The parasite release hypothesis and the success of invasive fish in New Zealand

A thesis
submitted in partial fulfilment
of the requirements for the degree
of
Master of Science in Biological Science
at
The University of Waikato
by

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The University of Waikato
2012

Abstract

Non-indigenous species are commonly released from their native enemies, including parasites, when they are introduced into new geographical areas. This has been referred to as the enemy release hypothesis and more strictly as the parasite release hypothesis. The loss of parasites is commonly inferred to explain the invasiveness of non-indigenous species. I examined parasite release in New Zealand non-indigenous freshwater fishes. A literature review was undertaken in order to collate lists of the known parasite fauna of 20 New Zealand non-indigenous freshwater fish species. Records were collated from their home range, New Zealand, and some other introduced ranges, to determine whether these species have a reduced parasite diversity in the New Zealand and other introduced ranges. Five non-indigenous freshwater fish, mosquitofish (*Gambusia affinis*), rudd (*Scardinius erythrophthalmus*), goldfish (*Carassius auratus*), koi carp (*Cyprinus carpio*) and catfish (*Ameiurus nebulosus*), and one native freshwater fish, common bullies (*Gobiomorphus cotidianus*), were sampled and examined for metazoan parasites. Mosquitofish and bullies, of similar size and habitat, were examined with greater intensity than the other species. Based on the literature review and fish examination, I found that the non-indigenous freshwater fish in New Zealand have seemingly lost their parasites. Being "lost overboard" is likely to have caused the loss of some parasites as most of the additional hosts required for non-indigenous parasites are no present in New Zealand. However, the loss of most of mosquitofish's parasites is likely due to "missing the boat", as introduction into New Zealand was a two-step process, from their native range in North America, via Hawaii, before release in New Zealand. Additionally, other hosts required for parasites of mosquitofish are not present in New Zealand. The native common bullies were found to harbour more parasites than the non-indigenous mosquitofish. Two parasites were found from common bullies, the cysts of the trematodes *Eustrongylides ignotus* and *Telogaster opisthorchis*, and no parasites were found on mosquitofish. A lack of spillback of *Eustrongylides ignotus* from bullies to mosquitofish, despite being parasititised by this species in its native range, may due to mosquitofish not being able to feed on intermediate the hosts present in New Zealand. The establishment and spread of non-indigenous fish in New Zealand waters is likely not the sole result of parasite release, but given their

apparent reduction or lack of parasites, it may be a factor contributing to their success.

Key words: *Parasite release hypothesis, non-indigenous freshwater fish*, *New Zealand*, *digestion method*, *parasite, mosquitofish*, *common bullies*

Acknowledgements

I owe my deepest gratitude to my supervisors, Dr Jonathan Banks and Dr Ian Duggan. Their patience, encouragement, guidance, and support from the initial to the final level enabled me to work smoothly on the project. Their efforts to go out collecting samples with me have made my research more rewarding.

I would also like to show my gratitude to Lee Laboyrie for teaching me everything I needed to know about the lab, about the handling and examination of my fish and its parasites.

In particular, my thanks go to my colleagues: Dr Dai Morgan, Dr Adam Daniel and Brennan Mahoney for supplying me with fish whenever I needed.

This thesis would not have been possible without the support of my mum, Miao Fan. Her constant checking of my grammar and sentence structures has made my writing smoother. I would also like to thank my dad, Dr Xiaomin Zhang for his expertise in biological science. He has made available his support in a number of ways. My thanks also go to my girl-friend, Jia Luo. Her accompany at fish sampling and fish measurement has made my research more enjoyable.

Lastly, I would like to thank all of those who supported me in any respect during the completion of the research.

Table of Contents

List of figures

List of tables

Chapter 1: Introduction

1.1 Parasitism

Parasitism has long been a popular subject, because parasites often cause serious harm to the health of humans and other animals (Friend & Franson, 1999). By definition, parasitism is a symbiotic relationship between two organisms where one, the parasite, lives inside or on the other, the host (Friend & Franson, 1999). Parasitic organisms are extremely diverse. They include single-celled protozoans (Durborow, 2003; Hoffman, 1999), and multicellular metazoans such as nematodes, trematodes and cestodes (Doyle, 2003; Knox, 2004; Zrzavý, 2001).

Parasites can be divided into two groups based on their location: endo-parasites, where parasitic individuals live internally, and ecto-parasites, where the parasite lives externally (Friend & Franson, 1999). Parasitic organisms are enormously diverse and many require multiple hosts to complete their life cycle. The host that harbours the sexual stage of fertile females is called the definitive host, while the host that holds immature parasites that usually do not sexually reproduce is called the intermediate host (Friend & Franson, 1999).

Parasites have one of two life cycles: direct life cycles or indirect (or complex) life cycles (Friend & Franson, 1999). Parasites with direct life cycles, such as monogenean trematodes, spend their entire life on or inside a single host; parasites with an indirect life cycles such as digenean trematodes and nematodes, require multiple hosts of different species to reach reproductive adulthood (Bunkley-Williams & Williams, 1994; Friend & Franson, 1999).

1.2 Invasive species

Invasive organisms are those that have been introduced into new habitats, either accidentally or deliberately by humans, and have caused significant damage to the economy or to the native flora and fauna (Macdonald, King, & Strachan, 2006; Torchin & Mitchell, 2004). Invasive animals have become a crisis globally as they are a major cause of biodiversity loss and lead to extirpation of the native plant and animals (Allan & Flecker, 1993). Invasive species can adversely affect native biodiversity through a number of interactions including predation, hybridization, competition and disease transmission (Gozlan, Britton, Cowx, & Copp, 2010; Mouritsen & Poulin, 2010; Moyle & Light, 1996). For example, the introduction of Nile perch (*Lates niloticus*) into Lake Victoria, Africa, has eliminated more than 200 species of haplochromine cichlids mainly through competition (Gozlan, et al., 2010; Mouritsen & Poulin, 2010; Moyle & Light, 1996). Similarly, the range and population size of New Zealand native bird species has been greatly reduced following the introduction of mammals, such as rats (*Rattus rattus*), possums (*Trichosurus vulpecula*) and stoats (*Mustela ermine*) (Macdonald, et al., 2006).

The fate of non-indigenous species introduced to a new range can be summarised into six patterns: 1) the introduced species does not establish; 2) artificial breeding is needed to maintain the introduced species; 3) introduced species establish locally in an unusual habitat; 4) introduced species establish but at low numbers; 5) introduced species establish with a rapid increase in both abundance and distribution, but with a major decline at later stages; 6) introduced species become significantly dominant (Lehtonen, 2003). Species conforming to pattern 6 are deemed invasive and (Torchin, Lafferty, & Kuris, 2002) summarized three key factors that contribute to the invasiveness of a non-indigenous species: 1) better environmental quality and availability; 2) fewer or poorer competitors for resources; 3) a paucity of natural enemies, such as predators and parasites compared with their home range.

