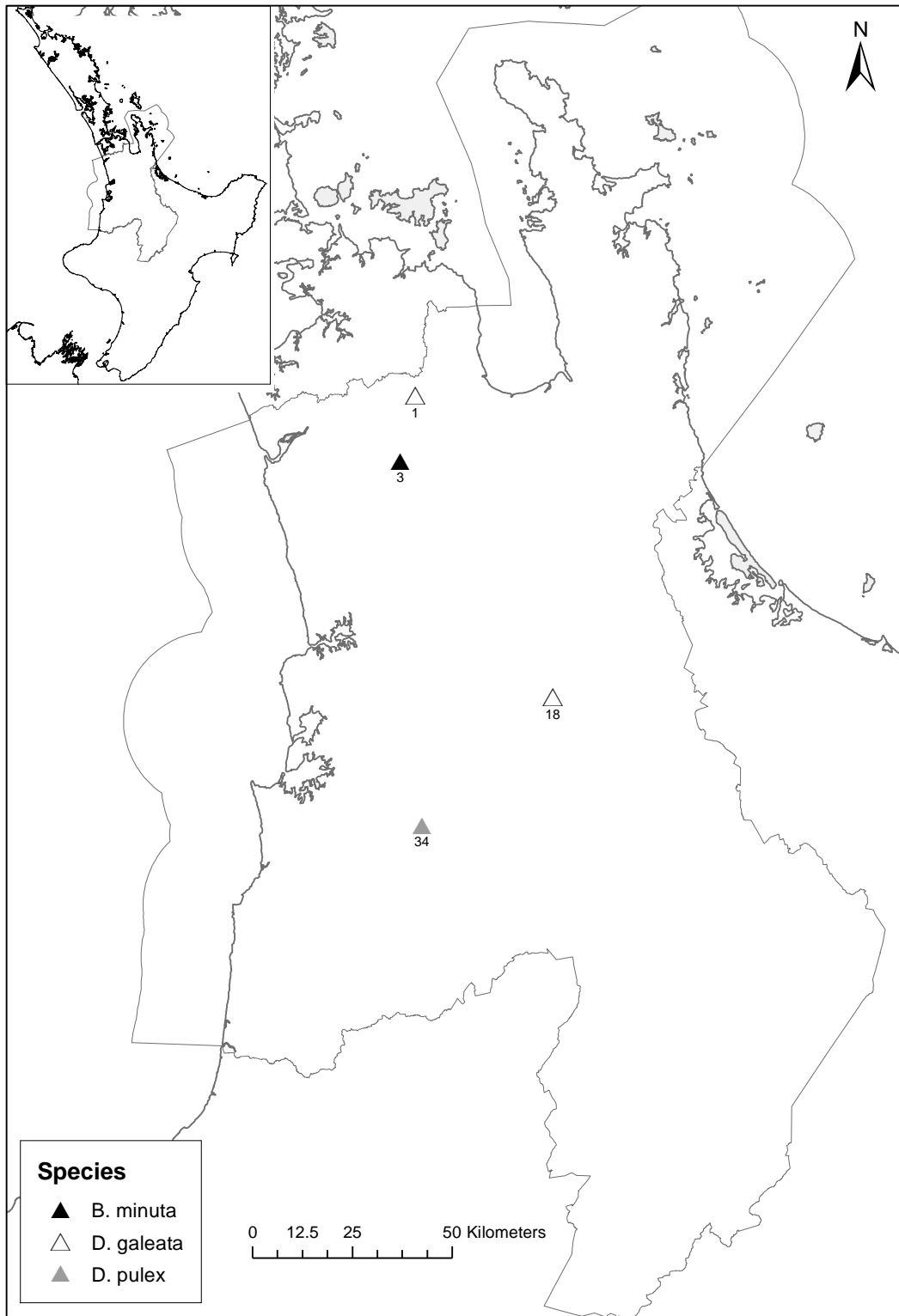


Figure 2. Site location of three non-indigenous species sampled throughout the Waikato region during this study.

Table 3. Chao-1 estimated species richness (ordered highest to lowest) for 19 farm dams and 19 natural ponds within the Waikato region. Map number refer to Figure 1.

Map number	Pond type	Species richness	Map number	Pond type	Species richness
1	Farm dam	81.5	5	Farm dam	25.1
30	Natural	52.5	15	Farm dam	25.0
8	Natural	51.0	9	Natural	24.0
4	Natural	44.3	35	Farm dam	24.0
11	Natural	40.0	32	Natural	23.9
20	Natural	39.0	24	Natural	23.5
37	Farm dam	37.4	26	Natural	22.1
13	Farm dam	36.3	22	Farm dam	21.0
27	Farm dam	36.2	10	Natural	21.0
7	Natural	34.9	25	Farm dam	20.5
28	Farm dam	31.1	29	Natural	20.3
23	Natural	31.1	38	Farm dam	19.0
14	Farm dam	30.5	17	Farm dam	19.0
19	Farm dam	29.1	21	Natural	16.3
33	Natural	29.0	12	Natural	16.0
6	Farm dam	28.0	31	Natural	13.3
2	Farm dam	26.5	16	Natural	13.1
3	Farm dam	25.9	18	Farm dam	13.0
36	Farm dam	25.2	34	Natural	8.0

3.2.1 Variation in zooplankton species richness

3.2.1.1 Natural ponds

Correlation coefficients (R^2) were used to identify relationships between estimated species richness and environmental variables in natural ponds. An R^2 value equal to or close to one indicates a strong relationship between the variables. In natural ponds, Chao-1 estimated species richness was not strongly correlated with any of the environmental variables (Figure 3 a to j). Temperature had the highest R^2 value of 0.2637 (Figure 3 a), followed by pond surface area ($R^2 = 0.2288$) (Figure 3 b).

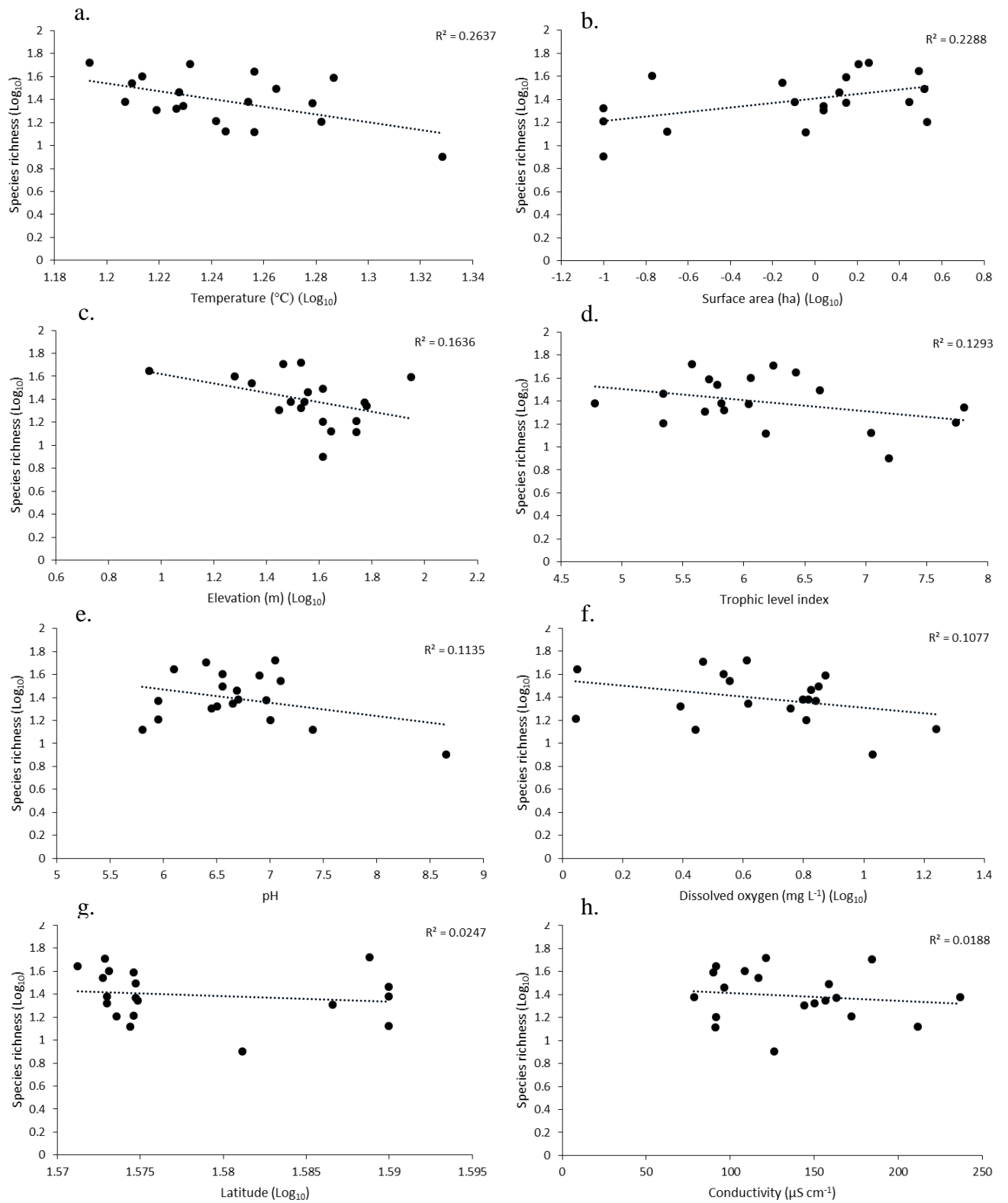


Figure 3 (a) to (h). Relationships between Chao-1 estimated zooplankton species richness and environmental variables from 19 natural ponds throughout the Waikato. Plots are ordered by decreasing correlation coefficients (R^2).

