ARE ZOOPLANKTON INVASIONS IN CONSTRUCTED WATERS FACILITATED BY SIMPLE COMMUNITIES?

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Abstract

The invasion of non-indigenous species is considered to be one of the leading causes of biodiversity loss globally. My research aimed to determine if constructed water bodies (e.g., water supply reservoirs, dams and ponds) were invaded by zooplankton with greater ease than natural water bodies, and whether this was due to a lower biodiversity, and therefore lower 'biotic resistance', in constructed water bodies. Sediment cores were collected from a cross-section of 46 lakes, ponds and reservoirs (23 natural and 23 constructed) throughout the North Island, New Zealand. Diapausing zooplankton eggs were separated from the sediments and hatched to assess species composition and richness. In addition, the distributions of non-indigenous zooplankton were examined to determine if they occurred more frequently in constructed water bodies than in natural ones.

Species composition results showed that natural water body zooplankton communities appeared to consist mainly of a core group of truly planktonic species. However, the species assemblages of constructed water bodies were more varied, comprising of a number of littoral and benthic species, and a large number of species that were recorded from only a single water body. A canonical correspondence analysis indicated that Trophic Level Index explained a significant amount of variation in zooplankton community composition of natural waters ($p = 0.002$). Distance to nearest water body and number of water bodies within a 20 km radius explained significant amounts of variation in community composition of constructed water bodies ($p = 0.040$ and 0.038 respectively). Average species richness was slightly higher for natural water bodies than constructed water bodies (18.47 and 15.05 respectively), although overall there was a lot of variation for both natural and constructed water body datasets. A stepwise linear regression indicated that latitude and approximate maximum depth of water body were significant predictors of natural water body species richness (p = 0.002 and 0.016 respectively). However, no significant predictors of species richness were elucidated for constructed water bodies. The non-indigenous calanoid copepods *Sinodiaptomus valkanovi* and *Boeckella minuta* were only found in constructed water bodies. However, the non-indigenous cladoceran *Daphnia galeata* was recorded in both natural and constructed water bodies. The non-indigenous calanoid copepods are more likely to establish populations in constructed water bodies due to the absence of key species (i.e. native calanoid copepods), whose presence in natural waters seemingly provides 'biotic resistance'. The invasion success of *D. galeata* in constructed and natural waters may be attributed to the absence of a superior competitor, as native *Daphnia* populations, for example, are rare in the North Island.

My results suggest that species richness may not be as important as species composition in influencing the ease with which non-indigenous species invade constructed water bodies. The core group of species found in natural water bodies are likely to be better adapted to pelagic conditions, and therefore better at resisting invaders, than the more varied constructed water body assemblages.

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Chapter One: Introduction

1.1 Background to invasions

Biological invasions are a naturally occurring phenomenon. The spread of species around the globe has occurred at a modest pace throughout history as a result of natural processes (e.g. ocean currents, wind and natural dispersal abilities) (Olden *et al.*, 2004; Hollebone & Hay, 2007). For example, the Australian longfinned eel *Anguilla reinhardtii* was first recorded in the Waikato River, New Zealand, in 1996 and has since established populations in a number of waterways (McDowall *et al.*, 1998). Prior to their discovery in the Waikato River the known distribution of *A. reinhardtii* was restricted to eastern Australia (northern Queensland to Tasmania), New Caledonia, Norfolk Island and Lord Howe Island (McDowall *et al.*, 1998). No live eels are imported into New Zealand so populations of *A. reinhardtii* could not have established from eels that had escaped captivity. Instead, the arrival of the species is likely to have occurred naturally via transoceanic dispersal from sub-tropical spawning grounds north of New Zealand (McDowall *et al.*, 1998). Flight is a common means of natural dispersal. The New Zealand short-tailed bat (*Mystacina tuberculata*), for example, is thought to have originated from Australian populations 20 to 25 million years ago, probably reaching New Zealand by flying across the Tasman Sea (Gibbs, 2006). Birds have arrived by similar means. The Australian spur-winged plover, for example, established relatively recently in Southland, New Zealand, in 1932. After establishing in several localities it then spread to the North Island, New Zealand, in the 1970s, and is now present in large numbers throughout both islands (Moon, 2001). It is thought the birds crossed the Tasman Sea with the aid of the prevailing westerly wind (Barlow, 1983). Other recent bird examples include the Australian Coot, the White-faced Heron and the Welcome

Swallow. All of these bird species are thought to have arrived from Australia within the past 60 years, without the aid of humans, and have now established breeding populations throughout New Zealand (Moon, 1979).

Humans are responsible for a rapid increase in the rate of species introductions across the globe (Mooney & Cleland, 2001; Olden *et al.*, 2004; Hollebone & Hay, 2007). For example, international trade has been identified as one of the most important pathways for the introduction of non-indigenous species (i.e. species introduced to areas beyond their native range; Kolar & Lodge, 2001) into North America (e.g. Jenkins, 1996). Activities such as agriculture, recreation and the transportation of goods and biota (e.g. the aquarium trade (Chang *et al.*, 2009), fish stocking (Crawford & Muir, 2008) and the transport of species in ballast tanks of transoceanic ships (Floerl & Inglis, 2005)) are all potentially responsible for the accidental, or intentional, spread of species across their natural dispersal barriers on both a national and international scale (Kolar & Lodge, 2001). Not only is this accelerated rate of invasions resulting in the alteration of local community composition and function, it is also leading towards a global homogenisation of species and thus intensifying the world biodiversity crisis (i.e. the rapid loss of global biodiversity) (Olden *et al.*, 2004; Hollebone & Hay, 2007).

Coupled with the anthropogenic-aided dispersal of species around the globe are the ways in which humans are constantly altering their surrounding environment to suit their needs. This is also aiding in the establishment of non-indigenous species across the globe (Olden *et al.*, 2004; Havel *et al.*, 2005). One such example of this environmental alteration is the construction of standing freshwater bodies, such as dams, water supply reservoirs and farm and ornamental ponds, which provide extensive new habitat for non-indigenous species to enter and establish (Havel *et al.*, 2005). Other examples of humans altering their surroundings include clearing forests or draining wetlands to expand or improve areas of farmland (Walker & del Moral, 2003b).

The study of biological invasions and their effects is a relatively new area of investigation. Whilst some mention of non-indigenous species was made by 19th Century naturalists, such as Charles Darwin, Joseph Hooker and Charles Lyell, these were simply observations (Richardson & Pysek, 2008). At the time it was not considered that these occurrences may be a threat to biodiversity on a global scale (Richardson & Pysek, 2008).

In the early 1900s biological invasions became more widespread but there was still very little attention being paid to the phenomenon. Many ecologists still considered the invasions as nothing more than anomalies (Ricciardi & MacIsaac, 2008). It was not until the publication of Charles S. Elton's book (1958) *'The ecology of invasions by plants and animals'* that biologists began to realise that biological invasions were events that needed to be researched in order to try and better understand the factors and processes involved (Richardson & Pysek, 2008).

Biological invasions can potentially result in high economic and ecological costs. In the United States the average annual figure for environmental damage and economic losses attributed to non-indigenous species (i.e. species not previously found in a given region) is around $120 billion (Pimentel *et al.*, 2005). One of the largest modern vertebrate extinction events ever recorded occurred in Lake Victoria, East Africa, following the release of the predacious Nile perch *Lates niloticus* in the 1950s (Kolar & Lodge, 2001). Since this introduction over two-thirds of the endemic fish populations have become extinct and heavy predation on grazing phytoplanktivores has resulted in a change of the entire food web of the lake (Bulleri *et al.*, 2008). Almost half of the extinct or endangered species in the United States owe their fate to at least a partial involvement of non-indigenous species (Lodge & Shrader-Frechette, 2003).

Many early biological invasion studies were of little use for the prediction and prevention of invasions in the respect that they generally only consisted of a qualitative assessment of species or community characteristics based on introduced species that had already successfully established, or ecosystems that had been invaded (Elton, 1958; Kolar & Lodge, 2001; Bailey *et al.*, 2005a). However, the growing awareness that the establishment of non-indigenous species is a major threat to global biodiversity (Drake & Lodge, 2004; Bailey *et al.*, 2005; Strecker & Arnott, 2008; Engel & Tollrian, 2009) has sparked the realisation that in order to better manage non-indigenous species and their potential effects there needs to be a shift in focus to take measures before establishment occurs (Jerde & Lewis, 2007; Westphal *et al.*, 2008). This could be achieved by identifying major introduction pathways to reduce the risk of new introductions (Bertolino, 2009) and identifying areas that are potentially at risk of biological invasions (i.e. 'hot spots') (Drake & Lodge, 2004).

Invasions follow a sequence of events which involves several different stages, including uptake (or entrainment), transportation, introduction, establishment and spread (Duggan *et al.*, 2006c) (Figure 1). Recent studies have focused on each of these stages separately, rather than treating an invasion as a single event (Bailey *et al.*, 2005a), as different factors determine whether a species will successfully complete each transition (Figure 1). For example, the survival of a fish in a ballast tank may be aided by an adaptation to feeding in the darkness (survival in transport, Figure 1), but this adaptation may impede its establishment if the water clarity is high in the new environment or there are already a lot of nocturnal fish in the recipient environment (Kolar & Lodge, 2001).

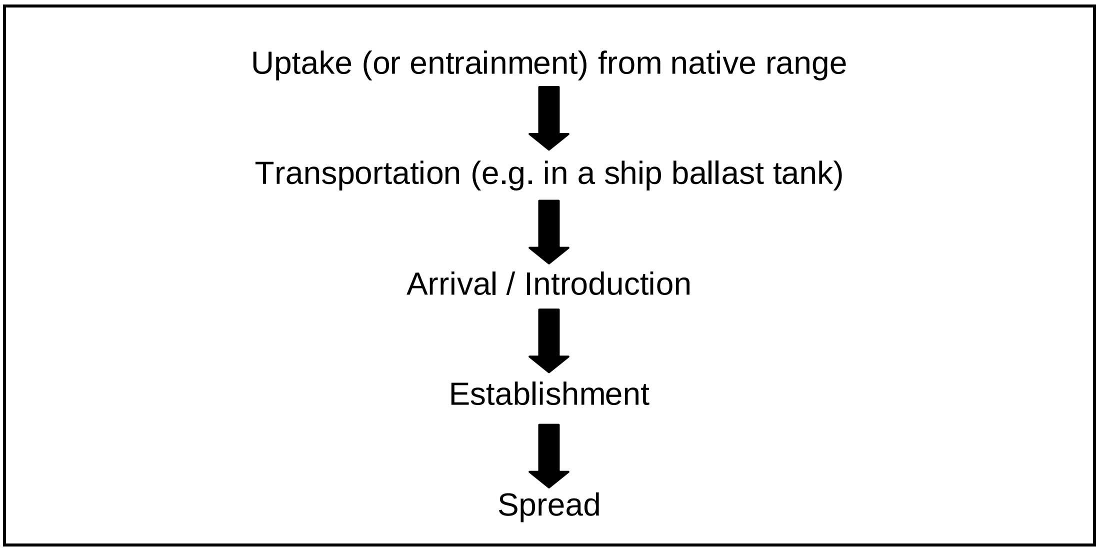


Figure 1: Stages of the invasion pathway. Diagram is based on Kolar & Lodge (2001) and Lockwood et al. (2005).

One factor that is largely agreed upon in determining establishment success is introduction effort or ‘propagule pressure’, which is the number and / or frequency of propagules released at introduction (Duggan *et al.*, 2006c). Colautti *et al.* (2006) state there is a significant positive association between propagule pressure and the establishment of non-indigenous species. This suggests successfully established species are generally introduced in greater numbers and / or more frequently than those which are introduced but fail to establish populations (Lockwood *et al.*, 2005; Colautti *et al.*, 2006; Simberloff, 2009). For example, in a study of the worldwide distribution of squirrels, Bertolino (2009) found that the success of their establishment in new environments was positively correlated to the number of animals introduced. A large number of studies have suggested that the establishment success of non-indigenous bird species in New Zealand, such as mallards (*Anas platyrhynchos*), pheasants (*Phasianus colchicus*) and California quails (*Lophortyx californicus*), was positively correlated to the number of introduction events and / or the number of individuals released (Veltman *et al.*, 1996; Green, 1997; Cassey, 2001; Forsyth & Duncan, 2001). The successful establishment of non-indigenous ungulates, such as alpaca (*Lama pacos*), white-tailed deer (*Odocoileus virginanus*) and red deer (*Cervus elaphus*), has also been attributed, at least partly, to the introduction of large numbers of individuals (Forsyth & Duncan, 2001).

By describing existing patterns of invasions, and focusing on the earlier stages of the invasion sequence it may be possible to make advancements towards predicting future invasions and invasion 'hot-spots' (Drake & Lodge, 2004). Once a non-indigenous species has established management options are generally limited, time-consuming and costly, while eradication is typically impossible (Kolar & Lodge, 2002). Therefore, identifying and understanding patterns that might reduce establishment and spread of non-indigenous species is a crucial part of managing biological invasions.

1.2 The biodiversity debate

Biodiversity and biotic resistance (defined below) are commonly cited as important factors responsible for regulating the ease with which non-indigenous species enter and establish in a new environment (Levine & D'Antonio, 1999; Shurin, 2000; Kennedy *et al.*, 2002; Havel *et al.*, 2005; Stachowicz & Byrnes, 2006; Battaglia *et al.*, 2009; Daleo *et al.*, 2009). However, there is still a lot of disagreement about whether biodiversity has a positive or negative influence on invasion success, and if biotic resistance is assigned more importance than it actually deserves.

Work by Elton (1958) is largely considered to be the origin of the biodiversity debate (Levine & D'Antonio, 1999; Ricciardi & MacIsaac, 2008; Richardson & Pysek, 2008). Elton put forward the theory that species-rich communities (i.e. those with a high biodiversity) are more resistant to invasions than communities with much smaller numbers of species, which is now widely known as the ‘biotic resistance hypothesis’ (Kennedy *et al.*, 2002; Ricciardi & MacIsaac, 2008).

A number of experimental tests have suggested that high diversity in an area exerts a negative effect on establishment success of new arrivals. Tilman (1997) reported that the proportion of introduced species to become successfully established in experimental grassland plots was negatively correlated to initial species diversity. Furthermore, in a study on the biological resistance of plant communities, Kennedy *et al*. (2002) found there was a significant negative effect of plot species richness on establishment (fewer invaders) and success (smaller maximum size) of invading plants. Shurin (2000) tested the invasion resistance of zooplankton communities by introducing a diverse mixture of species into intact local pond communities. His results inferred that the success of introduced species was negatively correlated with resident species diversity. In a similar study Dzialowski *et al.* (2007) noted that the non-indigenous cladoceran, *Daphnia lumholtzi*, was only able to establish in experimental mesocosms when the biomass and diversity of native zooplankton were significantly reduced.

The most commonly cited mechanism by which increased biodiversity could prevent invasions from occurring is that species-rich communities will utilise the resources available to them more efficiently than species-poor communities (Elton, 1958; Daleo *et al.*, 2009). This can result in a decrease in the number of "empty niches" available for invaders to move in and occupy (Shea & Chesson, 2002; Mwangi *et al.*, 2007). This assumption relates to classic niche theory, which suggests each species requires a particular set of conditions in order to survive in any given environment (Hutchinson, 1959), and that establishment could be minimised or prevented if the non-indigenous species occupies a similar niche to a native species (Hubbell, 2005). For example, deRivera *et al.* (2005) demonstrated how the native North American blue crab, *Callinectes sapidus,* appeared able to limit the abundance and distribution of the non-indigenous European green crab, *Carcinus maenas*, in eastern North America. Both species occupy shallow, soft-sediment habitats of bays and estuaries, and their ranges overlap in eastern North America (deRivera *et al.*, 2005). The results of this study showed that *C. sapidus* preyed heavily on *C. maenas* and the abundance of *C. maenas* was significantly lower at sites and depths where *C. sapidus* were present compared to sites where they were absent. Also, *C. maenas* were completely absent from Chesapeake Bay, which was where the highest abundance of *C. sapidus* were found (deRivera *et al.*, 2005). Therefore it appears the native *C. sapidus* is very effective at limiting the establishment of its non-indigenous rival.

In a study of the invasibility (i.e. the susceptibility of an area to invasion; Richardson, 2001) of artificial rock pools, Romanuk & Kolasa (2005) found that increasing resource availability through nutrient enrichment increased the invasion success of an introduced midge. They also noted that within the nutrient - enriched treatments, invasion success was highest in the low diversity treatments (Romanuk & Kolasa, 2005). Therefore, whilst an increase in resources can promote invasion success, the availability of the resources can still be determined by the diversity of the local community (Romanuk & Kolasa, 2005).

Another possibility is that a high biodiversity does not necessarily mean resources are being utilised efficiently, but instead signifies the possibility that a high ranking competitor is present (Shea & Chesson, 2002). Invasion success is not necessarily based on simply filling an empty niche, but may instead be achieved by exploiting available resources or avoiding a predator more effectively than resident species. Even in this situation a high biodiversity can still be maintained as the competitors strength may vary over space and time (Chesson, 2000).

It has been suggested that the scale of the study can influence whether diversity appears to have a positive or negative effect on invasion success. Small scale studies generally demonstrate negative correlations between diversity and invasion success. However, many large scale studies have suggested that communities with a high diversity are more easily invaded (Shea & Chesson, 2002; Byers & Noonburg, 2003). For example, Smith & Knapp (1999) found a positive correlation between native and exotic plant species richness in a native grassland in Kansas, U.S.A. In a 23 year study of the invasion of a non-indigenous herb into a New Zealand mountain beech forest, Wiser *et al.* (1998) noted that areas invaded by the herb typically had more species than those areas that were not invaded. These differences in correlations between diversity and invasion success could be attributed to the fact that most small scale studies only manipulate numbers of native and non-indigenous species whilst keeping environmental variables constant (Byers & Noonburg, 2003). However, patterns over large scales may be associated with underlying environmental factors such as resource availability, resource heterogeneity, predators, competitors and physical stress that may influence both biodiversity and invasion success (Shea & Chesson, 2002; Byers & Noonburg, 2003; Knight & Reich, 2005). Therefore, failure to account for these other factors may make a relationship that is negative on a small scale appear positive across a large area that incorporates variation in these factors (Byers & Noonburg, 2003).

The discrepancy over the nature of the relationship between diversity and invasion success may also be linked to the presence of specific species within communities. Communities with a high diversity may contain key species that act as facilitators of invasions, termed by Palmer & Maurer (1997) as ‘diversity promoters’, thereby making diverse communities more susceptible to invasions (Levine & D'Antonio, 1999). For example, Smith *et al.* (2004) found that reducing the abundance of dominant native grasses within experimental plots by up to 50% cause a significant decrease in the invasion success of a non-indigenous legume species. They suggested that, when present, dominant species alleviated stressful environmental conditions and acted as facilitators of invasions. Then when the dominant species were removed the environment was no longer suitable for non-indigenous species to establish (Smith *et al.*, 2004). It may also be that communities have a low diversity because they are dominated by a particular species that is both good at out-competing other native species and effective at resisting invaders. Robinson *et al.* (1995) found that seeds of the Californian poppy (*Eschscholzia californica*) introduced to grassland plots of varying diversity were more likely to germinate, flower and fruit in the more diverse plots. They suggested this result could be at least partially related to the fact that the low diversity plots contained high numbers of *Bromus diandrus*, which is a strong suppressor of poppies and other plants. Similarly Peart & Foin (1985) found it was easier to invade plots containing a variety of mixed annual grasses than plots dominated (close to 100% cover) by a single perennial grass (Levine & D'Antonio, 1999).

