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**The potential for waterbirds to act as a vector for zooplankton
dispersal in the North Island, New Zealand.**

A thesis

submitted in partial fulfilment

of the requirements for the degree

of

Master of Science (Research) in Ecology and Biodiversity

at

The University of Waikato

by

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THE UNIVERSITY OF
WAIKATO
Te Whare Wānanga o Waikato

2022

Abstract

Zooplankton are essential components of freshwater ecosystems by controlling algal growth and sustaining higher trophic levels. Freshwater zooplankton are geographically isolated and are incapable of active dispersal to new freshwater sites. The dispersal of zooplankton can occur through natural dispersal vectors (e.g., wind, rain or waterfowl) or through human-mediated dispersal vectors (e.g., accidental or deliberate introductions). Dispersal of zooplankton is vital for maintaining gene flow between isolated sites and colonising new habitats. Zooplankton diapause eggs are well suited for dispersal as they are resistant to harsh conditions, e.g., digestion, drying and freezing. Diapause eggs increase the chance of survival in unfavourable conditions and are an important part of a zooplankton's life cycle. This paper analyses New Zealand waterbirds' dispersal of zooplankton internally (endozoochory) and externally (ectozoochory).

This study quantified the dispersal of zooplankton internally (endozoochory) using the faecal droppings collected from waterbirds at two New Zealand Lakes. Faecal droppings were collected from Mallard Ducks, Canadian Geese, Greylag Geese, Black Swans and Australian Coots from Lake Rotorua and Lake Rotorua. A total of 50 eggs were found in the faecal droppings of waterbirds, with a mean number of 0.75 eggs found per dropping. These results indicate that waterbirds are consuming zooplankton eggs. However, no significant difference was observed in the propagule count among waterbird species. Therefore it was unlikely that the waterbird species impacted the abundance or viability of diapause eggs.

The sediment experiment showed zooplankton are inhabiting the shores of Lake Rotorua and Lake Rotorua, where waterbirds are likely to come in contact with diapause located within the sediment. In Lake Rotorua, diapausing eggs from six species of rotifers, cladocerans, copepods and ostracods hatched from the littoral sediments. Strikingly, no hatching was observed in the littoral sediments from Lake Rotorua. These results suggest that diapausing eggs are readily available to be picked up by waterbirds for external dispersal (ectozoochory). This study quantified the potential for zooplankton to be dispersed by waterbirds internally (endozoochory)

and externally (ectozoochory). Results suggest that waterbird dispersal of zooplankton is occurring, but the numbers being transported are low. Although, the transport of a few individuals may be enough to achieve gene flow. Waterbirds are not be the primary vector for the dispersal of zooplankton. Human-mediated contributions e.g., shipping-related activities (ballast tanks), may play a more significant role than waterbirds in the dispersal of zooplankton.

Acknowledgements

A special thank you to my academic supervisor, Ian Duggan for all your help and time you have put into helping me with trial sampling, laboratory work and a lot of editing. I have learnt so much these past two years and I appreciate all your ideas, advice, and assistance over this stressful period. I would have not been able to do it without you. Also, a big thank you to Kat, for the lab inductions, sorting equipment for us, keeping us organised and for just being a friendly face around R block every day.

A special mention to Gaby and Amber who I've gone through this entire process with. Gaby has been my flatmate, field assistant, and stress buddy throughout these last two years, and I don't know what I would have done without her. Also, to Amber who has been the biggest emotional support with countless hours of writing together, just as many hours distracting each other and endless procrastination coffee outings.

Finally thank you to my family for the endless support I have received. You've been my biggest support and have kept me accountable and motivated me to finish it. I'm sure you will read the entire thing when its finished.

I couldn't have done it without any of you,

Thank you very much

Kelly.

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Chapter 1: Introduction

1.1 Importance of Zooplankton

Zooplankton communities are diverse in freshwater environments, with more than 70,000 species described globally (Brönmark & Hansson, 2002). They are essential components in the functioning of freshwater ecosystems, playing a vital role in food chains through the transfer of energy from primary producers (phytoplankton) to the larger invertebrates and fish that feed on them (Jeppesen et al., 2011). Zooplankton also help control algal growth through grazing, improving water quality and increasing clarity in the water column (Elser & Goldman, 1991).

Biological indicators are valuable tools to assess the physical, chemical and biological factors of water quality in lakes, ponds and streams. Due to the sensitivity of zooplankton, they are considered universal indicators of ecosystem health and are utilised in several biotic indices assessing water quality (Jeppesen et al., 2011). Rotifers are particularly sensitive to environmental conditions (nutrient concentration, temperature and pH) and are a more accurate biological indicator in freshwater environments (Duggan et al., 2001). Several studies have identified relationships between the trophic state of lakes and zooplankton abundance (Pederson et al., 1976; Gannon & Stemberger, 1978; Chapman et al., 1985). Zooplankton community composition is an appropriate measure for assessing trophic states due to their response to environmental conditions (nutrient content) and short generation times (Lyche-Solheim et al., 2013).

1.2 Importance of Dispersal

Unlike aquatic insects, zooplankton taxa are incapable of active dispersal between isolated sites. Instead, they rely on the natural (e.g., wind, rain, surface waters and animals) (Jenkins & Underwood, 1998; Green et al., 2013; Moreno et al., 2019) and human introductions as passive transport vectors to colonise lakes (Bilton et al., 2001; Louette & Meester, 2005). Ronce (2007) defined dispersal as “any movement of individuals or propagules with potential consequences for gene flow across space”. Dispersal influences many important ecosystem characteristics,

including population structure, extinction, competition and biodiversity. Dispersal allows the escape from unfavourable conditions with low resources and predators to find a new ecosystem with reduced competition and more abundant resources (Bilton et al., 2001). Dispersal increases genetic diversity by introducing new individuals into populations, contributing to a lower probability of extinction and inbreeding depression (Freeland et al., 2000). However, some limitations prevent the successful dispersal and colonisation of organisms, including the inability to locate a mate, predation, failure to establish in a suitable site and outbreeding depression (Bilton et al., 2001).

Mechanisms that facilitate the dispersal of aquatic invertebrates are important to understand as dispersal shapes community structure and ecosystem biodiversity (Cohen & Shurin, 2003). These processes occur on different biological scales, spatially and temporally, due to the differences in dispersal capabilities and the ability of zooplankton to colonise new freshwater habitats (Cohen & Shurin, 2003; Moreno et al., 2019). The dispersal rates between lakes depends on several factors; distance to source and the ability of the dispersal vector (rain, wind, waterbird, human) that transports the dispersing agent (Hobaek et al., 2002). Insight into the dispersal of aquatic species is critical for protecting our freshwater heritage due to the ability of invasive aquatic invertebrates displacing native species (Sanchez et al., 2012; Reynolds and Cummings et al., 2015). In addition, understanding dispersal patterns may help manage the invasions of non-indigenous species, this is critical as eradication is unlikely once they have established in an environment (Parkes and Duggan, 2012).

A number of studies have examined the different vectors facilitating zooplankton dispersal. Human-related dispersal involves the intentional or accidental introduction of zooplankton. Recreational and commercial boating, especially shipping-related activities are a major case of human-related dispersal of zooplankton (Havel & Stelzleni-Schwent, 2000). Another vector is through aquaculture techniques can lead to accidental introductions as zooplankton can hitchhike during the introduction of other aquatic organisms e.g., fish (Carlton, 1992; Duggan & Pullan, 2017). Natural vectors e.g., Wind (Brendonck & Riddoch, 1999; Cáceres & Soluk, 2002), rain (Moreno et al., 2016), flowing water (Thorp et al., 1994), and animals (Green et al., 2008) have been studied across America, Europe, Australia. As far as I am aware, no studies

have analysed the natural dispersal of invertebrate propagules in New Zealand. Dispersal of zooplankton is commonly achieved through the diapausing stages of the zooplankton's lifecycle.

1.3 Zooplankton diapause eggs

The passive dispersal of zooplankton is primarily achieved by diapausing stages, and in particular using 'resting' eggs. Diapause eggs are well suited for the harsh conditions of overland transport as they are known to resist drying, freezing and digestion (Mellors, 1975; Panov et al., 2004; Reynolds & Cummings, 2015). Diapausing propagules are the dormant part of a zooplankton's life cycle, allowing for arrested development. An internal cue initiates diapause egg production after an external stimulus, such as photoperiod, predator density, food quality and population density indicates unfavourable conditions (Brendonck & De Meester, 2003; Conde-Porcuna et al., 2014). This stage in development can give species living in unsuitable environments an increased chance of survival and will hatch and resume development when conditions become favourable again (Brendonck & De Meester, 2003; Conde-Porcuna et al., 2014). However, some populations, particularly those inhabiting temporary waters, rely on resting stages for survival (Brendonck & De Meester, 2003). From this, some authors have concluded that the production of diapausing eggs is an adaptation for dispersal (Panov et al., 2004).

Cladocerans, rotifers and ostracods can reproduce asexually through parthenogenesis. Under the right conditions, they have the capability for a single hatching to establish a new population (Havel & Stelzleni-Schwent, 2000; Havel & Shurin, 2004). Diapausing zooplankton eggs are produced when their reproductive mode switches from parthenogenesis to sexual reproduction (gametogenesis). The change in reproductive mode is often triggered by environmental stimuli (Aránguiz-Acuña & Ramos-Jiliberto, 2014), such as changes in photoperiod (Stross, 1969), temperature, food concentration (Alekseev et al., 2007) or salinity (Hagiwara et al., 1988). The three major zooplankton groups, rotifers, copepods and cladoceran (Hairston et al., 2000), as well as other freshwater taxa such as large branchiopods (Brendonck & Riddoch, 2000) and tardigrades (Nelson & Marley, 2000), are known to produce diapause eggs.

The hatching of diapause eggs depends on the completion of an essential diapause period, suitable environmental conditions, and the viability of the diapause egg (García-Roger et al., 2006). Diapause eggs commonly sink and settle into the bottom sediments. However, hatching can only occur in the upper layer of the sediment, in the active egg bank where the eggs are exposed to hatching stimuli (e.g., light, temperature and food (Conde-Porcuna et al., 2014). The active egg bank ranges from 2 cm to 5 cm below the sediment surface, restricting the number of diapause eggs that are able to hatch (Cáceres, 1998; García-Roger et al., 2006). Some eggs can float or attach to plants or sediment particles (Brendonck & De Meester, 2003), leading to accidental ingestion by waterbirds feeding on aquatic vegetation. Eggs can persist in the sediment egg bank of lakes and hatch after decades; some have recorded hatching eggs that are hundreds of years old (Hairston et al., 1995). The extent of the sediment egg bank exposed to hatching cues is dependent on sedimentation rates of lakes, burial and sediment disturbances, i.e. Storm disturbance, bioturbation by aquatic species and boat anchoring (Hairston et al., 1995).