The probability of a species becoming invasive in a new area is dependent on a number of factors including transport, establishment and demographic expansion (Torchin & Mitchell, 2004). Establishment success is controlled by the numbers of individuals introduced, and environmental and biotic interactions (Moyle & Light, 1996). For fish, establishment and spread are influenced by environmental factors, such as water temperature, flow rate and chemistry, biological factors such as prey availability, competition, predation, disease, and parasitism, and demographic factors such as the number of individuals introduced and the ability of the organisms' population to expand when numbers are small and/or at low densities (Keane & Crawley, 2002; Moyle & Light, 1996; Torchin, et al., 2002).

1.3 Enemy Release Hypotheses

The enemy release hypothesis is a widely accepted explanation for the invasiveness of non-indigenous organisms and states that individuals introduced into the new habitats, either naturally or by humans, are released from their natural enemies present in their native ranges (Keane & Crawley, 2002). Enemies include predators, pathogens and/or parasites. Release from natural enemies can result in faster population growth rates for the newly established species, which allows the introduced species to dominate in the introduced range (Blossey & Notzold, 1995; Mitchell & Power, 2003).

The enemy release hypothesis is based on two principles: 1) natural enemies regulate population size, whereby the introduced species are able to increase their abundance in the absence of their natural enemies; 2) the impact of enemies on the native species is greater than the impact on the introduced species (Torchin, et al., 2002). For example, boneseed (*Chrysanthemoides monilifera*), a plant native to South Africa that has become an invasive weed in Australia and New Zealand, produces twice as many seeds in its introduced range compared with its native South Africa (Blossey & Notzold, 1995). The absence of their natural browsers has been evoked as explanation for the greater fecundity of boneseed. Another example of enemy release allowing an organism to become a pest is that of the cane toad (*Bufo marinus*), in Australia. These animals reach population densities ten times higher in Australia than in their native region, South America, because of the absence of their native predators such as various species of snakes, eels, killifish, ibis and catfish (Torchin, et al., 2002)

The enemy release hypothesis has risen in popularity but not without controversy (Zetlmeisl, 2011). Colautti, Ricciardi, Grigorovich, & MacIsaac (2004) suggested that the causal connection between the loss of enemies and invasion success are not always clear and that non-indigenous species do not necessarily have fewer enemies than the native species in an area. Therefore researchers must be careful in linking the reduction of parasites on non-indigenous species with the invasiveness of these non-indigenous species in the introduced ranges without considering the importance of environmental factors.

1.3.1 Parasite Release Hypothesis

Predators, parasites and pathogens have long been recognized as playing a crucial role in the population growth, spread and establishment of a species (Campbell & Reece, 2005; Cornet, Sorci, & Moret, 2010). Recent studies have generated the parasite release hypothesis by applying the principles of the enemy release hypothesis to parasitism (Cornet, et al., 2010; Drake, 2003; MacLeod, Paterson, Tompkins, & Duncan, 2010; Ross, Ivanova, Severns, & Wilson, 2010; Torchin, Lafferty, Dobson, McKenzie, & Kuris, 2003; Torchin, et al., 2002; Torchin & Mitchell, 2004). Studies comparing parasite species richness and abundance of hosts in both their native and introduced ranges found that introduced species typically have reduced parasite diversity and abundance and researchers hypothesised that a loss of parasites may increase the ability of a species to establish and spread (e.g., Torchin et al., 2002; Drake, 2003).

The parasite release hypothesis has been examined for animals including birds, fish, amphibians, crayfish, aquatic and terrestrial molluscs (MacLeod, et al., 2010; Ross, et al., 2010) and plants (Mitchell & Power, 2003). Parasite diversity of 26 host species of molluscs, crustaceans, fishes, birds, mammals, amphibians and reptiles was significantly reduced in the introduced ranges comparing with that in their native habitats (Torchin, et al., 2003). Mitchell & Power (2003) examined 473 plant species that were introduced from Europe to the United States and found these species also had fewer parasites in their introduced ranges than in their native ranges (Mitchell & Power, 2003; Torchin, et al., 2003). In Australia, native fish carry significantly more parasites than the introduced fishes (Lymbery, Hassan, Morgan, Beatty, & Doupe, 2010).

The loss of parasites from a host can occur at several parts of the invasion process and has been summarised as:

1) Missing the boat: introduced populations are often established from a small number of individuals reaching the new range. As parasites tend to have a “patchy” distribution (i.e. a few host individuals tend to be heavily parasitized in contrast to the majority of hosts that do not carry the parasite species). Thus the parasite species may not reach the new host’s range for stochastic reasons (MacLeod, et al., 2010).

2) Lost overboard (drowning on arrival):

a) Parasites often require a series of intermediate hosts before reaching their definitive hosts to complete their growth and reproductive cycles. If any of these hosts are missing from the new range, or alternative hosts are not found, the parasite will go extinct.

b) Sinking with the boat: a parasite may reach the new range with its host but the host becomes extinct. Parasites introduced with their host may go extinct if the parasite population cannot reproduce sustainably. Alternatively, host population fragmentation may occur, which results in insufficient parasite transmission for the parasite to survive in its new environment. Sinking with the boat is more likely if the parasites have no alternative host species in the new region.

(Bunkley-Williams & Williams, 1994; MacLeod, et al., 2010; Torchin, et al., 2003; Torchin, et al., 2002; Torchin & Mitchell, 2004).

It is not clear which point of the introduction process is most critical for the successful establishment of parasites in new ranges. Some studies have suggested the pre-arrival stages are more important than the post-arrival stages (Paterson & Gray, 1997; Paterson, Palma, & Gray, 1999; Zetlmeisl, 2011), while others suggested the opposite (MacLeod, et al., 2010; Torchin, et al., 2003; Torchin & Mitchell, 2004). Zetlmeisl (2011) suggested that the pre-arrival stages are very important, as the high variation of parasite prevalence and intensity can influence the population size of the parasite being introduced with their hosts. Also, some hosts are transported as juveniles such as plant seeds and larval invertebrates, which rarely harbour parasites (Torchin, et al., 2002). On the other hand, MacLeod et al. (2010) tested the different processes and mechanisms that have caused parasite loss on New Zealand introduced birds. They suggested that establishment failure was more crucial than the failure of arriving with their host; i.e., the parasites arrived with their hosts in the new range, but then went extinct (MacLeod, et al., 2010).

1.4 Parasite transfer between native and non-indigenous species

There are potentially adverse effects associated with parasites that can occur with the introduction of hosts to a new area. Host species in new areas can alter the parasite fauna of native fishes by acting as additional hosts for endemic parasites (parasite spill back) (Kelly, Paterson, Townsend, Poulin, & Tompkins, 2009). Furthermore, parasites can disperse from a heavily infected population to a more susceptible non-infected sympatric population (parasite spill over or host switching) (Colla, Otterstatter, Gegear, & Thomson, 2006; Kestrup, Thomas, Rensburg, Ricciardi, & Duffy, 2011).