It may be possible that some combinations of species are simply more effective at inhibiting invasions than others of equal diversity (Law & Morton, 1996). For example, a well structured community (i.e. a community consisting of a non-random sub-set of the regional species pool; Pimm, 1991; Law & Morton, 1996), may be better at resisting invasions than a community consisting of a more 'random' or varied assemblage of species.

Taking all of the above into account, it is clear that a lot of research is still required before a more substantial conclusion can be reached on the effects biodiversity has on biological invasions. Factors which control variation in community diversity, such as disturbance, resource availability, competitors and physical stress also have the potential to influence invasibility, which can make understanding the link between biodiversity and the success of biological invasions difficult (Levine & D'Antonio, 1999; Von Holle & Simberloff, 2005).

1.3 The role of constructed waters

Humans have played a significant role in accelerating the rate of aquatic invasions both by introducing new transport vectors and through environmental manipulation (Havel *et al.*, 2005). One such example of this environmental manipulation that is currently a growing cause for concern is the construction of new water bodies. Downing *et al*. (2006) estimated large impoundments (e.g. dams and reservoirs) cover approximately 0.26 million km^2 of the earth's surface (compared to 4.2 million km^2 covered by natural lakes), with a further 77,000 km^2 covered by smaller impoundments (e.g. farm and ornamental ponds). These figures are expected to rise as more water bodies are constructed to try and meet the growing demands placed upon the Earth's freshwater resources as a result of growing human populations and changing climate (Palmer *et al.*, 2008). In the U.S.A the number of constructed water bodies is increasing at a rate of roughly 1% per year (Downing *et al.*, 2006).

Constructed waters provide a huge increase in area, number and spatial distribution of standing bodies of freshwater in many countries and are believed to aid the establishment and spread of non-indigenous species (Havel *et al.*, 2005; Johnson *et al.*, 2008). As a combined force, the construction of water bodies and biological invasions are having a major impact on the biodiversity of freshwater ecosystems, which exceed both terrestrial and marine systems in rates of extinction and proportions of endangered species (Ricciardi & Rasmussen, 1999; Dudgeon *et al.*, 2006; Johnson *et al.*, 2008). It is thought dams are particularly good sites for the establishment of passively distributing organisms such as many zooplankton species, aquatic plants and planktonic larvae of invertebrates, which may be unable to survive in strong unidirectional flows (Havel *et al.*, 2005). Once species have established, these constructed waters may act as invasion 'hubs', resulting in the subsequent spread and establishment of non-indigenous species into natural water bodies (Muirhead & MacIsaac, 2005; Johnson *et al.*, 2008).

Much of the research currently being conducted on how constructed water bodies facilitate biological invasions has focused only on reservoirs (i.e. dammed rivers), such as that in North America by Havel *et al.* (2005) and Johnson *et al.* (2008). There are a number of factors, both abiotic and biotic, that these authors suggest contribute to the ease with which organisms can establish in, and spread among, reservoirs as opposed to natural lakes. They highlight likely important factors as being greater connectivity, propagule pressure, disturbance and environmental variability, although many of these theories remain untested.

Since reservoirs are situated within riverine networks they have a high connectivity both to river systems and other reservoirs (Havel *et al.*, 2005). This high connectivity ties into the propagule pressure hypothesis, which is based on the idea that the greater the introduction effort (i.e. number of individuals released and number of introduction attempts) the more likely a species is to become successfully established (Kolar & Lodge, 2001). It is highly likely that the downstream transport of water will enhance the delivery rates of non-indigenous species, as opposed to natural water bodies, which are generally more isolated and thus may have a lower introduction effort. Shurin & Havel (2003) conducted a study on the spread of the non-indigenous cladoceran *Daphnia lumholtzi* between reservoirs in Missouri, U.S.A. They found that, in general, reservoirs downstream of known source populations had a higher chance of being invaded than those found upstream or completely isolated from these populations (Shurin & Havel, 2003). Nonetheless, *Daphnia lumholtzi* was still found in some upstream reservoirs, which indicates other modes of transport (e.g. boating traffic; Leung *et al.*, 2006) are also important for dispersal.

The idea that anthropogenic disturbance (i.e. an event in time that disrupts ecosystem, community or population structure and changes resource availability or the physical environment – definition adapted from White & Pickett, 1985) increases an ecosystems susceptibility to invasion has been around for many years (Orians, 1986). Disturbances may reduce the abundance of native species, which can open up available resources to potential invaders (Havel *et al.*, 2005). In addition to this, resource availability may be temporarily increased by events such as nutrient inputs, thus creating opportunities for invaders (Davis *et al.*, 2000).

Reservoirs are subjected to regular anthropogenic disturbance through the release of water for flood control and to produce power; they also tend to have much faster and more variable flushing rates than natural water bodies. Reservoirs also tend to receive higher loads of organic materials and nutrients than natural lakes, owing to a larger watershed area:volume ratio. This can increase the potential for eutrophication and associated algal blooms (Havel *et al.*, 2005).

Spatial and temporal heterogeneity of reservoirs may also provide multiple niches for invaders to occupy. The upper reservoir (riverine) end tends to be thermally unstable with high turbidity, sedimentation rates, and nutrient loading. On the other hand the lower reservoir (lacustrine) zone is generally associated with high water clarity, pronounced stratification, and nutrient limitation in the summer months (Havel *et al.*, 2005). Therefore, there are a large variety of conditions to cater to the needs of a whole range of organisms should they have the opportunity to invade.

Whilst studies such as those conducted by Havel *et al.* (2005) and Johnson *et al.* (2008) appear to provide some compelling evidence as to why invasions may be occurring in reservoirs it is key to note that the term 'constructed water body' does not relate exclusively to reservoirs. In New Zealand invasions are occurring in many other types of constructed water bodies, for example ornamental ponds and old mine pits (Banks & Duggan, 2009). These water bodies are far less likely to be influenced by factors such as high connectivity and regular disturbance related to dammed rivers, which therefore makes biotic resistance a much more compelling factor.

It is thought that constructed waters may have a lower diversity than natural water bodies due to the fact that they are considerably younger (e.g. < 50 years as opposed to > 500 years in NZ) and have therefore had less time to accumulate species (Havel *et al*. 2005). Shea & Chesson (2002) suggest that the more mature a system is (i.e. those which have had more time to accumulate species), the better it will be at resisting invaders. Younger communities are likely to have fewer species with broader niches, which have had less time to adapt to local conditions. They will therefore be expected to have lower competitive abilities and poorer invasion resistance than those better adapted species found in more mature communities (Shea & Chesson, 2002). Therefore, if constructed waters do indeed have a lower biotic diversity it will result in them having low ‘biotic resistance’ (Shurin, 2000), allowing non-indigenous species to become established with relative ease.

There are a growing number of documented cases of species invading freshwater bodies, but one well known example of a species of zooplankton that has spread rapidly over a large area via reservoirs is the tropical cladoceran *Daphnia lumholtzi* (Havel et al., 2005; Engel & Tollrian, 2009). It originates from the tropics and subtropics of Africa, Asia and Australia but, following its first sighting in a Texas reservoir in 1990, has spread throughout the whole of the United States (Engel & Tollrian, 2009). The majority of the United States population of *Daphnia lumholtzi* is found in reservoirs, although they have also been found in large rivers and lakes (e.g. the Great Lakes; Havel *et al.*, 2005). Although it is not known exactly how or when this species was introduced it is highly likely that the introduction occurred when Lake Fairfield, in Texas, U.S.A, was stocked with the non-indigenous Nile perch (*Lates niloticus*) in 1983 (Havel & Hebert, 1993). These fish were taken from Lake Victoria in east Africa, where *Daphnia lumholtzi* is known to be a dominant species amongst the zooplankton community (Havel & Hebert, 1993). The success of the species is thought to be linked to its ability to thrive in the hot summer conditions, during which time the abundance of the native *Daphnia* species (*Daphnia pulicaria*) declines (Havel *et al.*, 2005). In addition, *Daphnia lumholtzi* produces large head and tail spines in the presence of predators, which the native *Daphnia pulicaria* does not produce. Therefore, *Daphnia lumholtzi* is competitively superior in the presence of fish (Engel & Tollrian, 2009). Since its initial introduction, *Daphnia lumholtzi* appears to be increasing its distribution beyond the United States, as it was recorded for the first time in October 2000 in the Três Irmãos reservoir in Sao Paulo, Brazil (Zanata *et al.*, 2003).

Johnson *et al*. (2008) conducted a study in the Laurentian Great Lakes region to explore the suggestion that impounded water bodies facilitated invasions into natural lakes. They compiled data on 5281 water bodies (4200 lakes and 1081 impoundments) and found that for each of the five widespread nuisance invaders impoundments were significantly more likely to be invaded than natural lakes. They also found that for the 189 water bodies that they surveyed for the three most common invaders (zebra mussels, Eurasian watermilfoil and rusty crayfish) the impoundments were far more likely to be able to support multiple invaders (Johnson *et al.*, 2008). They also found that the number of boat landings and / or the proximity to the nearest Great Lake was a good predictor of the occurrence of spiny water fleas, rainbow smelt, zebra mussels and Eurasian watermilfoil. This highlights the potential importance of connectivity and human use for increasing invasion success, and also supports the ideas I have previously mentioned by Havel *et al*. (2005).

1.4 Invasions of constructed waters in New Zealand

There are several species of non-indigenous zooplankton that have been recorded from constructed water bodies throughout New Zealand. Two species of calanoid copepod, *Boeckella symmetrica* and *Boeckella minuta*, are thought to be recent arrivals from Australia, owing to their limited distribution, with their successful establishment facilitated by the availability of new habitats (i.e. reservoirs) (Duggan *et al.*, 2006b). Banks & Duggan (2009) recorded three additional species of calanoid copepods in the North Island of New Zealand that were seemingly confined to constructed waters. These were the North American species *Skistodiaptomus pallidus,* the Japanese species *Sinodiaptomus valkanovi,* and *Boeckella triarticulata*. All these species have been recorded from multiple constructed water bodies in the North Island, except for *Boeckella triarticulata*. This species has only been recorded from a single farm dam in the North Island (Burns, 1984), but is found in natural waters throughout the South Island of New Zealand and Australia (Maly & Bayly, 1991; Jamieson, 1998). These findings suggest that constructed waters in the North Island, New Zealand, may indeed be facilitating invasions of non-indigenous zooplankton. Constructed waters also appear to be responsible for range expansion of native species. The native calanoid copepod *Boeckella propinqua* was once confined to natural water bodies within a small section of the central North Island, encompassing a narrow area from Ohakune to Mayor Island. Their distribution is associated with the Taupo Graben and Haast Schist basement terranes (i.e. geographical regions with a common geological history) (Banks & Duggan, 2009). Its range now encompasses constructed water bodies as far north as Auckland (Banks & Duggan, 2009).

It is also important to note that these non-indigenous calanoid copepods have been found in a variety of constructed water bodies, such as ornamental ponds and old mine pits, and not just reservoirs (Banks & Duggan, 2009). Sites such as ornamental ponds and old mine pits have very similar environments to natural lakes and ponds. Therefore factors such as high levels of disturbance, high connectivity and unusual chemical and physical properties, which authors like Havel *et al.* (2005) suggest facilitate invasions into reservoirs, are not applicable (Banks & Duggan, 2009). This suggests that other variables, such as reduced biotic resistance, may be responsible for the facilitation of non-indigenous species invasions into New Zealand constructed water bodies (Banks &

Duggan, 2009). It is highly likely that this biotic resistance is particularly strong for calanoid copepods as species of similar size are generally not able to co-occur within the same water body (Chapman & Green, 1987). The discovery of non-indigenous species in constructed water bodies would be far less concerning if they were permanently confined to these locations. However it appears (from studies such as Havel et al. 2005, Ferrari & Rossetti 2006) that constructed waters may simply act as a stepping-stone and, once established, the species may spread to other sites, including natural lakes, and potentially exert detrimental effects on the local biota. For example, the Australasian calanoid copepod *Boeckella triarticulata* was identified as a non-indigenous species in fish ponds in northern Italy in the mid 1980s. It was not until 2005 that its presence was recorded in natural water bodies (i.e. the Po River) (Ferrari & Rossetti 2006). Whilst this spread has not yet been documented in New Zealand (Banks & Duggan, 2009) the presence of non-indigenous calanoid copepods confined to constructed water bodies could mean it is only a matter of time before some, or all, of these species spread to natural water bodies.

1.5 Aims, objectives and hypotheses

The main aims of this research were focused on comparing biodiversity and community composition of natural and constructed water bodies in the North Island, New Zealand. My results also aim to examine whether establishment frequency of non-indigenous zooplankton species is higher in constructed waters than natural waters. Through carrying out this research I hope to make advancements towards understanding if constructed waters are more easily invaded than natural waters, and if so what factors could be aiding successful establishment. Results from this study may not only help with identifying future invasion ‘hot-spots’, but also reduce the establishment and spread of non-indigenous species in constructed water bodies. They could also be used to inform management bodies (i.e. local and regional councils) of the risks associated with the construction of new water bodies.

My hypotheses are that species richness will be lower in constructed water bodies than natural ones and that non-indigenous zooplankton will occur at a higher frequency in constructed water bodies.

Chapter Two: Materials and Methods

2.1 Site selection

Initial water body selection was conducted using a variety of different sources including books (e.g. Lowe & Green, 1987), maps (e.g. Penguin Books (NZ) Ltd, 1999; KIWI MAPS Ltd, 2004), Google Earth (http://earth.google.com/), and through conversing with colleagues and friends about my research. All North Island water bodies that appeared accessible by boat, or shallow enough for wading, were recorded on a spreadsheet along with their nature of origin (i.e. constructed or natural), location, age, trophic status and area. Surface areas were estimated using a ruler and map books (e.g. Penguin Books (NZ) Ltd, 1999; KIWI MAPS Ltd, 2004). Trophic states of water bodies were acquired from journal articles (e.g. Ryan *et al.*, 2006), or estimated based on either the purpose of the water body (e.g. water reservoirs were assumed to be oligotrophic to mesotrophic) or the surrounding landscape (e.g. those enclosed by extensive farm land were assumed to be eutrophic). If any of these factors were unknown then the land owner or the associated regulatory authority were contacted for information. Other environmental variables were later added, such as latitude, altitude, number of water bodies within a 20 km radius, distance to nearest major highway and distance to nearest water body. Information on these variables was collected using Google Earth (http://earth.google.com/).

Several water bodies identified from initial searches were later deemed inaccessible, usually owing to some physical aspect. For example, some water bodies were accessible only by a long trek on foot, whilst others were present in areas that meant they were geothermal or saline influenced.

Steps were taken to ensure that comparisons were being made between water bodies with similar characteristics in order to minimise bias for statistical analyses. For example, natural water bodies with an area greater than 14 km^2, such as Lake Taupo (622.63 km^2) and Lake Rotorua (79.78 km^2) (Irwin, 1975), were discarded. A figure of 14 km^2 was selected as a maximum for water body area as it was equivalent to the largest accessible constructed water body (Lake Arapuni, 13.8 km^2).

Having recorded all potential study sites, lakes and ponds were then sorted by origin (i.e. natural or constructed) and entered into two separate spreadsheets. To select the water bodies for my final site list I used a process of directed randomisation. The first step was to sort the water bodies by area. Small water bodies were deemed as those with an area less than 0.1 km^2, medium water bodies had areas between 0.1 and 5 km^2, and large water bodies had areas greater than 5 km^2. Microsoft Excel was then used to generate a series of random numbers for each group. The water bodies represented by the three highest numbers in each group were then highlighted for use in the final site list. A similar process was carried out for age and trophic status, selecting either the two or three highest numbers depending on the number of groups in the category. There were some instances where the same water body was selected twice in different categories. When this occurred I used the water body associated with the next highest number.

Directed randomisation was used in the selection process because, whilst it was important to have a random selection of water bodies to minimise bias, I still needed to ensure that the final sites chosen represented a wide range of ages, sizes, trophic states and geographical locations to make certain that the whole of the North Island was going to be represented. Had the water bodies simply been split by origin there was the risk that some types of water bodies, for example large natural ones, could be over-represented whilst others, for example large constructed ones, could be missed altogether, thereby reducing the comparability of the final results.

In total 46 water bodies were sampled (Figure 2); 23 of natural origin and 23 constructed. These ranged from small ponds to lakes and reservoirs.
This was the maximum I was able to analyse due to time constraints brought about by the time required to undertake hatching experiments. However, my sites provide a good representation of the water bodies found throughout the North Island of New Zealand.

