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New Zealand Calanoid Copepod Invasions: Has Artificial Lake
Construction Facilitated Invasions, and are our Coastal Waters
Uninvaded?

A thesis submitted in partial fulfilment
Of the requirements for the Degree of
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Abstract

Non-indigenous species have become a global issue of increasing importance in recent years, with many causing significant environmental and economic damage. Identifying locations vulnerable to invasion allows for focus of management efforts towards prevention of invasions at those locations. In order to determine whether constructed water bodies, such as reservoirs, ornamental lakes or retired mines, are more easily invaded environments than natural water bodies, owing to decreased biotic resistance, the distributions of native and non-indigenous freshwater calanoid copepod species in the North Island were examined. Calanoid copepods in ports and other coastal environments were also examined, in order to determine whether ports are more frequently invaded owing to increased propagule supplies from visiting ships and other sources.

The distributions of the native freshwater calanoid copepod species *Boeckella hamata*, *B. propinqua*, *B. delicata* and *B. tanea* are confined in the North Island of New Zealand to specific technostratigraphic terranes when natural waters only are examined, and as such each species can be considered to have a native range. The recently colonised calanoid copepod species *Boeckella minuta* (6 locations), *Skistodiptomus pallidus* (3 locations) and *Sinodiptomus valkanovi* (2 locations) are to date confined to constructed water bodies. *Boeckella symmetrica* (2 locations) may be confined to constructed water bodies, but the status of one location is unclear. *Boeckella triarticulata*, a species common in the South Island, is known only from a single farm dam in the North Island. The native species *Boeckella hamata*, *B. propinqua* and *B. delicata* were found to occur in constructed waters, but only *B.*

propinqua was found in constructed water bodies outside their natural ranges (9 locations). *Calamoecia lucasi* is found in lakes throughout most of the North Island, and is not confined to any one terrane. My results indicate that constructed water bodies are more easily invaded by non-indigenous species than natural water bodies, represents a potential pathway for future invaders to establish, and provides locations for species to spread.

In order to determine whether recently established freshwater calanoid copepod species have the potential to spread from their present habitats into other water bodies, the prosomal lengths of non-indigenous calanoid copepod species were measured and compared with those for native species. The results suggest that dietary overlap should prevent the non-indigenous species present to date from spreading into any water bodies with established *Boeckella* populations, although *Sinodiaptomus valkanovi* and *Boeckella triarticulata* could potentially spread to lakes containing only *Calamoecia lucasi*. Data on the co-occurrences of native freshwater calanoid copepod species support the theory of dietary exclusion, as *Boeckella* species have not been found to coexist.

In order to test whether New Zealand marine environments have been invaded by non-indigenous calanoid copepods, and whether ports have been more regularly invaded than non-port areas, calanoid copepods were sampled from various coastal locations around the North Island. With the possible exception of *Sulcanus conflictus*, no non-indigenous species were found, indicating that non-indigenous marine calanoid copepod species are not establishing in New Zealand despite a history of invasion elsewhere.

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Chapter 1:

Introduction

1.1: Thesis Introduction

Non-indigenous species have become a subject of increasing importance in recent years. Global movement of humans has led to both deliberate and accidental spread of non-indigenous species across natural geographical barriers worldwide (Vitousek et al., 1997). Although these organisms might eventually have migrated across these barriers by natural dispersal, the rate and spatial scale of spread has been greatly increased by human intervention (Hebert & Cristescu, 2002). The introduction of non-indigenous species into an ecosystem can result in severe ecological and economic impacts (Vitousek et al., 1997; Ricciardi & MacIsaac, 2000).

It is apparent that for a species to invade a new region it requires both a propagule supply and suitable environmental conditions in the recipient region (Forsyth & Duncan, 2001; Forsyth et al., 2004). Once a species has become established within an ecosystem, however, it can be very difficult, or even impossible, to remove (Mack et al., 2000). For this reason, it is preferable to prevent non-indigenous species from becoming established in the first place, rather than attempting to check their spread once they are established (Kolar & Lodge, 2001). Finding patterns in the invasion process is key to preventing future invasions.

1.2: Biotic Resistance and Propagule Pressure

The traditional view of invasions, as presented by Elton (1958), is that the probability of establishment of non-indigenous species will decrease with an increasing species richness of the recipient region, as a diverse community will more effectively utilise available resources, leaving few available “niches” for potential invaders to exploit. Such a process has become known as “biotic resistance”. Research conducted into biotic resistance has revealed mixed results, however (Levine & D’Antonio, 1999). Experiments on zooplankton have indicated that biotic resistance can play a strong role in preventing new species from establishing in ponds (Shurin, 2000). In some cases however, it was found that diverse communities were more easily invaded, owing to other factors such as richness of resources, which can covary with species diversity, as shown by studies on exotic plants on Lord Howe Island (Pickard, 1984), and the exotic herb *Hieracium lepidulum* in a New Zealand Beech forest (Wiser et al., 1998).

A more recent idea is the theory of propagule pressure, which states that all communities are able to be invaded, given sufficient supply of individuals of the potential invader, or if enough introduction attempts are made (Moyle & Light, 1996; Kolar & Lodge, 2001). Studies have shown that propagule pressure is a powerful predictor of invasion success in birds (Forsyth & Duncan, 2001; Cassey et al., 2005) and mammals (Forsyth et al., 2004), along with climatic suitability and life history traits. For aquatic taxa also, Colautti (2005) found that the explaining factor for establishment success for salmonid fish in Nevada was introductory effort by humans, rather than life history traits. Similarly, Semmens et al. (2004) correlated

propagule pressure from the aquarium trade with sightings of non-native tropical fish on the reefs of Florida, and Duggan et al. (2006b) established that there was a relationship between aquarium fish occurrences in stores and records of introduction and establishment for the United States and Canada. Biotic resistance may thus slow or prevent the spread and impact of non-indigenous species, rather than preventing their establishment (De Meester et al., 2002; Levine et al., 2004).

To date, there have been few studies aimed at examining interactions between biotic resistance and propagule pressure. However, propagule pressure was demonstrated to overwhelm biotic resistance in a series of experiments on forest understory plants which manipulated resident diversity, physical disturbance and abiotic conditions, and propagule pressure (Von Holle & Simberloff, 2005). The Great Lakes also display a pattern of facilitation, where non-indigenous species that have become established in the ecosystem have progressively altered the environment, creating conditions more favourable to the establishment of further species, and creating a “biological meltdown” effect; this is despite non-indigenous species providing more species rich communities that would be expected to have a greater biotic resistance (Ricciardi & MacIsaac, 2000).

1.3: Aquatic invasions

Aquatic ecosystems are particularly vulnerable to invasion owing to vectors such as trans-oceanic shipping, unintentionally carrying species by hull fouling and ballast water, and the aquarium trade, intentionally carrying fish, aquatic plants and snails, to and from areas of varying biogeographical origin. Both of these vectors are important in the Great Lakes of North America. As of 2001, 162 non-indigenous species had

been identified within this system of lakes (Ricciardi, 2001). Invasions of this ecosystem have been well documented (Mills et al., 1993; Grigorovich et al., 2003a), including a progressive mass invasion of species originating from the Ponto-Caspian region among other sources, introduced through ballast water from shipping. San Francisco Bay is perhaps the most invaded estuarine environment in the world, with 324 non-indigenous species found, with origins from several continents, around half of which have become established after 1960, indicating an accelerating rate of invasion (Cohen & Carlton, 1998). These invaders have caused significant economic and ecological impacts, the best documented example being the zebra mussel in the Great Lakes. The zebra mussel has, through blocking intake pipes for industrial and municipal water supplies, cost an estimated US\$2 billion to manage to date (Office of Technological Assessment, 1993, from Vitousek et al., 1997). In addition, the zebra mussel has been shown to cause massive declines in phytoplankton biomass, due to increased grazing pressure (Caraco et al., 1997).

Within the marine environment, ports are particularly vulnerable to invasion (Cohen & Carlton, 1998; McGee et al., 2006). The primary vector for aquatic invasions worldwide has been identified as transoceanic shipping (Carlton & Geller, 1993), either through hull fouling organisms, or through the discharge of ballast water. Even those ships which declare no ballast water on board retain residual ballast water and sediments in their tanks (Bailey et al., 2005; Gray et al., 2005), resulting in the release of organisms capable of surviving long term transportation in such environments. Other vectors, such as the aquarium trade, are also important for the introduction of non-indigenous species (Semmens et al., 2004). Both vectors for invasions are present in New Zealand, with container ships docking regularly at ports

around the country. Although regulations require that ballast water be exchanged outside the country's exclusive economic zone, residual water may still provide a vector for invasions.

1.4: Reservoirs as facilitators of invasions

Much work has gone into identifying potential invaders, for example using characteristics of past invaders to identify species which share these characteristics, and are thus potential future invaders (Ricciardi & Rasmussen, 1998; Kolar & Lodge, 2001). To date, however, there have been few studies aimed at identifying locations vulnerable to invasion.

A key feature of human modification to landscapes is the construction of reservoirs and other constructed water bodies (e.g., ornamental ponds, retired mine pits). Although the worldwide rate of reservoir construction peaked in the 1970s (Rosenberg et al., 2000), the construction of new water bodies (and the significant modification of natural water bodies) is an ongoing process, particularly in urban areas. Constructed water bodies now make up a significant proportion of the landscape, greatly increasing the areas of standing water worldwide (Rosenberg et al., 2000). This has led to both an increase in the number of lake environments open to invasion and greater connectivity amongst these and natural lakes (e.g., Havel et al. 2005).

Initially empty of the species assemblages that would be found in natural lakes, constructed water bodies will have little or no biotic resistance to invasion of non-indigenous species (Havel et al. 2005). Reservoirs are therefore an environment into which non-indigenous species can become established with a minimal number of

introductions, and a low density of propagules. Once established in such an environment, the species would potentially be able to spread out into surrounding lakes, driven by a regular supply of propagules from the initial point of establishment. Havel et al. (2005) identified several other characteristics of reservoirs that may increase their vulnerability to invasion, including high physical disturbance, higher and more variable fertility, higher salinity, and altered food webs. Studies suggest that the cladoceran *Daphnia lumholzi*, now established in 125 reservoirs in the United States, spread using reservoirs as stepping stones for its invasion (Havel & Herbert, 1993; Havel et al., 2005). Duggan et al. (2006a) recorded three new non-indigenous species of zooplankton in New Zealand, two of which are seemingly restricted to reservoirs.