Parasites from introduced species can switch to native hosts (Lymbery, et al., 2010; Torchin, et al., 2002). For example, the nematode swim bladder parasite *Anguilicola crassus* has been introduced into Europe from Asia with their native Asian eel host. This parasite has spread throughout Europe and has had adverse impacts on the native fauna. The absence of native swimbladder nematodes in Europe was thought to be an explanation for the great success of the introduced parasite *A. crassus*, as there were no competitors for the niche and the native hosts had not developed any resistance to the parasite (Lehtonen, 2003).

Alternatively, an introduced species may offer a new niche for native parasites (parasite spillback). Most species of the freshwater tilapia (family: Cichlidae), for example, are free from parasites in their native habitat. However, tilapia populations were infected by immature monogeneans, such as *Neobenedenia melleni*, when tilapia were introduced and reared in the Caribbean (Bunkley-Williams & Williams, 1994).

It has been suggested that of all animals, fish host the most diverse parasite fauna (Poulin & Morand, 2000). In New Zealand, a number of non-indigenous freshwater fish species, including mosquitofish (*Gambusia affinis*) and koi carp (*Cyprinus carpio*), have established and had severe impacts on the native aquatic fauna (Pearson, 2005).

1.5 New Zealand Introduced Freshwater Fishes

Globally, fish have been introduced into aquaculture for food production (51%), as ornamental fish (21%), for sport fishing (12%) and fisheries (7%) (Gozlan, et al., 2010). The introduction of freshwater fish into New Zealand started in the 1860s, following European settlement (McDowall, 1990). More than 20 non-indigenous fish species have become established in New Zealand (McDowall, 1980; McDowall, 1990) (Table 1), although 11 of these species have restricted distributions (Champion, Clayton, & Rowe, 2002). Two species are restricted to geothermal waters, guppies (*Poecilia reticulate*) and sailfin molly (*Poecilia latipinna*) (Champion, et al., 2002). Of the remaining introduced species, some are valued for recreational fishing (for example, brown trout, *Salmo trutta*, rainbow trout, *Oncorhynchus mykiss*, and perch, *Perca fluviatilis*), while others are considered pests (such as catfish, *Ameiurus nebulosus*, rudd, *Scardinius erythrophthalmus*, goldfish, *Carassius auratus*, koi or European carp, *Cyprinus carpio*, and mosquitofish, *Gambusia affinis*; (Champion, et al., 2002). These five pest fishes are the major focus of my study. Except for trout, the parasite fauna of New Zealand introduced fish species has not been extensively investigated (Hine, Jones, & Diggles, 2000).

Table 1. Established non-indigenous freshwater fish species in New Zealand (McDowall, 1980; McDowall, 1990)

Family	Species
Cyprinidae	Tench (*Tinca tinca*)
	Rudd (*Scardinius erythrophthalmus*)
	Goldfish (*Carassius auratus*)
	Koi or European carp (*Cyprinus carpio*)
	Orfe (*Leuciscus idus*)
	Grass carp (*Ctenopharyngodon idella*)
	Silver carp (*Hypophthalmichthys molitrix*)
Poeciliidae	Mosquitofish (*Gambusia affinis*)
	Guppy (*Poecilia reticulata*)
	Sailfin molly (*Poecilia latipinna*)
	Green swordtail (*Xiphophorus helleri*)
Percidae	Perch (*Perca fluviatilis*)
Salmonidae	Brown trout (*Salmo trutta*)
	Rainbow trout (*Oncorhynchus mykiss*)
	Atlantic salmon (*Salmo salar*)
	American brook trout (*Salvelinus fontinalis*)
	Lake trout (*Salvelinus namaycush*)
	Quinnat salmon (*Oncorhynchus tshawytscha*)
	Sockeye salmon (*Oncorhynchus nerka*)
Ictaluridae	Catfish (*Ameiurus nebulosus*)

1.7 Thesis objectives

Introduced fish species have adversely impacted New Zealand's native organisms (Pearson, 2005). However, few studies have been conducted on these species to investigate their parasite fauna and whether their success is potentially due to parasite release. According to Hewitt & Hine, (1972) and Hine et al., (2000), no more than 50% of the New Zealand freshwater fishes have been systematically examined for parasites.

My specific objectives are to:

1) Conduct a literature review to determine the currently know parasite fauna of the introduced freshwater fish species in New Zealand.

2) Study intensively to compare the parasite fauna of mosquitofish and common bullies.

3) Determine the parasites hosts, introduced koi carp, goldfish, catfish and rudd in the Auckland, Northland, Rotorua and Waikato region.

4) Investigate variation in the parasite fauna of mosquitofish and common bullies in different regions.

5) Compare the parasite fauna of several introduced fish species in their native range with that in their introduced ranges to see if these species have been released from their parasites and to see if they acquire new parasites after the introduction.

1.8 Hypotheses

1. Introduced fish will have fewer parasites in New Zealand than in their native ranges.

   Introduced fish will have fewer parasites than similar sized native fish within the same habitat, as introduced fish are released from their native parasites and they will not acquire new parasites (i.e., native common bullies will have more parasites than the introduced mosquitofish).

2. Parasites which are generalist are more likely to establish in a new environment when they are introduced with their hosts than specialists.

3. Fish from different regions in New Zealand will have a different parasite fauna, and fish hosts should have higher parasite diversity at their first release site comparing with later release sites.

Chapter 2: Materials and Methods

2.1 Parasite checklist

Metazoan parasite species were focused in my study as they are more diverse, easier to handle and identify, and pose a greater impact to hosts than protozoan parasite species (Pearson, 2005). A literature search identified the metazoan parasite species that were recorded from the twenty non-indigenous freshwater fish established in New Zealand: tench (*Tinca tinca*), rudd (*Scardinius erythrophthalmus*), goldfish (*Carassius auratus*), koi or European carp (*Cyprinus carpio*), orfe (*Leuciscus idus*), grass carp (*Ctenopharyngodon idella*), silver carp (*Hypophthalmichthys molitrix*), mosquitofish (*Gambusia affinis*), guppy (*Poecilia reticulate*), sailfin molly (*Poecilia latipinna*), green swordtail (*Xiphophorus helleri*), perch (*Perca fluviatilis*), brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), Atlantic salmon (*Salmo salar*), American brook trout (*Salvelinus fontinalis*), lake trout (*Salvelinus namaycush*), quinnat salmon (*Oncorhynchus tshawytscha*), sockeye salmon (*Oncorhynchus nerka*) and catfish (*Ameiurus nebulosus*) ((McDowall, 1980; McDowall, 1990). Records were collated for their home ranges, New Zealand and some other introduced ranges. The parasite fauna of New Zealand native freshwater fish were summarised to make comparisons with those introduced freshwater fishes. A comparative host-parasite checklist was generated.