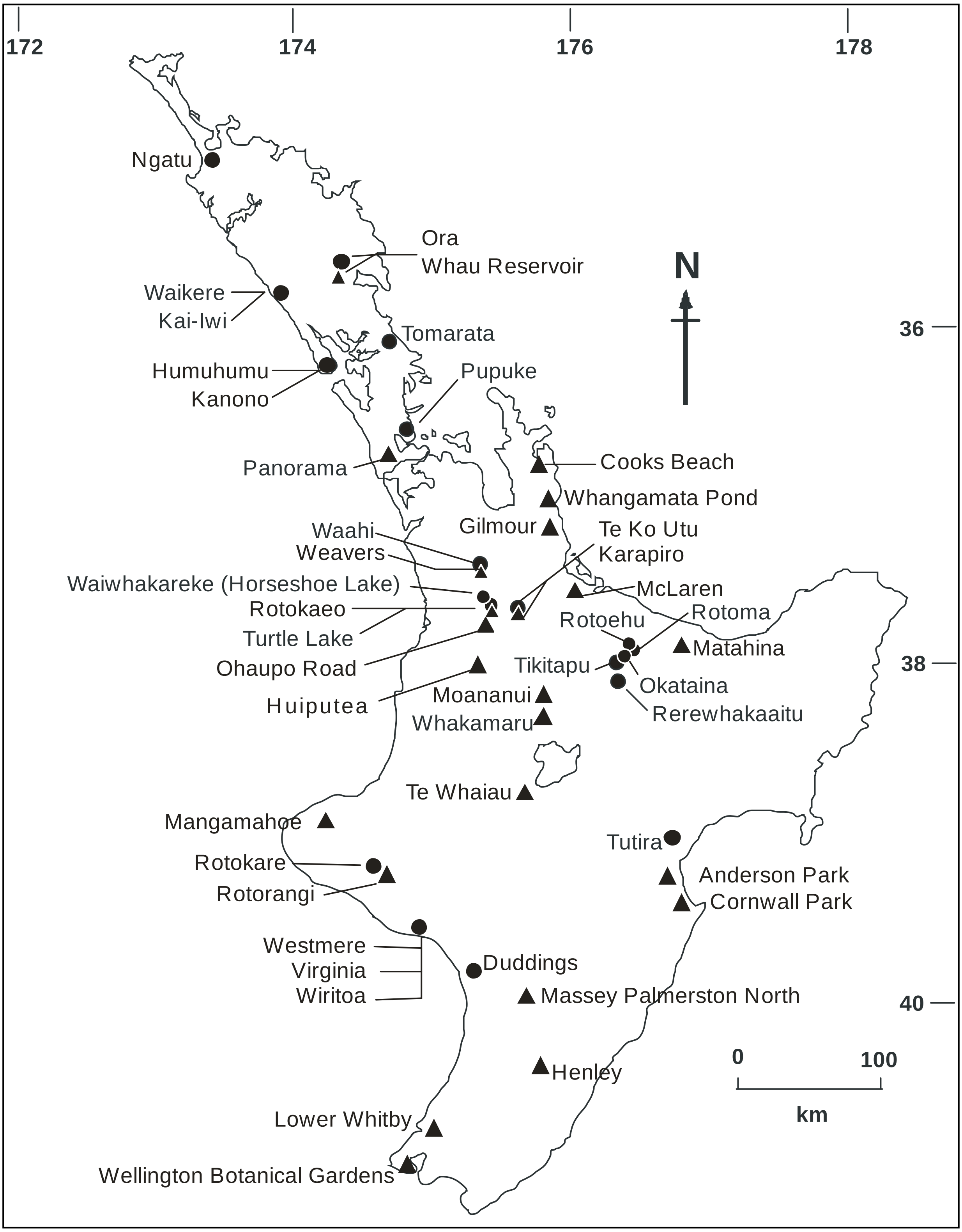


Figure 2: Locations of water bodies sampled in the North Island, New Zealand

▲ = Constructed water bodies ● = Natural water bodies

2.2 Sample collection

Sample collection took place over the months of February and March 2009 (austral summer and early autumn). A gravity corer (length: 50 cm; inner-diameter: 6 cm) was used to obtain surface sediment samples from the selected sites. A corer was used rather than an Ekman grab as the amount of sediment collected could be more accurately quantified. In addition, the corer disturbs the surface sediment less thereby ensuring only the top sediments were collected, which will have the highest number of viable eggs and also the most recently deposited diapausing eggs (Brendonck & De Meester, 2003). The corer was cleaned between sites to prevent any cross-contamination among samples and to reduce the potential spread of non-native species.

Sediment samples were used to assess species richness because lake sediments contain diapausing eggs of zooplankton species present in a water body. Water sampling using nets or traps on a single visit only provides an indication of what species are present in the water column at that time. Zooplankton populations can display significant seasonality, i.e. be present in large numbers for short time periods and completely absent the rest of the year (Herzig, 1985; May, 1986; Caceres & Hairston, 1998; Hairston *et al.*, 2000; Brendonck & De Meester, 2003). Therefore, water sampling would need to be carried out multiple times at each location during the course of the year. Owing to the nature of my work and the time constraints applied to it this was not logistically possible.

Five sediment cores were collected from randomly selected, widely distributed points in each water body. At each site, if possible, one core was taken from approximately the deepest part of the water body. Coring at several different locations is preferential to taking all the cores at one site for a number of reasons. Firstly, the horizontal distribution of diapausing eggs is not uniform across the bottom of a water body (Brendonck & De Meester, 2003). Therefore, collecting cores at only one site could result in all the cores being taken in a ‘dead patch’, where very few diapausing eggs are present. However, sampling a series of random sites has a much greater chance of coring a patch of sediment containing a high number of viable eggs, or simply attaining a representative sample of species. Secondly, it has been suggested (Harvey *et al.*, 2009) that by sampling at a number of widely spread sites there is a greater probability of obtaining organisms that may only be present in small numbers, such as newly introduced non-indigenous species. Harvey *et al*. (2009) also found that whilst the number of samples collected is important for detecting low density species, it was the spatial arrangement that had the greatest influence on the success of detection.

Some water bodies were shallow enough to wade into. However, in most cases the corer was deployed from a boat. Only the top 5 cm were retained from each core. This figure was based on studies that suggest the greatest number of viable diapausing eggs could be found in the top 4-6 cm of the sediment (Herzig, 1985; Carvalho & Wolf, 1989; Hairston & Van Brunt, 1994; Caceres, 1998). Furthermore, negative relationships can exist between hatching success and sediment depth (Herzig, 1985; Hairston & Van Brunt, 1994; Hairston *et al.*, 1995).

Upon collection the sediment samples were placed in labelled 400 ml plastic containers for transport to the laboratory. Samples were wrapped in aluminium foil, to keep the sediment in the dark, and placed in the refrigerator (3 to 6 ^{o}C). These steps were taken to ensure the eggs completed their refractory period, and to provide a cue for hatching once they were exposed to light and higher temperatures.

In addition to the sediment cores, two 400 ml plastic containers of surface water were also collected from each water body. One of these was used for chlorophyll *a* analysis. Upon returning to the laboratory a known volume of water (20 ml for water bodies with a high algal content to 100 ml for those with a low algal content) was filtered at a low vacuum through a

0.5 µm glass microfiber filter. The filter paper was then wrapped in a piece of aluminium foil, labelled, and stored in the freezer until processing. The second water sample was used for total phosphorus analysis. Water clarity was recorded at each site using a 25 cm Secchi disk. This was done by lowering the Secchi disk into the water to find the point between disappearance and reappearance of the disk, and then recording the depth from the attached tape measure. Depth readings were also taken at various points at each site using a portable depth sounder (Eagle, 'Fish Easy' model). These readings were used to estimate the maximum depth of each water body.

Copepods were sampled at each site using a 40 µm mesh net, which was towed horizontally through the water in shallow water bodies and vertically through the water column in deeper lakes and reservoirs. The samples were then transferred into labelled 400 ml plastic containers and preserved in 70% ethanol (final concentration) for later identification. This sampling was carried out as copepods, one of the major groups of zooplankton, are difficult to rear to a life stage where they can be identified using hatching experiments; immature copepods cannot be identified to species level (Hairston *et al.*, 2000; Vandekerkhove *et al.*, 2004).

2.3 Laboratory analyses

Chlorophyll *a* extraction was carried out in a room with minimum lighting in order to reduce degradation of the samples. The filter paper was torn into small pieces and placed in the bottom of a glass grinding tube, to which 5 ml of aqueous buffered acetone solution was added. An electric grinder was used to process the contents into a slurry, making sure that any heat generated by friction was kept to a minimum. The slurry was then poured into a labelled 15 ml screw-cap Vulcan tube. Another 5 ml of acetone solution was used to rinse out the glass grinding tube, and this was then added to the Vulcan tube containing the slurry. If necessary, the Vulcan tube was topped up with acetone to the 10 ml mark.

Once all the samples had been processed, the tubes were shaken and then kept in the dark at 4 ^{o}C for approximately 20 hours. The samples were shaken an additional two times during this period.

Following the 20 hour period the samples were given another vigorous shake, and then centrifuged at 1157 G for 10 minutes. Samples were then left to stand for half an hour, allowing them to come to ambient temperature and giving the fluorometer (Turner Designs 10 – AU Fluorometer) sufficient time to warm up. Firstly, un-acidified and acidified blank values were obtained by adding buffered acetone solution and acetone solution plus 3 drops of hydrochloric acid, respectively, to the glass cuvette. These samples were measured using 5 ml of the supernatant in a cuvette. If the fluorometer gave a reading of ‘OVER’, signifying the solution was too concentrated, then the solutions were diluted by half using the acetone solution; all dilutions were recorded. To prevent any risk of contamination, the cuvette was rinsed with a small amount of supernatant prior to the sample reading being taken.

Acidified readings for the samples were acquired by mixing 3 drops of hydrochloric acid into the supernatant. All values were then filled into a pre-programmed Microsoft Excel spreadsheet, based on calibration curves derived from samples of known concentrations, to produce results for total chlorophyll *a*.

Total Phosphorous Analysis was carried out by Hill Laboratories, Hamilton. Together with the Secchi disk measurement taken at each site, the phosphorous and chlorophyll *a* readings were used to calculate Trophic Level Index values (Burns *et al.*, 1999) to provide an estimate of the trophic state of each water body. The equations used to calculate trophic level values for chlorophyll *a* (TLc), Secchi depth (TLs) and total phosphorus (TLp) are as follows (Burns *et al.*, 1999):

$$TLc = 2.22 + 2.54 \log (\text{Chl } a) \quad (1)$$

$$TLs = 5.10 + 2.27 \log (1 / SD - 1 / 40) \quad (2)$$

$$TLp = 0.218 + 2.92 \log (TP) \quad (3)$$

Obtaining these values enables the average Trophic Level Index (TLI) to be calculated:

$$TLI = 1 / 3 (TLc + TLs + TLp) \quad (4)$$

2.4 Zooplankton analyses

Unprocessed sediments were kept refrigerated in the dark for at least two months prior to the commencement of hatching experiments to allow for a refractory period (Bailey *et al.*, 2005; Duggan *et al.*, 2006a). Diapausing eggs have a very low hatching success rate unless they undergo this initial refractory period (Chen & Marcus, 1997; Marcus & Lutz, 1998).

Four cores from each water body were processed. The first step involved in processing the samples was to give them a thorough stir to homogenise the sample, thereby ensuring the eggs were spread throughout the sample. Following this, two 40 g wet-weight sub-samples were weighed out into small plastic dishes. Each sub-sample was washed through a 40 μm sieve, thus removing any fine sediment, and leaving behind the courser sediment along with the rotifer and cladoceran eggs. The sieve was thoroughly rinsed between samples to prevent any cross-contamination.

The material retained on the sieve was then washed into a labelled 50 ml centrifuge (Vulcan) tube using a 1:1 weight:volume mixture of sugar and water. This sugar / water solution created a density gradient, which resulted in all organic material floating to the surface and any inorganic material remaining at the bottom of the tube. The tubes were then shaken, to ensure the solution had mixed right through the sediment, and placed in a centrifuge for 5 minutes at 54 G.

The supernatant was poured off into the 40 µm sieve and rinsed to remove any sugar solution coating the organic material. Synthetic pond water was then used to rinse the organic matter retained into labelled Petri dishes (Hebert & Crease, 1980). A concentrated solution of the synthetic pond water was made up by adding 480 mg $NaHCO_3$, 380 mg $CaSO_4.2H_2O$, 300 mg $MgSO_4$ and 5 mg KCl to one litre of Milli-q water. When being used to rinse the sugar solution off the organic matter the synthetic pond water solution was diluted by a factor of 10 (i.e. 50 ml:500 ml of Milli-q water) in a wash bottle. This same dilution was used for the synthetic pond water in which the diapausing eggs were incubated.

Two incubators (Thermoline Scientific Incubators, model: TRIL320–1– SD) were set up, one at 12 ^{o}C and the other at 20 ^{o}C, to represent an approximation of summer and winter water temperatures in water bodies in the North Island of New Zealand (Green *et al.*, 1987). One sub-sample from each core was placed in each incubator. The incubators were programmed to undergo a 16:8 hour light:dark cycle. The samples were left for 21 days and checked for emergence every Monday, Wednesday and Friday. This was done by removing the Petri dishes from the incubators and examining them under a stereo dissecting microscope (Olympus SZ60) at 30x magnification. Any zooplankton found were removed, identified, and their presence recorded (Duggan *et al.*, 2002; Duggan *et al.*, 2006a) (Appendix 1).

It has been suggested that a period of four weeks is ideal when assessing zooplankton diversity through hatching experiments (Vandekerkhove *et al.*, 2004). However, in preliminary experiments the only emergence occurring after 21 days was of individuals of species that had already been recorded. The first group of 10 cores to be processed were left for a period of 30 days, after which there were still no new species of zooplankton emerging. Therefore, it was decided that an incubation period of 21 days would be suitable for this work. It has also been found that separating the eggs from the sediment greatly increases hatching success (Vandekerkhove *et al.*, 2004). Furthermore, by keeping the incubation period consistent across all samples there is no risk of biasing any of the estimates of species richness.

Cyclopoid copepods were identified to species level by dissecting the rear end of a female (straight antennae as opposed to curled). The dissection was made between the third and fourth pairs of pleopods (P3 and P4) using a pair of fine needles and a stereo dissecting microscope. The P4 were folded back to expose the small pair of fifth pleopods (P5), which were mounted onto a slide and examined under a compound microscope (Olympus BH-2) at 200 to 400x magnification. The technique for identifying calanoid copepods to species level is similar except that a male is used (articulated antennae) and the P5 is dissected. The guides in Chapman & Lewis (1976), Bayly (1992) and Duggan *et al.* (2006b) were used for copepod identifications. The first step in identifying rotifers was to remove a live specimen from the Petri dish, using a pipette, place it on a glass slide in a small drop of water, and examine it under a stereo dissecting microscope at 30x magnification. If a positive identification could not be made then a coverslip was placed over the specimen. A small drop of sodium hypochlorite was placed along the edge of the coverslip and drawn under using filter paper. The sodium hypochlorite erodes the rotifer body, leaving behind only the trophi (jaws). The trophi were then examined under a compound microscope at 200 to 400x magnification. Rotifers were identified using the guides in Koste (1978), Nogrady (1995) and Shiel (1995).

2.5 Statistical analyses

2.5.1 Zooplankton species composition

One of the aims of this study was to compare species composition of natural and constructed water bodies. Two-tailed Pearson chi-squared tests of independence were run on all species found in at least five natural and five constructed water bodies to determine if they were more likely to occur in a water body of a particular origin. This test was chosen as it has been shown to be effective for this type of analysis (Johnson *et al.*, 2008). The presence / absence data for natural water bodies represented the expected statistic and the presence / absence data for constructed water bodies represented the observed statistic. This method was used to test my hypothesis that non-indigenous zooplankton would occur at a higher frequency in constructed water bodies than natural water bodies. However, the test could only be conducted on the data for one of the non-indigenous species (*Daphnia galeata*) as there was not enough data available for any of the non-indigenous calanoid copepod or rotifer species.

Canonical correspondence analyses (CCA) were performed on the natural and constructed data sets, using Canoco for Windows version 4.5 (Centre for Biometry, Wageningen, The Netherlands), to infer the environmental variables that were responsible for variation in species composition in both natural and constructed water bodies. Forward selection and Monte Carlo permutation tests were then carried out to determine which variables were statistically the most significant in determining the species composition of the water bodies. The species data for the CCA was based on species that were present in three or more natural or constructed water bodies. Where necessary, the environmental data was either $\log_{10}$ or $\log_{10}(x + 1)$ transformed to normalise its distribution. Variables were then standardised to zero mean and unit variance to eliminate any influence of the differing scales of measurement (ter Braak & Smilauer, 1998).

2.5.2 Zooplankton species richness

My study also aimed to determine whether constructed water bodies were more easily invaded than natural water bodies owing to a lower biological diversity and therefore biotic resistance. It is near impossible to measure biodiversity with absolute certainty as one cannot census an entire community (Arnott *et al.*, 1998). To overcome this problem I used the ‘Chao2’ non-parametric estimator to extrapolate species richness for each water body from species numbers observed in experimental replicates.

$$S^*_2 = S_{obs} + (L^2 / 2M) \tag{5}$$

Where ‘S^*_2’ is estimated species richness, ‘S_{obs}’ is the number of species observed, ‘L’ is the number of species found in only one sample, regardless of abundance, and ‘M’ is the number of species found in just two samples (Coddington *et al.*, 1996). Copepods were not included in the calculations as they were only taken from a single water sample, but they were included in the total number of observed species based on species recorded in the water sample (S_{obs}). The 'Chao2' method of estimating species richness was chosen as it has been used in a number of zooplankton studies and has been cited as a reliable and relatively unbiased method (Dumont & Segers, 1996; Arnott *et al.*, 1998; Muirhead *et al.*, 2006).

Species richness was plotted against the environmental variables to try and determine whether there were any relationships present. The variables included water body age, trophic state, surface area, distance to nearest neighbouring water body, distance to nearest major highway, the number of water bodies within a 20 km radius, approximate maximum depth of water body, latitude and altitude. A stepwise linear regression was then carried out, using Statistica version 9 (Statsoft Inc., Tulsa, USA) to determine what factors were the underlying cause for variation in species richness in both natural and constructed water bodies. Stepwise linear regression was used because it identifies the most significant variable, and then selects the variables that account for the remainder of the variation. Correlation coefficients, on the other hand, give relationships but do not take into account that not all the variables are independent. As with the CCA, where appropriate, environmental data was either $\log_{10}$ or $\log_{10}(x + 1)$ transformed to normalise its distribution. Species richness data was also $\log_{10}$ transformed to increase the normality of the data distribution.

Chapter Three: Results

3.1 Primary environmental variables

The primary environmental variables used for initial water body selection were water body surface area, trophic state and geographic spread. Every effort was made to ensure that the water bodies sampled during this study were evenly distributed throughout the North Island, and that they covered a wide variety of areas and trophic states, so as to allow valid comparisons between natural and constructed water bodies and reduce bias. There were some differences in the surface areas of water bodies sampled, with constructed waters in the final data set approximately 1 km^2 smaller, on average, than natural waters (Table 1). Nevertheless, for both natural and constructed water bodies a wide range of areas were covered, including a wide overlap, which is most important for identifying the major determinants leading to gradients in species richness and composition between the two data sets (Table 1). The range of TLI values covered was similar for both natural and constructed water bodies (Table 1), with there being less than one TLI unit difference between the data sets. The geographical distributions of natural and constructed water bodies were also very well matched (Table 1; Figure 2), thereby allowing reliable comparisons to be made between the different water bodies.

Table 1: Range of primary data for natural and constructed water bodies sampled in the North Island, New Zealand.

	Natural			Constructed		
	Mean	Min.	Max.	Mean	Min.	Max.
Surface area (km^2)	2.215	0.059	11.200	0.995	0.001	7.200
TLI value	4.00	2.31	6.67	4.49	1.58	6.27
Latitude	-37.75	-40.10	-35.03	-38.54	-41.28	-35.71

3.2 Zooplankton species composition

3.2.1 Zooplankton species diversity

A total of 71 species of zooplankton were found in natural and constructed water bodies throughout the North Island, New Zealand, during this study (Table 3). All species have been previously recorded in New Zealand, except for the rotifer *Cephalodella stenroosi* (Shiel *et al.*, 2009), which was recorded from a constructed pond in Whangamata on the east coast of the North Island. Overall, natural and constructed water bodies had a similar average number of species per water body (10.4 & 9.3 respectively). However, constructed water bodies had a greater total number of species than natural waters (60 and 54 respectively) and a much larger number of singularly occurring species (31 and 18 respectively) (Table 3).

Natural water bodies appeared to have a core group of species with 36 out 54 species (67%) recorded in two or more water bodies. However, constructed water bodies appeared to have a much more varied assemblage, with only 29 out of 60 species (48%) recorded in two or more water bodies.