1.5: Zooplankton Invasions

Invasions by zooplankton species into both marine and freshwater habitats are common worldwide (Ricciardi & MacIsaac, 2000; Cohen, 1998). Invasions are most common within the same hemisphere, likely owing to the difficulty of temperate organisms dispersing across the inhospitable tropics, and because the dominant trade routes tend to be between ports in the same hemisphere. However, there are examples of cross-hemisphere invasions, following human intervention (Ferrari et al., 1991; Duggan et al., 2006a). New Zealand has a long history of human-aided invasions by non-indigenous species, including of aquatic ecosystems by fish, plants and zooplankton (Cranfield et al., 1998), and the recent discovery of three non-indigenous freshwater zooplankton species by Duggan et al. (2006a).

Calanoid copepods are found worldwide in both freshwater and marine habitats, have distinctive species in different regions, and have a history of invasion in both environments. In the marine environment, numerous cross-continental invasions have been recorded. For example, the Asian species *Pseudodiaptomus inopinus* has become established in the Columbia River Estuary (Cordell et al., 1992), and *P. forbesi* and *P. marinus* have been found in California's Sacramento-San Joaquin Estuary (Orsi & Walter, 1991). Despite their record of invasion however, no definitive non-indigenous marine calanoid copepod species have been recorded from New Zealand (Cranfield et al., 1998). The question is whether these species are present but remain thus far unrecorded, or whether they are not being transported to or fail to establish in, New Zealand harbours in the first place.

Calanoid copepods also have a history of intercontinental invasions in freshwater environments (Reid & Pinto-Coelho, 1994; Bollens et al., 2002). Examples include *Boeckella triarticulata*, an Australasian species, which has been found in a constructed fish pond in northern Italy (Ferrari et al., 1991), and has subsequently spread to natural waterways (Ferrari & Rossetti, 2006). The Asian species *Sinodiaptomus sarsi* has been found in Turkey (Gündüz, 1998), and *S. valkanovi* has been recorded in North America, Bulgaria and New Zealand (Ueda & Ohtsuka, 1998; Duggan et al., 2006a). Freshwater calanoid copepods within Australia have also been found to have established themselves outside of their normal ranges, particularly in the case of species not normally found in Western Australia establishing in artificial water bodies in urban areas (Maly & Bayly, 1991; Maly et al., 1997).

1.6: Calanoid copepods in New Zealand

Freshwater calanoid copepod distributions in New Zealand have been well studied, with records stretching back for over a century (e.g. Bayly, 1964; Jamieson, 1988). To date, ten species have been recorded in the North Island (Chapman & Green, 1987; Duggan et al., 2006a). Of the calanoid copepod species occurring in the North Island, six are considered to be good native species – *Calamoecia lucasi*, *Boeckella tanea*, *B. delicata*, *B. hamata*, *B. propinqua* and *B. triarticulata*. Based on their restricted distributions, *Boeckella minuta* and *B. symmetrica* are thought to be recent arrivals from Australia (Chapman & Green, 1987). *Skistodiaptomus pallidus* and *Sinodiaptomus valkanovi* are recent arrivals from North America and Japan, respectively (Duggan et al., 2006a).

Freshwater calanoid copepods of similar sizes do not typically co-occur in the same water bodies, owing to dietary overlap (e.g. Kobayashi, 1993). Hutchinson (1967) stated that a size difference of 35% would be necessary to prevent dietary overlap. Co-occurrences between established species are well documented, being limited in the North Island to instances of *Calamoecia lucasi* coexisting with *Boeckella minuta*, *B. propinqua* and *B. hamata* (Chapman & Green, 1987). However, it is unknown what species the more recently arrived non-indigenous species, *Skistodiaptomus pallidus* and *Sinodiaptomus valkanovi*, may coexist with if they are able to spread.

Several *Boeckella* species have been shown to have distributions more-or-less related to certain technostratigraphic terranes (Jamieson, 1998). Terranes, or micro-plates, are geographical regions with a common geological history, distinct from

neighbouring terranes (Cooper, 1989; Heads, 1989). New Zealand is divided into several distinct terranes, including seven major features in the North Island (Fig. 1). Just as each terrane has a common geological history, they can also have common assemblages of organisms, which they carry with them as they move, separating once continuous populations and bringing together formerly separate ones. Perhaps the best known examples in New Zealand of species confined to particular terranes are those of populations separated by movement along the alpine fault, such as the angiosperm *Celmisa petriei* and the oligochaete worms *Deinodrilus benhami* and *Diprochaeta intermedia*, which are confined to the Western Province terrane (Heads, 1989). Heads (1989) also outlines other examples of such distributions, such as the lichen *Anzia jamesii*, which is confined in the North and South Islands to the Western Province and Murihiku terrane. Jamieson (1998) examined four *Boeckella* species, and determined distributions were similarly more-or-less related to specific terranes. *Boeckella dilatata* and *B. delicata* were primarily found in the Tuhua and Caples terranes, while *B. hamata* and *B. triarticulata* were found in the Torlesse terrane, though there was considerable overlap in some areas. Although species distributions have been mapped for the North Island (Chapman & Green, 1987), to date, no study has attempted to relate these to technostratigraphic terranes, or what effect construction of reservoirs and other waters might have on this distribution.

As calanoid copepods are well defined taxonomically (e.g. Bayly, 1964; Bradford-Grievess, 1994; 1999), have a history of invasion, typically have defined native ranges, and tend to exclude one another from freshwater habitats, they are a very useful group for studying the establishment and spread of non-indigenous species.

1.7: Hypotheses

My hypotheses are as follows:

- 1) As more readily invaded environments, constructed water bodies in New Zealand will contain non-indigenous species not found in natural lakes, or will have non-indigenous species found at a greater frequency than in natural lakes.
- 2) Constructed water bodies will aid the spread of aquatic organisms, and will have changed the natural distributions of calanoid copepod species indigenous to New Zealand (i.e., distributions will be less confined to terranes when considering reservoirs than when considering natural lakes only).
- 3) That New Zealand coastal marine areas have been invaded by calanoid copepods, and that a higher proportion will be found in port areas than in other non-port areas owing to a high frequency of introductions (and hence propagule pressure) from visiting ships.
- 4) That non-indigenous calanoid copepod species will be able to co-exist with native species, allowing them to spread from constructed waters to natural waters.

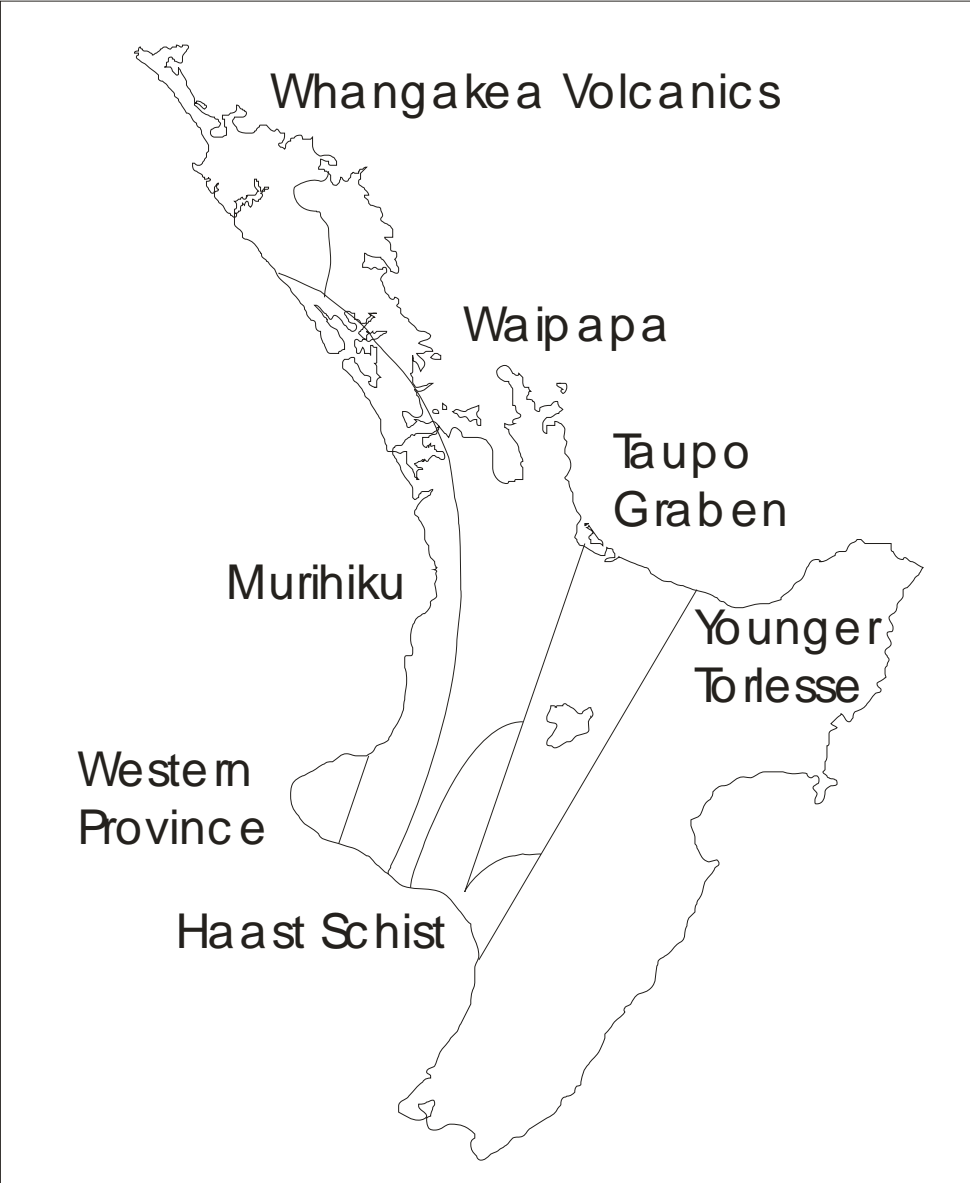


Figure 1: Technostratigraphic terranes of the North Island.

Chapter 2:

Methods

2.1: Lake and Reservoir Calanoid Copepods

To determine whether reservoirs facilitate invasions, I sampled both natural and constructed permanent lakes, ponds and reservoirs from across the North Island, New Zealand. Samples were collected using 40 μ m mesh nets, towed multiples times horizontally or vertically from shore for at least 5 minutes, or until copepods could be seen swimming in the samples. The samples were concentrated and preserved with ethanol for a final concentration of 50-70% ethanol. Historic samples held by the University of Waikato, in particular samples collected during the systematic survey of Duggan et al. (2002), were also included in the study, having been collected using similar methods to those described above.

Overall, 98 sites were sampled between March and November 2006, of which 40 contained mature male calanoid copepods. 74 stored samples dating from 1993 to 2006 were also examined, 50 of which contained mature male calanoid copepods. Standard taxonomic keys were used to identify the species (Chapman & Lewis, 1976; Bayly, 1992), based mainly upon the morphology of the male fifth legs. Specimens were selected and dissected under a binocular microscope at between 15X and 40X magnification. They were then transferred to slides and examined under a compound microscope at 400X magnification.