The books used were:

1) *Parasite of North American Freshwater Fishes* (Hoffman, 1999) was used to identify North American freshwater fish parasites.
2) *Checklist of parasites of New Zealand fishes and of their hosts* (Hewitt & Hine, 1972) and *A checklist of the parasites of the New Zealand fishes, including previously unpublished records* (Hine, et al., 2000) were used to identify parasites of New Zealand freshwater fishes

The online databases used were:

1) JSTOR (http://www.jstor.org);
2) ISI Web of Science (Thomson Reuters Web of Knowledge;

http://apps.webofknowledge.com);

3) Science Direct (http://www.sciencedirect.com);
4) Google Scholar (http://scholar.google.com);
5) Wiley Online Library (http://www.wiley.com)

The search terms used were:

1) Freshwater fish and parasite;

3) Parasite checklist and freshwater and fish;

4) Parasite checklist and (introduce* or invas* or alien) fish;

2.2 Fish sampling

2.2.1 Study fish

2.2.1.1 Mosquitofish (*Gambusia affinis* Baird and Girard 1853)

Mosquitofish, the major freshwater fish species focused during my study, are the most widely established and abundant non-indigenous freshwater fish found in New Zealand aquatic ecosystems (McDowall, 1978).

Mosquitofish originate from Central America (Baker, Rowe, & Smith, 2004; Bisazza, Santi, & Vallortigara, 1999; McDowall, 1978; Speirs, 2001), and have now been introduced into many continents (McDowall, 1978; Smith et al., 2011). Mosquitofish belong to the family Poecilidae. They have extremely high tolerance of harsh environmental conditions; they can live in water with temperatures from near freezing up to 44 ℃, salinities up to twice that of sea water, and among pollutants and pesticides (Chen, Lin, & Chen, 2008; McDowall, 2000). Mosquitofish are live-bearing fish, which range in size from 35 mm to 60 mm, with females larger than males (Chen, et al., 2008).

Mosquitofish were first introduced into New Zealand from Hawaii in 1930 and released into a pond in the Auckland Domain. The first release into the wild in New Zealand was in 1933, into Lake Ngatu in Northland (McDowall, 1978). Adverse effects of mosquitofish in New Zealand are competition for space and food with native fishes, such as inanga (*Galaxias maculatus* and *G. gracilis*) (Ling, 2004), smelt (*Retropinna retropinna*), and the common bully (*Gobiomorphus cotidianus*) which has reduced the numbers of these native fish species (McDowall, 1978; Speirs, 2001). Mosquitofish were also found to prey on mudfish (*Neochanna* spp.) fry and affect their recruitment (Ling, 2001, 2004).

Mosquitofish were transferred around New Zealand for mosquito control and the spread was thus mostly deliberate (Champion, et al., 2002). Mosquitofish are widely spread in the North Island with major concentrations around Northland, Auckland and north of Waikato. No records have been reported on the occurrence of mosquitofish in the South Island, except Nelson (Champion, et al., 2002;

Council, 2008; McDowall, 2000).

Poeciliidae are vulnerable to many types of parasite infections as a result of the diverse habitats they occupy (Deaton, 2011). Mosquitofish are considered to have a diverse parasite fauna in North America (Hoffman, 1999). For example, the nematode *Eustrongylides ignotus* was reported to heavily infect some Texas and Oklahoma mosquitofish populations (Deaton, 2009) Brock & Font (2009) found eight flatworms (Platyhelminthes) on mosquitofish in Louisiana, USA: *Ascocotyle ampullacea*, *Ascocotyle mcintoshi*, *Ascocotyle tenuicollis*, *Phagicola diminuta*, *Phagicola* sp., *Echinochasmus swartzi*, *Posthodiplostomum minimum*, and *Glossocercus* sp. The Asian trematode *Centrocestus formosanus* has been found on mosquitofish in a non-indigenous population in China (Chen, et al., 2008; Zeng, Liao, Nie, & Wang, 2005). However, no parasites have been reported to infect mosquitofish in New Zealand to date, although this may be due to the inadequate sampling.

2.2.1.2 Other introduced fishes in New Zealand

Koi carp (*Cyprinus carpio*; Linnaeus 1758) originated from Eurasia, but are now distributed worldwide in tropical and warm climates (McDowall, 1990). Carp were first introduced to New Zealand in the 1960s as an ornamental "aquarium" fish (Speirs, 2001). Carp are currently present in small lakes in the North Island and Nelson in the South Island (Champion, et al., 2002). Large populations are known from the lower Waikato River and around Auckland. Koi carp prefer stable waters, such as weedy ponds, river backwaters and lake margins. They tolerate poor water quality (Speirs, 2001).

Goldfish (*Carassius auratus*; Linnaeus 1758) are native to eastern Asia and were first introduced into New Zealand in 1864 and 1868 (McDowall, 1978). They can be found in many New Zealand lakes and ponds in North Island. Only isolated populations have been reported in South Island (Champion, et al., 2002). Goldfish are omnivores that prefer slow flowing water; and are widespread in New Zealand but only locally abundant (McDowall, 1990; McDowall, 2000). They do not appear to have serious deleterious effect on the native flora and fauna (Speirs, 2001).

North American brown bullhead catfish (*Ameiurus nebulosus*; Lesueur 1819) is the only catfish introduced to New Zealand (McDowall, 1978). This species is native to southern Canada and northern United States of America and was introduced to New Zealand from California in 1877 with no specific purpose, and it has no contemporary usage (McDowall, 1978). It has been suggested that this catfish was first introduced to Lake St John, Auckland in 1878, and later released into other streams and rivers (Speirs, 2001). Catfish are now found mostly in North Island lakes and rivers, and a few lakes in the South Island (Champion, et al., 2002). Catfish feed on invertebrates, plant matter and small fishes (McDowall, 2000). They compete with native fish for space and food (Speirs, 2001).

Rudd (*Scardinius erythrophthalmus*; Linnaeus 1758) originate from cooler ranges of Western Europe to the Caspian and Aral Sea basins (Fuller, Nico, & Williams, 1999). Rudd are mostly carnivorous, feeding on small invertebrates and fishes (McDowall, 2000). The first introduction of rudd into New Zealand was illegal, in the 1960s, in an attempt to create a coarse fishery. At present rudd are distributed throughout rivers and lakes in the North Island and Canterbury in the South Island (Speirs, 2001).

Many non-indigenous fishes in New Zealand have had deleterious effects on native freshwater ecosystems (Champion, et al., 2002). Species like catfish, rudd, koi carp and mosquitofish can tolerate harsh environmental conditions, thus they have an extensive distribution and their abundance is increasing. The distinct feeding strategy of koi carp of sucking up bottom or bank sediments and filtering out organic particles increases water turbidity and weakens river banks as well as prevents re-establishing the plant communities (Hamill, 2006). Rudd is a voracious consumer of aquatic plants especially native macrophytes resulting in the destruction of macrophyte communities (Speirs, 2001). Catfish have reduced eel populations through competition for food, and perch have reduced the abundance of small native fish in lakes and indirectly affected other top predators such as eels (Flecker & Townsend, 1994).