Table 2: Key to sample numbers for total zooplankton species list. Numbers 1 to 23 represent natural water bodies, and numbers 24 to 46 represent constructed water bodies.

n	Natural Water Bodies	n	Constructed Water Bodies
1	Duddings Lake	24	Anderson Park Pond
2	Lake Waiwhakareke (Horseshoe Lake)	25	Cooks Beach Pond
3	Lake Humuhumu	26	Cornwall Park Pond
4	Lake Kai-Iwi	27	Lake Gilmour
5	Lake Kanono	28	Lake Henley
6	Lake Ngatu	29	Lake Huiputea
7	Lake Okataina	30	Lake Karapiro
8	Lake Ora	31	Lower Whitby Lake
9	Lake Pupuke	32	Lake Mangamahoe
10	Lake Rerewhakaaitu	33	Massey Palmerston North Pond
11	Lake Rotoehu	34	Lake Matahina
12	Lake Rotokaeo	35	Lake McLaren
13	Lake Rotokare	36	Lake Moananui
14	Lake Rotoma	37	Ohaupo Road Pond
15	Lake Te Ko Utu	38	Lake Panorama
16	Lake Tikitapu	39	Lake Rotorangi
17	Lake Tomarata	40	Te Whaiau Reservoir
18	Lake Tutira	41	Turtle Lake
19	Lake Virginia	42	Weavers Lake
20	Lake Waahi	43	Wellington Botanical Gardens Pond
21	Lake Waikere	44	Lake Whakamaru
22	Lake Westmere	45	Whangamata Pond
23	Lake Wiritoa	46	Whau Reservoir

*Table 3: Total species list of zooplankton recorded during this study. Locality numbers refer to Table 2. Species in **bold** are those recorded in only one natural and / or one constructed water body.*

Species	Natural Water Bodies (n)	Constructed Water Bodies (n)
Rotifers		
Anuraeopsis fissa	4, 8, 10, 13, 22, 23	25, 27, 29, 30, 31, 32, 33, 34, 39, 41
Anuraeopsis navicula	**3**	
Ascomorpha ovalis	**42**	
Ascomorpha saltans	1, 7, 15, 18, 19, 20, 22, 23	28, 37
Asplanchna brightwelli	2, 10, 13, 19, 20, 22, 23	26, 28, 29, 31, 34, 35, 36, 41, 46
Asplanchna girodi	1, 15	**32**
Asplanchna priodonta	1, 13, 16, 17	**39**
Asplanchna seiboldi	**23**	
Bdelloids	2, 12, 19	24, 36, 41, 42
Brachionus angularis	1, 2, 18, 20, 22	25, 26, 28, 29, 31, 32, 33, 36, 37, 38, 39, 42
Brachionus budapestinensis		**26**
Brachionus calyciflorus	2, 15, 18, 20, 22	24, 25, 26, 28, 29, 31, 32, 33, 34, 36, 37, 38, 39, 41, 44
Brachionus caudatus	1, 18	24, 28
Brachionus quadridentatus	2, 15, 22	24, 25, 27, 28, 29, 33, 34, 44
Brachionus urceolaris	8, 13, 20	24, 34
Cephalodella catellina		**34**
Cephalodella stenroosi		**45**
***Collotheca* sp.**		**34**
Conochilus coenobasis	**10**	
Conochilus dossuarius	1, 3, 4, 7, 19	33, 36
Conochilus exiguus	**2**	
Conochilus unicornis		**24**
Filinia longiseta	1, 3, 7, 8, 15, 18, 20, 22	24, 28, 29, 31, 32, 33, 36, 37, 39, 41, 42
Filinia novaezealandiae	4, 13	**38**
Filinia terminalis	2, 10, 19, 21	**46**
Flosculariid	**19**	
Gastropus hyptopus	7, 10, 13, 14, 15, 18, 20	29, 38, 44
Hexarthra intermedia	1, 4, 5, 6, 7, 10, 11, 19, 23	39, 42
Hexarthra mira	2, 3, 17, 18, 22	24, 25, 28, 29
Keratella australis		**24**
Keratella cochlearis		**34**

Table 3 (cont.): Total species list of zooplankton recorded during this study. Locality numbers refer to Table 2. Species in ***bold*** *are those recorded in only one natural and / or one constructed water body.*

Species	Natural Water Bodies (n)	Constructed Water Bodies (n)
Rotifers (cont.)		
Keratella procurva	**8**	**36**
Keratella slacki		32, 33, 37
Keratella tecta		**39**
Keratella tropica	11, 14, 15, 19	25, 27, 29, 33, 37
Keratella valga	**1**	
Lecane bulla	**15**	
Polyarthra dolichoptera	1, 2, 4, 8, 11, 12, 15, 18, 19, 22	24, 25, 26, 27, 28, 29, 32, 33, 34, 35, 37, 39, 41, 42
Pompholyx sp.	1, 2, 3, 7, 10, 13, 14, 15, 18, 19, 20, 22	31, 38, 41, 42
Proales sp.	10, 17	**31**
Proalides sp.		**39**
Ptygura sp.	**19**	
Synchaeta oblonga	1, 2, 6, 7, 9, 13, 14, 15, 19	31, 32, 35, 36, 39, 42, 46
Synchaeta pectinata	1, 7, 18	28, 31, 33
Testudinella patina	**8**	**26**
Trichocerca mus		**41**
Trichocerca pusilla	2, 5, 7, 10, 11, 13, 14, 18, 19, 20	24, 29, 30, 42
Trichocerca similis	1, 7, 23	**37**
Cladocerans		
Alona quadrangularis	10, 11	
Biapertura affinis		**35**
Bosmina meridionalis	1, 7, 10, 13, 16, 17, 19, 20, 21, 22	27, 33, 34, 39, 41
Camptocercus australis		**25**
Ceriodaphnia dubia	1, 6, 7, 8, 10, 11, 13, 16, 17, 18, 19, 21, 22	26, 27, 28, 29, 31, 33, 35, 36, 38, 39, 46
Daphnia carinata	**18**	**24**
Daphnia galeata	1, 2, 9, 11, 12, 13, 15, 19, 20, 22, 23	29, 31, 32, 38, 41, 42, 44
Leydigia australis	**12**	**26**
Moina tenuicornis		**45**
Pseudomoina lemnae	**8**	

Table 3 (cont.): Total species list of zooplankton recorded during this study. Locality numbers refer to Table 2. Species in ***bold*** *are those recorded in only one natural and / or one constructed water body.*

Species	Natural Water Bodies (n)	Constructed Water Bodies (n)
Cyclopoid Copepods		
Acanthocyclops robustus	4, 12	26, 33, 36
Diacyclops bicuspidatus		**42**
Eucyclops serrulatus		**40**
Macrocyclops albidus	5, 17	
Mesocyclops leuckarti	1, 2, 6, 7, 8, 9, 11, 13, 15, 18, 19, 20, 22, 23	24, 25, 27, 28, 29, 30, 31, 32, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46
Paracyclops fimbriatus	**5**	**26**
Calanoid Copepods		
Boeckella delicata		**42**
Boeckella hamata	19, 23	24, 28
Boeckella minuta		**41**
Boeckella tanea	3, 4, 5	
Calamoecia lucasi	1, 3, 4, 5, 6, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 20, 21, 22, 23	31, 36, 38, 44
Sinodiaptomus valkanovi		**27**
Other crustaceans		
Ostracods	1, 8, 9, 12, 14, 17, 22	24, 26, 29, 33, 37, 38, 40, 43

3.2.2 Frequently occurring zooplankton species

There was a great deal of variation in zooplankton species composition amongst both natural and constructed water bodies. Cladocerans, copepods and rotifers were all found throughout the North Island of New Zealand, occupying water bodies of both origins. However, when focusing on the most commonly occurring species it is clear that natural water bodies appear to be dominated by a different group of zooplankton compared to constructed water bodies. Cladocerans and calanoid copepods were, on average, more frequently observed in natural waters than constructed waters (e.g. *Bosmina meridionalis* and *Calamoecia lucasi*). Many rotifers species, such as *Brachionus species* and *Polyarthra dolichoptera*, had a higher frequency of occurrence in constructed waters, with Crustacea being recorded in fewer water bodies (Table 3; Figure 3).

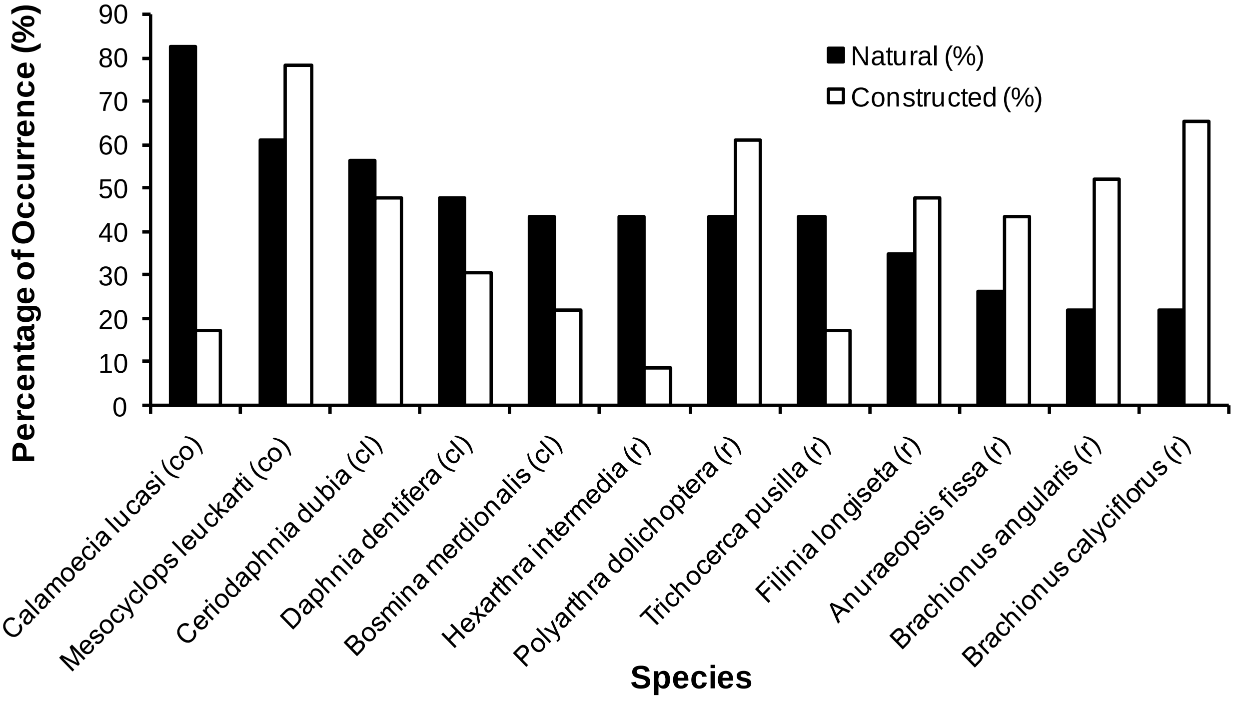


Figure 3: Percent occurrence of species found in at least ten natural or constructed water bodies. Species are ordered from highest to lowest occurrence in natural waters.

co = Copepod   cl = Cladoceran   r = Rotifer

Two-tailed Pearson chi-squared tests of independence were used to investigate whether any of the species found in a minimum of five natural and constructed water bodies were more likely to occupy natural or constructed water bodies. Native calanoid copepods (*Calamoecia lucasi, Boeckella hamata, B. delicata* and *B. tanea*) were significantly more likely to be found in natural water bodies (df = 1, $p < 0.05$) (Table 4). On the other hand, the rotifers *Brachionus angularis* and *B. calyciflorus* were significantly more likely to be found in constructed water bodies (df = 1, $p < 0.05$) (Table 4). These findings are in accordance with the results presented in Figure 3. The results for the remaining species (Table 4) infer they occur in both natural and constructed water bodies, with no strong, or statistically significant, preference for one or the other.

Table 4: Two-tailed Pearson chi-squared tests of independence results for species found in a minimum of five natural and constructed water bodies, and their percentage of occurrence in natural and constructed water bodies. Significant results are highlighted in **bold** *(df = 1, *p < 0.05, **p < 0.025, ***p < 0.001).*

Species	Natural (%)	Constructed (%)	X^2
Daphnia galeata	47.8	30.4	1.52
Native calanoid copepods***	**87.0**	**34.8**	**24.87**
Ceriodaphnia dubia	56.5	47.8	0.35
Mesocyclops leuckarti	60.9	78.3	1.75
Bosmina meridionalis	43.5	21.7	2.70
Polyarthra dolichoptera	43.5	60.9	1.44
Synchaeta oblonga	39.1	30.4	0.39
Filinia longiseta	34.8	47.8	0.82
Anuraeopsis fissa	26.1	43.5	1.61
Asplanchna brightwelli	30.4	39.1	0.39
Brachionus angularis**	**21.7**	**52.2**	**5.27**
Brachionus calyciflorus***	**21.7**	**65.2**	**11.18**

3.2.3 Variation in zooplankton species composition

3.2.3.1 Natural water bodies

Species such as *Brachionus calyciflorus, B. quadridentatus, B. angularis, B. urceolaris, Asplanchna brightwelli, Pompholyx* sp., and *Keratella tropica* were negatively associated with Axis 1 of the ordination diagram based on canonical correspondence analysis (CCA) of zooplankton species found in natural water bodies (Figure 4). *Conochilus dossuarius, Boeckella tanea, Gastropus hyptopus, Filinia terminalis, Hexarthra intermedia* and *Trichocerca similis* were positively associated with Axis 1.

The results of the forward selection and associated Monte Carlo permutation tests of the significance of environmental variables for natural water bodies are listed in Table 6. The lambda - 1 values represent the variance associated with each environmental variable when the variables are treated separately. The lambda - A column lists the variables in their order of inclusion in the CCA model (with the most important variable listed first) and the additional variance each explains at the time of inclusion (ter Braak & Smilauer, 1998; Duggan, 1999). The p - values show the significance of each variable at the time of inclusion. Axis 1 is largely constrained by the first variable in the lambda - A column (ter Braak & Smilauer, 1998).

For the natural water bodies sampled in this study (Figure 2; Table 2) Trophic Level Index (TLI) was the variable found to explain the greatest amount of variation in species composition (27%) when the variables were considered on an individual basis (lambda - 1). This was followed by approximate maximum depth (20%) and distance to nearest major highway (19%) (Table 6). Following the addition of TLI to the ordination (lambda - A) there were no other variables that explained any significant amount of the remaining variation ($p < 0.05$). Therefore, Axis 1 is largely constrained by TLI values. The eigenvalues and the percentage of variance of zooplankton species abundance accounted for by the first two axes in the CCA for natural water bodies are given in Table 5.

Taking into account that TLI explains the greatest amount of variation along the horizontal axis (Axis 1), and that it is negatively associated with Axis 1, it is inferred that the water bodies and species negatively associated with Axis 1 had a relatively high trophic state (i.e. high TLI values), and those positively associated had a low trophic state (i.e. low TLI values). Relating this to the TLI data (Table 7) it is apparent that this is justified. For example, Lake Te Ko Utu (TLI = 6.67), Lake Waahi (TLI = 6.27), Lake Waiwhakareke (TLI = 5.63) and Lake Westmere (TLI = 5.66) were all water bodies negatively associated with Axis 1 (Figure 4) and all had trophic states assessed as hypertrophic or supertrophic (Table 7). Conversely, sites such as Lake Humuhumu (TLI = 2.93), Lake Kai-Iwi (TLI = 2.36), Lake Tomarata (TLI = 3.01) and Lake Waikere (TLI = 2.50) were positively associated with Axis 1 (Figure 4), and were oligotrophic or mesotrophic (Table 7). Therefore, species such as *Brachionus calyciflorus, B. quadridentatus* and *Keratella tropica* were found in water bodies with a higher trophic state, whilst species such as *Conochilus dossuarius, Boeckella tanea* and *Gastropus hyptopus* were found in more oligotrophic water bodies (Figure 4).

The variables ‘approximate maximum depth’ and ‘distance to nearest major highway’, which were highlighted as important before the addition of TLI to the model (lambda – 1) (Table 6), were positively associated with Axis 1. Their importance at this stage may have been because there was a slight trend towards more oligotrophic water bodies being deeper and further away from major highways than hypertrophic or supertrophic waters (Table 7). However, after the addition of TLI to the model ‘approximate maximum depth’ and ‘distance to nearest major highway’ no longer explained a significant amount of variation in the data.

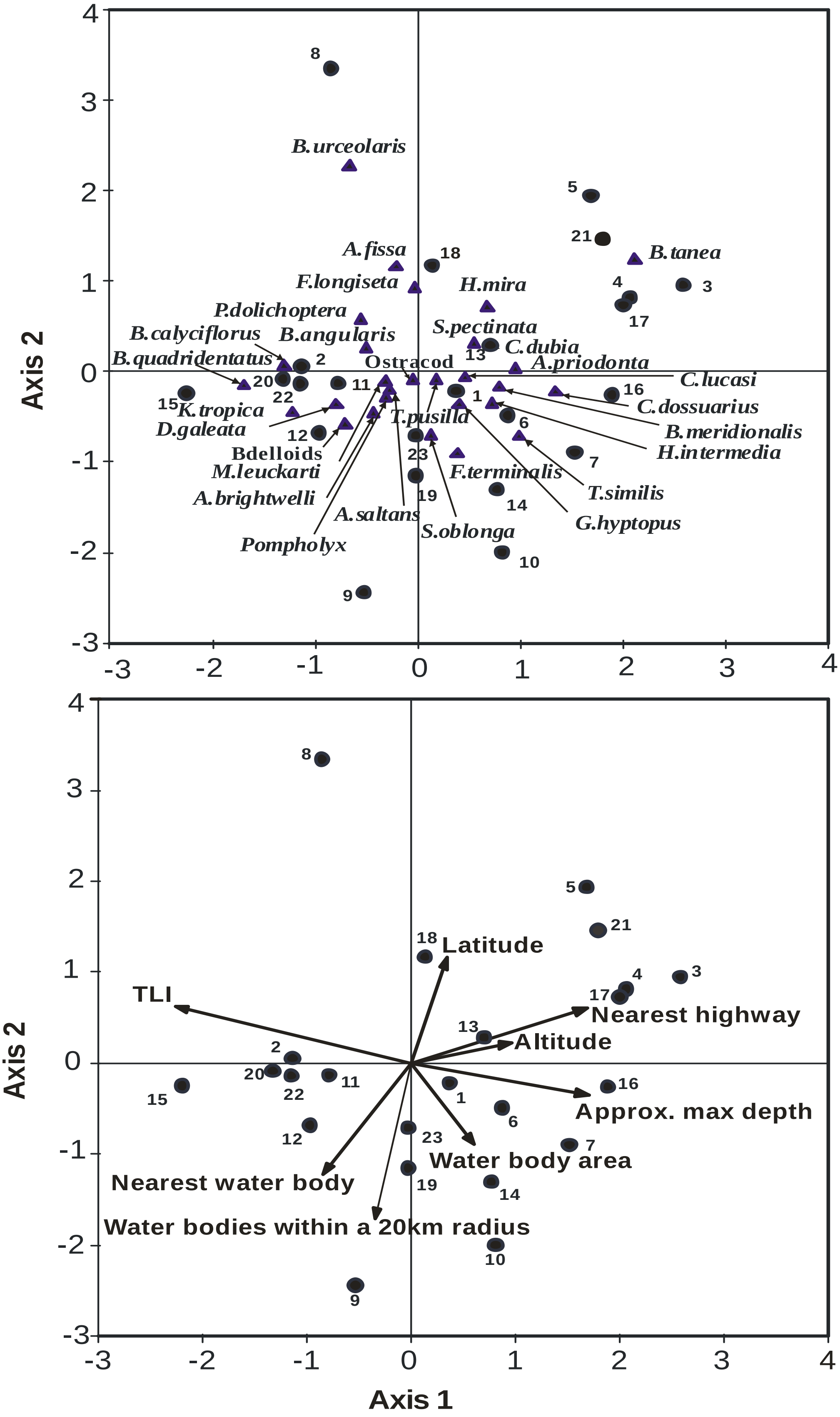


Figure 4: Ordination diagram based on CCA of natural water body zooplankton species with respect to environmental variables. Numbers (●) correspond to water body names (Table 2).