A review of the literature was also conducted, so as to include data from sites either not sampled or unsuccessfully sampled (i.e. no adult calanoids present) during the

course of this study, and not represented in historic samples. Sources consulted included Chapman & Green (1987), Bayly (1964), Chapman (1971), (2); Jolly (1955, 1957) Magadza (1973), Forsyth et al. (1983) and Duggan et al. (2006a).

The distributions of freshwater calanoid copepods in the North Island were plotted on maps, separated according to whether they occurred in natural or constructed water bodies. These plots were compared with the geographic terranes of the North Island, as detailed by Heads (1989).

2.2: Co-occurrence and exclusion among freshwater calanoid copepods

In order to examine whether recently established, currently spatially restricted, freshwater calanoid copepod species can spread to natural waters in New Zealand, and coexist with native calanoid copepod species, prosome lengths for the freshwater species *Skistodiaptomus pallidus*, *Sinodiaptomus valkanovi*, *Boeckella tanea* and *B. symmetrica* were obtained by measuring at least 30 individual adults from single populations, using an ocular at 100X magnification. Mean prosome lengths for New Zealand species (Chapman & Green, 1987) were compared to these measurements, with ratios for the mean prosome lengths of each species compared to determine whether there is sufficient difference between particular species to prevent dietary overlap, negating the effects of biotic resistance and allowing non-indigenous species to coexist with native species. Mean figures for each population were graphed, along with a dietary overlap range of 1.35 times the average prosome length, as suggested by Hutchinson (1967).

2.3: Marine and coastal calanoid copepods

To determine whether non-indigenous calanoid copepod species have established populations around major ports, I collected samples from harbours in the following areas: Waitemata, Raglan, Thames, Tauranga, New Plymouth and Wellington. Waitemata, Tauranga and Wellington Harbours contain major port facilities, and see frequent international shipping, whereas New Plymouth contains a less important port, and Raglan and Thames have little in the way of port facilities. Samples were also collected from coastal lagoons, some of which contained a mixture of freshwater and brackish/marine species. Samples were collected at varying distances from major port facilities in order to see whether species found varied away from the ports.

As with the freshwater samples, coastal marine samples were collected using 40µm mesh nets, towed multiple times horizontally or vertically from shore for at least 5 minutes, or until copepods could be seen swimming in the samples. The samples were concentrated and preserved with ethanol for a final concentration of 50-70% ethanol.

Standard taxonomic keys for marine calanoid copepods were used to identify the species (Bradford-Grieve, 1994; 1999), based mainly upon the morphology of the male fifth legs. Specimens were selected and dissected under a binocular microscope at between 15X and 40X magnification, transferred to slides, and examined under a compound microscope at 400X magnification.

Overall, eleven samples were collected between March and November 2006, of which five contained mature, identifiable calanoid copepods. Six samples from brackish water sites contained marine species, and were added to these results. Historical samples were not available to add to those collected. The species found

were compared to known distributions for marine calanoid copepod species in New Zealand as detailed in Bradford-Grieve (1994; 1999).

Chapter 3:

Results

3.1: Lake and reservoir calanoid copepods

The distributions of ten freshwater calanoid copepod species were recorded from my surveys of North Island lakes, examination of historic samples, and from published records, from both natural and constructed water bodies (Figures 2-5; Appendix 1-10); These were *Calamoecia lucasi*, the only species of its genus in the country; seven species of *Boeckella* – *B. tanea*, *B. propinqua*, *B. delicata*, *B. minuta*, *B. hamata*, *B. symmetrica* and *B. triarticulata* – *Skistodiaptomus pallidus*, a non-indigenous North American species, and *Sinodiaptomus valkanovi*, a non-indigenous Japanese species. Distributions of species were plotted according to whether the water bodies were natural or constructed, and compared to the terrane margins of Heads (1989; Figures 2-5). The distribution of *Calamoecia lucasi* in North Island natural waters is seemingly not restricted to any particular terrane, nor is its distribution apparently impacted by constructed water bodies (Figure 2). The distributions of native *Boeckella* species in North Island natural waters indicates that *B. tanea* is restricted to the Whangaeka Volcanics, *B. delicata* is restricted to the Waipapa Terrane, *B. propinqua* is restricted to the Taupo Graben and Haast Schist and *B. hamata* is restricted to the Younger Torlesse and Haast Schist (Figure 3).

The distributions of native *Boeckella* species in North Island constructed water bodies indicates that *B. tanea*, *B. delicata* and *B. hamata* have apparently not been greatly influenced by construction of new water bodies (Figure 4), as occurrences in constructed waters are restricted to their native terranes (Figure 3).

Boeckella tanea was not found in any constructed water bodies, *B. delicata* was found in one constructed water body on the Waipapa terrane, and *B. hamata* was found in four constructed water bodies on the Younger Torlesse. *Boeckella propinqua*, however, confined to the Taupo Graben and Haast Schist when examining natural waters, is found in five constructed water bodies on the Waipapa Terrane, two on the Murihiku Terrane, and one on the Younger Torlesse, indicating an expansion in its natural range.

With the possible exception of *Boeckella symmetrica*, the distributions of other freshwater calanoid copepod species in the North Island are confined to constructed water bodies, and cannot be assigned natural distributions related to any particular terrane (Figure 5). *Boeckella symmetrica* has been previously recorded from one unidentified pond in Pakuranga, Auckland. This study added a constructed lake formed in the former Wiri Quarry, Auckland to its range. *Boeckella minuta* has been previously recorded from four constructed water bodies in the Waikato region and the Karori reservoir in Wellington. This study added Turtle Lake in Hamilton to its range. *Boeckella triarticulata* has been recorded from the North Island only from a single constructed farm pond near Otatara Pa in Hastings. *Skistodiatomus pallidus* has been previously recorded in two constructed water bodies in Auckland. This study added Lake Rotomanu, a former quarry in New Plymouth to its range. *Sinodiatomus valkanovi* has been previously in one constructed water body in Auckland. This study added Gilmour Lake, a former mine in Waihi, to its range.

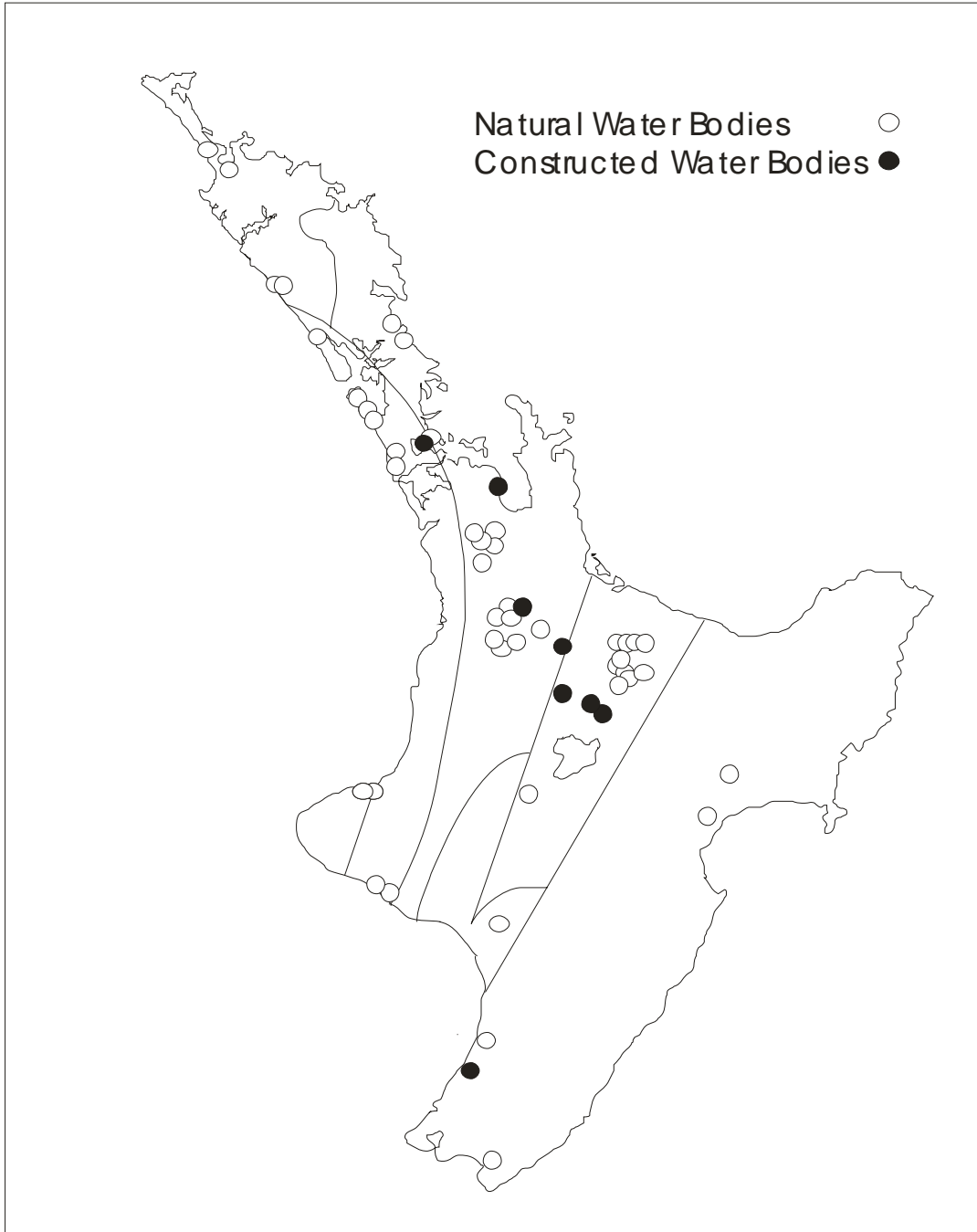


Figure 2: Distributions of *Calamoecia lucasi* in natural and constructed waters in the North Island.