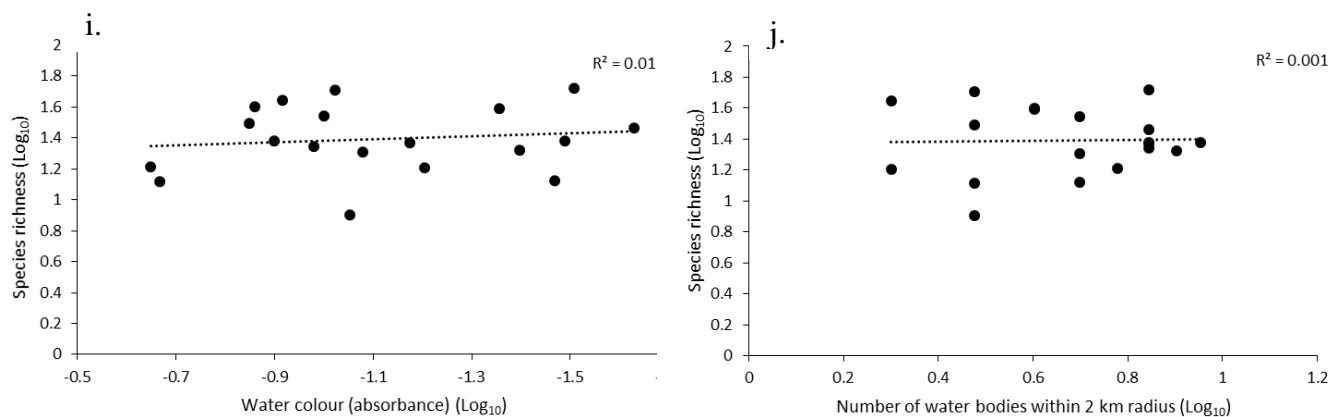


Figure 3 (i) to (j). Relationships between Chao-1 estimated zooplankton species richness and environmental variables from 19 natural ponds throughout the Waikato. Plots are ordered by decreasing correlation coefficients (R^2).

Overall, the stepwise linear regression model accounted for a significant amount of the variation in Chao-1 estimated zooplankton species richness in natural ponds at 54% (adjusted $R^2 = 0.540$; $p = 0.004$) (Table 4). The regression model inferred temperature to be the most significant predictor of the estimated species richness in natural ponds ($p = 0.025$) (Table 5). Additional significant variation was also explained by pond surface area ($p = 0.016$) (Table 5). Elevation, TLI, pH, dissolved oxygen, conductivity and the number of water bodies within a 2 km radius were not significant predictors of the estimated species richness in this model.

Table 4. Summary statistics for the stepwise linear regression model that tested the significance of environmental variables on Chao-1 estimated species richness in 19 natural ponds sampled in the Waikato region.

Statistic	Value
Multiple R	0.801
Multiple R^2	0.642
Adjusted R^2	0.540
F(4,14)	6.283
p	0.004
Standard Error of Estimate	0.149

Table 5. Stepwise linear regression summary for Chao-1 estimated species richness (dependent variable) in natural ponds. Significant variables and p-values are in bold.

Variable	Step	R ²	p-value
Temperature (log₁₀)	1	0.26	0.025
Surface area (log₁₀)	2	0.23	0.016
Latitude (log ₁₀)	3	0.08	0.121
Water colour (log ₁₀)	4	0.07	0.120

3.2.1.2 Farm dams

Correlation coefficients (R²) were used to identify relationships between Chao-1 estimated zooplankton species richness and environmental variables in farm dams. Estimated species richness was not strongly correlated with any of the environmental variables (Figure 4 a to j). Dissolved oxygen had the highest R² value of 0.2471 (Figure 4 a), followed by the number of water bodies within a 2 km radius (R² = 0.1061) (Figure 4 b).

Overall, the stepwise linear regression model indicated that the environmental variables measured did not account for significant variation in Chao-1 estimated zooplankton species richness in farm dams at 26.3% (adjusted R² = 0.263; *p* = 0.056) (Table 6). Consequently, the model inferred that no environmental variables were significant predictors of Chao-1 estimated species richness in farm dams.

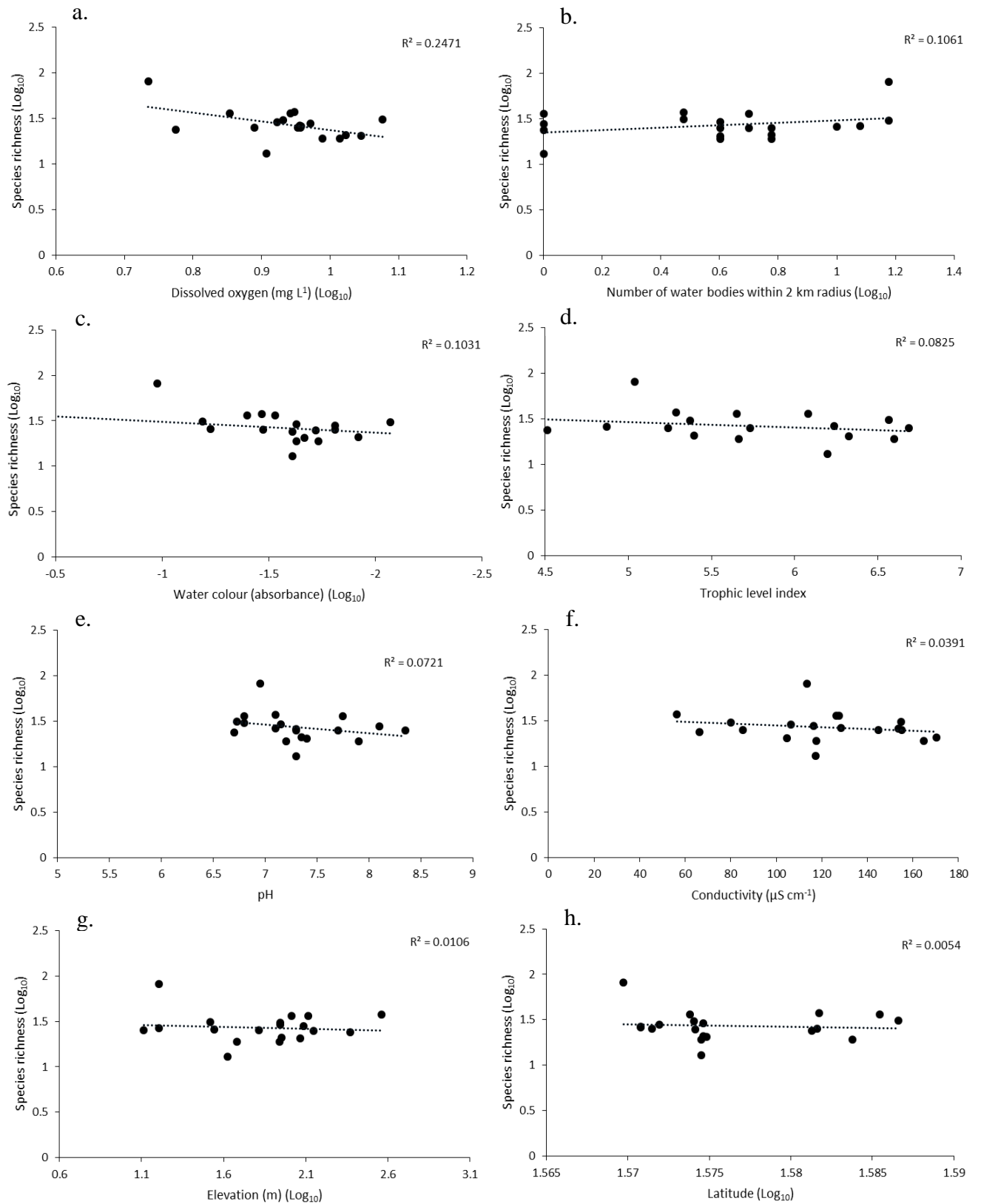


Figure 4 (a) to (h). Relationships between Chao-1 estimated zooplankton species richness and environmental variables from 19 farm dams throughout the Waikato. Plots are ordered by decreasing correlation coefficients (R²).