Table 5: Summary of CCA variables for natural water bodies.

Axes	Eigenvalue	Cumulative percentage variance of species data	Cumulative percentage variance of species – environment relation
1	0.324	13.2	29.1
2	0.227	22.5	49.4

Table 6: Results of forward selection and Monte Carlo permutation tests from CCA of natural water body zooplankton species. Environmental variables are listed by the order of their inclusion in the model (lambda – A). Significant variables and p-values for variables at their time of inclusion in the model are in ***bold*** *($p < 0.05$).*

Variable	Marginal effects	Conditional effects	
	Lambda - 1	Lambda - A	*p*
Trophic Level Index	**0.27**	**0.27**	**0.002**
Distance to nearest major highway (km)	0.19	0.15	0.076
Distance to nearest water body (km)	0.16	0.15	0.100
Number of lakes within a 20km radius	0.15	0.14	0.076
Lake area (km^2)	0.12	0.11	0.284
Latitude	0.13	0.11	0.342
Altitude (m)	0.12	0.10	0.388
Approximate maximum depth (m)	0.20	0.09	0.490

Table 7: Environmental variables identified as important in lambda – 1 (Table 6) in explaining variation in species composition of natural water bodies sampled in the North Island, New Zealand. Variables are ordered from highest to lowest TLI value. Numbers correspond to water body names in Table 2.

n	TLI value	Trophic state	Approximate maximum depth (m)	Distance to nearest major highway (km)
14	2.319	Oligotrophic	72.0	0.59
16	2.336	Oligotrophic	26.2	18.55
4	2.357	Oligotrophic	10.6	0.04
21	2.496	Oligotrophic	25.8	0.40
7	2.737	Oligotrophic	78.5	1.00
3	2.932	Oligotrophic	12.5	2.58
6	2.955	Oligotrophic	4.8	0.23
9	2.991	Oligotrophic	51.1	0.21
17	3.008	Oligotrophic	5.3	2.71
19	3.232	Mesotrophic	21.5	1.17
18	3.514	Mesotrophic	40.1	0.28
1	3.596	Mesotrophic	11.7	0.51
10	3.891	Mesotrophic	13.9	0.19
23	3.978	Mesotrophic	10.2	2.09
5	4.231	Eutrophic	14.4	1.06
13	4.827	Eutrophic	8.9	0.18
11	5.191	Supertrophic	10.8	8.50
12	5.255	Supertrophic	1.2	0.90
2	5.634	Supertrophic	2.5	7.32
22	5.664	Supertrophic	4.8	0.03
8	5.977	Supertrophic	7.8	1.22
20	6.268	Hypertrophic	1.3	0.68
15	6.671	Hypertrophic	2.0	2.60

3.2.3.2 Constructed water bodies

Species like *Keratella tropica, Trichocerca pusilla, Brachionus calyciflorus, B. quadridentatus* and *Anuraeopsis fissa* (i.e. predominantly rotifers) were negatively associated with Axis 1 on the ordination diagram based on CCA of zooplankton species found in constructed water bodies (Figure 5). *Synchaeta oblonga, Pompholyx, Ceriodaphnia dubia, Daphnia galeata, Calamoecia lucasi* and *Mesocyclops leuckarti* were positively associated with Axis 1, the most important axis in the ordination diagram.

The results of the forward selection and associated Monte Carlo permutation tests of the significance of environmental variables for constructed water bodies are listed in Table 9. For the constructed water bodies sampled in this study (Figure 2; Table 2) distance to nearest water body was the variable found to explain the greatest amount of variation in species composition (15%) when the variables were considered on an individual basis (lambda - 1). This was followed by number of water bodies within a 20 km radius (14%) and Trophic Level Index (11%) (Table 9). Following the addition of distance to nearest water body to the ordination (lambda - A) only the number of water bodies within 20 km explained any significant amount of the remaining variation ($p < 0.05$). Distance to nearest water body had a p – value of 0.040 and the addition of the number of water bodies within a 20 km radius had a p – value of 0.038 at the time of its inclusion (Table 9). TLI, which was the most significant variable for explaining species composition in natural water bodies, did not explain any significant amount of variation in species composition in constructed water bodies after the addition of the other variables to the model.

Distance to nearest water body is listed first in the lambda – A column (Table 9), which indicates that it explains the greatest amount of variation along the horizontal axis (Axis 1). The eigenvalues and the percentage of variance of zooplankton species abundance accounted for by the first two axes in the CCA for constructed water bodies are presented in Table 8. The Axis 1 eigenvalue is 0.26, which is less than the Axis 1 eigenvalue for the natural water bodies (0.32) (Table 5). This indicates that less of the variability is explained along Axis 1 for constructed water bodies than for natural water bodies.

Distance to nearest water body is negatively associated with Axis 1, and the number of water bodies within 20 km is positively associated with Axis 1 (Figure 5). This suggests that water bodies negatively associated with Axis 1, such as the Cooks Beach Pond (80.58 km from another water body, and zero water bodies within a 20 km radius) and Lake Gilmour (54.09 km and zero water bodies) are a relatively long distance from any other water body and have few water bodies within a 20 km radius of them (Figure 5; Table 10). On the other hand, water bodies positively associated with Axis 1, such as Weavers Lake (0.09 km and eight water bodies) Te Whaiau Reservoir (1.57 km and four water bodies) are within relatively close proximity to another water body, and have a number of water bodies within a 20 km radius (Figure 5; Table 10). Taking this into account it can be inferred that species negatively associated with Axis 1, such as the rotifers *Keratella tropica* and *Brachionus quadridentatus* (Figure 5), are perhaps able to disperse more easily over relatively large distances, whilst those positively associated with Axis 1, such as the crustaceans *Daphnia galeata* and *Calamoecia lucasi* (Figure 5), tend to disperse more slowly or over much shorter distances.

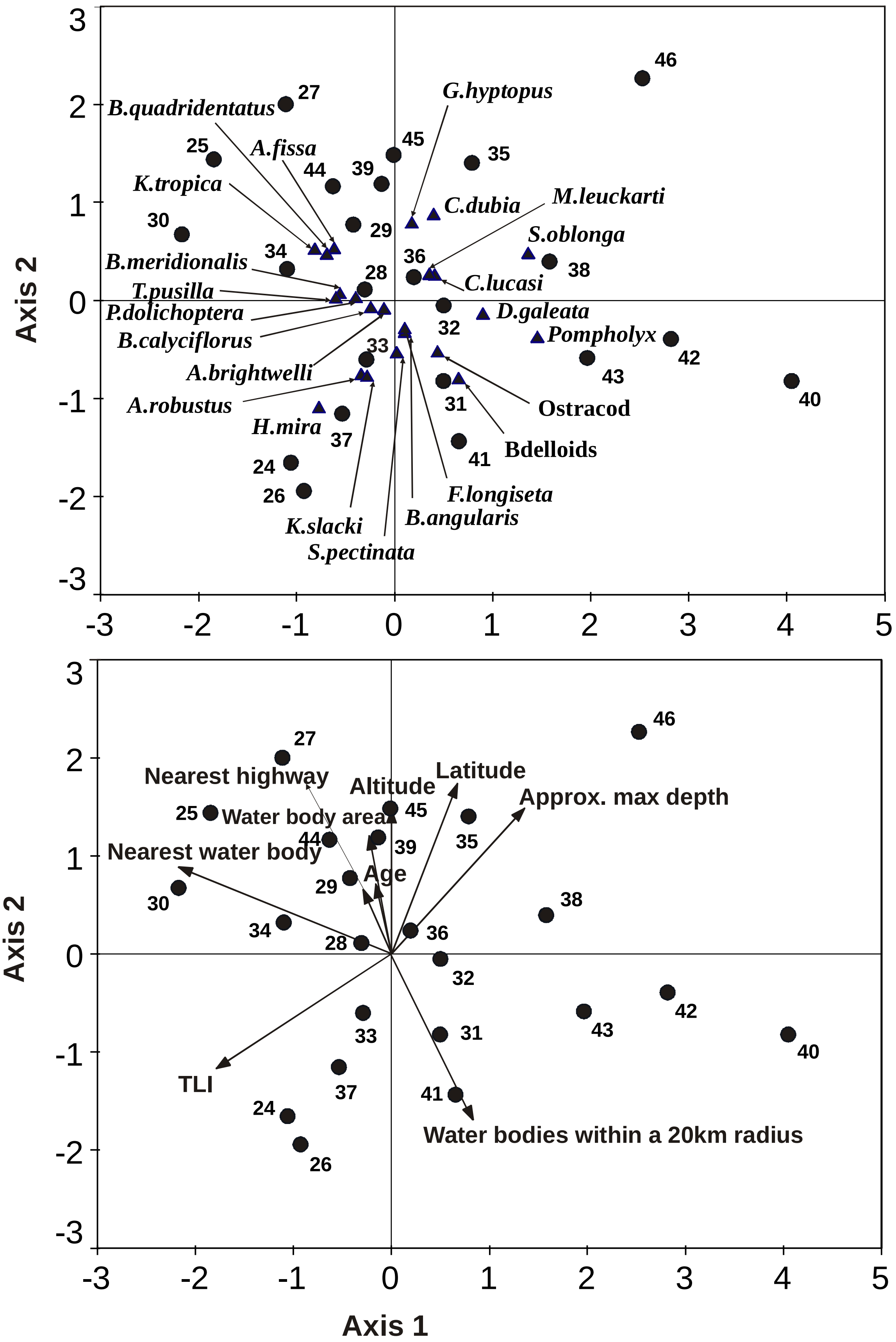


Figure 5: Ordination diagram based on CCA of constructed water body zooplankton species with respect to environmental variables. Numbers (●) correspond to water body names (Table 2).

Table 8: Summary of CCA variables for constructed water bodies.

Axes	Eigenvalue	Cumulative percentage variance of species data	Cumulative percentage variance of species – environment relation
1	0.261	12.5	30.4
2	0.162	20.2	49.3

Table 9: Results of forward selection and Monte Carlo permutation tests from CCA of constructed water body zooplankton species. Environmental variables are listed by the order of their inclusion in the model (lambda – A). Significant variables and p-values for variables at their time of inclusion in the model are in ***bold*** *(p < 0.05).*

Variable	Marginal effects	Conditional effects	
	Lambda - 1	Lambda - A	*p*
Distance to nearest water body (km)	**0.15**	**0.15**	**0.040**
Number of water bodies within a 20 km radius	**0.10**	**0.15**	**0.038**
Latitude	0.10	0.11	0.184
Approximate maximum depth (m)	0.14	0.11	0.222
Water body area (km^2)	0.08	0.09	0.422
Trophic Level Index	0.11	0.07	0.638
Distance to nearest major highway (km)	0.05	0.07	0.7
Altitude (m)	0.08	0.08	0.63
Age (years)	0.03	0.03	0.98

Table 10: Distance to nearest water body values and the number of water bodies within a 20 km radius for constructed water bodies sampled in the North Island, New Zealand. Numbers correspond to water bodies names in Table 2.

n	Water Body	Distance to nearest water body (km)	Number of water bodies within a 20km radius
24	Anderson Park Pond	10.95	3
25	Cooks Beach Pond	80.58	0
26	Cornwall Park Pond	10.20	4
27	Lake Gilmour	54.09	0
28	Lake Henley	39.29	0
29	Lake Huiputea	26.26	0
30	Lake Karapiro	7.47	5
31	Lower Whitby Lake	26.65	0
32	Lake Mangamahoe	19.23	1
33	Massey Palmerston North Pond	36.65	0
34	Lake Matahina	8.47	4
35	Lake McLaren	30.53	0
36	Lake Moananui	15.15	2
37	Ohaupo Road Pond	3.00	11
38	Lake Panorama	1.57	4
39	Lake Rotorangi	7.59	1
40	Te Whaiau Reservoir	1.57	4
41	Turtle Lake	2.20	9
42	Weavers Lake	0.09	8
43	Wellington Botanical Gardens Pond	21.03	0
44	Lake Whakamaru	4.35	4
45	Whangamata Pond	19.40	1
46	Whau Reservoir	1.14	1

3.3 Zooplankton species richness

The ‘Chao2’ non-parametric estimator was used to extrapolate species richness for each water body from species numbers observed in experimental replicates. Water bodies were ordered from highest to lowest species richness (Table 11). The water bodies with the highest estimated species richness were natural, whilst those with the lowest were constructed (Table 11). The highest richness recorded in a natural water body (Lake Rerewhakaaitu) was 53.50, whilst the highest richness in a constructed water body (Turtle Lake) was 44.00. Average species richness was slightly higher in natural water bodies (18.47) than in constructed water bodies (15.05). Although, overall there was a lot of variation in species richness for both natural and constructed water bodies.

Table 11: Water body species richness, estimated from species hatched from sediment cores. Data is ordered from highest to lowest species richness. 'N' denotes natural water bodies, and 'C' denotes constructed water bodies.

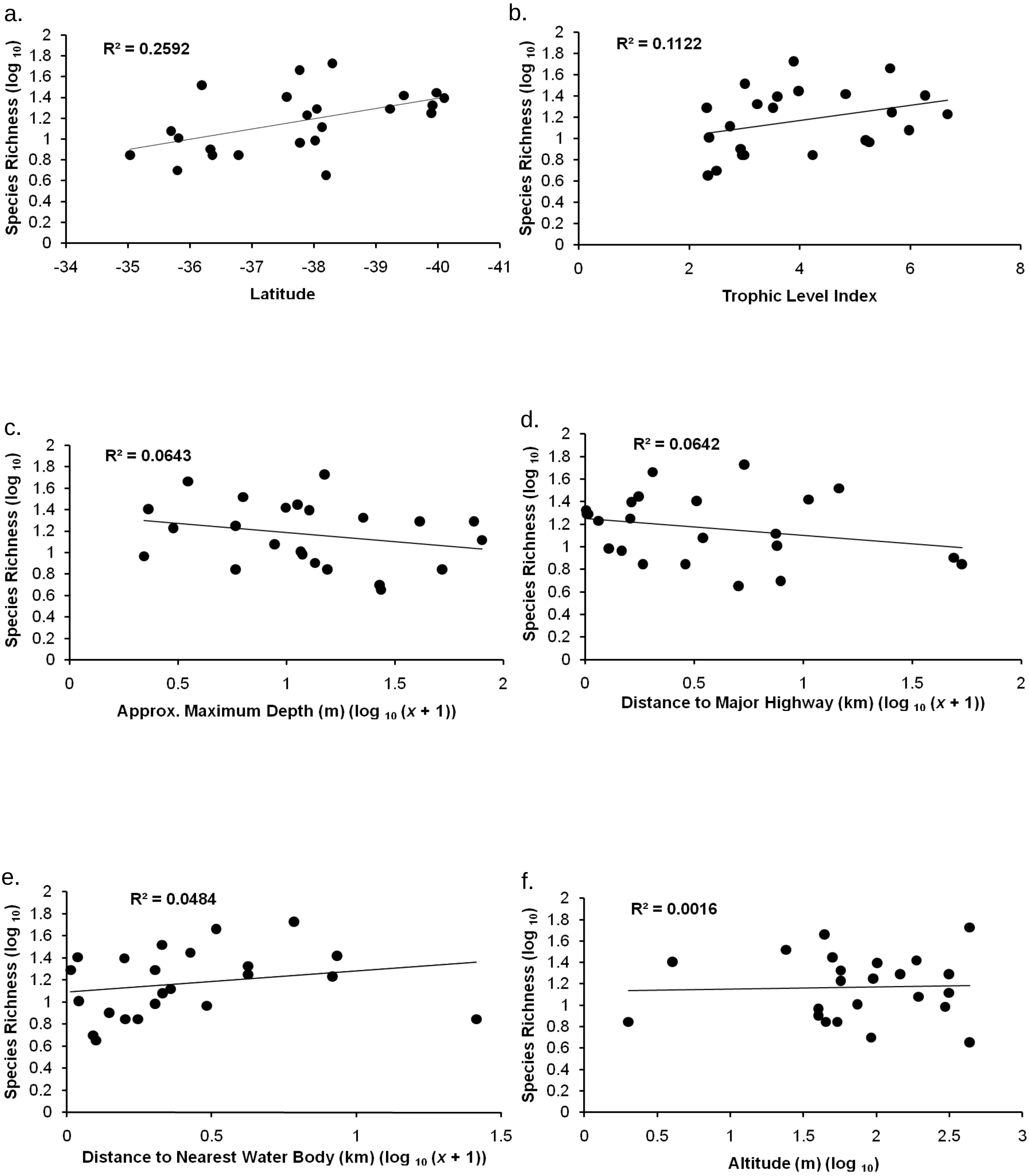
Origin	Water Body	Species Richness
N	Lake Rerewhakaaitu	53.50
N	Lake Waiwhakareke	46.00
C	Turtle Lake	44.00
C	Anderson Park Pond	40.00
N	Lake Tomarata	33.00
N	Lake Wiritoa	28.00
C	Lake Huiputea	27.50
N	Lake Rotokare	26.25
C	Lake Panorama	26.00
N	Lake Waahi	25.50
N	Duddings Lake	24.90
N	Lake Virginia	21.17
C	Lake Moananui	20.00
N	Lake Rotoma	19.50
N	Lake Tutira	19.50
N	Lake Westmere	17.79
C	Lake Rotorangi	17.17
N	Lake Te Ko Utu	17.00
C	Lake Henley	17.00
C	Weavers Lake	16.50
C	Lake Mangamahoe	14.50
C	Massey Palmerston North Pond	14.00
C	Lower Whitby Lake	13.33
N	Lake Okataina	13.10
C	Cornwall Park Pond	12.67
C	Lake Matahina	12.25
N	Lake Ora	12.00
C	Ohaupo Rd Pond	10.50
C	Lake Whakamaru	10.50
N	Lake Kai-Iwi	10.25
C	Cooks Beach Pond	10.25
N	Lake Rotoehu	9.67
N	Lake Rotokaeo	9.25
C	Whau Reservoir	9.00
C	Lake Gilmour	8.50
N	Lake Humuhumu	8.00
N	Lake Kanono	7.00
N	Lake Ngatu	7.00
N	Lake Pupuke	7.00
C	Whangamata Pond	7.00
N	Lake Waikere	5.00
C	Lake McLaren	5.00
N	Lake Tikitapu	4.50
C	Te Whaiau Reservoir	4.00
C	Lake Karapiro	3.50
C	Wellington Botanical Gardens Pond	3.00