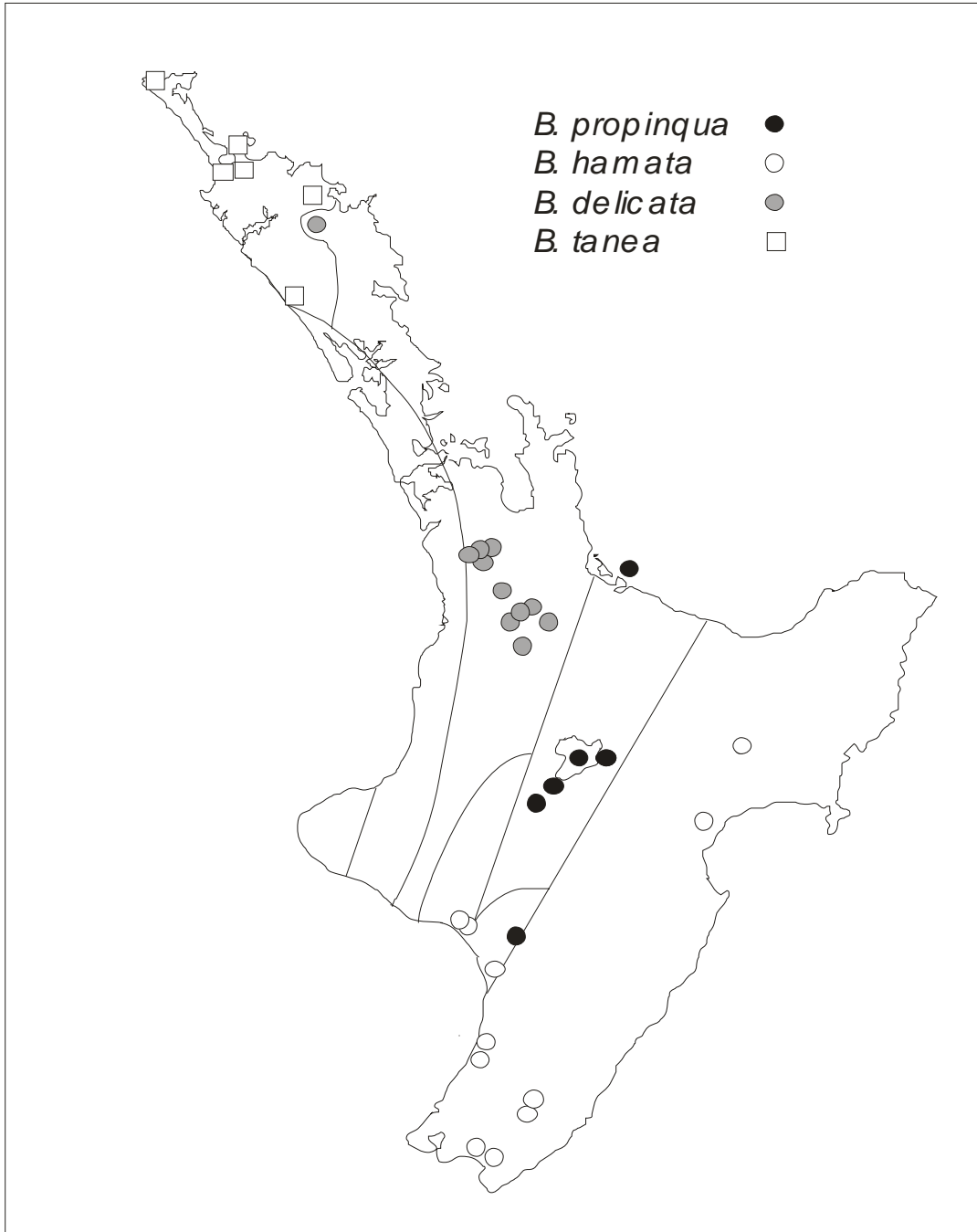


Figure 3: Distributions of the native *Boeckella* species *B. propinqua*, *B. hamata*, *B. delicata* and *B. tanea* in natural waters in the North Island

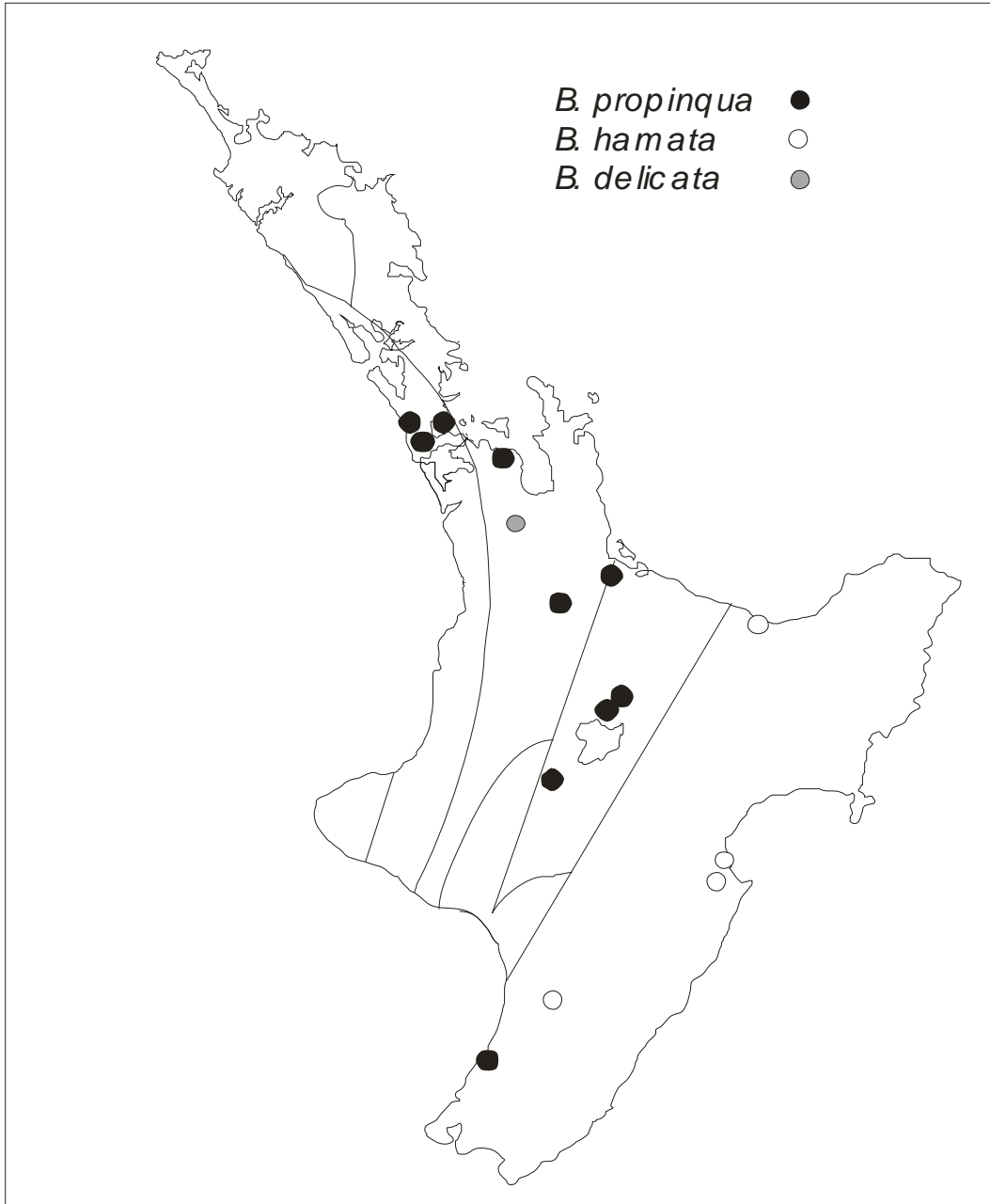


Figure 4: Distributions of the native *Boeckella* species *B. propinqua*, *B. hamata* and *B. delicata* in constructed water bodies in the North Island.

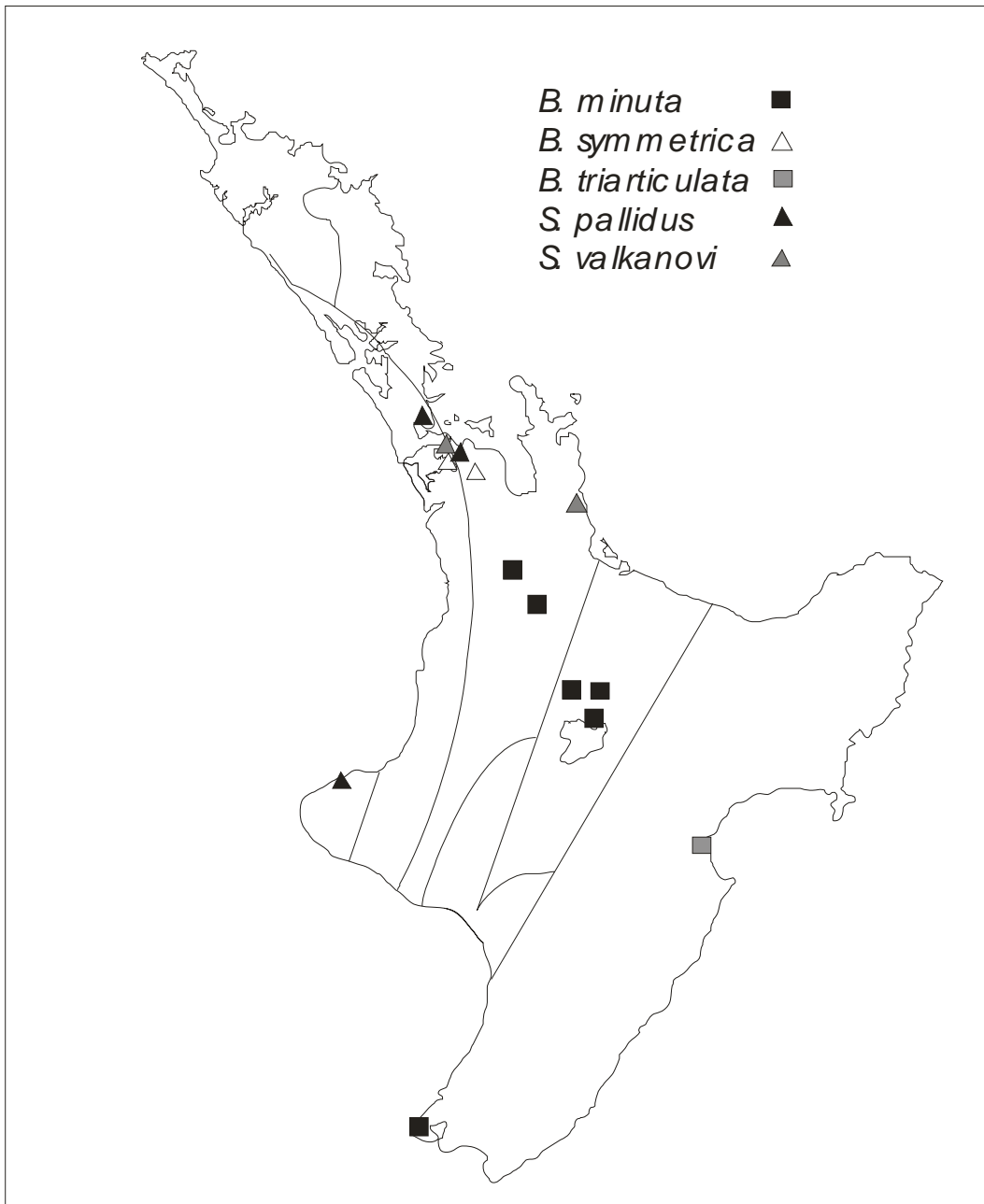


Figure 5: Distributions of the freshwater calanoid copepod species *Boeckella minuta*, *B. symmetrica*, *B. triarticulata*, *Skistodiaptomus pallidus* and *Sinodiaptomus valkanovi* in constructed water bodies in the North Island.