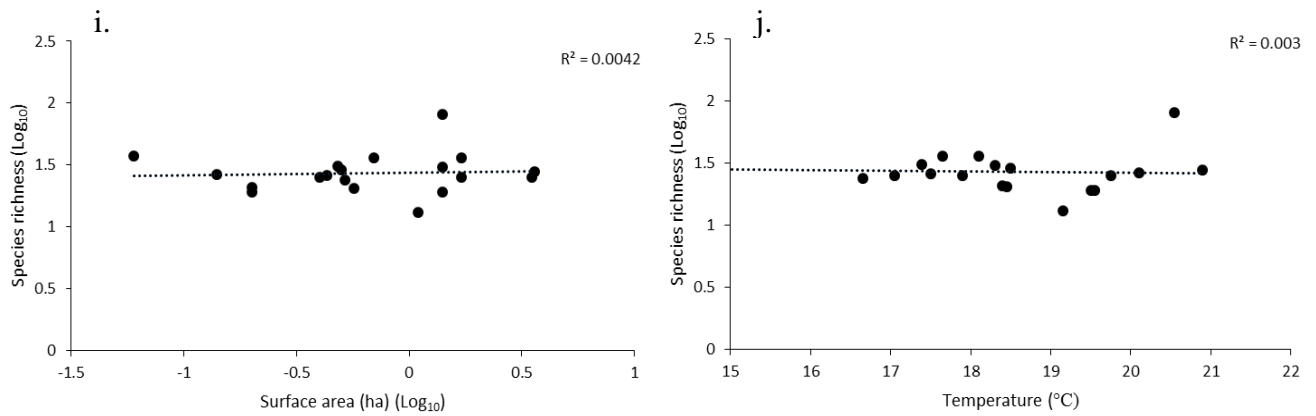


Figure 4 (i) to (j). Relationships between Chao-1 estimated zooplankton species richness and environmental variables from 19 farm dams throughout the Waikato. Plots are ordered by decreasing correlation coefficients (R^2).

Table 6. Summary statistics for stepwise linear regression model that tested the significance of environmental variables on Chao-1 estimated species richness in 19 farm dams sampled in the Waikato region.

Statistic	Value
Multiple R	0.621
Multiple R^2	0.386
Adjusted R^2	0.264
F(4,14)	3.150
p	0.056
Standard Error of Estimate	0.139

3.2.2 Frequently occurring species

The frequency of species occurrence in 50% or more of either natural ponds or farm dams were compared. On average, natural ponds had a slightly higher frequency of cladoceran occurrences (66%) compared to farm dams (60%) (Table 2; Figure 5). Farm dams had a higher average percent occurrence of rotifers (67%) compared to natural ponds (57%). Interestingly, the cyclopoid copepod *Acanthocyclops robustus* was found in all farm dams and natural ponds sampled. Species with the greatest dissimilarities between pond types were *Bosmina meridionalis* and *Ilyocryptus sordidus*, both of which occurred more frequently in natural ponds. In contrast, species such as *Alona* sp., *Brachionus quadridentatus*, *Keratella tecta* and *Lecane bulla* were more common in farm dams than natural ponds.

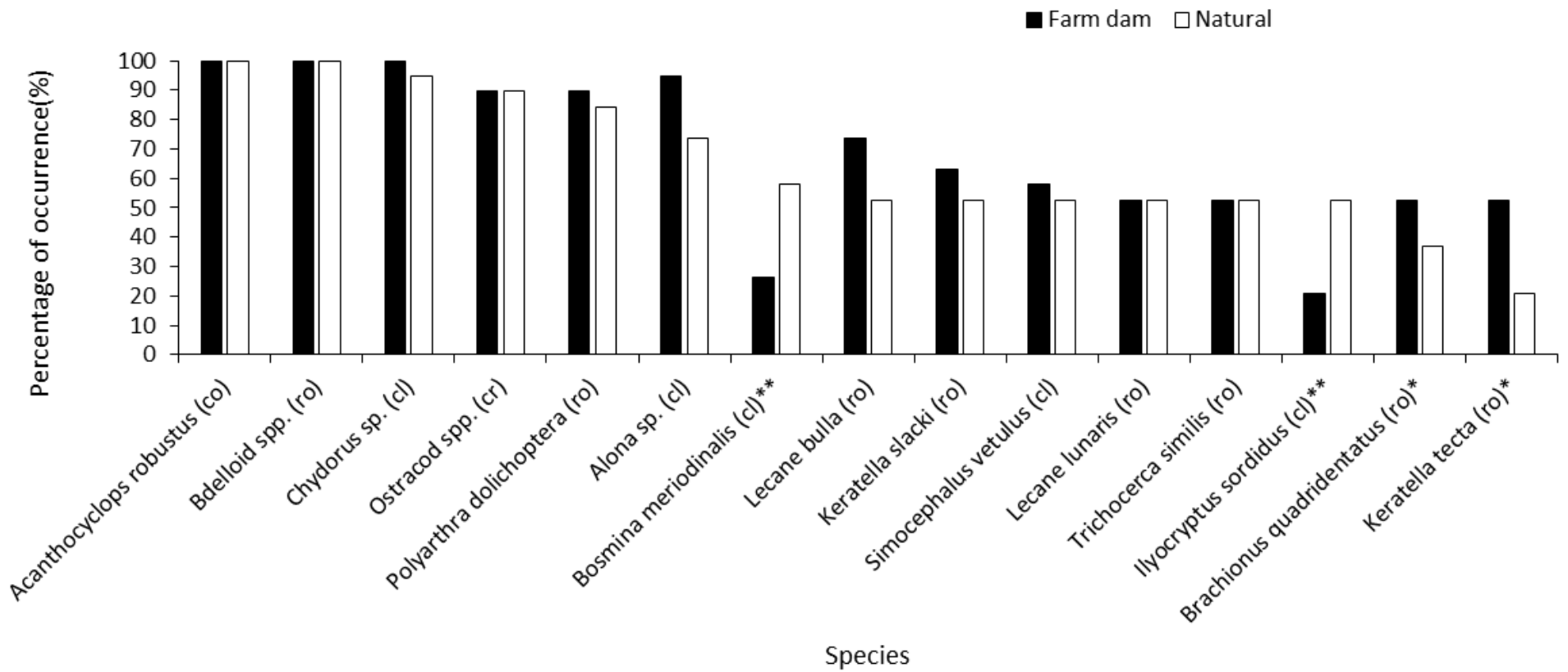


Figure 5. Percentage occurrence of zooplankton species present in 50% (or more) natural ponds or farm dams sampled during this study. Species are ordered from highest to lowest based on percentage occurrence in natural ponds. cl = cladocera, co = copepod and ro = rotifer. A single asterisk (*) denotes species not present in ten or more natural ponds. Double asterisks (**) denote species not present in ten or more farm dams.

3.3 Zooplankton community composition

A non-metric multidimensional scaling ordination (nMDS) was used to examine patterns in zooplankton community composition across pond types (Figure 6). The stress value (showing the fit of the ordination to the underlying matrix) was 0.23, which indicates a potentially useful picture, although little reliance should be placed on the fine structure of the plot. Natural ponds tended to be towards the left of the ordination while farm dams were typically on the right, with some overlap in the middle of the ordination, indicating that there is a difference between zooplankton composition in farm dams and natural ponds. A one-way ANOSIM indicated the difference in zooplankton composition between farm dams and natural ponds was significant ($p = 0.014$).

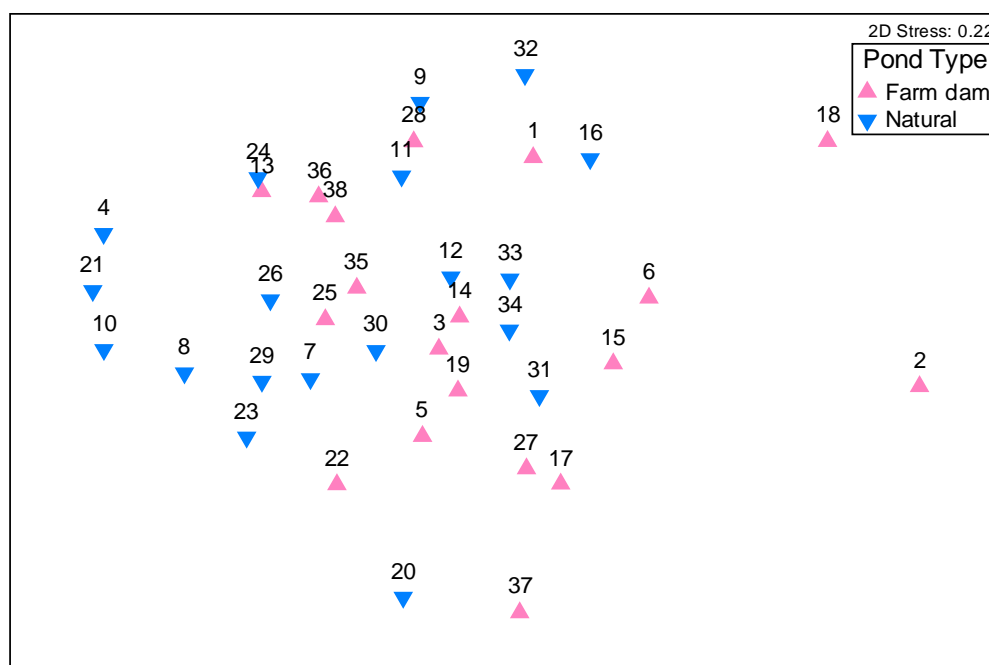


Figure 6. Non-metric multidimensional scaling ordination (nMDS) using $\log(x+1)$ transformed data showing zooplankton communities from Waikato farm dams and natural ponds. Numbers indicate site location (Figure 1). Stress = 0.22.