2.2.1.3 Common bully (*Gobiomorphus cotidianus* McDowall)

Common bullies are small freshwater benthic fish which is native to New Zealand coastal freshwater aquatic environments (Closs, Smith, Barry, & Markwitz, 2003; McDowall, 2000; Rowe, Nichols, & Kelly, 2001; Wilhelm, Closs, & Burns, 2007). They are found in many New Zealand lakes, streams and rivers (McDowall, 2000). Common bullies are naturally riverine and males establish and guard the territories (McDowall, 2000). Larval common bullies are planktonic spending three to four months in the sea after hatching in freshwater and feeding on zooplankton (McDowall, 2000; Rowe, 1999). However, landlocked populations are also present in many New Zealand lakes (Closs, et al., 2003; McDowall, 2000). Adult common bullies feed on many invertebrates (Closs, et al., 2003; McDowall, 2000; Rowe, 1999; Rowe, et al., 2001). Trout, salmons and eels were reported to prey on common bullies (Wilhelm, et al., 2007).

Mosquitofish are frequently encountered by common bullies as both species occupy the littoral zone of lakes and rivers (Champion, et al., 2002; Rowe, 1999; Wilhelm, et al., 2007). In the research I compared the parasite fauna of the two species.

Eight species of parasites have been reported from common bullies in New Zealand, which include five digeneans *Coitocaecum parvum*, *Coitocaecum zealandicum*, *Deretrema philippae*, *Stegodexamene anguillae* and *Telogaster opisthorchis*, two cestodes *Amurotaenia decidua* and *Ligula intestinalis*, and one acanthocephale *Acanthocephalus galaxii* (Hine, et al., 2000).

2.2.2 Locations

Mosquitofish (*Gambusia affinis*) and common bullies (*Gobiomorphus cotidianus*) were sampled in four regions of the North Island, New Zealand in 2011. Six lakes in the Waikato region were sampled monthly between May to September; two lakes in the Auckland region were sampled on 23 and 30 September; six lakes in the Northland region were sampled on 28, 29 and 30 September; and five lakes in the Rotorua region were sampled at 22 September (Figure 1). Lakes were chosen to cover a range of different lake types, size and trophic states; for their presence of both common bullies and mosquitofish; and the accessibility to the water.

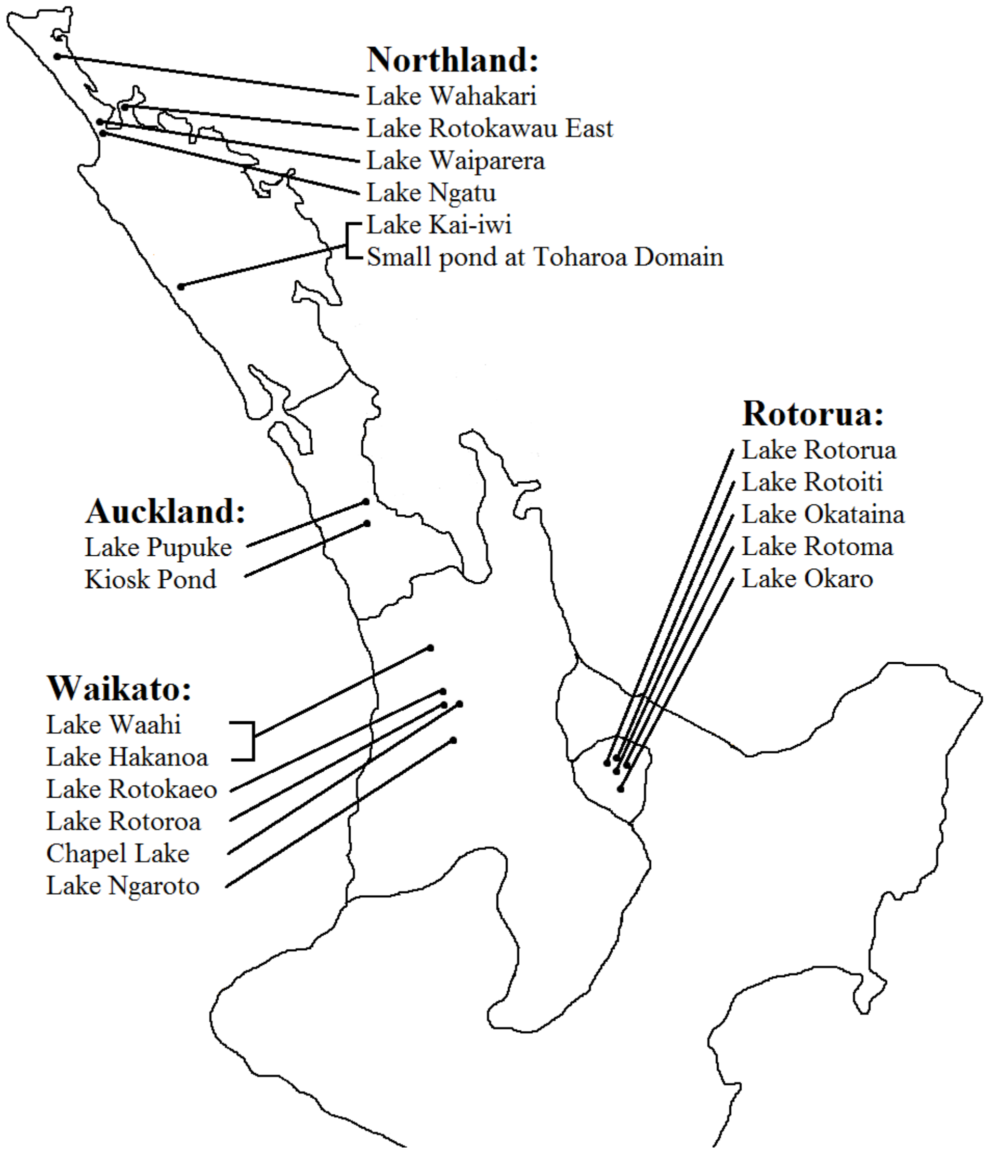

Figure 1. Map of North Island, New Zealand showing the approximate locations of sampled lakes (modified from Department of Conservation, 2012).

2.2.2.1 Waikato Region

a) Chapel Lake (37”47’18.30” S, 175”18’53.64” E, 51 metres above sea level; Google Earth, 2012) is a relatively small lake (0.44 ha) located at the University of Waikato with a maximum depth of 1.8 metres. Campus Lake contains catfish, common bullies, short-finned eels and mosquitofish (Hicks & Bryant, 2002) Figure 2).