1.4 Waterbird dispersal

Darwin (1859) was the first to propose the possibility of zooplankton dispersal through waterbirds. Several studies have identified waterbirds as an important vector for carrying diapausing stages of invertebrates and plants externally on their feathers and plumage (Ectozoochory) (Maguire, 1959, 1963; Figuerola and Green 2002b; Brochet et al., 2010; Reynolds & Cumming, 2015) and internally through their digestive tract (endozoochory) (Proctor, 1964; Brochet et al., 2010; Charalambidou & Santamaría, 2002; Figuerola et al., 2003; Frisch et al., 2007; Green et al., 2008; Van Leeuwen et al., 2012; Muñoz et al., 2014; Moreno et al., 2019). The abundance and distribution of waterbirds make them suitable dispersal vectors and allow for short-distance and long-distance transport of invertebrate eggs (Charalambidou & Santamaría, 2002). In addition, waterbirds can transport propagules over long distances, up to thousands of kilometres (Freeland et al., 2000; Clausen et al., 2002), which is likely related to migratory movements of waterbirds in winter during stopovers at sites (Farmer & Parent, 1997; Green & Figuerola, 2005).

1.5 Endozoochory

Few studies have addressed whether zooplankton diapause remains viable after passing through the waterbird gut (Proctor, 1965; Frisch et al., 2007; Green et al., 2008; Moreno et al., 2019). There are several requirements for the successful endozoochory dispersal of invertebrate propagules. Firstly, the waterbird must ingest the propagule voluntarily by feeding on aquatic invertebrates or foraging for aquatic plants with invertebrate propagules attached. Retention time in the waterbird gut and flight speed limits viable propagules' dispersal distances. Finally, establishing the propagule in the new site requires the waterbird to defecate in suitable habitat with appropriate hatching cues (Figuerola et al., 2002). Past studies analysing endozoochory have focused on understanding propagule viability, retention time and frequency of propagules passing through the gut to get a better understanding of dispersal probability and dispersal distances. Commonly used methods to achieve this include faecal studies and feeding experiments. Faecal studies give a good indication of the types of zooplankton species being transported internally by waterbirds and which species are more likely to remain viable after digestion (Figuerola et al., 2003; Charalambidou & Santamaría, 2005; Moreno et al., 2019). Whereas feeding experiments require captive waterbirds to ingest large amounts of zooplankton propagules and are useful for testing the proportion of propagules that remain viable after digestion. Feeding experiments are commonly coupled with retention time studies by feeding waterbirds plastic markers to quantify the number of time propagules would be exposed to digestive processes (Van Leeuwen et al., 2012).

Several studies have linked the viability of propagules after excretion to the retention time within the bird. The retention time is the amount of time the propagule takes to move through the avian gut while exposed to digestive processes (e.g., grinding). The longer the propagule retention time, the less likely it will pass through undamaged (Charalambidou & Santamaría, 2002). Differences in waterfowl gut and digestive efficiency can partially explain differences in the viability of propagules and retention time (Green et al., 2008). Several studies have examined different aspects of waterbird and gut morphology: crop, gizzard, caecae, intestine length and how it affects retention time and viability of the propagule (De Vlaming, 1968; Malone, 1965; Van Leeuwen et al., 2012). Moreno et al. (2019) speculated that small propagules with a hard shell would be more likely to be transported and remain viable as they

were more likely to survive gut passage. Due to the small size of rotifer propagules compared to copepods and cladoceran, rotifer eggs would likely suffer less physical damage from the gizzard and its grit content of waterbirds during digestion (Charalambidou & Santamaría, 2002). However, the small size of rotifer eggs makes them challenging to identify (Moreno et al., 2019).

1.6 Ectozoochory (Epizoochory or Exozoochory)

The transport of propagules through ectozoochory transport has several requirements for successful waterbird dispersal (Coughlan et al., 2017). Firstly, the vector (waterbird) and dispersal unit (propagule) must come in contact and attach. Propagules floating in the water column or from within the top few centimetres of sediment in the littoral zones of the lake can attach to the feet and plumage of water birds (Brochet et al., 2010). However, when the bird is in flight, the attached diapausing propagules are exposed to harsh conditions and must resist desiccation to remain viable (Coughlan et al., 2017). The ability of propagules to adhere to the plumage and feet of waterbirds may limit dispersal ability (Figuerola and Green, 2002b). Lastly, the propagule must detach from the waterbird in a suitable environment and establish in the receiving habitat (Coughlan et al., 2017)

Feather brushings (Figuerola & Green, 2002b; Brochet et al., 2010; Reynolds & Cummings, 2015), sediment analyses and experimental attachment studies (Banha et al., 2016; Rachalewski et al., 2013; Sánchez et al., 2012) have shown that some aquatic invertebrates can be carried externally on waterbirds. However, there is still little information on this topic. Figuerola and Green (2002b) collected propagules attached to several groups of waterbird species (2 Ducks, 2 Waders and 2 Rallids) in temporary wetlands in Spain through the feather brushing technique. Waterbirds were captured in traps and placed in plastic cups filled with distilled water to remove propagules from their feet. Each bird was then held in a cloth bag for an hour before the next step of collection. Next, using a soft shoe-brush each bird was brushed for 3 minutes over a plastic tray to carefully remove propagules attached to the plumage. Contents from the distilled water, cloth bag and plastic trays were analysed for propagules (Figuerola & Green, 2002b). Due to the large number of propagules found attached to waterbirds they speculated that dispersal is likely occurring at least at a local scale (Figuerola

& Green, 2002b). Past studies have used the experimental attachment method to measure the probability that invertebrates and invertebrate propagules will remain attached to waterbirds (Sánchez et al., 2012). In several studies, invertebrate propagules were attached to the carcasses of Mallard Ducks and were then put under swimming or flight conditions to mimic day-to-day activities undertaken by waterbirds (Banha et al., 2016; Rachalewski et al., 2013).

Zooplankton communities have been well studied in the open water of lakes, but few studies have examined the community composition at the lake shore. The psammon is a group of organisms that inhabit the sandy shoreline. The psammon habitat supports a variety of species but due to the unstable habitat, few plants are able to attach to the sediment and therefore it is an unfavourable habitat for grazing animals (Lokko et al., 2013). There is also little information regarding egg bank densities in the littoral zone, with most studies analysing the egg bank generally collected data using sediment cores from the deepest part of the lake (De Stasio, 1989; Conde-Porcuna et al., 2018). As a result, the species inhabiting the lake edge and the density of the sediment egg bank in this zone are underrepresented in the current literature compared to the species composition of the middle of the lake. On a regional scale, dispersal is an important influence on the community composition of zooplankton. Frequent dispersal between habitats is likely to increase the species richness and abundance of organisms in an ecosystem (Hobaek et al., 2002).

1.7 Aims and Hypotheses

The main aim of this research is to analyse the role waterbirds play in the dispersal of zooplankton. Specifically, I aim to examine the potential for organisms to be transported via waterbirds internally (endozoochory) and externally (ectozoochory). My first component specifically aims to analyse the number and viability of zooplankton eggs passing through the gut during endozoochory transport and whether the count and viability of eggs differ between waterbird species. My second component examines the sediments of shallow marginal habitats, with the aim of quantifying the variety of organisms living around the lake edge and the diapausing eggs found within the sediment, to understand what animals could be transported by waterbirds externally on feet and feathers (Ectozoochory). I also aim to examine how this

potential dispersal differs spatially between sites at each lake and between different lakes. This research can be used to improve the knowledge of the dispersal of zooplankton by waterbirds and the potential for long distance dispersal of isolated organisms. My hypotheses are that there are a wide variety of zooplankton on the lake shores for the potential dispersal externally by waterbirds and I expect that there will be a significant difference in the egg counts from different species of waterbird faecal samples and the probable viability of the zooplankton eggs.

Chapter 2: Methods

Faecal and sediment samples were collected from two lakes in the central North Island, New Zealand. Lake Rotorua is located in the Bay of Plenty region and is the second largest lake in the North Island, formed within a volcanic eruption crater. The lake has a maximum depth of 10.7 m and a catchment size of 42 400 ha, made up of pasture, exotic forest and urban area, which includes the city of Rotorua (Rutherford, 1984). Rotorua is known for its geothermal activity, which increases the temperature of the water flowing into the lake (Hoellein et al., 2012). Lake Rotorua has become highly eutrophic since the 1800s due to the intensification of land use increasing inputs of Nitrogen and Phosphorous into the lake (Smith et al., 2016). Lake Rotorua was formed within a collapsed magma chamber after an eruption, possibly around 100 000 years ago (Jolly & Brown, 1975).

Lake Rotoroa (Hamilton Lake) is located in the Waikato region in the city of Hamilton. It is significantly smaller than Lake Rotorua with a maximum depth of 6 m (Tanner et al., 1990). The catchment is 138 ha and is primarily made up of urban residential and recreational reserves. Hamilton Lake was formed 20 000 years ago when the Waikato River diverged from its course and redirected from Thames to Port Waikato (Lowe, 2014). Deposits of the Hinuera Formation formed dams that created Lake Rotoroa and several other lakes in the Hamilton Basin (Lowe, 2014). Water enters the lake from the catchment through 10 stormwater drains, groundwater, surface runoff and direct rainfall (Kane, 1995; Lowe, 2014). The lake is eutrophic due to the high levels of phosphorus and nitrogen, which have severely impacted the lake's water clarity (De Winton et al., 2002).

2.1 Waterbird species

In Lake Rotoroa, two birds were considered for the study, Mallard Ducks (*Anas platyrhynchos*) and Canada Goose (*Branta canadensis*) and in Lake Rotorua, three birds were considered, Greylag Goose (*Anser anser*), Black Swan (*Cygnus atratus*) and Australian Coot (*Fulica atra australis*). Mallard Ducks, Canada and Greylag Geese and Black Swans are all members of the family Anatidae family and the Eurasian Coot belongs to the Rallidae family. The Canada

Geese and Mallards were abundant at Lake Rotorua, and the Black Swan, Greylag Geese and Australian Coot were common around Lake Rotorua.

Many studies analysing the dispersal capabilities of waterbirds have focused on the Mallard duck as the primary disperser (Charalambidou & Santamaría, 2002). Mallards have a cosmopolitan distribution but are native to Europe, Asia and most of North America (Charalambidou & Santamaría, 2002). Mallard ducks are now widespread across New Zealand and inhabit a range of locations after being introduced into New Zealand in the 1860s (Guillemain et al., 2020). They are the largest dabbling duck, with an average body mass of 1 kg (Guillemain et al., 2020). They are an omnivorous species consuming various foods, including mostly aquatic plant material and aquatic invertebrates (Charalambidou & Santamaría, 2002).