A similarity percentages (SIMPER) analysis was used to identify the contribution of each species to the observed dissimilarity between natural ponds and farm dams (Table 7). The average dissimilarity between farm dams and natural ponds was 64%, with the greatest dissimilarity attributed to the rotifer *Polyarthra dolichoptera* (5.64%) followed by bdelloid rotifer species (5.60%). *Polyarthra dolichoptera* and *Keratella tecta* were more abundant in farm dams than in natural ponds, whereas

bdelloid rotifers, *Chydorus* sp., ostracod species, *Acanthocyclops robustus* and *Simocephalus vetulus* were all more abundant in natural ponds compared to farm dams.

Table 7. SIMPER analysis using log(x+1) transformed species data from 19 farm dams and 19 natural ponds throughout the Waikato Region. Species included are those contributing greater than 3.5% to the dissimilarity between farm dams and natural ponds.

Species	Natural ponds	Farm dams		Contribution (%)
	Average abundance	Average abundance	Average dissimilarity	
<i>Polyarthra dolichoptera</i>	2.89	2.96	3.61	5.64
Bdelloid spp.	3.88	1.80	3.58	5.60
<i>Chydorus</i> sp.	2.84	2.01	3.02	4.73
Ostracod sp.	2.04	1.28	2.50	3.90
<i>Acanthocyclops robustus</i>	3.64	3.25	2.41	3.76
<i>Keratella tecta</i>	0.53	1.42	2.37	3.70
<i>Simocephalus vetulus</i>	1.65	0.42	2.25	3.52

3.3.1 Canonical correspondence analysis of natural ponds

Ordination biplots were generated based on canonical correspondence analysis (CCA) of zooplankton species in natural ponds throughout the Waikato region (Figure 7). Sites and species are plotted on the ordinations and environmental variables are represented by arrows. The direction of the arrows indicate the association of sites and species with environmental variables and the length of the arrow indicates the strength of the association. The two most important axes, Axis 1 (eigenvalue = 0.265) and Axis 2 (eigenvalue = 0.167), were used in the biplots. On the CCA, species such as *Keratella procurva*, *Trichocerca similis*, *Dicranophoroides caudatus*, *Brachionus angularis* and *Ilyocryptus sordidus* were most strongly negatively associated with Axis 1. *Epiphanes macroura*, *Mytilina mucronata*, *Lepadella ovalis*, *Trichocerca brachyura* and *Platytias quadricornis* were strongly positively associated with Axis 1. There were only five ponds (sites 4, 10, 21, 8 and 26) positively associated with Axis 1. Also, five peat ponds (sites 8, 9, 16, 21 and 23) were strongly negatively associated with Axis 2, while there were four oxbow ponds (sites 30, 32, 33 and 34) strongly positively associated with Axis 2.

Forward selection and Monte Carlo permutation tests were performed to explore the environmental variables that explained patterns in zooplankton composition among natural ponds (Table 8). Lambda – 1 indicates the amount of variation in zooplankton community composition that a single environmental variable explains independently of the other environmental variables. The amount of variation each environmental variable explains at the time of inclusion into the CCA model is represented by Lambda-A (most important variable is listed first) (ter Braak & Smilauer, 1998). Dissolved oxygen, the most strongly negatively associated variable on Axis 1, explained the greatest amount of variation in zooplankton species composition (23%) in natural ponds when the environmental variables were considered individually (Lambda – 1) (Table 8.). Following this, conductivity, water colour, TLI and elevation all individually explained 14% of the variation in species composition in natural ponds. Lambda – A results indicated that dissolved oxygen explained the largest proportion of variation in community composition in natural ponds (Lambda - A = 0.23, $p = 0.002$) (Table 8). Following the addition of dissolved oxygen to the CCA model, conductivity explained a further 15% of the variation in zooplankton composition ($p = 0.020$) (Table 8). After the inclusion of dissolved oxygen and conductivity, no other environmental variables explained any further significant amount of variation in the zooplankton data. Dissolved oxygen was most strongly negatively associated with Axis 1 and conductivity was strongly negatively associated with Axis 2 and moderately associated with Axis 1 (Figure 7).

As dissolved oxygen explained the greatest amount of variation in zooplankton community composition, this indicates that natural ponds that were negatively associated with Axis 1 had higher dissolved oxygen levels. There were only five natural ponds that were positively associated with Axis 1 (Figure 7), and these all had low dissolved oxygen levels (Site 4 = 1.12 mg L⁻¹; Site 8 = 2.93 mg L⁻¹; Site 10 = 2.47 mg L⁻¹; Site 21 = 1.11 mg L⁻¹; Site 26 = 4.13 mg L⁻¹). Therefore, species that were negatively associated with Axis 1 were found in natural ponds with higher levels of dissolved oxygen compared to species positively associated with Axis 1. Conductivity also explained a significant amount of variation in zooplankton composition when included in the model, indicating that sites 8, 9, 21 and 23 (all peat ponds), all strongly negatively associated with Axis 2, had high conductivity

levels. In contrast, sites 10, 32, 33 and 34 (oxbow ponds) had lower conductivity levels. Therefore, species negatively associated with Axis 2 (e.g., *Euchlanis pyriformis*, *Brachionus budapestinensis*, *B. calyciflorus* and *Filinia novaezealandiae*) were found in natural ponds with low conductivity compared to species positively associated with Axis 2 (e.g., *Synchaeta pectinata*, *Filinia longiseta* and *Trichocerca similis*).

Table 8. Forward selection and Monte Carlo permutation test results from CCA of zooplankton species in natural ponds. Environmental variables are listed based on Lambda - A (inclusion in the model). Bold values indicate a significant result ($p < 0.05$).

Variable	Marginal effects	Conditional effects	
	Lambda - 1	Lambda - A	<i>p</i>
Dissolved oxygen (mg L ⁻¹)	0.23	0.23	0.002
Conductivity (μS cm ⁻¹)	0.14	0.15	0.020
Water colour (absorbance)	0.14	0.12	0.062
No. of water bodies within 2km radius	0.11	0.10	0.196
Trophic level index	0.14	0.10	0.284
Elevation (m)	0.14	0.10	0.166
Area (ha)	0.10	0.09	0.262
Temperature (°C)	0.07	0.08	0.464
pH	0.12	0.07	0.724
Latitude	0.12	0.06	0.702

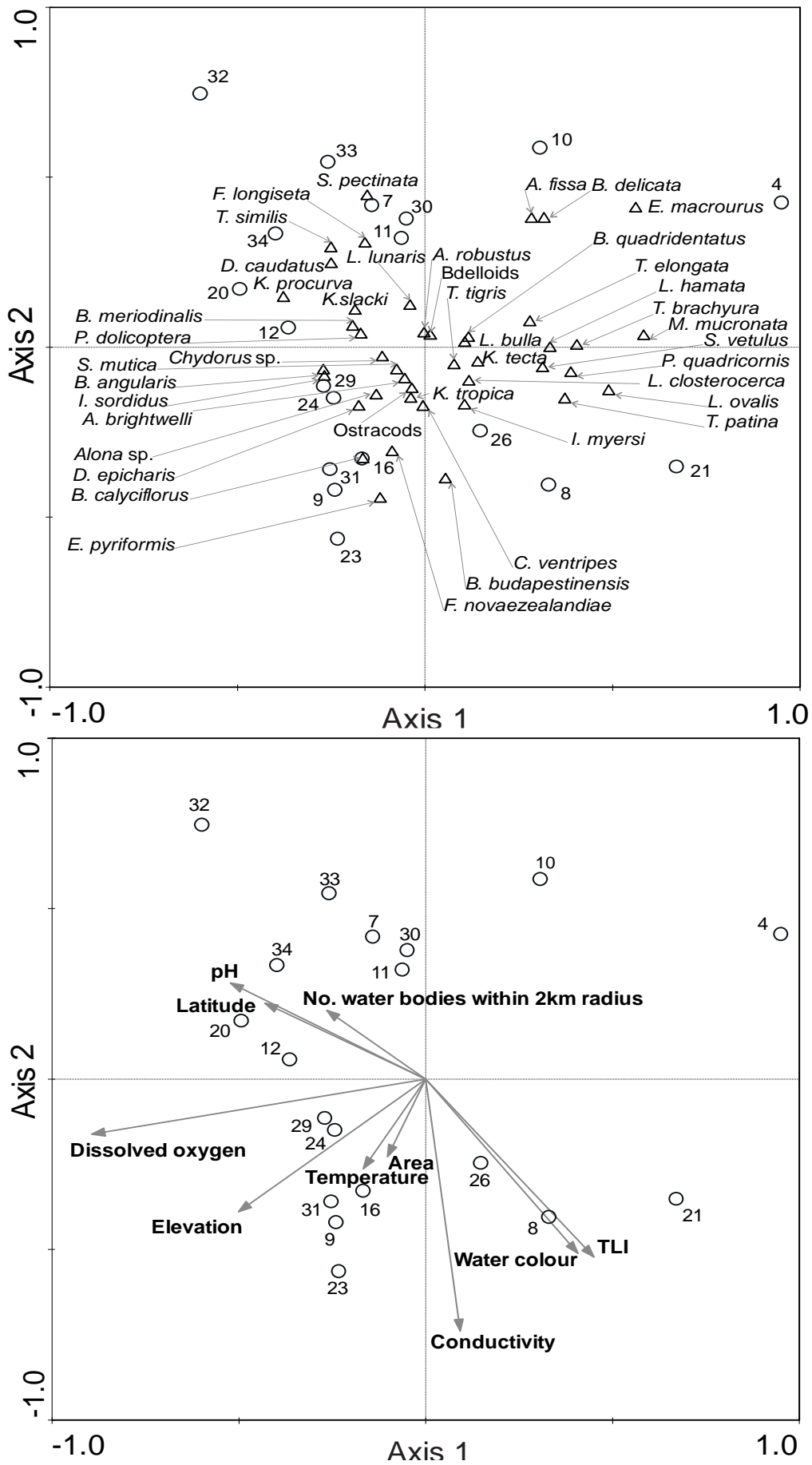


Figure 7. Ordination biplots generated from CCA of natural pond zooplankton species relative to environmental variables. Numbers indicate site location in the Waikato region (Figure 1).