Figure 2. Chapel Lake (cross marks the sample sites; Google Maps, 2012).

b) Lake Rotokaeo (37”46’24.90” S, 175”15’00.97” E, 41 metres above sea level; Google Earth, 2012) is a shallow lake with a surface area of 3.7 ha. Most parts of the lake are less than 1.8 metres deep. Goldfish, catfish, short-finned eels and mosquitofish have been found in the lake (Hicks, Brijs, & Bell, 2009) Figure 3).

Figure 3. Lake Rotokaeo (cross marks the sample sites; Google Maps, 2012).

c) Lake Ngaroto (37”57’18.37” S, 175”16’53.67” E, 37 metres above sea level; Google Earth, 2012) is heavily used for recreation such as power boating. Lake Ngaroto is a hypertrophic peat lake (Hicks, Reynolds, Jamieson, & Laboyrie, 2001), with an area of 24.9 ha and a maximum depth of 6.7 metres. Introduced fish recorded from this lake are goldfish, koi carp, catfish, rudd and mosquitofish. Native fish recorded are common bullies, smelt, longfin and shortfin eels (Edwards, Clayton, & Winton, 2005; Hicks, et al., 2001; LERNZ, 2011) (Figure 4).

Figure 4. Lake Ngaroto (cross marks the sample sites; Google Maps, 2012).

d) Lake Rotoroa (Hamilton Lake; 37”45’57.19”S, 175”16’31.58” E, 37 metres above sea level; Google Earth, 2012) is a eutrophic urban peat lake with an area of 54 ha and a maximum depth of six metres (T. Edwards, et al., 2005; T. Edwards, Winton, & Clayton, 2010). Introduced fish species recorded from Lake Rotoroa are catfish, rudd, perch, tench, goldfish and mosquitofish (Clayton & Winton, 1994; LERNZ, 2011). Lake Rotoroa is the most urbanized lake in the Waikato Region (Figure 5).

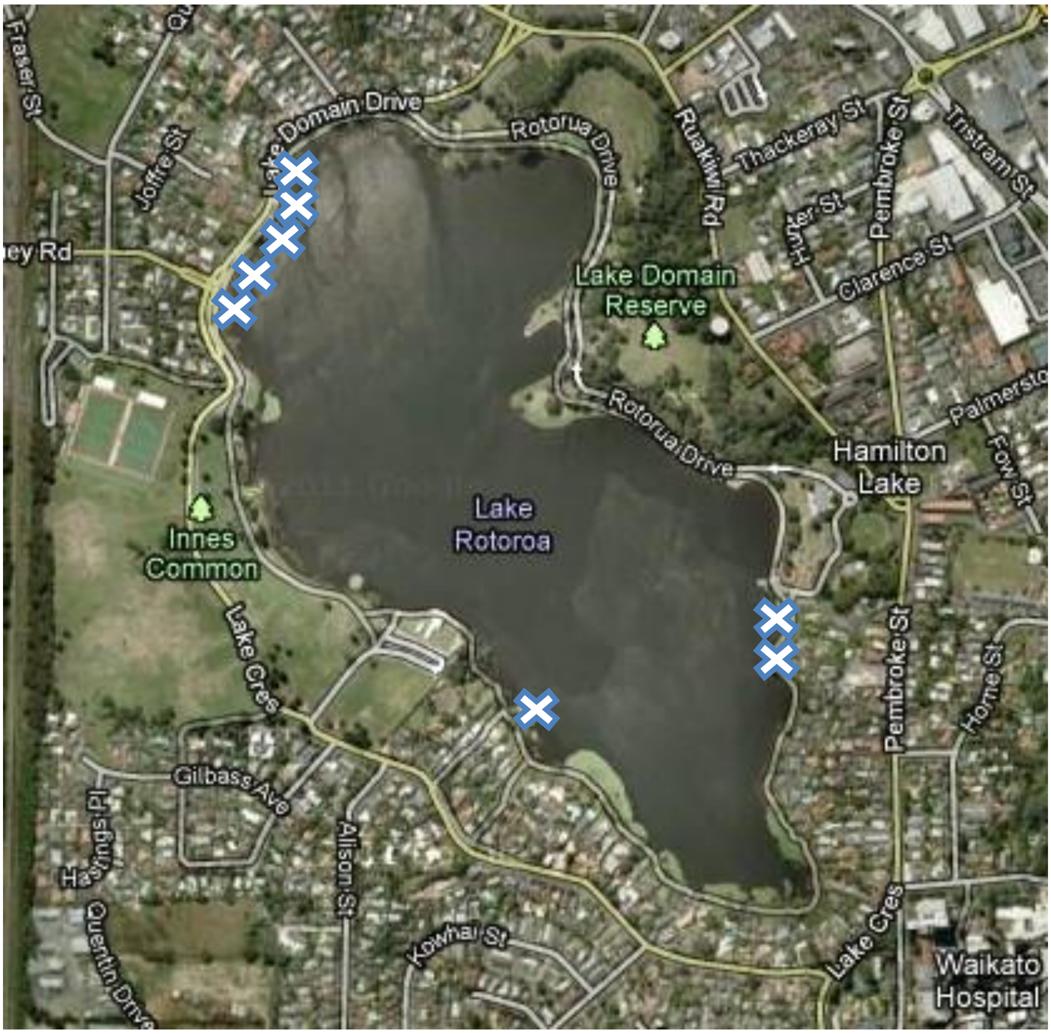

Figure 5. Lake Rotoroa (cross marks the sample sites; Google Maps, 2012).

e) Lake Hakanoa (37”33’07.78” S, 175”10’09.49” E, 9 metres above sea level; Google Earth, 2012) is a riverine lake with a size of 56 ha and a maximum depth of 2.5 metres (Edwards, et al., 2005; Edwards, et al., 2010) (Figure 6).

Figure 6. Lake Hakanoa (cross marks the sample sites; Google Maps, 2012).

f) Lake Waahi (37”33’43.19” South, 175”07’30.23” East, 5 metres above sea level; Google Earth, 2012) is a riverine hypertrophic lake. It has a size of 537 ha and a maximum depth of 5 metres (Edwards, et al., 2005; Edwards, et al., 2010). Lake Waahi has been surffering from high level of suspended sediment due to coal mining discharge. Catfish, mosquitofish and few species of carps have been found in the lake (Hayes, Rutledge, Chisnall, & Ward, 1992; LERNZ, 2011) (Figure 7).

Figure 7. Lake Waahi (cross marks the sample site; Google Maps, 2012).

2.2.2.2 Auckland Region

a) Kiosk Pond (36”51’35.32” S, 174”46’21.51” E, 58 metres above sea level; Google Earth, 2012) has a surface area of less than 0.1 ha. Mosquitofish and goldfish were found in the pond (Spiller & Forsyth, 1970). Kiosk Pond was the first release site of mosquitofish (McDowall, 1978) (Figure 8).

Figure 8. Kiosk Pond at Auckland Domain (cross marks the sample sites; Google Maps, 2012).

b) Lake Pupuke (36”46’48.67” S, 174”45’57.93” E, 1 metre above sea level; Google Earth, 2012) is a eutrophic crater lake with a size of 110 ha and a maximum depth of 57 metres (Cassie, 1989; Duggan & Barnes, 2005) (Figure 9).