Canada Geese were introduced to New Zealand from North America in 1905 and 1920 (White, 1986; Allan et al., 1995). They are entirely herbivorous, mainly feeding on terrestrial grasses and some aquatic plants (Conover, 1991). Canada Geese are large birds with a black head, neck, and a dark grey body (Adriaens et al., 2020). These Geese tend to be non-migratory in many areas around the world but are capable of migration in higher latitudes, where they can fly distances of up to 850 km non-stop (White, 1986). In New Zealand, movements are less migratory and tend to be restricted to breeding habits and wintering habitats (White, 1986).

The Greylag Goose were introduced to New Zealand by European settlers and now inhabit low lying or open areas with waterbodies and feed on roots, grain and insects and snails (Heather & Robertson, 2000). These Geese are large, on average weighing around 3.27 kg. (Hart & Downs, 2020). Sexual dimorphism of the plumage is prominent, with the male Greylag Geese being entirely white while the females having large patches of brown with distinctive orange bills and legs.

Black swan is a large native waterbird in New Zealand found to inhabit large constructed ponds, lakes and selected estuaries. These birds are flightless during moulting season, January – February. The Black Swan were introduced in the 1860s from Melbourne and due to their abundance it is speculated that some arrived naturally (Heather & Robertson, 2000). Black Swans are commonly found inhabiting lowland and coastal lakes like Lake Rotorua (Heather & Robertson, 2000). They are an entirely herbivorous species, feeding primarily on submerged aquatic freshwater plants (Heather & Robertson, 2000).

The Australian Coot, a sub-species of the Eurasian Coot, are a self-introduced species from Australia that invaded in 1957 and are now found throughout most of New Zealand but are absent from Northland (Heather & Robertson, 2000). The native range of *F. atra* ranges from North Africa, Europe, Asia and Australia (Heather & Robertson, 2000). Coot are primarily herbivorous, feeding on grass, algae and seeds but have also been found to consume aquatic invertebrates and eggs (Heather & Robertson, 2000).

2.2 Site selection

Based on preliminary location scouting, sample locations were selected where birds are known to inhabit the lake shore and that were accessible for collection of shallow water, shoreline bird faeces and marginal sediments samples. Collection of waterbird faeces and water samples from Lake Rotoroa and Rotorua was undertaken during late winter (August) and early spring (September) 2021, respectively. Sediment samples were collected from both lakes during early summer (December) 2021.

2.3 Faecal study – endozoochory

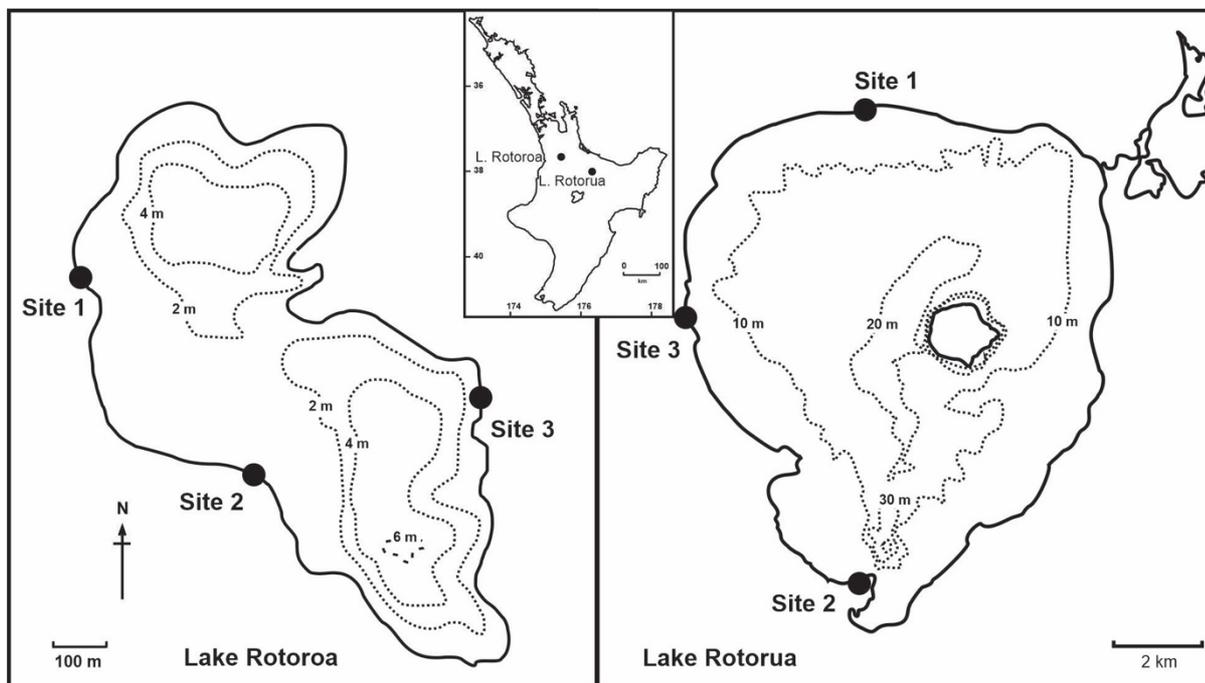


Figure 1. Site locations where faecal samples were collected from Lake Rotoroa and Lake Rotorua and the respective positions of both Lakes in the North Island

2.3.1 Fieldwork sampling

Table 1. Site number and coordinates for three sites around Lake Rotorua and the three sites around Lake Rotorua for the faecal study.

	Lake Rotorua	Lake Rotorua
Site 1	37°47'47"S 175°16'11"E	38°01'59"S 176°15'48"E
Site 2	37°47'58"S 175°16'21"E	38°07'46"S 176°15'49"E
Site 3	37°47'57"S 175°16'43"E	38°04'31"S 176°12'58"E

The collection protocol for the waterbird faeces followed Moreno et al. (2019). Waterbird faeces were collected from each site where waterbirds were found to be currently inhabiting to ensure they were fresh. Individual faeces were collected with a wooden spatula and placed into an airtight Falcon tube (50 ml), one sample per tube. Caution was taken when collecting the sample to minimise contamination by only selecting samples that were not in contact with soils or other materials that would be attached to the faeces. Any part of the faeces in contact with soil or other material was removed with a knife before being stored in the Falcon tube. A new spatula was used for every collected individual faeces to prevent cross-contamination among samples. The contents of each Falcon tube were weighed, recorded and labelled based on location, site, date and waterbird species present in the area. Each Falcon tube was individually wrapped with aluminium foil, transported to the laboratory in a cool box with ice, and then stored in the fridge at 4 °C before processing. The samples were stored in the fridge for a minimum four week refractory period (a temporal phase of dormancy that prevents premature hatching of diapause) (Ślusarczyk et al., 2019). A total of 31 faecal samples were collected from 3 sites around Lake Rotorua on 30 July and 36 samples were collected from 3 sites around Lake Rotorua on 29 September 2021 (Table 2).

Table 2. Number of faecal samples collected from waterbirds at Lake Rotorua and Lake Rotoroa.

Lake Rotorua			Lake Rotoroa	
<i>Anser anser</i> Greylag Goose	<i>Cygnus atatus</i> Black Swan	<i>Fulica atra</i> Australian Coot	<i>Anas platyrhynchos</i> Mallard Duck	<i>Branta canadensis</i> Canadian Goose
10	6	20	20	11

2.3.2 Laboratory analysis – sieved faecal samples

A preliminary analysis was conducted where ten faecal samples were incubated at 15 degrees with a photoperiod of 16 hr: 8hr (light: dark) cycle. However, due to a lack of hatching and issues with the incubators, egg counts were chosen to analyse the number of zooplankton in faecal droppings. Each faecal sample was washed through a 40 μm sieve with water to remove fine sediment from the coarser material. The material retained on the sieve was washed into a labelled 50 ml centrifuge tube with a 1:1 weight: volume sugar: water solution (i.e., 1 kg of sugar to 1 L water; Parkes & Duggan, 2012). Each sample was placed into the centrifuge (Hettich Zentrifugn: universal 320 R) for 5 minutes at 54 g. The top layer (supernatant), containing organic material, was washed with water through a 40 μm sieve to remove the remaining sugar solution. Finally, the organic material was poured into labelled Petri dishes using a solution of synthetic pond water (480 mg NaHCO₃, 380 mg CaSO₄ · 2H₂O, 300 mg MgSO₄ and 5 mg KCl in 10 L of Milli-q water; Hebert & Crease, 1980; Parkes & Duggan, 2012).

Each sample was immediately examined under a stereomicroscope to undertake an egg count. Any eggs found were examined under a compound microscope (Olympus BH2), with care taken to ensure no damage was done to the eggs. Any eggs found were placed into a separate Petri dish with synthetic pond water on a laboratory bench under natural light to observe for hatching. Four Petri dishes filled with synthetic pond water acted as control samples.

2.4 Active zooplankton – Shallow Littoral Water Column

2.4.1 Fieldwork sampling

To analyse existing near shore zooplankton communities found in the water column, where birds swim in the shallows, water samples were collected from three sites at both lakes at a depth of 1 m (Table 1). At each site, water samples were collected by wading from the lake edge to analyse existing near-shore zooplankton communities. Following methods described by Branford & Duggan (2017), a 2 L jug was plunged 30 cm below the water's surface (The total water depth where the sample was collected, 1 m) 5 times, with the 10 L of water collected filtered through a 40 μ m plankton net. The concentrated zooplankton sample retained was washed into a labelled container and immediately preserved in 100% ethanol (final concentration 70%) for analysis in the laboratory. Two replicate samples were collected at each site location at both lakes.

2.4.2 Laboratory analysis

Zooplankton samples were filtered through a 40 μ m sieve to remove ethanol from the sample prior to analysis. Zooplankton retained in the mesh was rinsed into a measuring cylinder to a known volume (between 25 mL to 100 mL). Zooplankton species were counted and identified under a stereo dissecting microscope (Olympus SZ40) using magnifications up to 40x. The water sample was auto pipetted onto a gridded counting tray in 5 mL aliquots to identify and count. Aliquots were counted until either at least 300 individual zooplankton had been counted and identified or, where fewer individuals were present in the sample, the whole filtered sample was finished. Zooplankton were identified to the species level where possible using standard taxonomic keys (e.g., Shiel, 1995; Chapman et al., 2011).

The rotifer taxa were identified by analysing their body or trophi (jaw) morphology. Soft-bodied rotifers were extracted with a pipette onto a slide under a coverslip and examined under a compound microscope up to 400x magnification (Olympus BH2). A small drop of sodium

hypochlorite (10%) solution is added to the slide to dissolve the body and reveal the trophi (Shiel, 1995).