3.3.2 Canonical correspondence analysis in farm dams

Ordination biplots were generated based on canonical correspondence analysis (CCA) of zooplankton species in farm dams throughout the Waikato region (Figure 8). Sites and species are plotted on the ordinations and environmental variables are represented by arrows. The two most important axes, Axis 1 (eigenvalue = 0.210) and Axis 2 (eigenvalue = 0.188), were used in the biplots. On the CCA, species strongly positively associated with Axis 1 were predominantly rotifers such as *Trichocerca teniour*, *Filinia novaezealandiae*, *Asplanchna brightwelli* and *Itura myersi* (Figure 8). Strongly negatively associated with Axis 1 were rotifer species such as *Keratella tecta*, *K. cochlearis* and *B. budapestinensis* (Figure 8).

Forward selection and Monte Carlo permutation tests were performed to explore which environmental variables explained patterns in zooplankton composition in farm dams (Table 9). On an individual basis (Lambda - 1), pond surface area (ha) explained the largest amount of variation in species composition (17%) followed by conductivity and elevation, which both explained 13% of variation in species composition. However, none of the measured environmental variables explained significant amounts of variation in zooplankton composition among farm dams (Table 9), suggesting that zooplankton communities in farm dams are relatively unstructured by the environmental variables examined in this study.

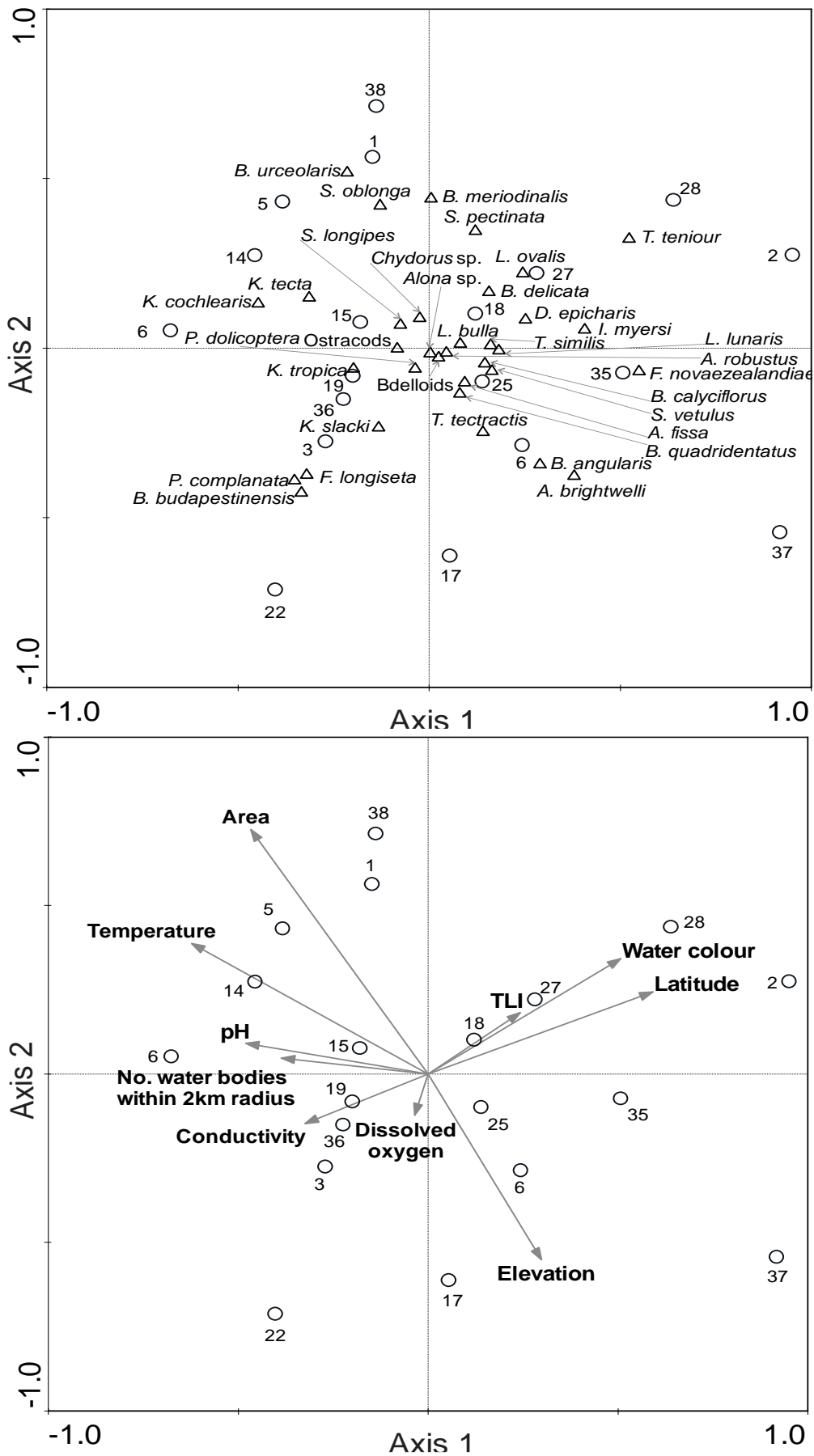


Figure 8. Ordination bipolots generated from CCA of farm dam zooplankton species relative to environmental variables. Numbers indicate site location in the Waikato region (Figure 1).

Table 9. Forward selection and Monte Carlo permutation test results from CCA of zooplankton species in farm dams. Environmental variables are listed based on Lambda - A (inclusion in the model).

Variable	Marginal effects		Conditional effects	
	Lambda - 1	Lambda - A	<i>P</i>	
Area (ha)	0.17	0.17	0.058	
pH	0.12	0.13	0.258	
Latitude	0.12	0.13	0.276	
Conductivity ($\mu\text{S cm}^{-1}$)	0.13	0.12	0.348	
Elevation (m)	0.13	0.11	0.343	
Dissolved oxygen (mg L^{-1})	0.10	0.11	0.484	
No. of water bodies within 2 km radius	0.09	0.10	0.516	
Water colour (absorbance)	0.12	0.09	0.646	
Trophic Level Index	0.08	0.09	0.644	
Temperature ($^{\circ}\text{C}$)	0.14	0.08	0.700	

Chapter 4

Discussion

4.1 Zooplankton communities in natural ponds and farm dams

All of the ponds examined were eutrophic to hypertrophic, and common species recorded in both pond types were typical of eutrophic conditions, including *Brachionus* species, *Keratella* species and *Polyarthra dolichoptera* (Gannon & Stemberger, 1978; Duggan *et al.*, 2002). Littoral and benthic species were also common (e.g., *Platylabus*, *Testudinella* and *Euchlanis* species) in both pond types, which is likely a result of the near shore sampling locations, small habitat size, and in some cases, the presence of macrophytes, which increases habitat heterogeneity (Pennak, 1966; Pejler, 1995; Castro *et al.*, 2005; Bielańska-Grajner & Gładysz, 2010).