3.2: Co-occurrence and exclusion among freshwater calanoid copepods

Known co-occurrences of freshwater calanoid copepod species in the North Island are detailed in Table 1. Co-occurrences of freshwater calanoid copepod species were rare, and mostly limited to shallow lakes or larger constructed waters. This study added several new instances of co-occurrence, including the co-occurrence of *Calamoecia lucasi* and *Boeckella propinqua* in Lake Karapiro, between *C. lucasi* and *B. delicata* in Lake Waikare, and between *C. lucasi* and *B. hamata* in Lake Tutira.

Based upon data combined from this study, Bayly (1964), Chapman et al. (1975), and Chapman & Green (1987), co-occurrences were also noted between *Calamoecia lucasi* and *Boeckella delicata* in Lakes Rotokauri, Rotomanuka, Rotongaro, Whangape and Waahi, and for *C. lucasi* and *B. hamata* in Lake Waikaraemoana.

Notably, co-occurrence between *Calamoecia lucasi* and *Boeckella tanea* was recorded for Lake Taharoa, based on the presence of each in separate samples. In addition, co-occurrence between three species – *Calamoecia lucasi*, *Boeckella minuta* and *B. propinqua* was recorded for Lakes Karapiro and Ohakuri, based upon combined data from this study and that of Magadza (1973). It is important to note that *Boeckella minuta* and *B. propinqua* were not recorded together in any one sample.

Out of the 32 constructed water bodies found to have calanoid copepods in this study, five were found to contain two or three different species of freshwater calanoid copepods.

Table 1: Known co-occurrences of freshwater calanoid copepod species in the North Island. Sources: This study (1); Chapman & Green (1987) (2); Jolly (1955, 1957) (3); Chapman et al. (1975) (4); Magadza (1973) (5); Lawless (1983) (6); Bayly (1964) (11); Balvert (2006) (15).

Species	Lake	Source
<i>C. lucasi/B. propinqua</i>	Chelsea Sugarworks Pond (Auckland)	3
	Duck Creek (Piha)	2
	L. Karapiro (Waikato River)	1
	L. Namunamu (Wanganui)	2
	L. Ohakuri (Waikato River)	1; 5
<i>C. lucasi/B. delicata</i>	Black Lake (Huntly)	2
	Lagoon on Komakura Stream (Near Huntly)	4
	L. Koutu (Cambridge)	2
	L. Mangakaware (Waipa)	2
	Ohinewai Lake (Huntly)	2
	L. Rotokauri (Waipa)	1; 2
	L. Rotomanuka (Waipa)	1; 2
	L. Rotongaro (Huntly)	4; 2
	L. Serpentine (Waipa)	2
	L. Waahi (Huntly)	1; 2
	L. Waikare (Huntly)	1
	Weavers Lake (Huntly)	15
	L. Whangape (Huntly)	4; 2

Table 1 (cont.): Known co-occurrences of freshwater calanoid copepod species in the North Island. Sources: This study (1); Chapman & Green (1987) (2); Jolly (1955, 1957) (3); Chapman et al. (1975) (4); Magadza (1973) (5); Lawless (1983) (6); Bayly (1964) (11); Balvert (2006) (15).

<i>C. lucasi/B. tanea</i>	L. Taharoa (Northland)	1
<i>C. lucasi/B. hamata</i>	L. Pounui (Wairarapa)	6
	L. Tutira (Hawkes Bay)	1
	L. Waikaraemoana (Hawkes Bay)	1; 11
<i>C. lucasi/B. minuta</i>	L. Atiamuri (Waikato River)	2
	L. Karapiro (Waikato River)	5
	L. Ohakuri (Waikato River)	5
<i>C. lucasi/B. minuta/B. propinqua</i>	L. Karapiro (Waikato River)	1; 5
	L. Ohakuri (Waikato River)	1; 5

Mean prosome lengths for the freshwater calanoid copepod species found in New Zealand have been determined based on data collected by this study (Measurements for *Boeckella tanea*, *B. symmetrica*, *Skistodiaptomus pallidus* and *Sinodiaptomus valkanovi* were taken), and collected from various sources by Chapman & Green (1987), as detailed in Table 3. *Calamoecia lucasi* has a mean length of 0.65mm, *Boeckella minuta* of 0.99mm, *B. delicata* of 0.94mm, *B. triarticulata* of 1.21mm, *B. hamata* of 0.89mm, *B. propinqua* of 1.31mm, *B. tanea* of

0.72mm, *B. symmetrica* of 0.76mm, *Skistodiaptomus pallidus* of 0.84mm and *Sinodiaptomus valkanovi* has a mean length of 1.09mm (Table 3).

Mean prosomal lengths have been plotted, along with the range for dietary overlap (a factor of 1.35 times the size of the average individual; Hutchinson, 1967; Figure 5). If the mean length of a species falls within the dietary overlap range for another, they are predicted to be not able to coexist, owing to dietary overlap (i.e. competition for the same food sources). Among the non-indigenous species of freshwater calanoid copepods in the North Island, the diet of *Boeckella symmetrica* is predicted to overlap with all species except *Sinodiaptomus valkanovi*, *B. triarticulata* and *B. propinqua*. The diet of *Skistodiaptomus pallidus* is predicted to overlap with all species except *Boeckella triarticulata* and *B. propinqua*. The diet of *Boeckella minuta* is predicted to overlap with all species except *Calamoecia lucasi*. The diet of *Sinodiaptomus valkanovi* is predicted to overlap with all species except *Calamoecia lucasi*, *Boeckella tanea* and *B. symmetrica*. The diet of *Boeckella triarticulata* is predicted to overlap with all species except *Calamoecia lucasi*, *B. tanea*, *B. symmetrica* and *Skistodiaptomus pallidus*.

Among the species of freshwater calanoid copepods native to the North Island, The diet of *Calamoecia lucasi* is predicted to overlap with *Boeckella tanea*, *B. symmetrica* and *Skistodiaptomus pallidus*. The diet of *Boeckella tanea* is predicted to overlap with *Calamoecia lucasi*, *B. symmetrica*, *Skistodiaptomus pallidus*, *B. hamata* and *B. delicata*. The diet of *Boeckella hamata* is predicted to overlap with all species except *Calamoecia lucasi* and *B. propinqua*. The diet of *Boeckella delicata* is predicted to overlap with all species except *C. lucasi* and *B. propinqua*. The diet of

Boeckella propinqua is predicted to overlap with *B. minuta*, *Sinodiaptomus valkanovi* and *B. triarticulata*.

Table 2: Mean prosome lengths (in mm) of freshwater calanoid copepod species.

Sources: This study (1); Chapman (1973a) (2); Maly (1984) (3); Jamieson (1985) (4); Green (1974) (5).

Species	Lake	Length	n	Source
<i>C. lucasi</i>	L. Rotoiti	0.65	2500	2
<i>B. minuta</i>	?	0.99	5	3
<i>B. delicata</i>	?	0.94	104	3
<i>B. triarticulata</i>	Dunedin pond	1.21	73	4
<i>B. hamata</i>	Tomahawk Lagoon	0.89	81	4
<i>B. propinqua</i>	Auxilliary Nihotopu Reservoir	1.31	1250	5
<i>B. tanea</i>	L. Taharoa	0.72	33	1
<i>B. symmetrica</i>	Wiri Quarry	0.76	40	1
<i>S. pallidus</i>	Albany pond, MacKinnon Rd	0.84	33	1
<i>S. valkanovi</i>	Auckland Domain	1.09	38	1

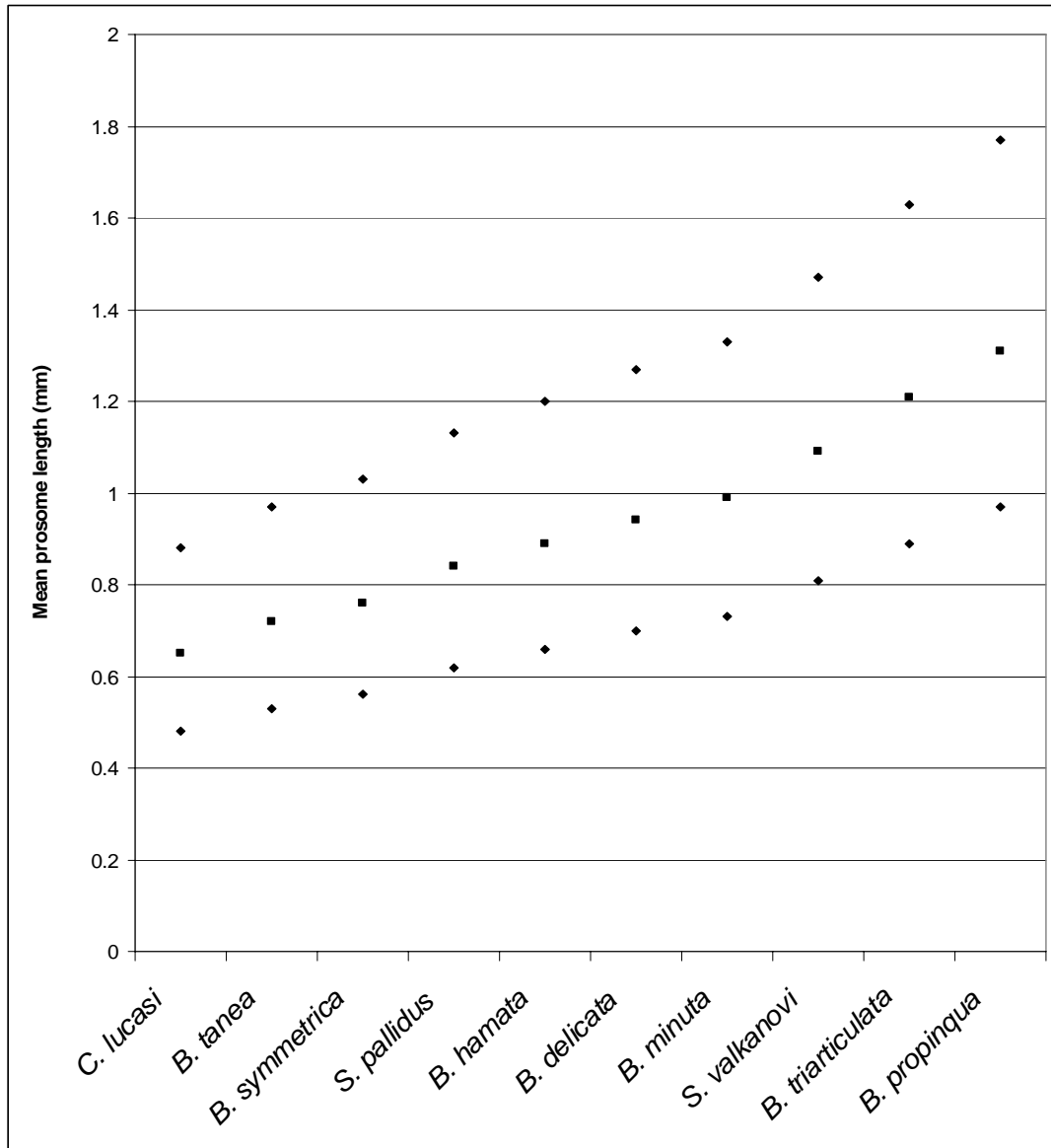


Figure 6: Mean prosomal lengths (in mm) of calanoid copepod species found in the North Island (Squares). Diamonds represent Hutchinson's limits for resource competition between species.