2.5 Sediment study – Ectozoochory

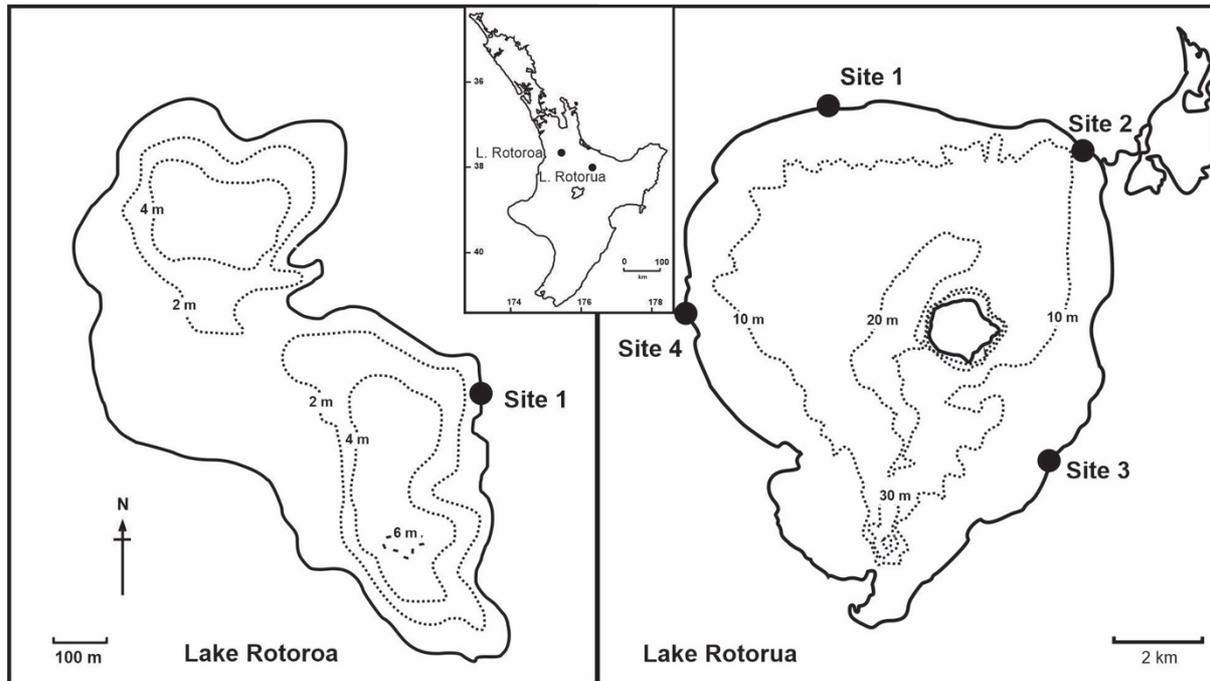


Figure 2. Site locations for the sediment study at both Lake Rotoroa and Lake Rotorua.

2.5.1 Field sampling

To analyse the zooplankton populations living in the littoral zone found within or in close association with the sediment, samples were collected from the shores of Lake Rotoroa and Lake Rotorua on 16 December 2021. Using a container, 17 cm² of sediment was collected from the shallow lake edge (5-10 cm water depth) at a water depth where waterbirds would be standing on the sediment in the water. During the collection of the sediment, I ensured only the uppermost layer of sediment (5-10 mm) was collected. The sampling of the top layer of sediment in the lake's shallow edges mimics where propagules are likely to come in contact with water birds' feet when they enter the lake from the water's edge. Due to limited accessibility or areas where shallow sediment was found at the lake edge, only one sampling site was chosen at Lake Rotoroa (Table 3). Three replicate sediment samples were collected at this site spaced 1 m apart. Due to the large size of Lake Rotorua and accessibility, four sites were sampled, with three replicates collected at each site, each spaced 1 m apart.

Table 3. Site number and coordinates for the site at Lake Rotorua and the four sites around Lake Rotorua for sediment study.

	Lake Rotorua	Lake Rotorua
Site 1	37°47'54"S 175°16'43"E	38°02'06"S 176°15'08"E
Site 2		38°02'47"S 176°19'27"E
Site 3		38°06'20"S 176°18'43"E
Site 4		38°04'31"S 176°12'58"E

2.5.2 Laboratory analysis – Preserved sediment samples

For each of the samples collected, the sediment was mixed and separated into two 40g subsamples and placed into separate falcon tubes. One tube was stored at 4 °C to undergo a four week refractory period (Schwartz & Hebert, 1987), while the other 40 g was centrifuged (Hettich Zentrifugn: universal 320 R) for 5 minutes at 54 g in a 1:1 weight: volume sugar: water solution (Parkes & Duggan, 2012). The supernatant was extracted with a pipette and washed through a 40 μ m sieve to remove the remaining sugar solution. From the mesh, the sample was washed into a labelled honey pot (250 mL) and preserved using 100% ethanol (final concentration 70%).

The preserved sediment sample was analysed to better understand the number of individuals and variety of species living within the littoral zone of the sediment. Before counting, the sediment samples were washed through a 40 μ m mesh sieve to remove ethanol. The mesh contents was rinsed into a measuring cylinder and made up to a known volume (between 25 mL to 100 mL). Next, zooplankton were counted and identified by autopipetting 5 mL aliquots onto gridded zooplankton counting trays under a compound (Olympus BH2) and stereo dissecting microscope (Olympus SZ40) up to 40x magnification. The analysis of a sample was completed when all zooplankton had been counted or identified in the filtered sample or when the count of zooplankton in the aliquots reached at least 300 individuals. All zooplankton were identified to the species level where possible using the taxonomic keys of Shiel (1995) and Chapman et al. (2011).

2.6 Hatching experiment on sediment samples

The sediment was stored at 4 °C for a two-month refractory period before the hatching experiment was initiated (Schwartz & Hebert, 1987). Each Falcon tube containing 40 g of sediment was filled with sugar solution (1:1 w: v sugar: water solution) and centrifuged at 54 g for 5 minutes (Hettich Zentrifugn: universal 320 R). The supernatant containing organic material was washed through a 40 μ m sieve to remove the remaining sugar solution on the organic material. The organic material was washed into labelled Petri dishes using a solution of synthetic pond (Herbert & Crease, 1980; Parkes & Duggan, 2012).

The 15 sediment samples were incubated (Thermoline Scientific, illuminated refrigerated incubator) at 15 degrees and a photoperiod cycle of 16hr:8hr (light:dark). The samples were monitored every 2 to 3 days for 21 days for potential new emergence of zooplankton using a stereo dissecting microscope at c.30 x magnification. Hatched zooplankton were removed from the Petri dish and identified to species level, where possible, under a compound microscope (Olympus BH2). Live copepod nauplii were moved into a new Petri dish containing synthetic pond water and placed back into the incubator and monitored for growth until mature enough to identify to species level.

2.7 Statistical analysis

Fisher Exact tests (Lowry, 2006) were used to compare the proportion of eggs among species. One test was performed comparing the waterbird species at Lake Rotorua and a second comparing the different waterbird species in Lake Rotorua. A third test was performed to compare the two study lakes and determine whether there is a difference between the proportion of waterbirds with propagules at Lake Rotorua versus the number of waterbirds with propagules at Lake Rotorua, irrespective of the waterbird species.

The Kruskal-Wallis test was used to determine whether a relationship existed between waterbird species and the abundance of propagules found in faecal samples. A Kruskal-Wallis test was performed as a number of samples contained no eggs. Using the sediment species composition data from four sites at Lake Rotorua, PRIMER 7 was used to create a non-metric multidimensional scaling plot using Bray-Curtis similarity as a distance metric. An ANOSIM was undertaken to determine whether there was a statistical difference in the species composition of zooplankton among the four sites at Lake Rotorua.

Chapter 3: Results

3.1 Species Composition of the Shallow Littoral Water Column

Active water samples were collected at each of the three sites at Lake Rotorua and Lake Rotorua (Hamilton) to obtain zooplankton community composition data on species present in the water column near the lake edge. Both lakes had a variety of different zooplankton taxa. In Lake Rotorua, seven species of rotifers, five species of cladocerans, and one species of copepod were identified. In Lake Rotorua, four species of rotifers, four species of cladocerans, and one species of copepod were identified (Table 4).

High densities of the rotifer *Polyarthra dolichoptera*, copepod *Calamoecia lucasi*, copepod nauplii and cladoceran *Chydorus* sp. were recorded at Lake Rotorua. Lake Rotorua had substantially lower abundances of zooplankton in the water column compared to Lake Rotorua, but had a higher diversity of species present (Table 4). Similar to Lake Rotorua, *Polyarthra dolichoptera* dominated the Lake Rotorua composition numerically but at a lower abundance of 6.03 ind./per L on average compared to 51.10 ind./per L in Lake Rotorua. *Synchaeta* species (*Synchaeta pectinata* and *Synchaeta oblonga*) and *Bosmina meridionalis* were also dominant species in Lake Rotorua.

Table 4. Table showing the zooplankton species composition in the shallow littoral water column at Lake Rotoroa and Lake Rotorua. The three sites where samples were collected at Lake Rotoroa, Hamilton (H1, H2 & H3) and Lake Rotorua (R1, R2 & R3) are displayed as a number of individuals per L, and as an average abundance (with standard deviation) for the lake.