Both natural ponds and farm dams had high species diversity (83 and 91 species respectively), with a similar species richness overall. Although species richness was similar between the pond types, the nMDS ordination and ANOSIM analysis ($p = 0.014$) indicated that there were differences in community composition between the two pond groups. A SIMPER analysis identified 7 taxa that contributed more than 3.5% of the dissimilarity between natural ponds and farm dams. Of these, crustacean zooplankton were identified as being more abundant in, and indicative of, natural ponds (e.g., the cladocerans *Chydorus* sp. and *Simocephalus vetulus*, ostracods, and the cyclopoid copepod *Acanthocyclops robustus*). In contrast, small planktonic rotifers such as *Polyarthra dolichoptera* and *Keratella tecta* were more common and abundant in farm dams. Similar findings have been made with respect to zooplankton species richness and composition in urban constructed and natural waters. For example, a global meta-analysis by Merrix-Jones *et al.* (2013) demonstrated pelagic crustacean zooplankton communities differ between natural and artificial lakes (e.g., dammed rivers and artificial ponds). Analogous to my study, these authors found species' richness in artificial and natural waters to be similar, but that community composition differed between the two water body types. Similarly, Parkes & Duggan (2012) examined zooplankton communities, including both crustaceans and rotifers, in 23 natural lakes and 23 constructed lakes in New

Zealand; these authors found that natural and constructed waters had similar species richness per water body, but community composition varied between them. In their study, zooplankton communities in constructed ponds were a collection of opportunistic species, comprising primarily small rotifers (e.g., *Keratella tropica* and *Trichocerca pusilla*) that were able to occupy new habitats, likely due to lack of adapted competitors and/or predators. These authors also found that crustaceans (e.g., *Bosmina meridionalis* and *Calamoecia lucasi*) were more common in natural lakes compared to artificial lakes.

While it is commonly possible to determine the age of constructed urban ponds, this is not the case for those in rural habitats. From 1840, European settlers began clearing, draining and developing the Waikato, and by the 1880s, most of the Waikato had been converted to pasture, as the dairy farming and agricultural industry grew (McKinnon *et al.*, 1997). Zooplankton are often slow to develop mature communities by natural vectors (taking 100s to 1000s of years to develop; Jenkins & Buikema, 1998), suggesting that natural ponds will have more structured and well adapted communities than newer ponds (e.g., farm dams), which have had less time to mature. Typically, immature communities consist of opportunistic species that are able to occupy a wide variety of habitats, and survive in a range of environmental conditions. Contrastingly, mature communities, which generally consist of species adapted to the local conditions (Shea & Chesson, 2002). In the present study, small eurytopic (i.e., able to survive a broad range of environmental conditions) and opportunistic species (e.g., the rotifers *Brachionus*, *Keratella* and *Polyarthra*) occurred more frequently in farm dams than in natural ponds, whereas crustaceans (e.g., *Chydorus* sp., *Ilyocryptus sordidus* and *Bosmina meridionalis*) were more common in natural ponds than in farm dams. Dispersal may be a factor affecting the frequency of rotifers and cladocerans in farm dams and natural ponds. For example, Jenkins (1995) found that rotifers were the dominant species to colonise newly created ponds. From a study on recently constructed treatment ponds in agricultural landscapes, Eivers *et al.* (2018) identified that zooplankton communities were different from adjacent lakes and drains owing to the dominance of rotifers. Furthermore, rotifer dispersal abilities are thought to be more effective over both short and long-distances as a result of their small size and the large number of diapausing eggs they produce relative to crustaceans (García-Roger *et*

al., 2006), which can be transported by wind, rain and water-fowl (Proctor & Malone, 1965; Pennak, 1966; Cohen & Shurin, 2003). Water-fowl were present at both natural and constructed sites examined in the present study, although no specific bird survey was conducted. Green & Figuerola (2005) considered dispersal of aquatic invertebrates by water-fowl to be infrequent. As such, the presence of more crustaceans in natural ponds is likely due to the age of natural ponds, which have had more time for the more slowly dispersing crustaceans to colonise by natural vectors. The results of the current study suggest that constructed farm dam communities are relatively unstructured and consist of eurytopic and opportunistic species, whereas natural ponds have more structured assemblages, with species adapted to the local conditions.

Local competition between larger cladocerans and smaller rotifers is a possible reason why rotifers were less common in natural ponds (with the exception of bdelloid rotifers). Interference competition from larger bodied cladocerans can damage and/or kill rotifers (MacIsaac & Gilbert, 1991; Pace & Vaque, 1994). Balvert *et al.* (2008) assessed the impact of the establishment of non-indigenous *Daphnia galeata* on rotifers in Lake Puketirini, New Zealand. These authors identified that the previously rotifer dominated system changed to one dominated by *D. galeata*. Further, exploitative competition for food resources from cladocerans can strongly affect rotifer abundances, as larger bodied cladocerans are more efficient grazers (MacIsaac & Gilbert, 1991).

Differences in zooplankton communities can influence the grazing pressure exerted on phytoplankton (Gerasimova *et al.*, 2018). Zooplankton, particularly cladocerans, have been reported to control algal biomass in lakes and ponds, and maintain clear-water states (Lampert *et al.*, 1986; Kagami *et al.*, 2002). However, as previously stated, fewer cladocerans were present in farm dams compared to natural ponds in the current study. This suggests that algae may not be processed as efficiently in farm dams compared to natural ponds, where cladocerans were more abundant.

Underlying environmental variables in natural ponds were found to structure zooplankton diversity and composition. Comparatively, a significant proportion of

the variation in zooplankton communities among farm dams was not explained by any of the measured environmental variables. In natural ponds, variation in species richness was attributed to temperature and pond surface area, and the variation in community composition was explained by dissolved oxygen and conductivity. This suggested that natural ponds had relatively structured zooplankton assemblages that are strongly influenced by the surrounding environment. Unlike natural ponds, variation in farm dam species richness and community assemblages was not explained by any of the measured environmental variables. The combination of the species richness and community composition results indicated that zooplankton communities in farm dams are a relatively unstructured subset of species from the regional pool. Parkes & Duggan (2012) also found zooplankton communities in natural lakes in New Zealand to be structured by underlying environmental gradients. A key difference between the findings of Parkes & Duggan (2012) and the current study, is zooplankton communities in the natural water bodies were governed by trophic state, while this variable was found to be insignificant in the current study. This variable was likely not significant in the current study due to the narrow trophic state gradient identified; all of the farm ponds were eutrophic to hypertrophic in this study, whereas the lakes surveyed by Parkes & Duggan (2012) ranged the spectrum from oligotrophic to hypertrophic. In constructed lakes, Parkes & Duggan's (2012) study indicated that zooplankton communities were governed by the opportunity for establishment; the significant variability in community composition was explained by distance to the nearest water body and number of water bodies within a 20 km radius. In the current study, these variables did not explain significant variation in zooplankton communities in farm dams. The opportunity for establishment in the current study was perhaps lower, given that all of the ponds were on private property in agricultural areas, therefore restricting human access to and from the ponds. In contrast, the lakes studied by Parkes & Duggan (2012) were in urban areas and readily accessible to the general public (e.g., for boat and swimming access), increasing the opportunity for species to be introduced and establish (Havel & Shurin, 2004). Additionally, water-fowl are also considered to transport small invertebrates, including zooplankton, between water bodies (Figuerola *et al.*, 2003; Green & Figuerola, 2005). Water-fowl, particularly ducks and geese, were present at most sites in the current study, and are likely the primary mechanism for zooplankton dispersal in and out of rural ponds. However, as discussed by Green & Figuerola (2005), dispersal by water-fowl is likely to be

infrequent. Further, Ricciardi (2007) also suggests that dispersal by natural vectors (e.g., water-fowl) is negligible compared to human vectors. As such, the opportunity for zooplankton dispersal and establishment in constructed waters in the current study is likely to be lower than that of Parkes & Duggan (2012).

4.2 Variation in natural pond species richness

Average water temperature (averaged between summer and winter samples) was identified as the most significant predictor of species richness for natural ponds, although this variable only explained a small amount of variation overall ($R^2 = 0.26$). The relationship between the average water temperature and species richness was slightly negative; indicating that as temperature increased, species richness decreased. The maximum average temperature of 21.3°C (site 34) and the minimum average temperature of 15.6°C (site 30) were both recorded in oxbow ponds within 10 km of each other. Shading may have been a factor influencing temperature among ponds; ponds with cooler average temperatures (15°C to 17°C) typically had more shading by macrophytes or more trees growing around the water's edge (Pers. Obs. Le Quesne, 2018). In contrast, sites with higher average temperatures (17°C to 21°C) lacked trees around their margins or had fewer macrophytes present (Pers. Obs. Le Quesne, 2018). Similarly, in their study of bdelloid rotifer occurrence in 220 small agricultural water bodies, Kuczyńska-Kippen (2018) found that shading from macrophytes and trees or shrubs surrounding pond margins had a positive effect on bdelloid rotifer species richness and abundance, and temperatures were cooler in shaded areas. At site 34, with the warmest average temperature, eight zooplankton species were recorded. In contrast, 28 species were recorded in site 30, which had the coolest average temperature. Site 30 was dominated by crustacean and rotifer species, including eurytopic species (e.g., *Brachionus* and *Keratella* species), whereas site 34 was dominated by *Daphnia pulex* and *Polyarthra dolichoptera*. Thermal tolerances of many zooplankton species are largely unknown, but it is likely that the species present in ponds with cooler waters, more riparian vegetation and more macrophytes (which provide shade and increase habitat heterogeneity (Castro *et al.*, 2005; Bielańska-Grajner & Gładysz, 2010)), are less tolerant of higher temperatures. In particular, daphnids have been recorded in experimental and field studies of lakes and ponds with temperatures reaching 30°C, illustrating a tolerance to warmer temperatures (Goss & Bunting, 1976;

MacArthur *et al.*, 1985; Yampolsky *et al.*, 2014). As temperature increases, so will light and associated UV radiation (Häder *et al.*, 2015). Therefore, temperature in my study may also be acting as a proxy for UV radiation. The shallow nature of the ponds in the current study likely exposed zooplankton to high levels of UV radiation, which can be lethal (Leech & Williamson, 2000; Leech *et al.*, 2005; Marinone *et al.*, 2006). However, shading by riparian vegetation or macrophytes can reduce the amount of UV radiation zooplankton are exposed to, and is perhaps another reason why species richness was higher in sites with cooler temperatures and more shading. Rhode *et al.* (2001) illustrated that *D. pulex* was able to tolerate relatively high UV exposure owing to pigmentation, and this is a possible reason why *D. pulex* dominated at the warmest and least shaded site in the current study.