Table 3: Marine and estuarine calanoid copepods recorded from coastal habitats in the North Island.

Location	Species
Waitemata Harbour – Kelley Tarltons	<i>Paracalanus indicus</i>
Waitemata Harbour – Orakei Basin	<i>Gladiferens pectinatus</i>
Chelsea Sugar Ponds (Auckland)	<i>G. pectinatus</i>
Kai Aua Quarry (Coromandel)	<i>G. pectinatus</i>
Onepoto Lagoon (Auckland)	<i>G. pectinatus</i>
	<i>Sulcanus conflictus</i>
Mangere Lagoon (Auckland)	<i>Acartia jilletti</i>
Wattle Downs Boat Lake (Auckland)	<i>G. pectinatus</i>
Tauranga Port (Tauranga)	<i>Temora turbinata</i>
Newlands (Wellington)	<i>P. indicus</i>
	<i>Metridia ilcens</i>
	<i>T. turbinata</i>
Porirua Harbour (Kapiti Coast)	<i>G. pectinatus</i>
Aotea Lagoon (Kapiti Coast)	<i>A. jilletti</i>
Waikane Beach Lagoon (Kapiti Coast)	<i>G. pectinatus</i>

3.3: Occurrences of marine and coastal calanoid copepods

Six species of marine and brackish water calanoid copepods were collected from harbour sites and coastal lagoons around the North Island (Table 2). All species recorded were native to New Zealand, with the exception of *Sulcanus conflictus*, which was found in Onepoto Basin, and which is listed by Bradford-Grieve (1999) as a possible non-indigenous species.

Chapter 4:

Discussion

4.1: Freshwater Calanoid Copepod Distributions

New Zealand is divided into several technostratigraphic terranes, or micro-plates, of distinct geological history, which impact the distributions of species around the country (Cooper, 1989; Heads, 1989). Movement along fault lines has resulted in the separation of once continuous populations, while previously separated populations have been brought closer together. Among natural North Island freshwater lakes, the distributions of four *Boeckella* species were confined to specific terranes. *Boeckella tanea* was confined to the Whangakea Volcanics terrane, *B. delicata* to the Waipapa terrane, *B. propinqua* to the Taupo Graben and Haast Schist, and *B. hamata* to the Younger Torlesse terrane and Haast Schist. The occurrence of two *Boeckella* species on the Haast Schist may be due to the fact that it is younger than the surrounding terranes, allowing colonisation from neighbouring terranes over time. Jamieson (1998) similarly found distributions of four New Zealand *Boeckella* species to be more-or-less restricted to terranes, with *B. dilatata* and *B. delicata* found largely on the Western Province and the Caples terrane group (consisting of the Caples, Dun Mountain, Brook St and Muruhiku terranes), while *B. hamata* and *B. triarticulata* were found largely on the Torlesse terrane, although there was considerable overlap on the terrane margins (particularly for the Haast Schist). *Calamoecia lucasi* is found in many natural lakes throughout the North Island, and is seemingly not confined to any particular terrane. The results of this study augment those of previous examinations of the distribution of freshwater calanoid copepod species (Chapman &

Green, 1987; Jamieson, 1998), adding fresh data points for the distribution of freshwater calanoid copepod species and correlating the data with terrane boundaries.

The general coherence of Boeckellid distributions to geological terranes indicates that distributions of this genus in New Zealand have remained reasonably constant for millions of years prior to human arrival, despite the periodic natural formation and colonisation of new lakes (Lowe & Green, 1987). Different Boeckellid species in the North Island can therefore be considered to have “native ranges”. This temporal consistency may be attributed to a low natural dispersal rate in the calanoid copepods, sufficient to spread locally to nearby lakes (i.e. typically those within their own terrane margins), but seldom over long distances (Maly & Bayly, 1991; Jamieson, 1998). In short, the nearest species to a new habitat will generally colonise it first.

There are four species of freshwater calanoid copepod seemingly confined to constructed water bodies in the North Island; *Boeckella triarticulata*, *B. minuta*, *B. symmetrica*, *Skistodiptomus pallidus* and *Sinodiptomus valkanovi* (but see below on *B. symmetrica*). *Boeckella minuta* and *B. symmetrica* are already considered recent arrivals to New Zealand, owing to their restricted distributions (Chapman & Green, 1987). In addition to the historical records, this study recorded *Boeckella minuta* in Turtle Lake, a large ornamental pond in Hamilton, and *B. symmetrica* was recorded in this study in a lake formed from the former Wiri Quarry in Auckland. These findings indicate a small expansion in their ranges, and that these species have the potential to expand further, given open habitats.

Boeckella symmetrica has formerly been recorded from a small pond surrounded by farmland in Pakuranga, Auckland (Chapman & Green, 1987). It is

unclear whether this pond was natural or constructed, and there is therefore an element of doubt as to whether it is found solely in constructed water bodies in New Zealand. It is notable that *Boeckella symmetrica* has a history as an invader of constructed water bodies in Australia (Maly & Bayly, 1991).

Skistodiatomus pallidus and *Sinodiatomus valkanovi* are very recent invaders, first recorded in New Zealand by Duggan et al. (2006a). These authors found *Skistodiatomus pallidus* in two interlinked ponds in the Auckland Regional Botanic Gardens, and a pond in Albany, North Auckland, and *Sinodiatomus valkanovi* from an indoor ornamental pond in the Winter Garden at the Auckland Domain. This study adds new records for these species from locations widely separated from these initial localities; *Skistodiatomus pallidus* from Lake Rotomanu (a former quarry) in New Plymouth, and *Sinodiatomus valkanovi* from Gilmour Lake (a former mine pit) in Waihi. Given the distances that lie between these new sites and those where the species were previously recorded, it is clear that both species are either spreading in New Zealand, or have been introduced to new habitats on multiple occasions. Management efforts aimed at curtailing their further spread are likely to be difficult.

Boeckella triarticulata is found in the Torlesse terrane in the South Island, but there is only one record of this species in the North Island, in a constructed farm pond near Otatara Pa in Hastings (Burns, 1984). Given that *Boeckella hamata* and *B. triarticulata* have not been recorded coexisting despite a shared range in the South Island (Jamieson, 1998), it seems unlikely that *B. triarticulata* will be able to spread into the natural water bodies surrounding its current location. Alternatively, it is possible that *Boeckella triarticulata* is significantly more widely distributed in the

North Island than has been recorded to date, as its habitat in the South Island is largely restricted to stagnant pools and ponds (Jamieson, 1998), which have seldom been sampled in the North Island, either in the course of this study or by previous studies. Burns (1984) suggested that this species might also be more widely distributed through other constructed farm ponds in the area. *Boeckella triarticulata* has also demonstrated an ability to spread, as evidenced by its establishment and subsequent spread in Italy (Ferrari et al., 1991; Ferrari & Rossetti, 2006).

Of the species occurring in natural water bodies, only *Boeckella propinqua* of the native species appears to be expanding its natural range through constructed water bodies. Historical patterns of the distribution of *Boeckella propinqua*, the natural range of which is restricted to a narrow strip of the Taupo Graben and Haast Schist, have been significantly altered by the inclusion of samples from reservoirs, resulting in an arced distribution encompassing the Wanganui area, the central North Island, Mayor Island and the Auckland Isthmus (Chapman & Green, 1987). This distribution is further altered by the inclusion of the results from this study, in particular the recording of *Boeckella propinqua* in Paekakariki wetland and in Lake Karapiro, which means that *B. propinqua* is now found in the Taupo Graben, the Haast Schist, the Waipapa Terrane, the Murihiku Terrane and the Younger Torlesse.

Although *Boeckella hamata* is still restricted to lakes within its natural range, it has proven able to colonise reservoirs within that range. By contrast, *Boeckella delicata* may have low powers of dispersal, as despite the presence of many constructed water bodies in the Waikato region, the only such water body it has dispersed into is Weavers Lake, which is separated from Lake Waahi by less than 100 metres, and was flooded by Lake Waahi during its filling (Balvert, 2006).

Jamieson (1998) did not distinguish between natural and constructed water bodies when compiling the distributions of South Island freshwater calanoid copepod species, and it is possible that, if such distinctions were applied to those distributions, they would adhere more closely to terrane boundaries. For instance, *Boeckella dilatata* is listed as being present in “ponds and newly formed dams on the Waitaki and Clutha River systems”, which are located in the Torlesse terrane, which is otherwise dominated by *B. hamata* and *B. triarticulata*.

The apparent ability of *Boeckella propinqua* to spread to a greater extent than other *Boeckella* species may be a result of its ability to produce resting eggs. Of the *Boeckella* species in New Zealand, only *B. triarticulata* and *B. hamata* are known to produce diapausing eggs (Chapman & Green, 1987; Hall & Burns, 2001). However, there is considerable circumstantial evidence that *Boeckella propinqua* also has the ability to produce diapausing eggs, as evidenced by its quick reappearance in a reservoir after it had been drained for three weeks (Green, 1974). Other *Boeckella* species may also be able to produce diapausing eggs, but the fact that only *B. hamata* and *B. propinqua* of the native North Island *Boeckella* species have colonised reservoirs to a significant extent suggests that they may have superior dispersal capabilities to *B. minuta* and *B. tanea*. The ability to produce diapausing eggs does not necessarily equate to greatly enhanced dispersal ability under natural conditions, as such eggs will generally sink to the bottom of the water column after they are laid (Geddes, 1983, from Maly et al., 1997). If they do become entrained into a dispersal vector, however, they are more likely to survive transportation than species without diapausing eggs (Bailey et al., 2005).