3.3.1 Variation in zooplankton species richness

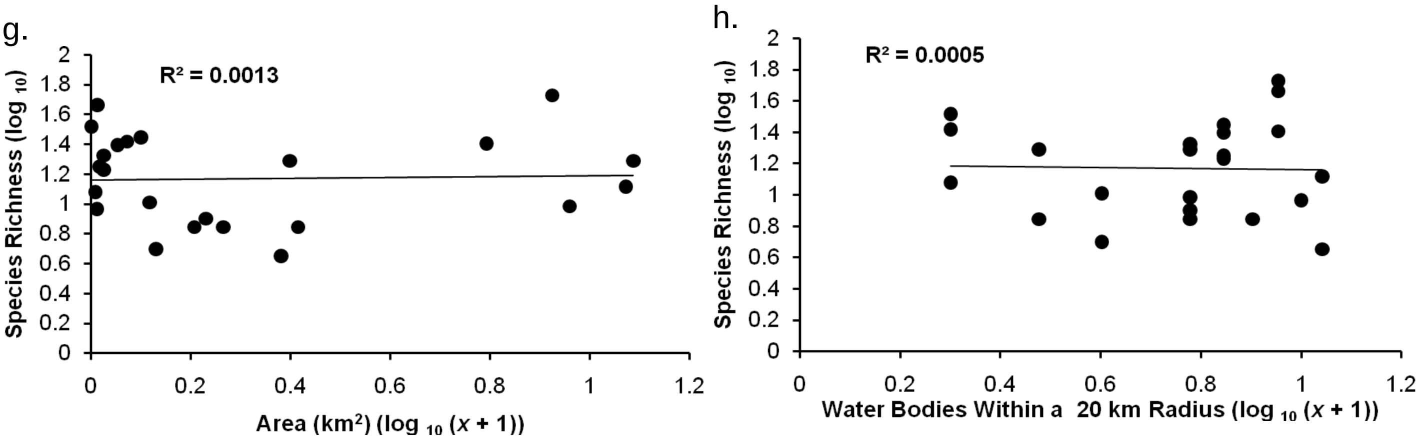
3.3.1.1 Natural water bodies

The initial step in trying to determine a relationship between species richness and the environmental variables was to create scatter plots and obtain the related correlation coefficients (R^2) (Figures 6 a to h). An R^2 value of close to or equal to 1 indicates that the variables being compared are related to each other in some way. The plots show that none of the variables share strong relationships with species richness. The highest R^2 value obtained was for latitude (0.2592) (Figure 6 a), followed by Trophic Level Index (0.1122) (Figure 6 b). With respect to latitude, the water bodies with high species richness tended to be located in the central and southern regions of the North Island, New Zealand (latitude – 37^o to – 40^o). For TLI, water bodies with mid to high TLI values (4 to 7) appeared to have higher species richness than ones with a low TLI value (1 to 3).

For a variables, such as the number of lakes within a 20 km radius, where $R^2 = 0.0005$ (Figure 6 h), the relationship was practically non-existent.



Figures 6 (a) to (f): Relationships between zooplankton species richness and environmental variables in natural water bodies. Plots are ordered based on decreasing correlation coefficients (R^2).



Figures 6 (g) to (h): Relationships between zooplankton species richness and environmental variables in natural water bodies. Plots are ordered based on decreasing correlation coefficients (R^2).

A stepwise linear regression model inferred latitude to be a highly significant predictor of species richness ($p = 0.0021$), whilst approximate maximum depth also added further significant information ($p = 0.016$) (Table 13). The summary statistics (Table 12) indicate the model accounted for 37% of the variance in species richness (Adjusted R^2 = 0.371). A p – value of 0.013 indicates the significance of the model ($p < 0.05$).

Table 12: Summary statistics for stepwise linear regression model to test the significance of environmental variables on species richness of natural water bodies.

Statistic	Value
Multiple R	0.697
Multiple R^2	0.486
Adjusted R^2	0.372
F (8 , 14)	4.256
p	0.013
Standard Error of Estimate	0.237

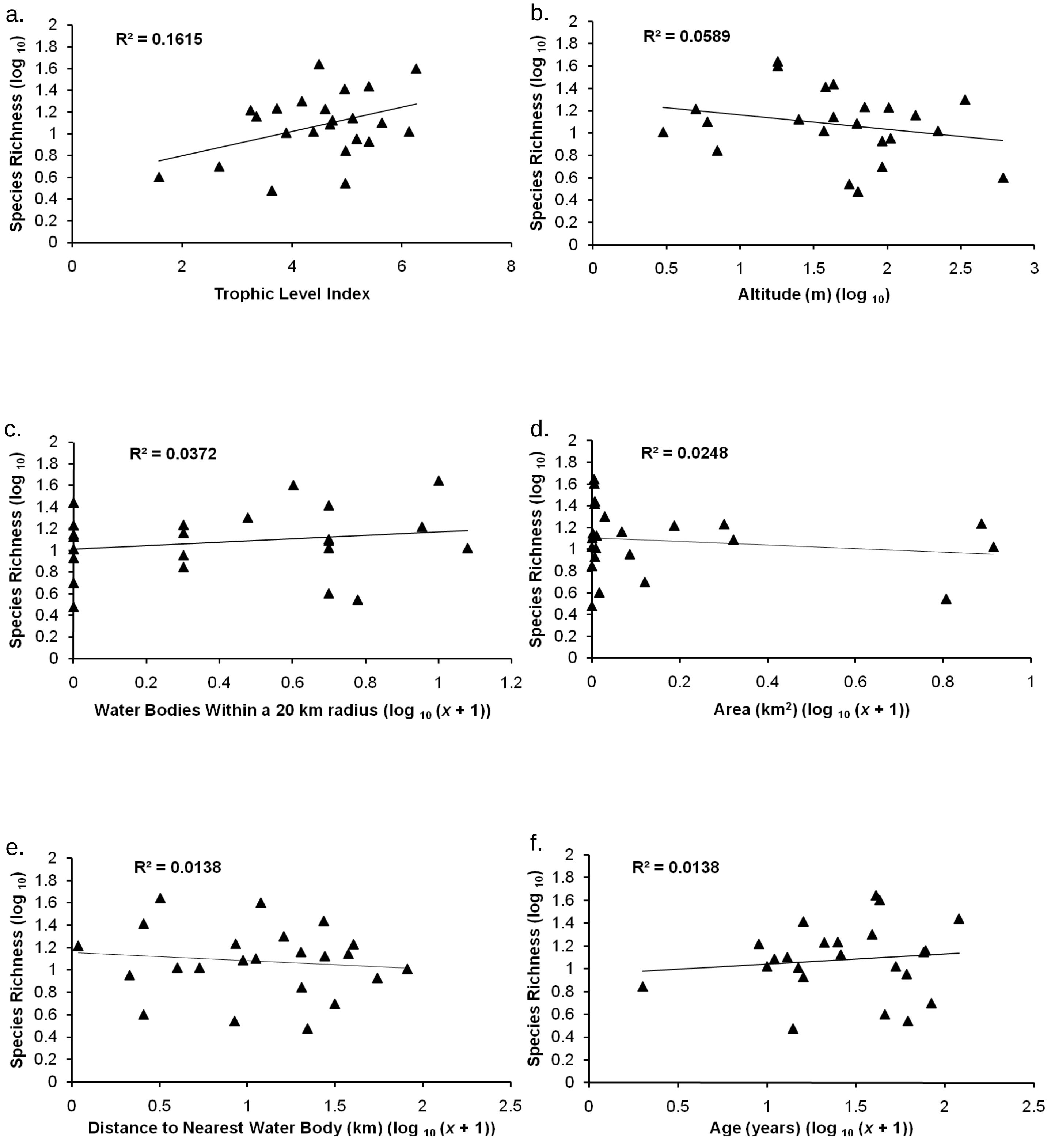
*Table 13: Stepwise linear regression summary for natural water bodies for the dependent variable: species richness. Variables listed are those included in the model. Significant variables and p – values ($p < 0.05$) are highlighted in **bold**.*

	b*	Std. error of b*	b	Std. error of b	p - value
Intercept			**2.81107**	**1.250258**	**0.037316**
Latitude	**0.632903**	**0.176880**	**0.12314**	**0.034414**	**0.002149**
Approximate maximum depth ($\log_{10}(x + 1)$)	**0.556573**	**0.209489**	**0.37556**	**0.141359**	**0.016056**
Number of water bodies within a 20 km radius ($\log_{10}(x + 1)$)	0.377132	0.199171	0.48007	0.253536	0.074479
Water body area ($\log_{10}(x + 1)$)	0.398749	0.217432	0.31800	0.173403	0.083257

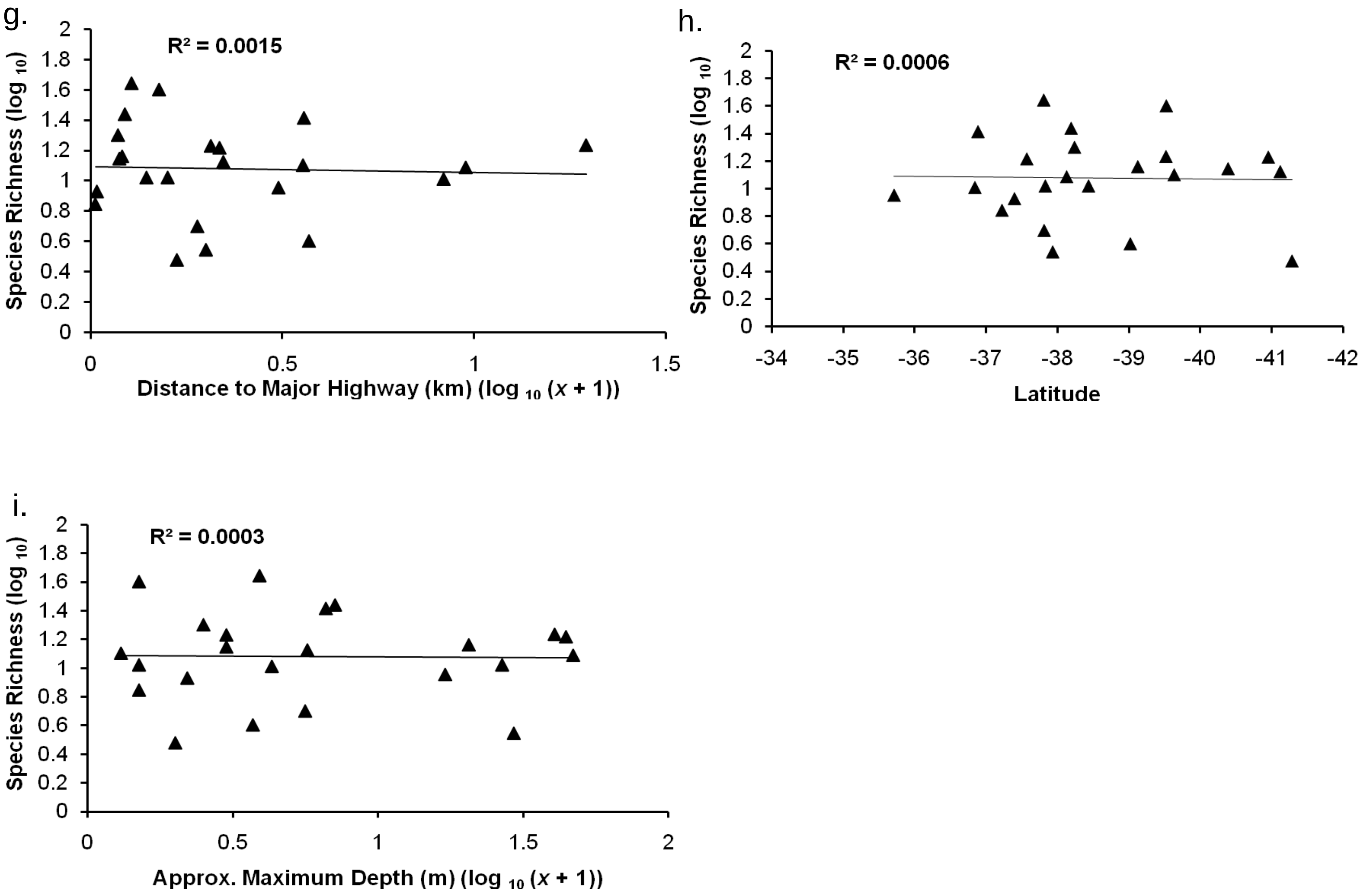
Trophic Level Index, distance to nearest major highway, altitude and distance to nearest water body were not significant predictors in this model.

3.3.1.2 Constructed water bodies

The scatter plots and associated correlation coefficients (R^2) (Figures 7 a to i) indicated that none of the environmental variables shared a strong relationship with species richness. The highest R^2 value obtained was for Trophic Level Index (0.1615) (Figure 7 a), followed by altitude (0.0589) (Figure 7 b). The strength of these relationships is noticeably lower than the relationships were for latitude and TLI for natural water bodies (0.2592 and 0.1122 respectively). This suggests that species richness is more strongly related to environmental variables in natural water bodies than it is in constructed water bodies, and that richness in constructed waters is therefore relatively unstructured.



Figures 7 (a) to (f): Relationships between zooplankton species richness and environmental variables in constructed water bodies. Plots are ordered based on decreasing correlation coefficients (R^2).



Figures 7 (g) to (i): Relationships between zooplankton species richness and environmental variables in constructed water bodies. Plots are ordered based on decreasing correlation coefficients (R^2).

A stepwise linear regression model inferred that none of the variables were significant predictors of species richness (i.e. they all had p – values > 0.05) (Table 15). The variable closest to being statistically significant was TLI (p = 0.057) (Table 15). The stepwise linear regression model for natural water bodies highlighted two significant independent environmental variables, whilst the model for constructed water bodies was not statistically significant (p > 0.05). This suggests that species richness was more strongly related to environmental variables in natural water bodies than in constructed water bodies. The summary statistics (Table 14) indicate the model for constructed waters only accounted for 12% of the variance in species richness (Adjusted R^2 = 0.121). This is much lower than the value of the adjusted R^2 for the natural water bodies (0.371).

Table 14: Summary statistics for stepwise linear regression model to test the significance of environmental variables on species richness for constructed water bodies.

Statistic	Value
Multiple R	0.402
Multiple R^2	0.162
Adjusted R^2	0.122
F (8 , 14)	4.045
p	0.057
Standard Error of Estimate	0.289

*Table 15: Stepwise linear regression summary for constructed water bodies for the dependent variable: species richness. Variables listed are those included in the model. Significant variables and p – values ($p < 0.05$) are highlighted in **bold**.*

	b*	Std. error of b*	b	Std. error of b	p - value
Intercept			**0.575568**	**0.257311**	**0.036272**
TLI	0.401899	0.199819	0.112013	0.055691	0.057302

Altitude, the number of water bodies within a 20 km radius, area, distance to nearest water body, age, distance to nearest major highway, latitude and approximate maximum depth were not significant predictors in this model.

3.4 Non-indigenous zooplankton distribution

One of the hypotheses stated in Chapter One was that non-indigenous zooplankton would occur at a higher frequency in constructed water bodies than natural water bodies. Four species of non-indigenous zooplankton were recorded during this study. The first of these was the non-indigenous cladoceran *Daphnia galeata* (Duggan *pers. comm.,* 2010), which was hatched from diapausing eggs found in the sediment of 18 water bodies. The two calanoid copepods, *Boeckella minuta* and *Sinodiaptomus valkanovi*, were identified from adult copepods collected using a 40 µm mesh net. Finally, the rotifer *Conochilus exiguus* was recorded in a single natural water body (Table 3). The distributions of these species are presented below.

3.4.1 Non-indigenous cladoceran

The non-indigenous cladoceran *Daphnia galeata* was recorded in 11 natural water bodies and 7 constructed water bodies sampled in the North Island, New Zealand during this study (Table 3). A two-tailed Pearson chi-squared test of independence inferred that *D. galeata* was not significantly more likely to be found in natural or constructed water bodies (Table 4).

However, whilst its latitudinal distribution spanned most of the length of the North Island, from Lake Pupuke on the North Shore, Auckland down to Lower Whitby, Wellington, its longitudinal distribution was found to be much more restricted (Figure 8). *Daphnia galeata* was only recorded from water bodies found on either the west coast or central North Island, New Zealand. It was not recorded from any of the water bodies sampled along the east coast.

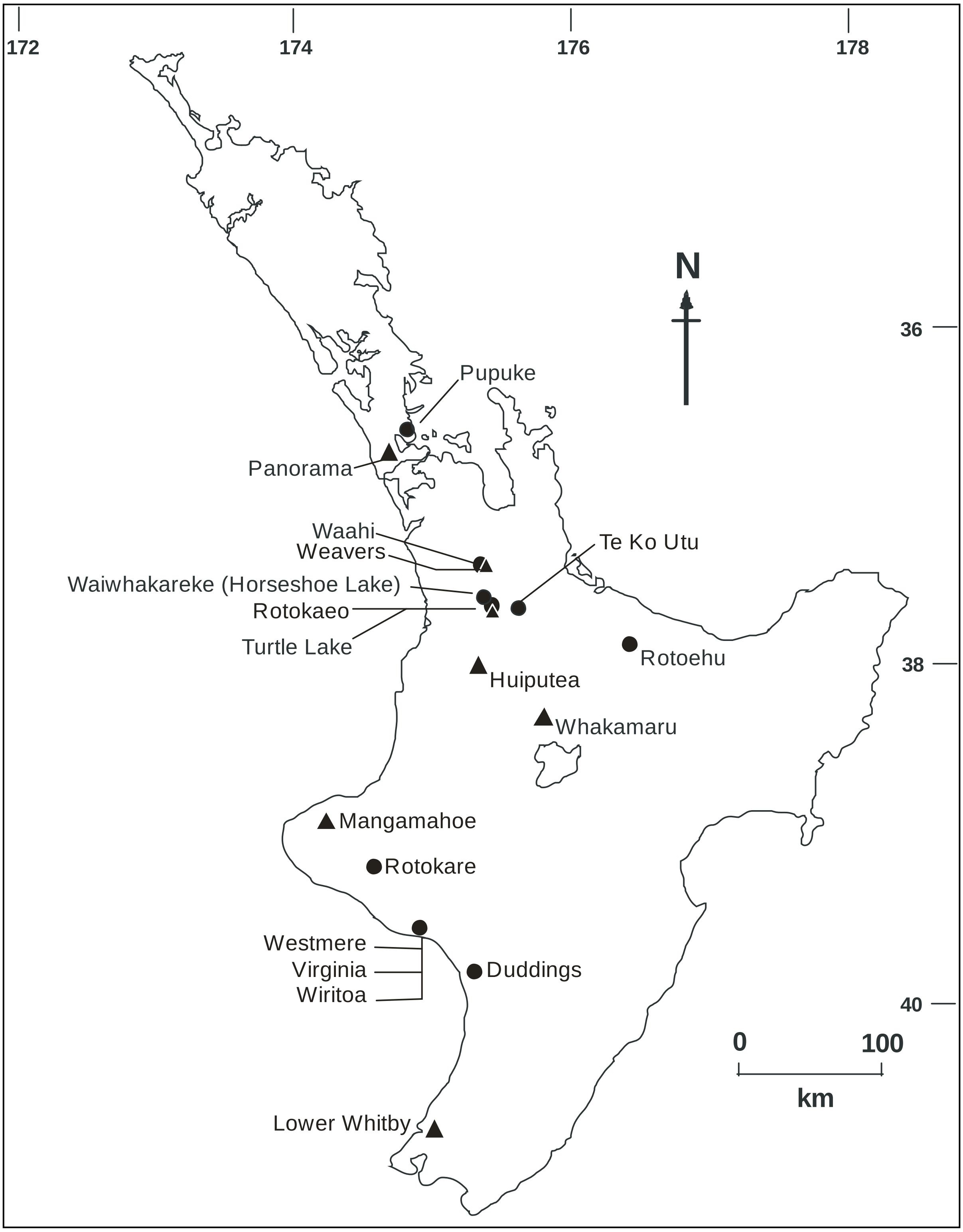


Figure 8: Distribution of the non-indigenous cladoceran Daphnia galeata from water bodies sampled in the North Island, New Zealand.