Of note, the oxbow with the highest average temperature (21.3°C) was one of the smallest and shallowest ponds, with a surface area of 0.1 ha during the winter. During the summer sampling period, the surface area of this pond had reduced by over half compared to the winter surface area, and the landowner stated that the pond is known to dry out in particularly warm summers. According to NIWA National Climate Centre (2019), the 2018/2019 summer was recorded as the third-warmest summer for New Zealand and the Waikato region since records began in 1981, with temperatures between 0.5°C and 1.2°C warmer than what is typical for that time of the year. The combination of an increase in temperature and a reduction in water volume (i.e., enabling the pond to heat faster) is a possible reason that the average temperature of this pond was 2°C higher than the next highest average pond temperature recorded (19.3°C). This may also be another factor in why this pond had a low zooplankton species richness (8 species recorded) compared to the other sites. However, the species richness of temporary ponds is considered highly variable, and may exhibit low or high species richness' (Pérez-Bilbao *et al.*, 2015).

Pond surface area was an additional significant predictor of species richness in natural ponds. However, as with temperature, surface area only explained a small amount of variation ($R^2 = 0.2288$). There was a positive correlation between species richness and pond surface area, suggesting that as the pond surface area increases, species richness also increases. Intuitively, this follows the ecological theory

proposed by MacArthur & Wilson (1967), whereby increasing the area of an island will increase the number of species that can be supported by the island. Richness-area relationships, with increased richness with an increased lake area, have also been demonstrated in zooplankton studies elsewhere (Dodson, 1992; Hessen *et al.*, 2007; Dodson *et al.*, 2009).

4.3 Variation in zooplankton community composition of natural ponds

In natural ponds, variation in zooplankton assemblages among ponds was attributed to dissolved oxygen and conductivity. Dissolved oxygen concentration explained the greatest amount of variation in zooplankton among ponds ($\Lambda - A = 0.23$, $p = 0.002$). The highest average dissolved oxygen levels were 17.4 mg L^{-1} and 10.7 mg L^{-1} , and species such as *Keratella procurva*, *Brachionus angularis*, *Bosmina meridionalis* and *Ilyocryptus sordidus* were associated with these ponds. The pond with the lowest average dissolved oxygen concentration (1.1 mg L^{-1}) was a shallow peat pond, which is known to dry up during the summer, and the shallow depth is perhaps the reason for recording low oxygen levels. *Epiphanes macroura* and *Mytilina mucronata* were abundant in this pond. For all other ponds, the dissolved oxygen concentrations ranged between 2.4 mg L^{-1} and 7.4 mg L^{-1} , which are relatively low being comparable to the hypolimnion of eutrophic lakes in summer (Heberger & Reynolds, 1977; McCarthy *et al.*, 2007; Wilhelm & Adrian, 2008; Araoye, 2009). The large range of dissolved oxygen concentration is indicative of different processes that are likely occurring in these natural ponds (e.g., photosynthesis and decomposition). For example, high dissolved oxygen levels can indicate relatively high levels of photosynthesis (from algae and macrophytes) (Wetzel, 2001; Misra, 2010). Further, macrophyte and algal photosynthesis could be playing a major role in oxygen generation (Wetzel, 2001; Pflugmacher *et al.*, 2006; Araoye, 2009). In the site with the highest dissolved oxygen, both macrophytes (Pers. Obs. Le Quesne, 2018) and algae (average chlorophyll-*a* concentration = $177.3 \text{ } \mu\text{g L}^{-1}$) were relatively abundant, suggesting that photosynthesis was an important factor influencing dissolved oxygen in these sites. The sites associated with high dissolved oxygen had taxa that commonly occurred in the current study (e.g., *Keratella* and *Brachionus* species), and many planktonic species, such as *Filinia longiseta*, *Polyarthra dolichoptera* and *Bosmina*

meridionalis. In contrast, the sites with the lower levels of dissolved oxygen ($<3 \text{ mg L}^{-1}$) indicate that bacterial decomposition was an important process in these ponds (Wetzel, 2001; Shade *et al.*, 2007). Of the five sites with dissolved oxygen concentrations of less than 3 mg L^{-1} (sites 4, 8, 10, 16 and 21), three were peat lakes. Low dissolved oxygen levels in these ponds may be explained by the substrate associated with these lakes. Peat lakes consists of partially decomposed organic matter (Paavilainen & Päivänen, 1995; Faithfull *et al.*, 2005), which can increase the rate of decomposition, and therefore oxygen consumption (Wetzel, 2001; Pflugmacher *et al.*, 2006). Additionally, bacterivorous species such as *Epiphanes macroua* were found in the sites associated with the lowest dissolved oxygen concentration. This species is regularly found in sewage treatment ponds, which commonly experience extremely low dissolved oxygen levels (Teltsch *et al.*, 1992; Nandini, 1999; Milstein & Feldlite, 2014).

Conductivity explained additional significant variation in community composition in natural ponds when included in the CCA model (Lambda – A = 0.15, $p = 0.020$). Notably, in the present study, there were four ponds (sites 8, 9, 21 and 23) that were associated with high conductivity levels in the CCA ($184.4 \mu\text{S cm}^{-1}$, $236.9 \mu\text{S cm}^{-1}$, $172.2 \mu\text{S cm}^{-1}$ and $158.9 \mu\text{S cm}^{-1}$ respectively). The substrate of these ponds was peat, which consists of accumulations of partially decomposed vegetation (Paavilainen & Päivänen, 1995; Faithfull *et al.*, 2005). Associated with the five ponds and high conductivity were species such as *Brachionus budapestinensis*, *B. calyciflorus*, *Euchlanis pyriiformis* and *Filinia novaezealandiae*. Positively associated with Axis 2 were four oxbow ponds (sites 30, 32, 33 and 34), which all had lower conductivity levels ($121.3 \mu\text{S cm}^{-1}$, $78.5 \mu\text{S cm}^{-1}$, $96.4 \mu\text{S cm}^{-1}$ and $126.3 \mu\text{S cm}^{-1}$ respectively). *Synchaeta pectinata*, *Filinia longiseta*, *Trichocerca similis* and *Dicranophoroides caudatus* were associated with these oxbow ponds. As such, pond origin may play a major role in variation among natural ponds, with conductivity a proxy for this in my study. The group of peat ponds linked with high conductivity also typically had yellow water colour, high Trophic Level Index (TLI) values and slightly acidic pH levels (these were not significant variables at the time they were added to the CCA in the final Monte-Carlo permutation model, but associated with conductivity in the ordination). In contrast, the oxbow ponds were associated with lower TLI levels, more neutral pH levels and lower concentrations

of humic substances. Conductivity varies among lakes based on underlying geology and edaphic factors (Canavan & Siver, 1994). Peat lakes are unique systems, typically exhibiting high concentrations of organic matter (>50%), acidic pH levels and dark brown colouration (Faithfull *et al.*, 2005). Historically, these ponds were associated with the Waikato region's peat wetlands, which offered a buffer to external nutrient and silt loading, and were typically low in nutrient concentrations (i.e., low conductivity). As a result of significant drainage and the conversion of 75% of the bog area to farmland, the wetland buffer has been severely reduced and ponds have become eutrophic, which may be indicated by higher conductivity levels (Schipper & McLeod, 2002). High conductivity levels have also been attributed to seepage from peat soils beneath a restored peatland lake in northern Israel (Hambright *et al.*, 1998). The naturally low inflow and outflow of these ponds may also be contributing to the higher concentration of ions compared to oxbow ponds (Faithfull *et al.*, 2005). For example, Vanhoutte *et al.* (2006) suggested that humic substances concentrated in Tasmanian lakes, where inflows and outflows were slow, whereas in lakes in the South Island, New Zealand, there was a lack of humic substances likely due to high flushing rates.