Recent changes in the pattern of freshwater calanoid copepod distribution (i.e. in constructed waters) can be attributed to human intervention. This can occur through the construction of many new water bodies in a short period of time, allowing species to colonise new, uninhabited sites, and possibly by transporting organisms between these sites. Vectors for transport of calanoid copepods to and among reservoirs may include the international and domestic transfer of reservoir construction equipment used in lakes (Koste & Shiel, 1989), or movement of recreational boats (Havel & Herbert, 1993). Another potential vector is with the transport of live fish for the stocking of new water bodies (Ferrari et al., 2001), or with the introduction of tropical plants (Duggan et al., 2006a). The dispersal of *Boeckella propinqua* into the Waikato hydroelectric dams may also be from passive dispersal downstream from Lake Taupo, with the dams providing suitable habitat.

Boeckella minuta, *B. symmetrica*, *B. triarticulata* and *Calamoecia lucasi* have been found to be extending their ranges in Western Australia, likely due in some degree to human disturbance (Maly & Bayly, 1991). In particular, *Boeckella minuta* is known in Western Australia only from ten constructed farm ponds (Maly et al., 1997). This, along with the fact that many freshwater non-indigenous species have been initially recorded in constructed water bodies (e.g. Ferrari et al., 1991; Reid & Pinto-Coelho, 1994; Havel et al., 2005), lends weight to the theory that constructed water bodies facilitate invasions.

In addition to the constructed water bodies included in this study, there are countless dammed farm ponds and other constructed water bodies scattered around the country. As a result, there are a considerable number of available sites for non-

indigenous species to colonise, given an appropriate vector for transportation to these water bodies.

4.2: Co-occurrence and exclusion among freshwater calanoid copepods.

The coexistence of freshwater calanoid copepod species in New Zealand is rare, being mostly restricted to shallow lakes and reservoirs (Chapman & Green, 1987). For the most part, *Boeckella* species are found coexisting only with *Calamoecia lucasi*, not each other. The results for prosome length measurements tend to agree with recorded co-occurrences among native species, with native *Boeckella* species falling within each others' dietary exclusion ranges. The exception to this is *Boeckella tanea*, which the results suggest should be able to coexist with *B. triarticulata* and *B. propinqua*, although its distributional range does not intersect with those of either species.

Of the recent calanoid copepod arrivals in New Zealand, *Boeckella minuta* and *Sinodiaptomus valkanovi* fall within the dietary overlap range for all native species except *C. lucasi* and *B. tanea*. Again, this suggests that neither species should be able to spread into habitats occupied by other *Boeckella* species, with the exception of *B. tanea*. Although *Boeckella minuta* has been found to co-occur with *B. triarticulata* in Australia, it is unclear whether the two species were found at the same time, owing to the dispersed spatial and temporal nature of the study (Maly et al., 1997).

Although *Boeckella propinqua*, *B. minuta* and *Calamoecia lucasi* have been recorded in Lakes Ohakuri and Karapiro (both constructed water bodies), all three species were never found in the same sample. *Boeckella propinqua* was found during

my surveys, while *B. minuta* was found by Magadza (1973). *Calamoecia lucasi* was found in both lakes by Magadza, and in Lake Karapiro in this study. Although instances of three species co-occurring have been noted in Australian studies (Maly & Maly, 1997; Maly et al., 1997), these samples were often separated temporally, as in the current study, so it is unclear whether these species can truly coexist together. It is notable that there have been no records of *Boeckella minuta* and *B. propinqua* coexisting from Australian or New Zealand studies to date (Chapman & Green, 1987; Maly et al., 1997). It is probable that different life history strategies between the two species mean that they are dominant in the lakes that both species occur in at different times of the year.

Additionally, this study found an instance of co-occurrence between *Calamoecia lucasi* and *Boeckella tanea* in Lake Taharoa. These species would be expected to exclude one another from their habitats, due to dietary overlap (Chapman & Green, 1987). Two samples were examined from Lake Taharoa, one of which was dominated by *Calamoecia lucasi*, and one by *Boeckella tanea*. It is probable that the two species are important in the lake at different times of the year, though further study would be necessary to determine the details of their interactions.

Of the non-indigenous calanoid copepods, *Boeckella symmetrica* and *Skistodiaptomus pallidus* fall within the range for dietary exclusion by *Calamoecia lucasi*, *B. tanea*, *B. hamata*, and *B. delicata*, which suggests that they will not be able to spread into natural water bodies, since between them these species cover most of the North Island. That *Boeckella symmetrica* and *Calamoecia lucasi* have not been recorded as coexisting in Australia (Maly et al., 1997) lends weight to this. There is,

however, a possibility that they will be able to establish themselves in lakes occupied solely by *Boeckella propinqua*.

Finally, *Boeckella propinqua*, a species which has demonstrated considerable ability to spread, falls within the dietary overlap for *B. hamata*, *B. delicata* and *B. minuta*, which suggests that this species will also be unable to spread to natural lakes containing *Boeckella* species other than *B. tanea*, which is not found adjacent to its current distribution.

Although it is too early to draw conclusions on the ability of *Skistodiptomus pallidus* or *Sinodiptomus valkanovi* to spread into natural water bodies based upon the recorded distributions of either species in New Zealand (though *S. pallidus* does have a record of spread in North America; Duggan et al., 2006a), *Boeckella minuta* has been established in New Zealand since at least 1967 (Vidal, 1968), and has yet to establish itself in any natural water bodies in New Zealand. This suggests that dietary overlap with native species may be preventing its spread, and will likewise check the spread of the other non-indigenous freshwater calanoid copepods established in New Zealand to date. Although freshwater calanoid copepod species may be slowed from spreading by biotic resistance due to dietary overlap, such patterns do not necessarily hold true for other classes and orders of zooplankton. *Daphnia lumholtzi* was initially recorded in a reservoir in Texas (Sorensen & Sterner, 1992), and has subsequently spread through 125 reservoirs in the United States, as well as into large rivers and natural lakes (Havel et al., 2005). *Daphnia dentifera*, a recent invader to New Zealand, has also recently become widespread in New Zealand natural lakes (Duggan et al., 2006a).

Havel et al. (2005) stated that dammed rivers were more vulnerable to invasion, owing to constant levels of disturbance, greater connectivity, and unusual physical and chemical properties. However, many of the constructed water bodies containing non-indigenous calanoid copepods in this study were not dammed rivers (e.g., *Skistodiaptomus pallidus* in ornamental ponds and a disused quarry; *Sinodiaptomus valkanovi* in an ornamental pond and disused mine). As these environments will not have the greater connectivity or unusual conditions associated with dammed rivers, it is likely that low biotic resistance is the key factor in facilitating invasions into constructed waters across landscapes.

4.3: Marine and coastal calanoid copepod distributions

The majority of species recorded in this study have been previously documented as common either around the coastline of the North Island of New Zealand, or within the wider region (Bradford-Grieve, 1994; 1999). The notable exception is *Sulcanus conflictus*, which was found in Onepoto Basin (a constructed habitat), in Auckland. It has been recorded previously in Orakei Basin, also in Auckland (Bradford-Grieve, 1999) as a possible invader (first recorded in Western Australia), and as an important species in Tauranga Harbour (Warr, 2001). Since zooplankton distributions as listed by Bradford-Grieve (1994; 1999) are based largely on deepwater (off shore) hauls, it is possible that *Sulcanus conflictus* is more widely distributed through New Zealand estuaries than is currently recognised. If it is an invader, then its presence in both Waitemata and Tauranga Harbours is suggestive that port environments are more prone to invasion than other coastal waters. More data on the distributions of *Sulcanus conflictus* in New Zealand is required to answer the question of whether it is a non-

indigenous species, however. The three other records of its distribution to date have placed *Sulcanus conflictus* in Western Australia, New South Wales and Tasmania (Bradford-Grieve, 1999), suggesting it has a reasonably widespread (though perhaps patchy) native range.

Overall, with the possible exception of *Sulcanus conflictus*, this study did not reveal any non-indigenous calanoid copepod species in New Zealand coastal waters, either around ports or in other environments. This result mirrors studies to date, which have shown that planktonic species are not well represented among marine non-indigenous species in New Zealand (e.g., Cranfield et al., 1998). It is possible that measures to reduce the release of non-indigenous species through ballast water have proven effective in preventing their establishment in New Zealand waters. Alternative explanations include abiotic conditions unsuitable for the establishment of planktonic species (as in Lake Superior; Grigorovich et al., 2003b), or biotic resistance preventing such species from becoming established. Neither explanation seems likely to apply for all the harbours in the country. A more likely explanation is that the distance of New Zealand from other major ports is limiting the chance of these organisms surviving prolonged transport in this vector. However, given the history of invasions by these species elsewhere (e.g., the establishment of *Pseudodiaptomus marinus* in the Sacramento-San Joaquin Estuary; Orsi & Walter, 1991), calanoid copepods represent a significant threat for future invasion.

Additional study, over a range of zooplankton species, on finer temporal scales, will be necessary in order to determine whether greater numbers of non-indigenous species can be found around ports in New Zealand than in other coastal environments.

Chapter 5:

Conclusion

5.1: Thesis conclusion

This study provides solid evidence that constructed water bodies are more easily invaded than natural water bodies, facilitating the establishment and spread of non-indigenous species of freshwater calanoid copepods. Construction of waters has also allowed the native species *Boeckella propinqua* to expand its range, effectively invading much of the central North Island. As such, constructed water bodies represent an important direction for future management efforts for the prevention of establishment and spread aquatic non-indigenous species.

Although constructed water bodies have allowed new non-indigenous freshwater calanoid copepod species to establish in the North Island, their spread into natural water bodies has to date apparently been prevented by biotic resistance, in the form of competitive exclusion due to dietary overlap between similarly sized species. Unfortunately, biotic resistance is likely less strong in other groups of zooplankton, allowing them to spread from an initial invasion site into natural water bodies (e.g., *Daphnia lumholtzi* in North America; Havel et al., 2005, and *Boeckella triarticulata* in Italy; Ferrari & Rossetti, 2006). This makes preventing non-indigenous species from becoming established in constructed water bodies doubly important.

Reservoirs may also facilitate co-occurrences between freshwater calanoid copepod species, due to being more variable environments, which provides optimal conditions for different species at different times (Chapman & Green, 1987; Havel et al., 2005). Such co-occurrences normally occur mainly in shallow lakes.

In the marine environment, *Sulcanus conflictus* was the only potential non-indigenous calanoid copepod species recorded, which supports the contention that calanoid copepods are underrepresented among recorded marine non-indigenous species in New Zealand.

5.2: Future Study

The next step following on from this study would be to conduct similar research for South Island lakes, and possibly for other countries, investigating whether constructed water bodies have changed the natural distributions of calanoid copepod species there. Given the abundance of historical records, a review of the literature to collate distributions of each species within natural and constructed water bodies could prove illuminating.