▲ *= Constructed water bodies* ● *= Natural water bodies*

3.4.2 Non-indigenous calanoid copepods

There were two non-indigenous calanoid copepods recorded from the water bodies sampled during this study. The first is the Australian species, *Boeckella minuta*, and the second is the Japanese species, *Sinodiaptomus valkanovi* (Banks & Duggan, 2009). These species were only found in constructed water bodies. *Boeckella minuta* was identified from the adult copepods collected from Turtle Lake in the Hamilton Gardens, whilst *Sinodiaptomus valkanovi* was recorded from Lake Gilmour in Waihi (Figure 9).

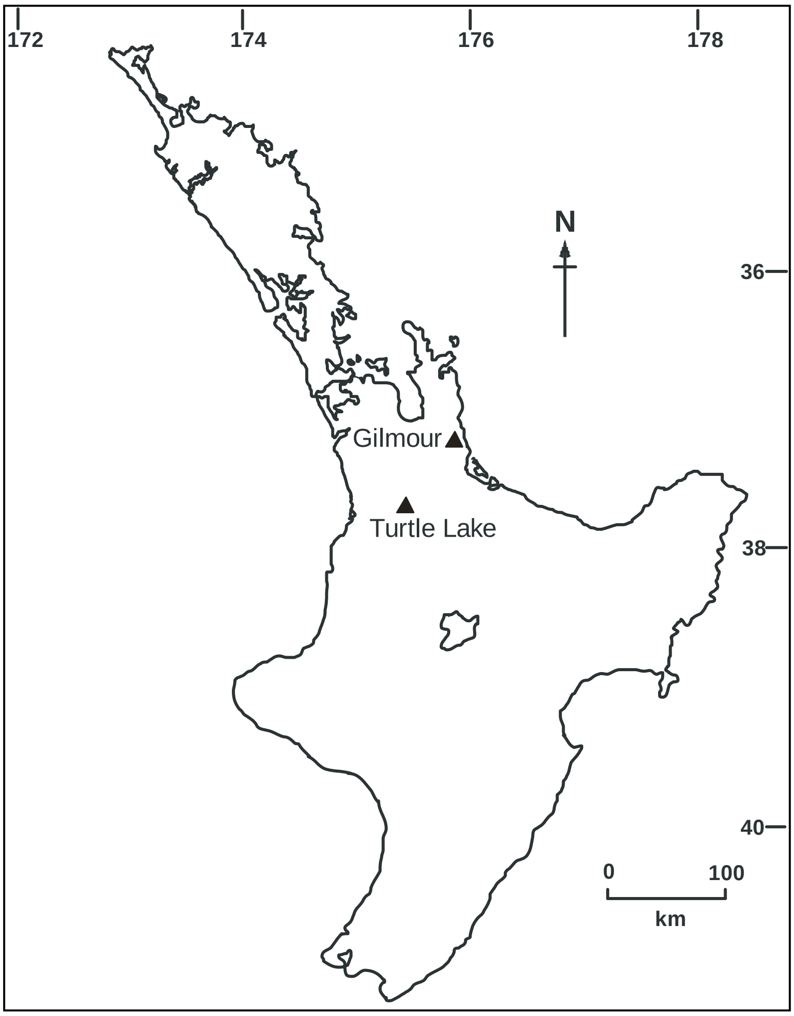


Figure 9: Distribution of the non-indigenous calanoid copepods Boeckella minuta and Sinodiaptomus valkanovi from water bodies sampled in the North Island, New Zealand.

▲ *= Constructed water bodies*

3.4.3 Non-indigenous rotifer

The rotifer *Conochilus exiguus* was only recorded in Lake Waiwhakareke (Horseshoe Lake), Hamilton (Figure 10), during my study.

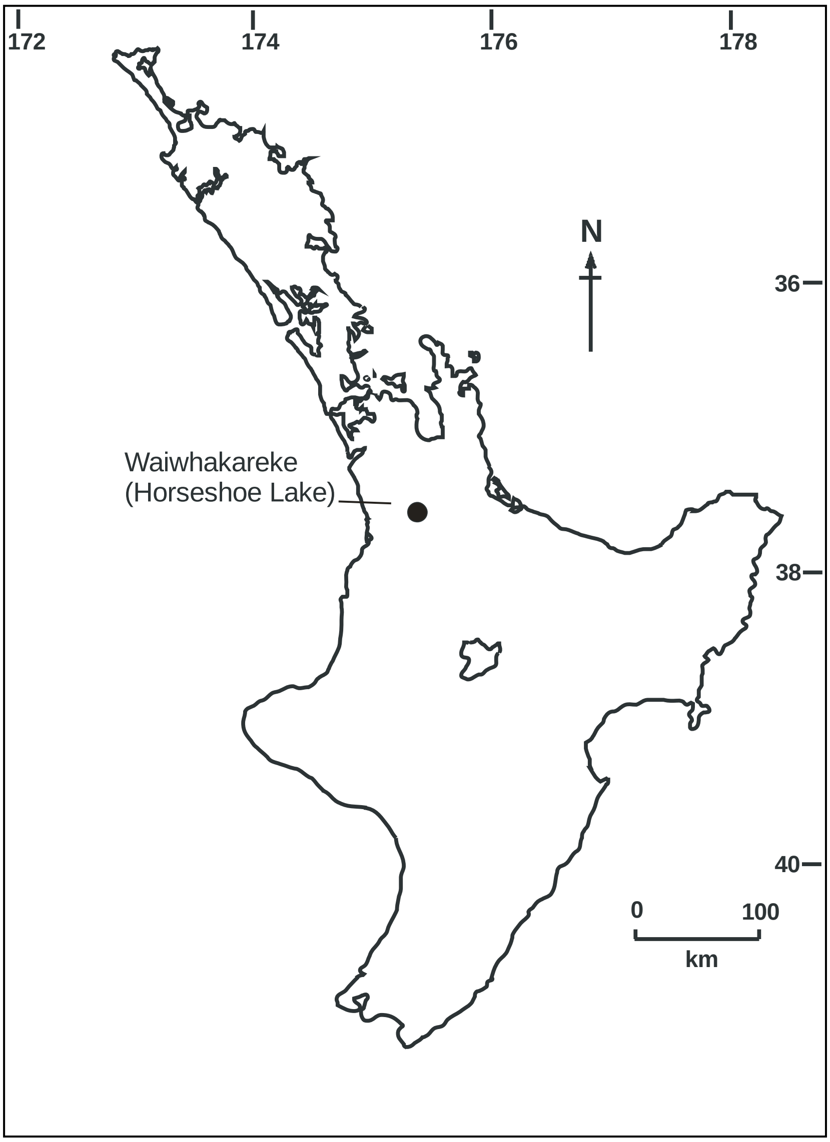


Figure 10: Distribution of the non-indigenous rotifer Conochilus exiguus from water bodies sampled in the North Island, New Zealand.

● = *Natural water bodies*

Chapter Four: Discussion

4.1 Zooplankton species composition

4.1.1 Zooplankton assemblages and community maturity

Natural and constructed water bodies had a similar number of species per water body (10.4 and 9.3 respectively). However, the 23 constructed water bodies had a greater total number of species than the 23 natural water bodies (60 and 54 respectively), and a much larger number of singularly occurring species (31 and 18 respectively). Based on these results I suggest that the community composition of natural water bodies has developed to a point where they have accumulated a core group of mainly planktonic species (e.g. *Ceriodaphnia dubia, Calamoecia lucasi, Hexarthra mira* and *Filinia longiseta;* Pennak, 1966; Chapman & Lewis, 1976; Duggan, 2001a), which are well adapted to the pelagic conditions. On the other hand, the assemblages in constructed water bodies appeared to be much more varied, consisting of a number of species commonly associated with benthic and littoral habitats (e.g. ostracods, *Acanthocyclops robustus, Diacyclops bicuspidatus, Brachionus calyciflorus,* and *Testudinella patina;* Pennak, 1966; Chapman & Lewis, 1976; Duggan, 2001a). Shea & Chesson (2002) suggest that more mature systems (i.e. those that have had a long time to accumulate species) are likely to have species that are well adapted to the local conditions. In contrast, species found in less mature systems may occupy much broader niches and / or be less suited to the environmental conditions, thus lowering their competitive ability (Shea & Chesson, 2002). For example, in their study of relatively 'young' (i.e. ~ 30 years old) mining lakes in the Siessian Upland, Poland, Bielanska-Grajner & Gladysz (2010) found that many of the rotifer species were eurytopic (i.e. able to survive under a wide range of conditions in a variety of habitats; Eversham *et al.,* 1996). Eurytopic rotifer species include *Brachionus angularis, B. calyciflorus, Keratella cochlearis* and *Polyarthra* sp. (Radwan *et al.*, 1991; Bielanska-Grajner & Gladysz, 2010). The maturity theory put forward by Shea & Chesson (2002) can be related back to the current study as most of the natural water bodies sampled were thousands of years old (e.g. Lake Te Ko Utu is ~ 18,000 years old, and Lake Okataina is ~ 7,000; Lowe & Green, 1987), whereas the average age of the constructed water bodies was only 37 years at the time of sampling. The oldest constructed water body sampled was approximately 119 years old (Lake Huiputea), whilst the youngest had only been constructed approximately 1 year prior to being sampled (Whangamata Pond). Therefore, the constructed water bodies have had considerably less time to accumulate species than the natural water bodies.

Communities may vary greatly during the initial stages of community assembly owing to the stochastic nature of dispersal and colonisation processes (Louette *et al.*, 2008). Over time communities may converge, thus resulting in a decrease in differences of community composition (Louette *et al.*, 2008). It is therefore possible that, given enough time, zooplankton assemblages in constructed water bodies may develop to match those of natural water bodies. This alteration in community composition can be related back to the general theory of ecological succession. Primary succession occurs when the original ecosystem is virtually lifeless, such as the area left behind by a retreating glacier (Laliberte & Payette, 2008). In terrestrial ecosystems, this process starts with the formation of soil, then over time the vegetation changes from mosses to grasses and shrubs, and eventually trees. This process may take hundreds to thousands of years (Laliberte & Payette, 2008). Early colonisers in terrestrial ecosystems undergoing primary succession are usually plants like mosses and ferns because they have very miniscule, buoyant spores that are effectively dispersed by the wind over long distances (Walker & Del Moral, 2003a). The process of primary succession in newly created water bodies is similar to that of terrestrial ecosystems. The arrival of zooplankton is likely facilitated by the initial presence of algae and bacteria (i.e. their food sources). Following this, early colonisers, such as benthic species which are more likely to be transported on the feet of water fowl or in streams than planktonic species, are likely to establish until such time as they are outcompeted by better adapted, slower moving planktonic species.

4.1.2 Dominant species groups and variation in species composition

Another striking difference in the community composition of natural and constructed water bodies are the dominant groups of species. Crustacea (i.e. cladocerans and copepods) tended to have a higher frequency of occurrence in natural waters than constructed waters. On the other hand, rotifers generally had a higher frequency of occurrence in constructed water bodies (Table 3; Figure 3). This is further supported by the results of the two-tailed Pearson chi-squared tests of independence which inferred that native calanoid copepods (e.g. *Boeckella hamata, B. delicata* and *Calamoecia lucasi*) were significantly more likely to be found in natural water bodies, whilst the rotifers *Brachionus angularis* and *B. calyciflorus*) were significantly more likely to be found in constructed water bodies (Table 4).

One of the main factors likely responsible for this variation in distribution was the difference in dispersal abilities of rotifers and crustaceans (i.e. cladocerans and copepods). This difference in dispersal abilities is highlighted by the results of the CCA for constructed water bodies. Distance to nearest water body and the number of water bodies within a 20 km radius were identified as the environmental variables explaining significant ($p < 0.05$) amounts of variation in species composition of constructed water bodies (Table 9). These variables were not significant

($p > 0.05$) for natural water bodies. The ordination diagram for constructed water bodies suggests that, in general, rotifers (e.g. *Keratella tropica, Trichocerca pusilla* and *Brachionus calyciflorus*) were capable of dispersing over relatively large distances as they were recorded at a higher frequency in more isolated water bodies. On the other hand, cladocerans and copepods (e.g. *Ceriodaphnia dubia, Daphnia galeata, Calamoecia lucasi* and *Mesocyclops leuckarti*) were typically found in water bodies located near to other water bodies, thereby implying that they are perhaps good at dispersing over shorter distances but not as effective at long-range dispersal. Ruttner-Kolisko (1974) suggested that most rotifers potentially have cosmopolitan distributions as nearly all species can be spread as tiny resting eggs by the wind, grazing animals or birds. However, it is increasingly becoming accepted that not all rotifer species have unlimited dispersal abilities, with some species (e.g. some *Brachionus* and *Keratella* species) apparently confined to distinct geographical regions (Segers & De Smet, 2008). Despite this, rotifers are still considered to be much better at dispersing over long distances than crustaceans. In a study of the dispersal mechanisms of freshwater zooplankton, Cohen & Shurin (2003) found that rotifers, cladocerans and copepods were all good dispersers over short distances (e.g. < 1 km). However, rotifers were the group identified as the most capable of effectively dispersing over larger distances (e.g. > 1 km). In a study of processes regulating zooplankton assemblages in newly constructed water bodies, Holland & Jenkins (1998) also found that rotifers dominated the species colonising the new pools.

In addition to having high dispersal abilities (e.g. Pennak, 1978), the high reproductive rates of rotifers (e.g. Shiel, 1995) could also contribute to their frequent occurrence in constructed waters. Rotifers are able to produce large numbers of diapausing eggs in comparison to cladocerans and copepods. For example, Gray *et al.* (2005) found diapausing rotifer egg densities in excess of 200 eggs per 40 g of sediment collected from natural lakes and ponds. Egg densities for cladocerans and copepods, on the other hand, generally ranged from 1 to 15 eggs per 40 g of sediment (with a one-off maximum of 66 copepod eggs in one sample; Gray *et al.,* 2005). This high reproductive rate could allow rotifers to rapidly establish populations in new habitats, such as those created by the construction of new water bodies, owing to the large supply of potential propagules. For example, eutrophic waters typically have higher diapausing egg densities than oligotrophic waters (Duggan *et al.*, 2002), and Brachionids, one of the most common rotifer species recorded during my study, are generally associated with eutrophic water bodies (e.g. Duggan *et al.*, 2001). The variety of rotifer species in constructed water bodies was also seemingly boosted by the prevalence of benthic or littoral species (e.g. bdelloids, *Cephalodella stenroosi* and *Proales* sp.; Nogrady *et al.*, 1995; Shiel, 1995), which may have already been present in streams or wetlands at or close to the site of the water body construction.

Another possible reason for rotifers exhibiting a higher frequency of occurrence in constructed water bodies could be related to the lower frequency of occurrence of crustaceans in constructed water bodies. In general, larger zooplankton are more efficient feeders than smaller ones (Hall *et al.*, 1976; Mourelatos & Lacroix, 1990). Therefore, rotifers could be outcompeted by the larger crustaceans. For example, in their study of the zooplankton assemblage of Lake Puketirini (Weavers Lake), New Zealand, Balvert *et al.* (2009) found that with the arrival of the non-indigenous *Daphnia dentifera* there was a dramatic change from rotifer dominance in the community to *Daphnia* dominance. In addition to this there was also a decrease in species richness, with rotifer species such as *Polyarthra dolichoptera, Filinia longiseta* and *Ascomorpha ovalis* being present at the beginning of the study (*Daphnia* absent) and absent at the end of the study (*Daphnia* present; Balvert *et al.*, 2009). As well as outcompeting rotifers for food, some crustaceans (e.g. cyclopoid copepods; Brandl, 2005) also prey upon them, which could limit their numbers in crustacean - dominated natural water bodies (Couch *et al.*, 1999).

Calanoid copepods (e.g. *Calamoecia lucasi*) are thought to have low powers of natural dispersal, which allows them to spread to neighbouring water bodies within a defined geographical area, but they very rarely spread over large distances (Maly & Bayly, 1991; Jamieson, 1998; Banks & Duggan, 2009). The CCA ordination for constructed water bodies identified *Calamoecia lucasi* as being more likely to be found in water bodies that are close to other water bodies. Also, *C. lucasi* was recorded from 83% of the natural water bodies sampled, but only 17% of the constructed water bodies. Both of these results indicate that *C. lucasi* is far more likely to be found in natural water bodies, although it appears to be slowly spreading to nearby constructed water bodies. The poor dispersal ability of calanoid copepods is thought to be linked to obligatory sexual reproduction and a low rate of survivorship to adulthood (Maly, 1984). Cladocerans are also thought to be slow dispersers over large distances. However, because they are able to produce unfertilised, parthenogenetic eggs, like rotifers, cladocerans may be able to disperse faster than copepods, which are obligatorily sexual (Chapman & Lewis, 1976). Louette *et al.* (2008) noted that cladocerans were very quick to colonise newly constructed pools, but the pools used in their study were located within 100 m of each other.

The suggestion that distance to nearest water body is a significant predictor of species composition in constructed water bodies can be related back to the theory of island biogeography. This theory states that the immigration rate to an island declines as the isolation of the island increases (i.e. an island close to the mainland or other islands will be colonised by a large number of naturally dispersing species, whilst more isolated islands will receive far fewer species; MacArthur & Wilson, 1967; Whittaker *et al.*, 2008). For example, in their study of non-indigenous and native plant species on 25 islands within the Boston Harbor, Long *et al.* (2009) found that species richness of both groups of plants was negatively related to isolation. Stracey & Pimm (2009) conducted a study on the visitation rates of migratory birds to a number of British islands. They concluded that islands far away from the mainland received far fewer visits from migratory bird species than islands close to the mainland (Stracey & Pimm, 2009). My study found that constructed water bodies that were close to other water bodies generally had higher numbers of crustaceans, which are slow natural dispersers (Maly, 1984), than those water bodies that were more isolated (Table 3; Figure 5). Therefore, this trend is most likely driven by natural dispersal methods rather than human vectors as slowly dispersing crustaceans would be able to reach nearby water bodies, but would take a long time to reach more isolated water bodies.