	H1	H2	H3	H		R1	R2	R3	R	
	Ind./L	Ind./L	Ind./L	Mean Ind./L	SD	Ind./L	Ind./L	Ind./L	Mean Ind./L	SD
Rotifers										
<i>Ascomorphella volvocicla</i>	0.83	0.35	0.30	0.49	0.29	0.00	0.00	0.00	0.00	0.00
Bdelloid spp.	0.00	0.00	0.00	0.00	0.00	0.00	0.70	0.06	0.25	0.39
<i>Polyathra dolichoptera</i>	12.86	0.45	140.00	51.10	77.24	4.04	0.40	13.64	6.03	6.84
<i>Pompholyx complanata</i>	0.25	0.00	0.00	0.08	0.14	0.00	0.00	0.00	0.00	0.00
<i>Synchaeta pectinata</i>	1.38	7.64	10.10	6.37	4.50	4.56	0.00	5.70	3.42	3.02
<i>Synchaeta oblonga</i>	0.76	17.54	4.00	7.43	8.90	3.96	0.00	8.71	4.22	4.36
<i>Trichocerca longiseta</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.30	0.00	0.10	0.17
<i>Trichocerca porcellus</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.90	0.18	0.36	0.48
<i>Trichocerca similis</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.38	0.30	0.22	0.20
Cladocera										
<i>Alona</i> sp.	0.88	6.25	2.20	3.11	2.80	0.04	0.00	0.06	0.03	0.03
<i>Bosmina meridionalis</i>	5.84	0.74	1.10	2.56	2.85	5.63	6.65	1.66	4.65	2.64
<i>Ceriodaphnia dubia</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.23	0.06	0.10	0.12
<i>Chydorus</i> sp.	22.09	21.31	1.70	15.03	11.55	0.00	0.05	0.24	0.10	0.12
<i>Daphnia galeata</i>	0.63	0.00	0.70	0.44	0.38	0.00	0.00	0.18	0.06	0.10
Copepod										
<i>Calamoecia lucasi</i>	10.00	1.39	24.20	11.86	11.52	2.06	1.80	3.98	2.61	1.19
Copepod nauplii	14.73	1.30	30.00	15.34	14.36	2.36	1.80	1.54	1.90	0.42
Other										
Ostracods	4.05	0.86	1.50	2.14	1.69	0.58	0.05	0.18	0.27	0.28
Tardigrade: <i>Dactylobiotus dispar</i>	0.00	0.00	0.00	0.00	0.00	4.21	0.23	0.00	1.48	2.37

3.2 Egg count from waterbird faeces – endozoochory

In total, 50 eggs were obtained from 67 waterbird faecal droppings collected in the study. In Lake Rotorua, 8 eggs were found in the 10 droppings from Australian Coot, 26 eggs were found in the 20 Black Swan droppings, while only 6 eggs were found in the 6 Greylag Goose droppings collected (Table 4). In Lake Rotorua, only 2 eggs were found in the 11 Canadian Goose droppings and 8 eggs were found in the 20 Mallard duck droppings.

From Lake Rotorua, the frequency of waterbirds with eggs was similar between the Greylag Goose and Black Swan, with 33% of Greylag Goose faecal samples found to contain eggs, while 30% of the Black Swan faecal samples contained eggs. Mallard Ducks and Canadian Geese droppings from Lake Rotorua also contained similar numbers, with 20% of the Duck faecal samples having eggs, and 18% of the Canadian Geese samples having eggs in their faeces. The Australian Coot sample had the lowest frequency of propagules found, with only 10% observed to have eggs present. There were no significant differences in the proportion of birds that contained propagules among the different waterbird species at each lake (Lake Rotorua 2 x 3 Fisher Exact test, $P = 0.5179$; Lake Rotorua 2 x 2 Fisher Exact test, $P = 0.7605$). There was also no significant difference between the proportion of birds that had propagules between the two lakes irrespective of bird species (2 x 2 Fisher exact test, $P = 1.000$).

Table 5. Count and frequency of eggs from 67 faecal samples collected from waterbirds around Lake Rotorua (Greylag Goose, Black Swan and Australian Coot) and Lake Rotorua (Mallard Duck and Canadian Goose).

Sites	Rotorua			Hamilton	
	<i>Anser anser</i> Greylag Goose	<i>Cygnus atatus</i> Black Swan	<i>Fulica atra</i> Australian Coot	<i>Anas</i> <i>platyrhynchos</i> Mallard Duck	<i>Branta</i> <i>canadensis</i> Canada Goose
Droppings examined	6	20	10	20	11
Droppings containing eggs	2	6	1	4	2
Frequency of birds with eggs (%)	33	30	10	20	18
Average number of eggs per bird	1.00	1.43	0.80	0.40	0.18
Total propagules found	6	26	8	8	2
Mean Faecal Sample weight (g)	18.7	13.1	11.7	9.3	15.3
Average egg count per g	0.05	0.11	0.07	0.04	0.01

On average, 1.43 propagules were found per faecal sample from Black Swans. Black Swan had the highest egg count with a total of 26 eggs, with a maximum of 16 eggs found in one faecal sample. Greylag Goose on average had 1.00 propagule per sample, similar to the Australian Coot, with 0.8 propagules per sample. Of the waterbirds at Lake Rotorua, Mallard Ducks and Canadian Geese contained the fewest propagules per bird, with 0.4 and 0.18 eggs per bird, respectively. However, the number of zooplankton propagules in each faecal sample were not statistically significant between Ducks and Geese in Lake Rotorua (Kruskal-Wallis test, $H = 0.043$; $P = 0.836$) or among Geese, Swans and Coot in Lake Rotorua (Kruskal-Wallis test, $H = 0.7574$; $P = 0.68477$). There were also no statistically significant differences between the number of eggs recorded in the faecal samples from Lake Rotorua and Lake Rotorua irrespective of bird species (Kruskal-Wallis test, $H = 0.313$; $P = 0.576$).

The larger birds, Greylag Goose and Canada Goose, had greater mean faecal weights (18.7 g and 15.3 g, respectively) than the other waterbird species in this study. Black Swan also had a large mean faecal weight of 13.1 g. The mean faecal weights of Australian Coot (11.7 g) and Mallard Duck (9.3 g) both had smaller mean faecal weights, likely due to the smaller body mass of the Coot and Duck (Table 4).

3.3 Littoral sediment – ectozoochory & epizoochory

The preserved sediment analysis from one site at Lake Rotorua (Hamilton) and four sites at Lake Rotorua was used to analyse the species composition of eggs and zooplankton individuals in the shallow littoral zones of each lake, where waterbirds are likely to wade. The results show that Lake Rotorua had higher densities of zooplankton and eggs per gram of sediment in the littoral zone of the lake compared to Lake Rotorua (Table 6)

Thirteen species of microfauna were identified from the Lake Rotorua sediments. The singular site had large numbers of bdelloid rotifers present, with 17.05 ind./g of sediment present, with the next most abundant being tardigrades, with 3.89 ind./g of sediment (Table 6).

Lake Rotorua had lower population densities and diversity of microfauna and eggs in the lake edge sediments. Sites 2, 3 and 4 at Lake Rotorua had low species diversity. Only three species of adult zooplankton were identified at site R2, six species at site R3 and five species at site R4. *Phyllognathopus volcanicus* and *Alona* sp. were the only taxa found across all four sites at Lake Rotorua.

Table 7. Species composition per g of sediment of one site at Lake Rotorua (H) and four sites at Lake Rotorua (R1-R4).

	H	R1	R2	R3	R4	AVERAGE Rotorua	STDEV Rotorua
Copepods							
<i>Calamoecia lucasi</i>	0.00	0.01	0.00	0.00	0.00	0.00	0.00
<i>Phyllognathopus volcanicus</i>	0.55	0.03	0.42	0.03	0.04	0.13	0.19
Copepod nauplii	0.54	0.03	0.43	0.00	0.00	0.11	0.21
Rotifers							
Bdelloid spp.	17.05	0.59	0.04	0.02	0.00	0.16	0.29
<i>Euchlanis dilatate</i>	0.03	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lecane closterocerca</i>	1.30	0.01	0.00	0.00	0.00	0.00	0.00
<i>Lecane bulla</i>	0.00	0.13	0.00	0.00	0.05	0.05	0.06
<i>Lecane luna</i>	0.23	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lepadella acuminata</i>	0.03	0.00	0.00	0.00	0.00	0.00	0.00
<i>Pompholyx complanata</i>	0.28	0.00	0.00	0.00	0.00	0.00	0.00
<i>Trichocerca longiseta</i>	0.00	0.03	0.00	0.00	0.00	0.01	0.01
<i>Trichocerca porcellus</i>	0.00	0.02	0.00	0.00	0.00	0.00	0.01
<i>Trichocerca similis</i>	0.00	0.01	0.00	0.00	0.00	0.00	0.00
<i>Trichotria tetractis</i>	0.03	0.00	0.00	0.00	0.00	0.00	0.00
Cladocerans							
<i>Alona</i> sp.	0.26	0.21	0.14	0.03	0.44	0.21	0.17
<i>Bosmina meridionalis</i>	0.00	0.04	0.00	0.10	0.00	0.04	0.05
<i>Chydorus</i> sp.	0.06	0.00	0.00	0.00	0.00	0.00	0.00
<i>Daphnia galeata</i>	0.00	0.00	0.00	0.04	0.00	0.01	0.02
Other							
Ostracods	0.20	0.00	0.00	0.00	0.07	0.02	0.03
Tardigrades	3.89	0.08	0.00	0.03	0.33	0.11	0.15
Eggs							
Tardigrades	0.18	0.00	0.00	0.00	0.00	0.00	0.00
Harpacticoid copepods	0.04	0.00	0.00	0.00	0.00	0.00	0.00
<i>Alona</i> sp.	0.00	0.03	0.00	0.00	0.12	0.04	0.06
Unknown round eggs	0.06	0.00	0.10	0.00	0.00	0.03	0.05
Unknown oval eggs	0.04	0.08	0.22	0.04	0.26	0.15	0.10

3.4 Hatching experiment

Strikingly, no hatched propagules were obtained from the littoral sediments of Lake Rotorua (Hamilton), with all the hatching from the experiment observed in Lake Rotorua (Table 7). In Lake Rotorua, hatched propagules were observed from six species: *Phyllognathopus volcanicus*, *Filinia terminalis*, *Conochilus dossuarius*, bdelloid rotifers, *Alona* sp., and ostracods. The main taxon found in the hatching experiment were rotifers, with three different species hatched, whereas only one copepod and one cladoceran taxon were observed to hatch throughout the experiment. No zooplankton were observed from any of the control samples of synthetic pond water. Further, three charophyte oospores were present at site four in Lake Rotorua, but did not germinate.

Site 2 at Lake Rotorua had the highest biodiversity and number of hatched zooplankton in the sample. Five species of zooplankton, the copepod *Phyllognathopus volcanicus*, rotifers *Filinia terminalis*, *Conochilus dossuarius*, the cladoceran *Alona* sp., and ostracods hatched (Table 7), and a total of 21 live individual zooplankton were recorded in the sample (Figure 3).