An examination of species distribution patterns for other taxonomic groups among natural and constructed water bodies, such as for cyclopoid copepods or cladoceran species, could also prove useful in determining whether particular taxonomic groups are better able to extend their natural ranges through constructed water bodies. In addition, given the record of establishment of non-indigenous calanoid copepod species in constructed water bodies, such sites should be considered at risk of invasion, and monitored for non-indigenous species, particularly in urban areas.

Research should also be conducted into methods to minimise the risk of invaders establishing themselves in constructed water bodies. Stocking such sites with native species following construction would be one possible way of reducing the risk of non-indigenous species becoming established.

Although constructed water bodies are clearly more vulnerable to invaders than natural water bodies, some questions remain unanswered. Are all constructed water bodies equally invasible? Or do they accumulate species richness and hence biotic resistance over time? Studies of species richness in constructed water bodies of varying ages could be conducted and compared to those for natural lakes in order to answer these questions.

Although both natural and constructed permanent lakes were well covered by this study, constructed farm ponds were not. These water bodies represent a considerable number of habitats potentially open to invasion across the country. A survey of such water bodies would be useful for determining whether any non-indigenous species, more specialised to these smaller habitats, are spreading through such water bodies.

The question of whether areas of similar vulnerability in other environments exist also arises. An example in the terrestrial environment would be of roadside vegetation in otherwise undisturbed environments, as road construction would be expected to disrupt biotic and abiotic conditions around the road in the terrestrial environment in a similar manner to that of reservoir construction in the aquatic environment. Additionally, studies of species assemblages in areas such as former mines, abandoned building sites, and other areas similarly stripped of vegetation and subsequently left alone could be compared to those for areas of comparatively undisturbed terrain.

In the area of identifying potential future invaders, a list of calanoid copepod species (both marine and freshwater) with a history of invasion could be compiled (e.g. *Sinodiaptomus sarsi*; Gündüz, 1998). This method has been identified as one of

the best ways to identify potential future invaders (Ricciardi & Rasmussen, 1998), likely because these species are already known to have an ability to move associated with human mediated dispersal vectors. Investigating the average size of these species would be useful for determining whether these species can potentially co-occur with native New Zealand species.

Given that non-indigenous marine calanoid copepod species do not appear to have established populations in New Zealand (a pattern which also holds for other planktonic species; c.f., Cranfield et al. 1998), despite a history of invasion elsewhere, it seems possible that adequate propagule supplies are not being transported to these ports. A study of organisms present in the ballast water of international ships entering New Zealand waters could be conducted, both to determine which, if any, species are surviving long-term transportation through this vector, and to compare the species assemblages found to those invaders found in New Zealand waters to date. Alternative explanations for this lack of planktonic invaders include unsuitable abiotic conditions for planktonic establishment in New Zealand ports, and biotic resistance. In order to test these theories, abiotic conditions and species richness in New Zealand ports could be compared to those in overseas ports with histories of invasion (e.g. San Francisco Bay; Cohen & Carlton, 1998).

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Appendix:

Freshwater calanoid copepod distributions in the North Island

Sources: This study (1); Chapman & Green (1987) (2); Jolly (1955, 1957) (3); Chapman et al. (1975) (4); Magadza (1973) (5); Lawless (1983) (6); Bayly (1962) (7); Green (1974) (8); Forsyth et al. (1983) (9); Jamieson (1985) (10); Bayly (1964) (11); Chapman (1973) (12); Burns (1984) (13); Duggan et al. (2006a) (14); Balvert (2006) (15).

Appendix 1: Distributions of *Calamoecia lucasi*

Lake	Lake Type	Source
L. Atiamuri (Waikato River)	A	2
Barrett Lagoon (New Plymouth)	N	1
Black Lake (Huntly)	?	2
Chapel Lake (Hamilton)	A	1
Chelsea Sugarworks Pond (Auckland)	A	3
Duck Creek (Piha)	A	2
Hamilton Lake (Hamilton)	N	1
Hawera Pond (Hawera)	N	1
L. Herengawe (Wanganui)	N	1
L. Horowhenua (Kapiti Coast)	N	1
Kai Aua Quarry (Coromandel)	A	1

L. Kai-Iwi (Northland)	N	1
L. Karapiro (Waikato River)	A	1
L. Kereta (Kaipara Harbour)	N	1
Lagoon on Komakurau Stream (Huntly)	?	4
L. Koutu (Cambridge)	N	2
L. Kuwakatai (Kaipara Harbour)	N	1
L. Mangakaware (Waipa)	N	2
L. Maraetai (Waikato River)	A	5
L. Namunamu (Wanganui)	N	2
L. Ngaroto (Waipa)	N	1
L. Ngapouri (Rotorua Lakes)	N	1
L. Ngatu (Northland)	N	1
L. Ohakuri (Waikato River)	A	5
Ohinewai Lake (Huntly)	N	2
L. Okareka (Rotorua Lakes)	N	1
L. Okaro (Rotorua Lakes)	N	1
L. Okataina (Rotorua Lakes)	N	1
L. Ototoa (Kaipara Harbour)	N	1
L. Panorama (Ranui)	A	1
L. Parawanui (Northland)	N	1
L. Pounui (Wairarapa)	N	6
L. Pupuke (Auckland)	N	1
L. Rerewhakaaitu (Rotorua Lakes)	N	1

L. Rotoehu (Rotorua Lakes)	N	1
L. Rotoiti (Rotorua Lakes)	N	1
L. Rotokare (Wanganui)	N	1
L. Rotokauri (Waipa)	N	2
L. Rotoma (Rotorua Lakes)	N	1
L. Rotomahana (Rotorua Lakes)	N	1
L. Rotomanuka (Waipa)	N	2
L. Rotongaro (Huntly)	N	4
L. Rotorua (Rotorua Lakes)	N	1
L. Serpentine (Waipa)	N	2
L. Spectacle (Northland)	N	1
Summerset Village lake (Kapiti Coast)	A	1
L. Taharoa (Northland)	N	1
L. Tarawera (Rotorua Lakes)	N	1
L. Tikitapu (Rotorua Lakes)	N	1
L. Tomarata (Northland)	N	1
L. Tutira (Hawkes Bay)	N	1
L. Waahi (Huntly)	N	1
L. Waikaraemoana (Hawkes Bay)	N	1
L. Waikare (Huntly)	N	1
L. Waikopiro (Hastings)	N	1
L. Wainamu (Piha)	N	1
L. Waiparera (Northland)	N	1

L. Waipu (New Plymouth)	N	1
Weavers Lake (Huntly)	A	15
L. Whangape (Huntly)	N	4

Appendix 2: Distributions of *Boeckella propinqua*

Lake	Lake Type	Source
L. Aratiatia (Waikato River)	A	1
L. Aroarotamahine (Mayor Island)	N	7
Auxilliary Nihotopu Reservoir (Auckland)	A	8
Chelsea Sugarworks Pond (Auckland)	A	3
Cosseys Creek Reservoir (Auckland)	A	1
Duck Creek (Piha)	A	2
Huia Reservoir (Auckland)	A	7
L. Karapiro (Waikato River)	A	1
L. Mangapapa (Kaimai Ranges)	A	1
L. Namunamu (Wanganui)	N	2
Nihotopu Reservoir (Auckland)	A	7
L. Ohakune (Mt Ruapehu)	N	1
L. Ohakuri (Waikato River)	A	1
Paekakariki Wetland (Kapiti Coast)	A	1
L. Rotoaira (Taupo)	N	2
L. Rotongaio (Taupo)	N	9
L. Taupo (Taupo)	N	1

L. Te Paritu (Mayor Island)	N	7
Waitakere Reservoir (Auckland)	A	7
Te Whaio Dam (Taupo)	A	1

Appendix 3: Distributions of *Boeckella delicata*

Lake	Lake Type	Source
Black Lake (Huntly)	?	2
Henson's Pond (Hamilton)	N	1
Lagoon on Komakurau Stream (Huntly)	?	4
L. Koutu (Cambridge)	N	2
L. Mangakaware (Waipa)	N	2
Ohinewai Lake (Huntly)	N	2
L. Omapere (Northland)	N	10
L. Rotokauri (Waipa)	N	1
L. Rotomanuka (Waipa)	N	1
L. Rotongaro (Huntly)	N	2
L. Serpentine (Waipa)	N	2
L. Waahi (Huntly)	N	2
L. Waikare (Huntly)	N	1
Weavers Lake (Huntly)	A	1
L. Whangape (Huntly)	N	2

Appendix 4: Distributions of *Boeckella hamata*

Lake	Lake Type	Source
Anderson Park (Napier)	A	1
Boggy pond (Wairarapa)	N	1
Flaxmere Park (Hastings)	A	1
L. Kaitoke (Wanganui)	N	11
Massey University pond (Palmerston North)	A	1
L. Onoke (Wairarapa)	N	1
L. Pauri (Wanganui)	N	11
L. Pounui (Wairarapa)	N	6
Sullivan Lake (Whakatane)	A	1
L. Tutira (Hawkes Bay)	N	1
L. Virginia (Wanganui)	N	1
Waikane Beach (Kapiti Coast)	N	1
L. Waikaraemoana (Hawkes Bay)	N	11
L. Wairarapa (Wairarapa)	N	1

Appendix 5: Distributions of *Boeckella minuta*

Lake	Lake Type	Source
L. Atiamuri (Waikato River)	A	2
L. Karapiro (Waikato River)	A	5
Karori Reservoir (Wellington)	A	1
L. Maraetai (Waikato River)	A	5

L. Ohakuri (Waikato River)	A	5
Turtle Lake (Hamilton)	A	1

Appendix 6: Distributions of *Boeckella symmetrica*

Lake	Lake Type	Source
Pakuranga Pond (Auckland)	?	2
Wiri Quarry (Auckland)	A	1

Appendix 7: Distributions of *Boeckella tanea*

Lake	Lake Type	Source
Pond near Kaimaumautura (Northland)	N	12
Pond near L. Kawerua (Northland)	N	12
L. Ohia (Northland)	N	12
Lagoon near Cape Reinga (Northland)	N	12
L. Rotokawau (Northland)	N	12
L. Taharoa (Northland)	N	1

Appendix 8: Distributions of *Boeckella triarticulata*

Lake	Lake Type	Source
Otatara Pa pond (Hastings)	A	13

Appendix 9: Distributions of *Skistodiptomus pallidus*

Lake	Lake Type	Source
Albany pond, MacKinnon Rd (Auckland)	A	1
Auckland Botanic Gardens (Auckland)	A	1
L. Rotomanu (New Plymouth)	A	1

Appendix 10: Distributions of *Sinodiptomus valkanovi*

Lake	Lake Type	Source
Gilmour Lake (Waihi)	A	1
Winter Garden Pond (Auckland Domain)	A	14