4.4 Non-indigenous species

Three non-indigenous species were recorded in this study, *Daphnia galeata*, *D. pulex* and *Boeckella minuta*, all of which have been found in New Zealand previously. The non-indigenous species recorded occurred more frequently in farm dams than in natural ponds, although overall, the frequency of occurrence was low. Non-indigenous species were present in only 7% of farm dams (*D. galeata* in two ponds and *B. minuta* in one pond) and 2% of natural ponds (*D. pulex*). Previous studies have identified constructed waters to be more readily invaded by non-native species compared to natural waters (Kolar & Lodge, 2001; Taylor & Duggan, 2011; Mimouni *et al.*, 2018). However, the overall frequency of non-indigenous species in this study was low when compared with other studies. Branford & Duggan (2017), for example, found non-native *D. galeata* and *D. pulex* in 21% and 35% (respectively) of constructed ponds they examined in, Auckland, New Zealand. *Daphnia galeata* was also observed in high frequencies in natural lakes (nearly 50%) and constructed lakes (just over 30%) surveyed across the North Island, New Zealand, by Parkes & Duggan (2012). Duggan & Payne (2017) discuss how

constructed waters have altered the distribution of calanoid copepods in the British Isles. These authors concluded that constructed waters had facilitated the spread of *Eudiaptomus gracilis* from northern England into the southern and eastern parts of England. Furthermore, they reported the presence of an estuarine species, *Eurytemora velox*, in a number of constructed water bodies that were inland of the coast, suggesting that constructed waters were facilitating its invasion across England. Banks & Duggan (2009) also concluded that constructed water bodies had facilitated the invasion of non-indigenous calanoid copepod species in New Zealand. These studies all suggest that constructed waters act as ‘stepping stones’ for the dispersal and establishment of invasive species across landscapes. However, the low frequency of non-native species in the present study suggests that constructed farm dams are not facilitating the spread of non-indigenous species to the same extent.

Humans have mediated the introduction of non-native species to inland waters via vectors such as the aquarium trade, with construction equipment and fish stocking (Duffy *et al.*, 2000; Duggan, 2010; Duggan, 2011; Branford & Duggan, 2017). In contrast, Ricciardi (2007) argues that dispersal of non-indigenous species by natural vectors (e.g., wind or water-fowl) is negligible compared to human mediated vectors. As previously mentioned, the frequency of non-indigenous species may have been low in the current study owing to the rural nature of the ponds (all ponds were on private property), and therefore, relatively inaccessible to humans. Thus, it is likely that human activities are the main factors facilitating the spread of non-native species across landscapes, and it appears unlikely that farm dams are acting as ‘stepping stones’ for non-indigenous species across the landscape, primarily due to the lack of human access.

4.5 New species records for New Zealand

Two genera (*Erignatha clastopis* and *Octotrocha speciosa*) and one species (*Cephalodella theodora*) recorded in the farm ponds had not previously been identified in New Zealand (Shiel *et al.*, 2009). *Erignatha clastopis* was recorded in a single farm dam during this study; elsewhere, it is typically associated with weedy ponds, lakes and swamps (Dumont, 1992). This genus comprises six known species,

with *E. clastopis* widely distributed across the Palearctic, Nearctic, Arctic and Australia. Both *O. speciosa* and *C. theodora* were found in the same natural pond, and have been recorded among macrophytes in littoral zones (Jersabek & Bolortsetseg, 2010; Segers *et al.*, 2010; Bertani *et al.*, 2011). Typically found in cold water bodies and temperate regions, *C. theodora* was first described in Stechlinsee, Germany (Dumont, 1992), and has been reported in freshwaters across Europe and North America (Zhuge *et al.*, 1998; Bekleyen *et al.*, 2011; Bertani *et al.*, 2011). *Octotrocha speciosa* has been reported in Asia (e.g., China, Thailand and Vietnam) (Segers *et al.*, 2010), in various water bodies throughout the United States of America (Edmondson, 1959), and in Australia (Shiel, 1995). Shiel *et al.* (2009) explained that the documentation of rotifer species in New Zealand is severely restricted both spatially and temporally. Currently, it is believed that approximately 70% of New Zealand rotifers are shared with Australia, and that there are many more yet to be documented in New Zealand (Shiel *et al.*, 2009). As such, it is difficult to determine if these species are native or non-indigenous in status. Nonetheless, it is likely that all three species are naturally found in New Zealand, and have simply never been documented here previously (particularly as pond habitats are understudied in New Zealand).

4.6 Study limitations

There were some practical limitations of the current study. One of the constraints was the limited number of samples taken due to time restrictions of an MSc degree. Two zooplankton samples were collected and two *in-situ* measurements of environmental variables were recorded; one in winter/spring and one in summer. In future, collecting multiple samples (e.g., monthly samples) over the course of a year would improve our understanding of zooplankton biodiversity and community composition across seasons in dams and natural ponds on farms. Further research in this area is needed to improve our understanding of the underlying environmental factors affecting zooplankton assemblages, particularly in farm dams, as the environmental variables measured in this study did not account for the variation seen in community composition. Another constraint was that some pond characteristics were unable to be recorded (e.g., pond depth, Secchi depth and age). Secchi depth was not possible to measure owing to the shallow nature of the ponds. A black disc measurement was considered as this is a horizontal measurement of

water clarity, but based on the fine substrate of the water bodies, it was deemed impractical as the black disc measurement would be hindered by the suspension of fine sediment when moving across the substrate. Pond depth would be a useful measurement if the study were to be repeated, but due to factors such as time restrictions, lack of accessibility to the middle of the ponds (e.g., impractical to launch boat in these shallow waters), and health & safety reasons (e.g., pond substrate too soft to walk on safely), measurements of pond depth and Secchi depth was not feasible. Depth would be a particularly useful variable to record, as it is known to affect a range of other abiotic factors (e.g., dissolved oxygen and temperature), which in turn can influence zooplankton communities. Pond age (for both natural ponds and farm dams) was also not available. Although it is assumed that natural ponds are 100s to 1000s of years old and farm dams are recent constructions, it was impossible to determine when the farm ponds in this study were created.

In addition, the timing of sample collection may have affected the environmental characteristics governing zooplankton composition and richness. For example, multiple ponds were sampled in a single day. As such, some were sampled in the morning when temperatures were cooler, and others were sampled early in the afternoon when temperatures were warmer. This may have introduced artefacts to the data set, where the average of some variables was higher or lower than other ponds simply based on the timings of sample collection.

4.7 Implications and future research

My research has identified that zooplankton communities in farm dams were significantly different to those in natural ponds. As such, it would be beneficial to continue improving our knowledge of zooplankton in farm dams and natural ponds, as they are typically under-represented in many lakes databases, and may represent valuable conservation tools for enhancing biodiversity (Taylor & Duggan, 2011). Further, my results highlight that when examining environmental determinants of zooplankton community composition in water bodies across the landscape, natural and constructed ponds should be separated, as they appear to be structured by different variables; as such, including constructed ponds among databases of natural

water bodies may mask patterns with respect to community composition variability across landscapes.

Large proportions of variation remained unexplained by the analyses conducted; for example, only 38% of the variation in zooplankton community composition among natural ponds was explained by the measured environmental variables. This suggests that other stochastic processes and/or biotic interactions that were not measured in the current study may be important factors influencing zooplankton communities in farm dams and natural ponds. These processes and interactions (e.g., influence of water-fowl in dispersal or predation by fish) were not examined in the current study, but could improve our understanding of the factors defining zooplankton assemblages in farm dams and natural ponds. Also improving our understanding of zooplankton biodiversity, in general, could have implications for maintaining and improving biodiversity (Davies *et al.*, 2008; Casas *et al.*, 2012). Landowners may also be able to use this research to promote and manage zooplankton communities to improve their water quality, which is of high importance to the New Zealand agricultural sector; for example, by seeding farm dams with native species (Taylor & Duggan, 2011).

Another recommendation would be to more explicitly compare zooplankton communities between natural ponds of different origins (e.g., peat, oxbow and dune ponds). The results from the current study suggested that oxbow and peat pond zooplankton communities differed. These differences highlight that zooplankton communities in ponds are diverse, and also suggests that managing and conserving a variety of natural ponds (i.e., those of different origins) is important for maintaining and conserving zooplankton biodiversity. Further, given the similarities among peat ponds in this study, it would be interesting to specifically study the zooplankton communities in peat water bodies within the Waikato region to improve our understanding of the role of environmental variables, such as gilvin, in influencing trophic interactions.

Finally, the results of this study suggested that the spread of non-indigenous species across landscapes was not facilitated by the construction of farm dams. Future

studies could compare the frequency of non-indigenous species in constructed and natural water bodies that are more readily accessible by people relative to those that are isolated. Additionally, further research should be conducted to improve our understanding of the dominant factors facilitating the establishment and spread of non-indigenous species across the landscape (e.g., constructed water bodies or human mediated vectors).

4.8 Summary

In summary, natural and constructed ponds are diverse systems that also support rare species. Zooplankton species richness' were similar between farm dams and natural ponds, but community composition differed. Variation in natural pond zooplankton species richness and composition was explained by underlying environmental variables, whereas zooplankton communities in farm dams were not explained by the measured intrinsic factors. These findings suggest that farm dams have relatively unstructured communities compared to natural ponds. Two genera and one species were recorded that had not been identified in New Zealand prior to this study. Overall, the frequency of occurrence for non-indigenous species was low compared to other urban studies, suggesting that farm dams do not facilitate the movement of non-native species across the landscape. Further research should be conducted to improve our understanding of the influence of biotic and environmental factors in structuring both natural pond and farm dam zooplankton communities, as much of the variation remained unexplained. The current study will be a useful reference for future research on the biodiversity and structure of zooplankton communities in small natural and constructed waters in agricultural areas, and may also play a role in small pond management and conservation.

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