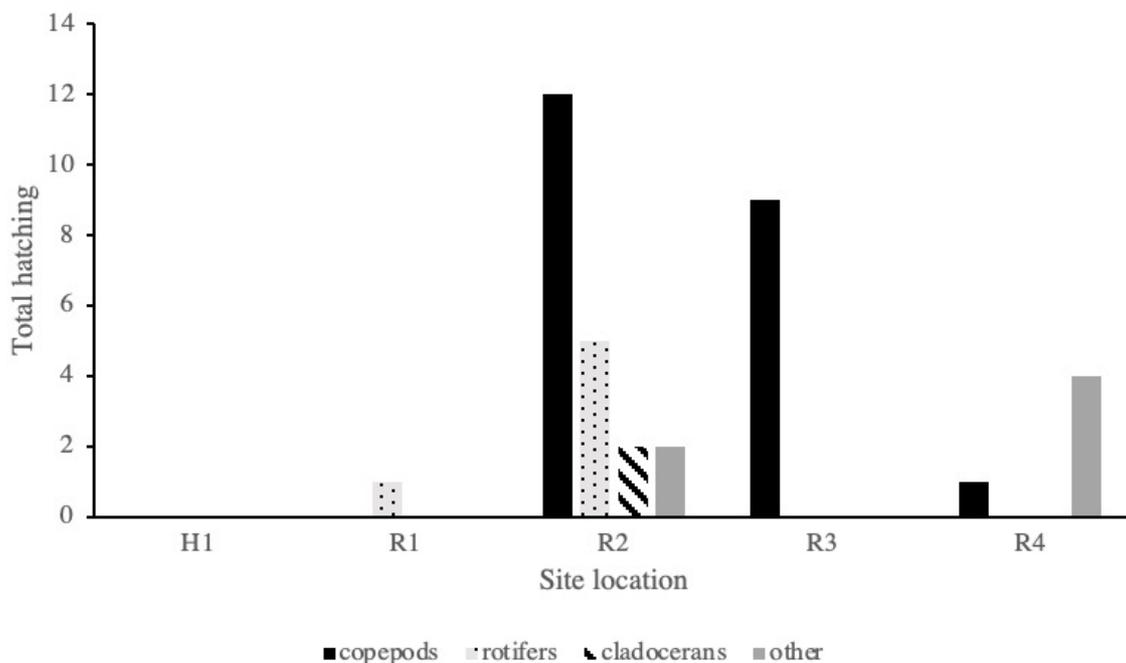


Figure 3. The number of zooplankton hatched from the sediment samples from the shallow littoral zone at Lake Rotorua and Lake Rotorua. One site was sampled at Lake Rotorua (H1) and four sites sampled at Lake Rotorua (R1 - R4).

Table 9. Total number of individuals hatched per 40g of sediment at Lake Rotoroa (one site, H) and Lake Rotorua (Four sites, R1-R4).

TOTAL sediment hatching	H1	R1	R2	R3	R4	Rotorua average	STDEV Rotorua
Copepods							
<i>Phyllognathopus volcanicus</i>	0.00	0.00	12.00	9.00	1.00	5.50	5.92
Rotifers							
Bdelloid spp.	0.00	1.00	0.00	0.00	0.00	0.25	0.50
<i>Conochilus dossuarius</i>	0.00	0.00	2.00	0.00	0.00	0.50	1.00
<i>Filinia terminalis</i>	0.00	0.00	3.00	0.00	0.00	0.75	1.50
Cladocerans							
<i>Alona</i> sp.	0.00	0.00	2.00	0.00	0.00	0.50	1.00
Others							
Ostracod spp.	0.00	0.00	2.00	0.00	1.00	0.75	0.96

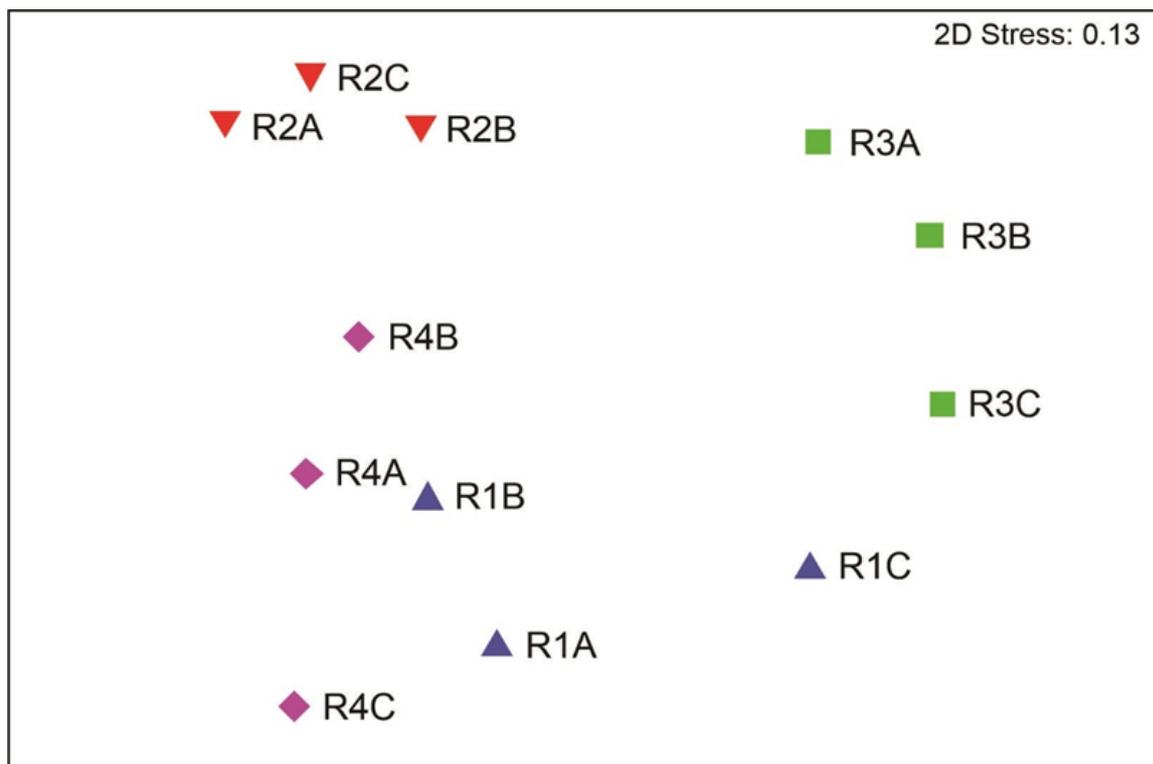


Figure 4. Non-metric multidimensional scaling diagram portraying how the species composition of zooplankton in the littoral zone at Lake Rotorua differed among samples and sites.

The non-metric MDS plot (figure 4) showed greater similarities between the species compositions within the subsamples at each of the four sites at Lake Rotorua than there was between sites. The replicates within each site spaced 10 m apart from one another were closely associated with each other showing the similarity of species composition within each site around the lake. This distribution indicates that Sites 1, 3 and 4 had the greatest dissimilarity (was the least similar) in species composition recorded in the subsamples across the site, whereas site 2 had the greatest similarity in species composition among subsamples.

Chapter 4: Discussion

The dispersal of zooplankton in association with waterbirds has not been extensively studied. Most research has been conducted in Europe, primarily analysing endozoochory (Charalambidou et al., 2003a,b; Figuerola et al., 2003; Green & Figuerola, 2005; Moreno et al., 2019), while less research has been undertaken on ectozoochory (Figuerola & Green, 2002a; Brochet et al., 2010; Rachalewski et al., 2013). My research represents the first to quantify the dispersal of zooplankton propagules by waterbirds in New Zealand. The only similar study in New Zealand examined the dispersal of aquatic plants through the digestive system of Mallard Ducks (Bartel et al., 2018).

4.1 Endozoochory

This study yielded evidence for the potential dispersal of zooplankton by endozoochory, with diapausing eggs passing through the digestive system of Coots, Ducks, Geese, and Swans. Diapausing eggs were obtained from all waterbird species investigated, indicating that various waterbird species act as dispersal vectors for zooplankton. There were no significant differences in the egg counts among the five waterbird species recorded in this study. The average number of eggs in the waterbird faeces varied between 0.18 and 1.00 eggs per faecal sample. The low number of eggs in the faeces across all bird species, suggests that low numbers of zooplankton are being dispersed internally by waterbirds. Similar to the present study, Moreno et al. (2019) in Spain, reported low numbers of propagules in faecal samples of several different waterbird species, including Mallard Ducks and common Coots. A mean number of 0.9 diapausing eggs of cladoceran and rotifers per dropping was recorded. Several factors can limit the potential for waterbird dispersal of invertebrate propagules. Zooplankton dispersal through waterbirds requires the ingestion of eggs, survival of eggs during digestion, and transport to a suitable habitat where they can be excreted to establish in the receiving environment.

4.1.1 Ingestion of propagules by the waterbird

Firstly, waterbirds must ingest propagules for dispersal by endozoochory. Many waterbird species are herbivorous, feeding only on vegetation, but some species are omnivores, and their diets consist of invertebrates and aquatic vegetation. Sieved faecal samples indicated that waterbirds were feeding on invertebrate eggs, as 50 eggs were found in the 67 faecal samples examined. The faecal contents from all waterbird species contained large amounts of plant material. Therefore, it is likely that ingestion of diapause eggs occurred through entrainment while feeding on aquatic vegetation. Following the production of diapause eggs, most will sink to the sediment, but some will float and attach to plants (Brendonck & De Meester, 2003). The diapausing eggs of several cladoceran species (*Polyphemus pediculus*, *Sida crystallina*, and *Pseudosida variabilis*) have a sticky outer envelope that allows the egg to attach to aquatic vegetation (Fryer, 1996). This trait could facilitate the dispersal of diapause eggs between lakes by waterbirds grazing on the vegetation (Gyllström & Hansson, 2004). Alternatively, the consumption of eggs could have occurred through the ingestion of live individuals if those individuals were carrying diapausing eggs. A similar study conducted in Australia analysing the sieved faecal samples from Grey Teal (*Anas gracilis*), Black Swan and Eurasian Coot showed significant differences in the number of propagules among the three waterfowl, with the highest number of species obtained from Coot faeces (Green et al., 2008). In contrast to my results, only 10% of the Australian Coot had propagules present, compared to the Black Swan (30%), Greylag Goose (33%), Mallard Duck (20%) and Canada Goose (18%). Although, there was no significant difference in the number of propagules among waterbird species.

The lack of differences in the number of eggs found among the waterbird species is surprising due to the varying diets of all five waterbird species. The Canada Goose, Black Swan and Australian Coot are all entirely herbivorous, feeding on aquatic vegetation. On the other hand, Mallard Ducks and Greylag Geese are omnivorous, and known to feed on both invertebrates and aquatic vegetation. Consequently, I expected variation in the number of eggs ingested among the waterbird species. Many of the faecal samples analysed in this study contained significant amounts of vegetation. Therefore, the waterbirds may be feeding not only on aquatic vegetation but terrestrial vegetation also, Canada Geese are known to feed on both aquatic and

terrestrial grasses (Conover, 1991). This diet would minimise the probability of the waterbirds ingesting zooplankton diapause eggs.

As in my study, Moreno et al. (2019) found no significant differences in egg counts among waterbird species. *Sterna* sp. (terns) had the largest number of eggs in their faecal samples, and notably, no eggs were found in 29 *Charadrius alexandrinus* (Kentish plover) faecal droppings. Rotifer eggs were the most abundant diapause found in their study, with 261 diapause eggs recorded from 327 waterbird faecal droppings. In contrast, only 26 cladoceran diapause eggs were identified, with the majority recorded in the faecal samples of Mallard Duck and Australian Coot droppings (Moreno et al., 2019). The majority of the eggs found in the faecal samples in the present study were oval shaped, and measured between 100 and 150 μm in length. As such, the eggs were likely derived from species of rotifer (Bailey et al., 2003). Some eggs found in the faecal samples were round and 160 μm , these were likely eggs from calanoid copepods (Cooney & Gehrs, 1980). Both Lake Rotorua and Lake Rotorua had an abundance of *Calamoecia lucasi* inhabiting the shallow littoral water.