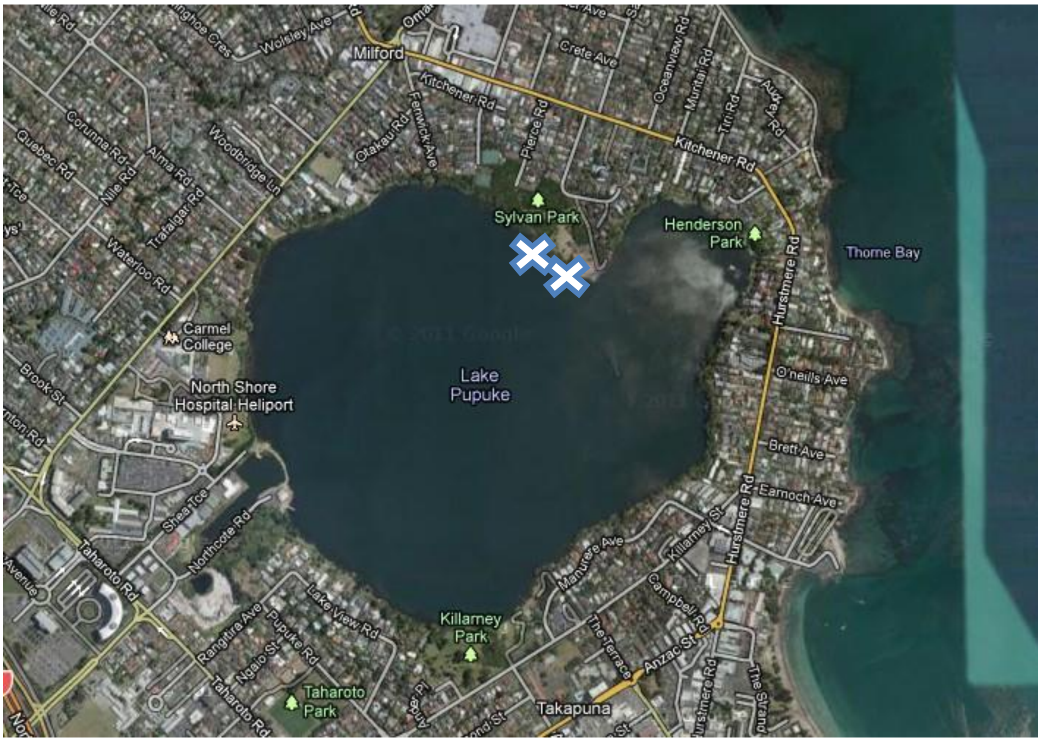

Figure 9. Lake Pupuke (cross marks the sample sites; Google Maps, 2012).

2.2.2.3 Northland

a) Lake Kai-iwi (35”48’52.49” South, 173”39’13.79” East, 76 metres above sea level; Google Earth, 2012) is a mesotrophic dune lake with a surface area of 22.6 ha and a maximum depth of 16 metres (Northland Regional Council, 2008). The fish species present include common bullies, rudd, mosquitofish, and a stocked population of rainbow trout (Wells, Champion, Winton, Edwards, & Whiting, 2006) (Figure 10).

Figure 10. Lake Kai-iwi (cross marks the sample sites; Google Maps, 2012).

b) A small pond at the Taharoa Domain (35”48’47.66” South, 173”38’47.01” East, 76 metres above sea level; Google Earth, 2012) with a surface area of less than 2 ha was sampled (Figure 11).

Figure 11. Small pond at the Taharoa Domain (red marks the shoreline; cross marks the sample site; Google Maps, 2012).

c) Lake Ngatu (35”01’55.04” South, 173”11’51.85” East, 36 metres above sea level; Google Earth, 2012) is a 50.3 ha mesotrophic dune lake with a maximum depth of 6.5 metres. It contains common bullies, mosquitofish, rudd, goldfish and rainbow trout (Ball, Pohe, & Winterbourn, 2009; Wells, et al., 2006) (Figure 12).

Figure 12. Lake Ngatu (cross marks the sample sites; Google Maps, 2012).

d) Lake Wahakari (34”39’11.49” South, 172”55’28.64” East, 47 metres above sea level; Google Earth, 2012) has a surface area of 84.4 ha and a maximum depth of 12 metres. It is a mesotrophic lake (Northland Regional Council, 2008). Common bullies and mosquitofish are present in this lake (Wells, et al., 2006) (Figure 13).

Figure 13. Lake Wahakari (crosses marked were individual sample site; Google Maps, 2012).

e) Lake Waiparera (34”56’42.72” South, 173”10’46.86” East, 34 metres above sea level; Google Earth, 2012) is a eutrophic lake with a surface area of 103 ha and a maximum depth of 6 metres (Ball, et al., 2009); Northland Regional Council, 2008). The fish species present in Lake Waiparera are common bullies, eels, mosquitofish and goldfish (Wells, et al., 2006) (Figure 14).