The CCA for natural water bodies highlighted trophic state as the only environmental variable that explained any significant amount of variation ($p < 0.05$) in species composition (Table 6). Species such as *Brachionus calyciflorus, B. quadridentatus, Pompholyx* sp. and *Keratella tropica* were found in water bodies with a higher trophic state, whilst species such as *Conochilus dossuarius, Boeckella tanea, Calamoecia lucasi* and *Gastropus hyptopus* were found in more oligotrophic water bodies.

Rotifers have been found to be good indicators of water body trophic state in both New Zealand (Duggan *et al.*, 2000; Duggan *et al.*, 2001, 2002a) and elsewhere (e.g. Gannon & Stemberger, 1978). Many of the *Brachionus, Pompholyx* and *Keratella* species are typically found in more eutrophic water bodies, whilst *Conochilus* and *Gastropus* species are generally indicative of water bodies with a lower trophic state (e.g. Gannon & Stemberger, 1978; Duggan *et al.*, 2001). In addition to this, the ordination diagram based on CCA of natural water body zooplankton species with respect to environmental variables (Figure 4) inferred that calanoid copepods were more likely to be found in water bodies with a low TLI value. Gannon & Stemberger (1978) found that calanoid copepods were good indicators of oligotrophic lakes, whilst studies of New Zealand calanoid copepods have identified them as one of the most abundant microcrustacea in water bodies with low trophic states (e.g. Chapman & Green, 1987).

It is important to note that trophic state is the primary determinant of species composition in natural water bodies, which have had a long colonisation period. However, community composition of constructed water bodies, which have had a much shorter colonisation period, was related more to connectivity and opportunity. This supports the suggestion that communities of natural water bodies are comprised of a core group of species that are well adapted to the environmental conditions. Constructed water bodies, on the other hand, have more varied assemblages, consisting of opportunistic species that have arrived in a new habitat and been able to establish in the absence of better adapted competitors.

4.2 Zooplankton species richness

4.2.1 Variation in species richness

The environmental variable highlighted as the most significant ($p < 0.05$) predictor of species richness in natural water bodies was latitude (Table 13). Natural water body species richness appeared to increase with increasing latitude (i.e. towards the southern end of the North Island). Latitudinal variation in zooplankton richness has been documented elsewhere. For example, in their study of rotifers in the Arctic, Chengalath & Koste (1989) found an increase in species richness as they travelled south from Bathurst Island (a central arctic island) towards the North American mainland. In a similar study, assessing zooplankton species richness and community stability of 35 lakes in North America and one in Europe, Shurin *et al.* (2007) found that high latitude lakes generally had lower species richness than lower latitude lakes. The results of Chengalath & Koste (1989) and Shurin *et al.* (2007) are in accordance with the 'latitudinal diversity gradient' theory, which states that species richness is generally higher in the tropics (low latitudes) than in more temperate regions (higher latitudes) (Hillebrand, 2004). There have been a number of explanations, both biological and non-biological, suggested for this diversity gradient (Hillebrand, 2004). These include: gradients in decreasing area and water supply (Currie, 1991; Allen *et al.*, 2002), differences in the intensity and specificity of biological interactions (e.g. predation and competition) between species and a decrease in habitat heterogeneity towards the poles (Pianka, 1966). In addition to these suggestions, 'mid-domain models' have been used to predict a peak in diversity in the middle of a domain (e.g. the equatorial region of Earth) with hard boundaries (e.g. the poles) (Colwell *et al.*, 2004; Hillebrand, 2004). Although the results of my study do not conform to the latitudinal diversity gradient theory (i.e. richness increased with latitude, rather than decreased), the 'mid-domain model' could explain why species richness was highest at the southern end of the North Island, as this is close to the middle of New Zealand. Another possible reason for the apparent increase in species richness with latitude is that zooplankton in the water bodies of the northern region of the North Island may produce fewer diapausing eggs as a result of the warmer water temperatures. To date, this theory does not appear to have been tested.

The approximate maximum depth of the water body was the only other variable that explained a significant ($p < 0.05$) amount of variation in species richness of natural water bodies after the addition of latitude to the stepwise linear regression model. In general shallower water bodies had a higher species richness than deeper ones (Figure 6 c). In a study of rotifer density and species distribution in lakes adjacent to the Yangtze River, China, Wang *et al.* (2010) found that high rotifer species richness was associated with lower lake depth. Shallow water bodies may support higher species richness because their littoral habitat provides a diverse range of ecological niches for species to occupy (Bielanska-Grajner & Gladysz, 2010). On the other hand, the pelagic habitat of deeper water bodies is much more homogenous, potentially leading to lower species richness (Tavernini *et al.*, 2009).

Whilst there were strong relationships present between environmental variables and species richness for natural lakes, a stepwise linear regression run on the data for constructed water bodies showed none of the environmental variables were significant predictors of species richness in constructed water bodies (Table 15). This suggests that species richness is more strongly related to environmental variables in natural water bodies than it is in constructed water bodies, and that richness in constructed waters is therefore relatively unstructured. A very similar pattern was observed when comparisons were made between environmental variables and the species compositions of natural and constructed water bodies (discussed above). Together, these findings provide some very compelling evidence to suggest that the community assemblages of natural water bodies have been shaped by their surrounding environments, whilst the assemblages in constructed water bodies are a much more random assortment of opportunistic species taking advantage of newly created habitats.

4.3 Species composition vs. Species richness: Who is the key player in invasion resistance?

Shea & Chesson (2002) put forward the theory that more mature systems are likely to contain species that are better adapted to local conditions, and are therefore more effective at resisting invasions than species from less mature systems. My study strongly relates to this theory. Natural water bodies had much more structured communities, as shown by the strong relationships between species composition and richness with environmental variables. On the other hand, species composition and richness in constructed water bodies only had very weak relationships with environmental variables. Constructed water body communities included a lot of opportunistic species that were only able to establish due to the absence of a better adapted competitor. In addition to this Law & Morton (1996) and Shea & Chesson (2002) suggested that certain species assemblages could be better at resisting invasions than other assemblages of similar richness. My study supports this theory as there was only a slight difference in average species richness between natural and constructed water bodies (18.47 and 15.05 respectively), with a wide variability in both (i.e. there were a number of natural and constructed water bodies assessed to have low species richness). However, natural water bodies had well structured communities consisting of a core group of species, whilst constructed water body communities consisted of a much more varied assemblage of species. Thus, my results suggest that better adapted communities, rather than species richness, is responsible for natural water bodies being more resistant to invasions than constructed water bodies.

It is also likely that constructed water bodies are more easily invaded than natural water bodies due to the absence of key species that are able to withstand invaders. For example, deRivera *et al.* (2005) demonstrated how the native North American blue crab, *Callinectes sapidus,* appeared able to limit the abundance and distribution of the non-indigenous European green crab, *Carcinus maenas*, in eastern North America. Robinson *et al.* (2005) found seeds of the Californian poppy (*Eschscholzia californica*) that were introduced to grassland plots established more successfully in plots of high species diversity then they did in low richness plots containing the species *Bromus diandrus*, which is a strong suppressor of poppies and other plants. Evidence of key species resisting invasions has also been recognised in the North Island, New Zealand, with regards to native and non-indigenous calanoid copepods. The two non-indigenous calanoid copepods recorded during this study were found only in constructed water bodies. This is potentially an important finding as, to date, the distributions of the four non-indigenous calanoid copepods in the North Island, New Zealand, appear to be confined to constructed water bodies (Banks & Duggan, 2009). The implications of these results are that native zooplankton communities, or key members of the zooplankton community, are very efficient at resisting invasions of non-indigenous calanoid copepods.

One underlying factor potentially related to this finding is that co-occurrence of calanoid copepods does not generally occur unless they are markedly different in size (Hutchinson, 1967; Chapman & Green, 1987). Some examples from North America include the co-occurrence of the calanoids *Hesperodiaptomus nevadensis* (3.5 mm) and *Leptodiaptomus sicilis* (1.1 to 1.5 mm) (Hutchinson, 1937), and *Hesperodiaptomus wardi* (1.24 to 1.6 mm) and *Hesperodiaptomus novemdecimus* (3.8 to 4.0 mm) (Wilson, 1953). It has been suggested that a difference in length of approximately 35% is enough to give almost non-overlapping food niches in calanoid copepods (Hutchinson, 1967). In New Zealand *Calamoecia lucasi* is able to co-occur with species of *Boeckella* (e.g. in my study *C. lucasi* and *B. tanea* were recorded from Lake Kai-Iwi, and *C. lucasi* and *B. hamata* were recorded from Lake Wiritoa), although co-occurrence is rare. This co-occurrence is thought to be possible as the *Boeckella* species are larger, and therefore probably feed on larger food particles, than *Calamoecia* (Chapman & Green, 1987). There are no known records of two *Boeckella* species co-occurring in New Zealand (Chapman & Green, 1987). In addition to this, I found the native calanoid *Calamoecia lucasi* was extremely common in natural water bodies (present in 83%), but very rare in constructed water bodies (present in only 17%). Native *Boeckella* species were also slightly more common in natural water bodies than constructed water bodies (22% and 13% respectively). The very high occurrence of *C. lucasi* in natural water bodies, coupled with the absence of records of two *Boeckella* species co-occurring, could explain why the two non-indigenous species of *Boeckella* in the North Island are seemingly restricted to constructed water bodies.

Duggan *et al.* (2006b) express the concern that the relatively low species diversity of New Zealand crustacean zooplankton communities relative to elsewhere (e.g. Chapman & Green, 1987) may put them at risk of being invaded more easily by a non-indigenous species. However, the results of this study, coupled with the findings of Banks & Duggan (2009), infer that calanoid copepods, at least, have to date been very successful at repelling non-indigenous calanoid copepods from natural water bodies.

The non-indigenous cladoceran *Daphnia galeata*, which is widely distributed throughout Europe and Asia (Benzie, 2005), was recorded from 48% of the natural water bodies sampled and 30% of the constructed water bodies. It is possible that this non-indigenous species was able to establish in natural as well as constructed water bodies due to the absence of an equal or superior competitor, rather than any differences in species composition or species richness. The native *Daphnia carinata* is a rare occupant of water bodies in the North Island, New Zealand (Chapman & Green, 1987). For example, my survey only recorded *D. carinata* from two water bodies, both of which were located on the east coast of the North Island; these were Lake Tutira (natural) and Anderson Park pond (constructed). *Daphnia galeata* was not recorded from any sites along the east coast, which suggests that *D. carinata* may be capable of outcompeting or repelling the invasion of *D. galeata*. Whilst the presence of *D. galeata* in New Zealand may be linked to the absence of a superior competitor, the case for the non-indigenous *Daphnia lumholtzi* in North America is slightly different. Work by Engel & Tollrian (2009) has shown that *Daphnia pulicaria,* which is the most widespread native *Daphnia* species in North America, occurring in lakes and ponds from Mexico to the Arctic, is a superior competitor to *D. lumholtzi*, but only in the absence of fish predators. The successful invasion of *D. lumholtzi* is not due to the absence of a superior competitor, but is instead linked to its very effective predator defence mechanisms. Another theory is that *D. lumholtzi* has been able to successfully establish in North America because its thermal tolerance is considerably higher than that of the native *Daphnia* species (Engel & Tollrian, 2009).

Havel *et al.* (2005) and Johnson *et al.* (2008) suggested that high connectivity, high disturbance, and unusual physical and chemical properties could make reservoirs easier to invade than natural water bodies. However, as identified by Banks & Duggan (2009), many of the constructed water bodies invaded by non-indigenous calanoid copepods in the North Island, New Zealand (e.g. ornamental ponds and old mine pits) have environments that are more similar to natural water bodies than reservoirs. Therefore, it is likely that some other factor, such as species composition or species richness, influences the ease with which non-indigenous species invade. The results of my study suggest that species richness *per se* may not be the determining factor behind whether constructed water bodies are more easily invaded than natural water bodies. There was a large degree of variation in species richness of natural and constructed water bodies, and no clear relationship (whether positive or negative) between species richness and invasion success. Instead, it seems that species composition plays a more important role. The core group of well adapted species found in natural water bodies appear to be more successful at repelling invaders than the more varied, and possibly less well adapted, species assemblages of constructed water bodies.

4.4 Potential confounding factors

4.4.1 Preliminary environmental variables

When compiling the preliminary list of water bodies careful attention was paid to ensure that the range of variables (i.e. surface area, trophic state and geographic range) covered was the same for natural and constructed water bodies, as failure to do so may produce invalid results. Although there were some slight differences in the ranges of environmental variables measured for natural and constructed water bodies these should not affect the results obtained during this study. Surface area was not highlighted as a significant variable in either the community composition or species richness analyses. Although TLI was a significant predictor of community composition in natural water bodies, and latitude was a significant predictor of species richness in natural water bodies, the ranges of these variables for natural and constructed water bodies were very similar so the results should not be affected.

4.4.2 Estimating zooplankton species richness and composition from diapausing eggs in water body sediments

Average species richness ranged from 15.05 in constructed water bodies to 18.47 in natural water bodies. Studies on rotifer richness in North Island water bodies (e.g. Duggan *et al.,* 2002a) have found an average richness of 21.1 species per lake. Crustacean richness, on the other hand, is typically much lower, consisting of one species of calanoid copepod (*Calamoecia lucasi* or a *Boeckella* species), one or two species of cyclopoid copepod (commonly *Mesocyclops leuckarti*), and one to three species of cladocerans (*Bosmina meridionalis* and *Ceriodaphnia dubia* being the most common) (Chapman & Green, 1987). The crustacean composition and richness sampled during my study was similar to that suggested by Chapman & Green (1987). However, the rotifer richness recorded in some water bodies was much lower than previous studies have shown it to be. For example, my study only recorded three zooplankton species from Lake Tikitapu bottom sediments (two cladoceran species: *Ceriodaphnia dubia* and *Bosmina meridionalis*, and one species of rotifer: *Asplanchna priodonta*). Yet in a similar hatching experiment Duggan *et al.* (2002) recorded a total of 13 species of zooplankton emerging from Lake Tikitapu bottom sediments. Accurately estimating species richness and composition of short-lived organisms such as zooplankton can be a difficult task as their community dynamics vary hugely in both space (diel vertical or horizontal migration) and time (seasonal and inter-annual variation) (Arnott *et al.*, 1998; Vandekerkhove *et al.*, 2005; Vandekerkhove *et al.*, 2005b; Garcia-Roger *et al.*, 2006). The sampling of diapausing eggs from lake bottom sediment has previously been assessed as an effective method. For example, May (1986) found sampling the diapausing eggs of rotifers gave her a much greater species richness than had been recorded in the water column during a single year. She found that rotifer richness assessed from diapausing eggs was similar to an assemblage observed over a six year period of sampling rotifers in the water column (May, 1986). However, there is also the risk that the areas sampled could be 'dead patches' (i.e. areas with low densities of diapausing eggs) (Brendonck & De Meester, 2003), which could lead to an under-estimation of species richness. In particular, the species richness of water bodies with a low tropic state (e.g. Lake Tikitapu) may have been underestimated due to these water bodies typically exhibiting much lower densities of diapausing eggs than more eutrophic water bodies (e.g. Duggan *et al.,* 2002). Despite the potential risk of under-estimating species richness, I still think the hatching of diapausing eggs from the sediment was an appropriate technique to use in this study. Methods were kept consistent for all water bodies sampled, so no water bodies were unduly biased. Further evidence for this being an appropriate method was that clear relationships were recognised between species richness and composition, and environmental variables for natural water bodies. On the other hand, relationships for constructed water bodies were either much weaker, or non-existent.

4.5 Rare elements of the fauna

4.5.1 A newly recorded species: *Cephalodella stenroosi*

A total of 71 species of zooplankton were recorded (Table 3) from water bodies sampled throughout the North Island, New Zealand. All of these species have been previously recorded in New Zealand, except for one. To date there has been no other record of the rotifer *Cephalodella stenroosi* in New Zealand (Shiel *et al.*, 2009). *Cephalodella stenroosi* was identified based on its toes with a dorsal lump, not tooth, the absence of an eye spot, and the trophi were as figured in Nogrady *et al.* (1995). It may be that this species is a new arrival to New Zealand, but it is much more likely that it has just never been documented or identified. Although studies of zooplankton in New Zealand now span over 150 years, many of the early studies are of little use to ecologists as they lacked comprehensive figures and keys to species (Shiel *et al.*, 2009). In addition to this, most rotifer collections have been from the open water of lakes and ponds, and therefore benthic and periphytic species are likely to be very poorly described (Duggan *et al.*, 1998; Shiel *et al.*, 2009).

Cephalodella stenroosi was recorded from a small constructed pond in Whangamata, on the east coast of the North Island, which was the 'youngest' (approximately 1 year old) of the constructed water bodies sampled. *Cephalodella stenroosi* is a benthic / periphytic rotifer (Nogrady *et al.*, 1995) so it is possible that it originated from the area surrounding the pond and was then able to take advantage of the available resources in the relatively undeveloped community of such a recently constructed water body. The only other zooplankton species recorded from the Whangamata pond were the cladoceran *Moina tenuicornis* and the cyclopoid copepod *Mesocyclops leuckarti* (Table 3).

4.5.2 A peat-lake rotifer: Non-indigenous or native?

A rotifer found during this study in Lake Waiwhakareke (Horseshoe Lake) was recorded as the non-indigenous rotifer, *Conochilus exiguus,* which is thought to have originated in North America. It has been suggested that its arrival in New Zealand was the result of an accidental anthropogenic introduction (Ruttner-Kolisko, 1974; Duggan *et al.*, 2002a). This species has previously been recorded from three other locations in New Zealand, which were Lakes Rotomanuka North and South (Duggan *et al.* 2002a), and Lake Serpentine East (Duggan, 2008) in the North Island. All four of the lakes that this species has been recorded from are very old Waikato peat lakes (~ 10,000 to 17,000 years old) (Lowe & Green, 1987). Therefore, the possibility exists that this species is actually a native rotifer that has not been previously identified (Duggan *pers comm.,* 2010). Genetic comparison with the North American *Conochilus exiguus* is necessary to properly identify this species.

Chapter Five: Conclusions

Although a slight difference in average species richness did exist between natural and constructed water bodies, this was seemingly not as great as the differences observed in species composition. The species assemblages of constructed water bodies were comprised of a wide variety of species, including many benthic and littoral species. Natural water bodies, on the other hand, had more structured communities consisting of a core group of predominantly pelagic species. In addition, the species composition and richness of natural water bodies had strong relationships with environmental variables. The relationships between environmental variables, composition and richness for constructed water bodies, on the other hand, were either weak or non-existent.

Overall, it appears that too much attention has been paid to the role of species richness of water bodies for resisting invasions, and the focus perhaps needs to be shifted towards looking at key differences in species composition. If we are able to identify species (or groups of species) that are particularly effective at resisting invasions of non-indigenous species, in the way that native calanoid copepods appear to resist non-indigenous calanoid copepods, then it may be possible to introduce these species to constructed water bodies in an attempt to reduce the establishment and spread of potentially harmful non-indigenous species.

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