Parasite eggs (e.g., Nematodes, Cestodes, and Trematodes), commonly found in Anatidae in New Zealand (Black Swan, Greylag Goose and Mallard Duck), are in the range of 10 to 25 μm in length (Presswell & Lagrue, 2016). In the current study, I used a mesh size of 40 μm , too coarse to retain the eggs of most parasite egg species; the eggs recorded from the faecal samples in the present study were mainly greater than 100 μm , with few eggs smaller than this size. As such, I can be confident that the eggs recorded in faecal samples in my study were not parasite eggs, despite none hatching, and thus likely belong to free-living invertebrates.

4.1.2 Survival of propagules after digestion

No hatching occurred from the eggs isolated from the waterbird faecal samples. The survival of propagules following digestion is the most critical factor during endozoochory dispersal. Gut morphology and retention time strongly influence propagule viability after digestion (Charalambidou & Santamaria, 2002). The results from sieved faecal samples showed no significant difference in egg count between the four waterbird species (Coots, Ducks, Geese and Swans). Nevertheless, previous studies have noted the limitations of a large body size of

the dispersal vector, the morphology of the crop, gizzard and caecae and the length of the intestine on the survival and retention time of propagules (Charalambidou & Santamaria, 2002). The varying digestive processes of waterbirds may explain the hatching success differences recorded in some studies (Moreno et al., 2019). Green et al. (2008) also performed an emergence study on faecal samples from the three waterfowl (Grey Teal, Black Swan and Eurasian Coot). They recorded the hatching of Protozoa, nematodes, ostracods, and rotifers (Green et al., 2008). Ostracods emerged in 33% of Coot samples and 7% of Teal and Swan samples, whereas rotifers were absent from Teal samples but emerged from 7% of Swan and 13% of Coot samples.

4.1.3 Endozoochory frequency and dispersal distances

The retention time of viable propagules within the gut of waterbirds is essential to better understand the potential dispersal distances by using existing knowledge of the flight speeds of key waterbird species. Few studies have analysed the retention time of invertebrate propagules utilising a variety of waterbird species (Proctor et al., 1967; Charalambidou et al., 2003a,b; Charalambidou et al., 2005). Past studies have used feeding experiments to test propagule survival and retention times by providing large numbers of propagules to captive waterbirds (Figuerola et al., 2002). Feeding experiments have quantified maximum retention times recorded in several different waterfowl groups. For example, Charalambidou et al. (2003b) recorded a maximum retention time of 44 hours and 32 hours for bryozoan statoblast *Crisatella mucedo* in the gut of two duck species. The mean retention time was four hours. As such, short-distance transport is likely more frequent than long-distance transport.

Using retention time data and waterfowl flight speed, we can better estimate the dispersal distances of propagules. For example, with mean retention times of 4 hours for Bryozoan statoblasts (Charalambidou et al., 2003b) and the average flight speed of *Anas* ducks is 60 to 78 km/h (Welham, 1994), we can assume that the maximum endozoochory dispersal distances of 250 to 315 kilometres. However, propagules are likely to be excreted before reaching their destination on a long-distance flight. Therefore, dispersal will likely occur over short distances (Clausen et al., 2002). Maximum recorded retention times of the cladoceran *Bythotrephes*

longimanus (22 hours) (Charalambidou et al., 2003a), and of the bryozoan statoblasts of *C. mucedo* (44 hours) (Charalambidou et al., 2003b), indicate that waterbirds can disperse propagules up to thousands of km (retention time x flight time) (Freeland et al., 2000; Clausen et al., 2002; Charalambidou & Santamaria, 2005). Nevertheless, such events are extremely unlikely as 67-95% of the propagules were released four hours after ingestion (Charalambidou et al., 2003a). Similar flight speeds have been recorded for Black Swan at 72 km/h (Welhun, 1994), therefore we might expect Black Swans to have similar dispersal distances to what was noted for Mallard Ducks.

In the present study, the mean fresh weight faecal samples of Mallard Ducks was 8.6 g. Assuming a daily faecal output for the Mallard Duck is 12.2 droppings per day (Marion et al., 1994), we could estimate that a single individual at Lake Rotorua excretes approximately 104 g of faeces per day. Considering the number of droppings per day (Marion et al., 1994) with the average number of eggs per dropping (0.4; my study), a total of 4.88 diapausing propagules could be excreted by a single Mallard per day. However, not all propagules ingested by waterbirds will hatch. Conde-Porcuna et al. (2018) observed a hatching success rate of only 25% in the faecal droppings of Mallards. Black Swan had a mean weight of 13.1 g per faecal dropping, although individuals of this species will excrete a daily faecal output of approximately 418 g of fresh weight (Mitchell & Wass, 1995). As such, the faecal samples of the Black Swans examined in the present study represent only 3.1% of the daily faecal output.

No hatching of propagules was observed in any of my faecal samples. Unlike the sediment samples from the shallow littorals, the faecal samples were not incubated at a set temperature or photoperiod but left on a bench top for three weeks to allow any potential hatching. From the number of digested propagules in all waterbirds observed in the present study, I would have expected some hatching. However, each faecal sample only represents a small proportion of the total daily faecal output. Therefore, we only see a fraction of the eggs being transported by waterbirds daily.

4.2 Ectozoochory (Exozoochory or Epizoochory)

The requirements for successful Ectozoochory limit the probability of waterbirds dispersing invertebrate propagules. Propagules must first come in contact with the dispersal vector and then attach to it. Next, they must remain viable during flight, and finally, the propagule must detach from the dispersal vector into a suitable environment to establish in the new habitat (Coughlan et al., 2017).

4.2.1 Contact and attachment

In the present study, the total density of active microfauna inhabiting the surficial sediments in the littoral of Lake Rotorua was 24.45 individuals per gram of sediment. High densities of bdelloid rotifers were observed, with 17.05 individuals per gram of sediment recorded. Lake Rotorua had a lower density of active microfauna inhabiting the littoral sediments compared to Lake Rotomahana, with only 0.85 individuals per gram of sediment on average. Several studies have highlighted the importance of propagule density, shallow water depths, and exposure time to increase the probability of dispersal by Ectozoochory (Banha & Anastácio, 2012; Rachalewski et al., 2013; Águas et al., 2014; Anastácio et al., 2014; Banha et al., 2016). These factors could increase the probability of propagules attaching to vectors, increasing the likelihood of dispersal. Rachalewski et al (2016) attachment experiment in Portugal used a dead duck's leg to investigate the adhesion of the amphipod, *Crangonyx pseudogracilis*, to Mallard Ducks. The experiment showed that the probability of *C. pseudogracilis* adhering and being transported by duck's feet or plumage was 1.6% and 1.84%.

Few diapausing eggs were found in the lakeshore sediments relative to what has been recorded in sediments at deeper points in lakes. In Lake Rotorua there were only 0.32 eggs observed per g of sediment and in Lake Rotomahana only 0.22 eggs observed per g of sediment. Cáceres, (1998) study analysed the sediment egg bank populations of *Daphnia galeata mendotae* and *Daphnia pulicaria* at various depths at a lake in New York, America. Cáceres, (1998) study took single sediment cores at the lake along a transect at water depths of 3, 7, 9 and 12 m and showed that the sediments at the deepest parts of the lake had the most diapausing eggs for both species of

Daphnia (Cáceres, 1998). Rotifer egg densities recorded in the deepest parts of two New Zealand lakes were 311.32 rotifers/ml of sediment in Lake Okaro, a eutrophic lake and 2.03 rotifers/ml of sediment in Lake Tikitapu, an oligotrophic lake (Duggan et al., 2002). Only a fraction of the egg densities recorded from deeper lake sediments in Duggan et al. (2002) were found in the littoral lake sediments of the present study. The low number of eggs found in the littoral zone in the present study, where waterbirds are wading at the shore, decreases the potential for ectozoochory dispersal. Although propagules inhabit the sediment in the littoral zone, I expect external waterbird dispersal numbers to be low due to the low density of diapausing eggs. When propagules are concentrated along the shoreline (i.e., within the sediment or at the water surface), they are more likely to attach to feathers and feet (Brochet et al., 2010).

The sediment samples collected in the present study at Lake Rotorua and Lake Rotorua were sandy substrates. Invertebrate propagules require passive attachment to waterbirds, where the dispersal vector (i.e. the waterbird) facilitates attachment. Lake characteristics, such as substrate type and aquatic vegetation, can aid in the attachment of propagules to waterbirds (Figuerola & Green, 2002b). Muddy substrates, for example, can assist in the adhesion of propagules. When the mud sticks to the feathers and feet of birds, the propagules become trapped within the mud. Lakes comprised of sandy substrates were observed by Figuerola and Green (2002b) to have lower numbers of propagules attached to waterbirds compared to lakes with muddy substrates (Figuerola & Green, 2002b). Similar results were seen in areas with more aquatic vegetation, as vegetation in the water column allowed more opportunities for waterbirds to come into contact with propagules. The sandy substrates present at Lake Rotorua and Lake Rotorua are therefore unlikely to aid in attachment to waterbirds.

4.2.2 Survival during transport

Invertebrate eggs of several zooplankton groups (rotifers, cladocerans and copepods) and active tardigrades, ostracods, rotifers, copepods and cladocerans were found inhabiting the littoral sediments of Lake Rotorua and Lake Rotorua. Tardigrades produce diapause eggs but can also enter a dormant stage of their lifecycle, known as cryptobiosis, which allows them to withstand freezing and desiccation and survive unfavourable conditions (Guidetti et al., 2011). Bdelloid rotifers can enter a dormancy called anhydrobiosis, which is caused by a loss of water

and allows them to dry out, rehydrate and survive, and thus inhabit temporary waters (Ricci, 1998; Marotta et al., 2010). Other rotifer species, like cladoceran species, will likely die unless kept moist. Active individuals were more abundant in the sediment than diapausing eggs, but diapause eggs are more likely to survive transport. Invertebrate diapause eggs often have a shell or envelope that can help protect them from environmental extremes, i.e., from desiccation during flight (Radzikowski, 2013). However, not all eggs are entirely resistant to desiccation, and some species that lose internal water may lose viability (Fryer 1996). Nevertheless, many species can rehydrate, remain viable and hatch after desiccation (Radzikowski, 2013). The plumage of ducks plays a key role during external transport by providing an added layer of protection from the exterior environment. The higher specific humidity within the plumage compared to the ambient air temperature reduces the desiccation rate of the propagule (Coughlan et al., 2015b). The waterbird plumage increases the likelihood of survival during extended periods of Ectozoochory (Coughlan et al., 2015 a,b).

Viable propagules of cladocerans and ostracods were removed from the plumage and feet of Eurasian Teal *Anas crecca* in a study conducted in Southern France (Brochet et al., 2010). Propagules of Anostraca, Bryozoa and Cladocera were found in 2.9% of the waterbirds sampled. Due to the difficulty of finding propagules among debris, emergence tests were carried out on 45 of the external samples to initiate the hatching of any remaining propagules. The emergence test showed the hatching of at least one propagule of cladoceran or ostracod species in 11.1% of the 45 external samples (Brochet et al., 2010). No seasonal trends were observed for the internal samples, but external sample results suggest that dispersal probability is more likely to occur during early winter than in late winter (Brochet et al., 2010). Seasonal trends may be more important in external than internal transport. The low abundance of propagules on the surface and in shallow water limits external transport, whereas propagules persist in the egg bank and are readily available for consumption year-round making internal transport challenging to predict and inconsistent (Figuerola et al., 2002; Brochet et al., 2010).

The results of Brochet et al. (2010) may not accurately represent all zooplankton dispersed through Ectozoochory. Rotifers were not considered in their study, as the mesh size of 63 μm was too large to retain the small propagules. The dispersal of diapausing eggs of rotifers may be crucial to understand due to the large quantities of diapause eggs they produce compared to

cladocerans and copepods (Parkes & Duggan, 2012), and their significant contribution to the sediment egg bank. The species composition of the littoral zone from the present study found large numbers of rotifers at Lake Rotorua and the hatching of *Filinia terminalis*, *Conochilus dossuarius* and emergence of bdelloid rotifers. Only six zooplankton species emerged from Lake Rotorua's shallow littoral sediment sample. The hatching of cladocerans, copepods, ostracods and rotifer species shows that diapause eggs are present in the littoral zone. Although no hatching occurred in Lake Rotorua and little hatching was observed in Lake Rotorua, they are available to be picked up by birds wading at the shore. However due to low numbers attachment to waterbirds in these areas will be minimal.

The survival rate and dispersal distances have been quantified by using waterbird carcasses to better understand the dispersal capabilities of waterbirds as a transport vector (Rachalewski et al., 2016). The experiment showed that active *Crangonyx pseudogracilis* could adhere to a flying duck, remain viable for 6.8 km and desiccation resistant for 88.6 minutes. These results gave a good indication that the dispersal of *C. pseudogracilis* could occur at least over a short distance by waterbirds. A similar experiment studying zebra mussel larvae in Spain examined the dispersal capabilities of Mallard duck carcasses and the resistance of larvae to desiccation (Banha et al., 2016). The desiccation experiment showed that lower relative humidity and higher temperatures decrease the survival rates of larvae. Although, zebra mussel larvae mortality increased with the amount of time spent out of the water, the maximum survival time of larvae attached to a Mallard Duck was 240 minutes. Combining the flight time of Mallard Ducks (60-78 km/hr) (Welhun, 1994) and the survival time of zebra mussel larvae out of the water it is suggest that they may remain viable long enough to undergo long distance dispersal by Mallard Ducks if they remain attached.

4.2.3 Detachment

For successful dispersal of diapausing propagules, the propagules need to detach from the dispersal vector in a suitable habitat to hatch and reproduce in a population (Coughlan et al., 2017). Propagules may detach before flight or during overland transport and end up in an unsuitable location and unable to hatch. Waterbird behaviours, such as preening, moulting and

washing, can also facilitate detachment but must occur after arrival at a new site for dispersal to be successful and establishment to occur (Coughlan et al., 2017).

4.3 Implications of waterbird dispersal

Anatidae (Ducks, Geese and Swans) and Rallidae (Coots) are widespread not only in New Zealand but globally (Heather & Robertson, 2000). My results have shown various waterbirds inhabiting lakes contribute to the dispersal of zooplankton propagules. The number of propagules transported by a single bird is low as the requirements for successful endozoochory and ectozoochory dispersal make transporting large numbers of viable propagules unfeasible. Only small numbers of invertebrate diapausing propagules were being transported internally through birds in the current study, and the low availability of invertebrates in the littoral zones of lakes limits the likelihood of external transport. Mallard distributions and tenancy for migration make them effective modes of transport for waterbird dispersal. Canadian Geese populations in the North Island, New Zealand, have increased rapidly since their establishment in 1970. Geese have a propensity to move around New Zealand as they inhabit inland rivers and lakes during the breeding season and then move to coastal rivers and lakes for the rest of the year. These small habitat changes during the year provide opportunities for potential long-distance dispersal (Spurr et al., 2005). Black Swan populations reside in estuaries and lakes year-round, but during moulting season non-breeding individuals are known to congregate in large estuaries where they graze on seagrass meadows (Williams, 1980; Dos Santos et al., 2012). As these waterbird species are abundant in New Zealand, even if only a small proportion of the population carries invertebrate propagules daily or during seasonal migrations, the impact of waterbird dispersal on zooplankton communities may be substantial (Brochet et al., 2010). Short distance dispersal is likely more frequent than long distance dispersal due to risk of desiccation, digestion, excretion, or detachment of the propagule during transport.

Dispersal of zooplankton from lakes typically occurs over short distances, with the occasional long-distance dispersal event occurring (Allen, 2007). Adult zooplankton are known to disperse across short distances in areas where there are abundant aquatic habitats (Allen, 2007). Adult

zooplankton are not desiccation resistant like diapause eggs therefore, can only travel short distances. Although, unlike diapause eggs, adults do not have to wait to hatch before colonising a new habitat (Allen, 2007). Retention time appears to be an important limitation affecting dispersal distances of endozoochory. However, low frequency dispersal still has consequences for the gene flow of species by homogenising populations (Havel & Shurin, 2004). Limited dispersal among populations results in divergence of genes through genetic drift (Havel & Shurin, 2004), but it is thought one immigrant per generation is enough to prevent divergence (Wright, 1949).

Several other studies have noted the minor importance of waterbird dispersal compared to other natural vectors of dispersal, such as air currents, wind and rain, that have been recorded to disperse large numbers of resting eggs (Green & Figuerola, 2005; Lopes et al., 2016). In contrast, the results from Moreno et al. (2016) and Moreno et al. (2019) have shown similar dispersal rates of rotifers between air currents and waterbirds. Although waterbirds contribute to zooplankton dispersal, it is on a small scale compared to numbers dispersed by human-mediated vectors. Deliberate releases, accidental introductions, and habitat modification have increased the rate of zooplankton dispersal (Carlton, 1992; Havel & Shurin, 2004). For example, ship ballast tanks have become an important mechanism for dispersing zooplankton in large quantities and potentially over long distances (Havel & Stelzleni-Schwent, 2000; Havel & Shurin, 2004). Sampling of Japanese ballast water tanks revealed zooplankton were present in 157 of 159 tanks sampled and a total 367 species described (Carlton & Geller, 1993). Copepod densities reached over 1.5 individuals per L, indicating great potential for dispersal in ballast tanks. Bailey et al. (2003) quantified the transport of zooplankton in residual ballast sediment with viable eggs of calanoid copepods, cladocerans and rotifers all recovered (Bailey et al., 2003). The density of diapausing eggs recorded from residual sediments were considered low, with fewer than 10 eggs recovered per 40 g of sediment. However, four samples presented densities of over 50 diapausing eggs per 40 g of sediment (Bailey et al., 2003). In the present study, most of the littoral sites had fewer than 10 diapausing eggs hatch per 40 g of sediment, except from one site in Lake Rotorua, where 21 diapausing eggs hatched in a 40 g sediment sample. The hatching observed in littoral lake sediments is similar to what was recovered in residual ballast sediments. As such, it is likely that ballast sediments play a more significant role in zooplankton dispersal what would occur by ectozoochory. The faecal samples also recorded less than 10 diapause per 40g of droppings in every bird species. There was no

significant difference in the propagule count among the five bird species sampled at Lake Rotorua and Lake Rotoroa. Recreational boaters also contribute to the dispersal of zooplankton through small live wells in the vessel. Unlike shipping ballast tanks, recreational wells only carry small volumes of water, but due to the abundance of recreational boaters frequent transport is likely (Kelly et al., 2013).

4.4 Study limitations

There were several limitations of the current study. The tight time restriction of an MSc degree, COVID lockdowns, self-isolations and equipment failings limited the number of experiments and samples I could collect and analyse. Sampling days were restricted to the winter months (July – September) as there was only a short time frame for sampling. Collecting another set of samples in the Summer would have improved the understanding of dispersal throughout the year. Seasonal variation in zooplankton diapausing egg production is apparent elsewhere (Jarnagin et al., 2004). Therefore, I expect dispersal results for at least ectozoochory to show variation between Winter and Summer. Having a single sampling day at each lake also limited the results, as I was restricted to sampling what waterbirds were present on the day of sampling. Mallard ducks are known to inhabit the water and shores of Lake Rotorua.

Several vital pieces of laboratory equipment were non-functional or malfunctioned during experiments (e.g., incubators and temperature-controlled room), reducing the number of replicates in my faecal samples' analysis. Further, obtaining replacement parts to fix these items was inhibited due to the COVID pandemic reduced the rate at which replacement parts could be imported into the country. Alternative incubators were used in the interim on initial samples, but these failed to maintain the set temperature and at times severely overheated, compromising the samples.

4.5 Implications for future research

My research has identified that waterbirds ingest zooplankton propagules and can transport them to new habitats. These propagules from faecal samples remain intact, but hatching could not be obtained. Further, my results highlighted the lack of information relating to ectozoochory as a method for dispersal. Further research examining the attachment of propagules to waterbirds and their survival during flight is essential to understanding the probability of ectozoochory. New Zealand's duck hunting season could provide a good opportunity to look at the number of viable propagules attached to Mallard Ducks during flight. This would increase the knowledge on Ectozoochory transport occurring in New Zealand and better understand the frequency of transport. I believe it would be beneficial to continue to sample littoral zone locations as they are underrepresented in the literature compared to what is known about the density of the egg bank in deeper parts of the lake. Littoral zone studies would provide a better understanding of the differences in the abundance of individuals and the sediment egg bank inhabiting the littoral zones of lakes.

Diapause production, lake characteristics and waterbird distribution are affected by seasonality and, therefore, cause a seasonal difference in zooplankton dispersal by waterbirds. Therefore, another recommendation for future research would be a variation in sampling times and having several sampling days in different seasons (e.g., Summer and Winter) to see if there were any seasonal variations in dispersal ability.

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