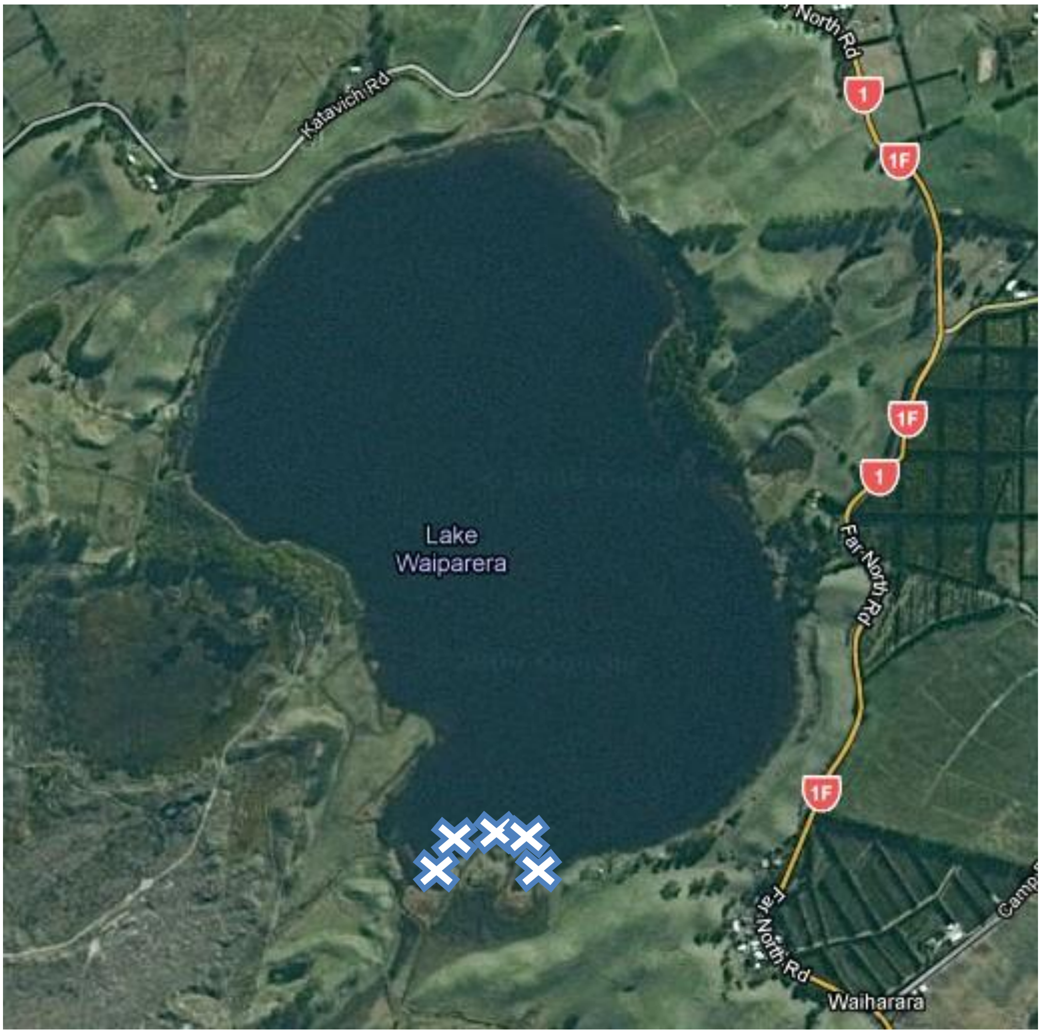

Figure 14. Lake Waiparera (cross marks the sample sites; Google Maps, 2012).

f) Lake Rotokawau East (34”52’17.81” South, 173”19’11.03” East, 5 metres above sea level; Google Earth, 2012) is a very shallow (< 1 metre) hypertrophic lake with a surface area of 21.3 ha (Northland Regional Council, 2008). Fish species which have been recorded from this lake include common bullies, eels and mosquitofish (Wells, et al., 2006) (Figure 15).

Figure 15. Lake Rotokawau East (cross marks the sample sites; Google Maps, 2012).

2.2.2.4 Rotorua Region

a) Lake Rotorua (38”04’41.87” South, 176”15’59.50” East, 293 metres above sea level; Google Earth, 2012) is a large eutrophic urban lake. It has a surface area of 8100 ha and a maximum depth of 45 metres. The water quality is very poor (Allan, Hicks, & Brabyn, 2007; Burns, McIntosh, & Scholes, 2009; Scholes, 2004; LERNZ, 2011; Parliamentary Commissioner for the Environment, 2006) (Figure 16).

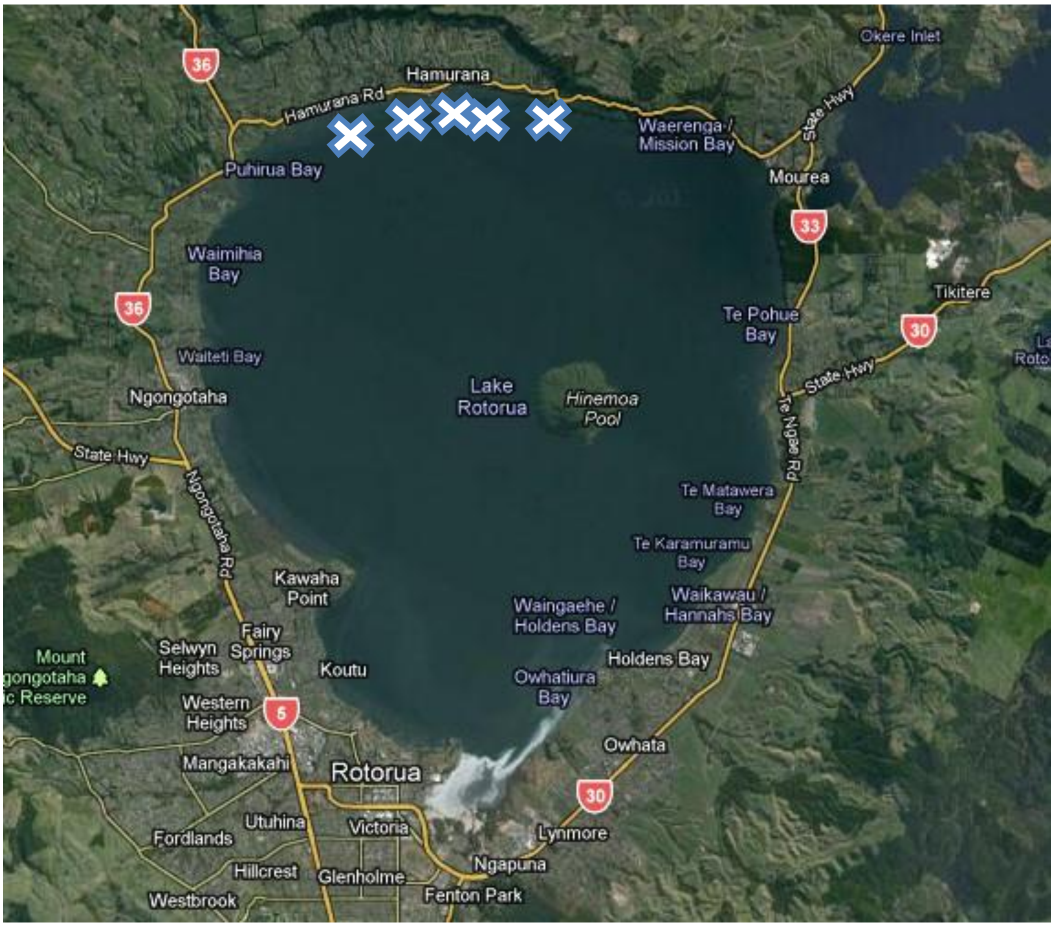

Figure 16. Lake Rotorua (cross marks the sample sites; Google Maps, 2012).

b) Lake Okaro (38”17’58.54” South, 176”23’40.91” East, 416 metres above sea level; Google Earth, 2012) is a eutrophic lake with a surface area of 32 ha and a maximum depth of 18 metres (Allan, et al., 2007; Burns, et al., 2009; Scholes, 2004). The nutrient level is very high due to geothermal activity, remobilisation from the bottom sediments and inputs from sounding farmland (LERNZ, 2011) (Figure 17).

Figure 17. Lake Okaro (cross marks the sample sites; Google Maps, 2012).

c) Lake Rotoiti (38”02’05.36” South, 176”25’25.42” East, 275 metres above sea level; Google Earth, 2012) is a eutrophic lake with a surface area of 3460 ha and a maximum depth of more than 90 metres (Allan, et al., 2007; Burns, et al., 2009; Scholes, 2004) (Figure 18).

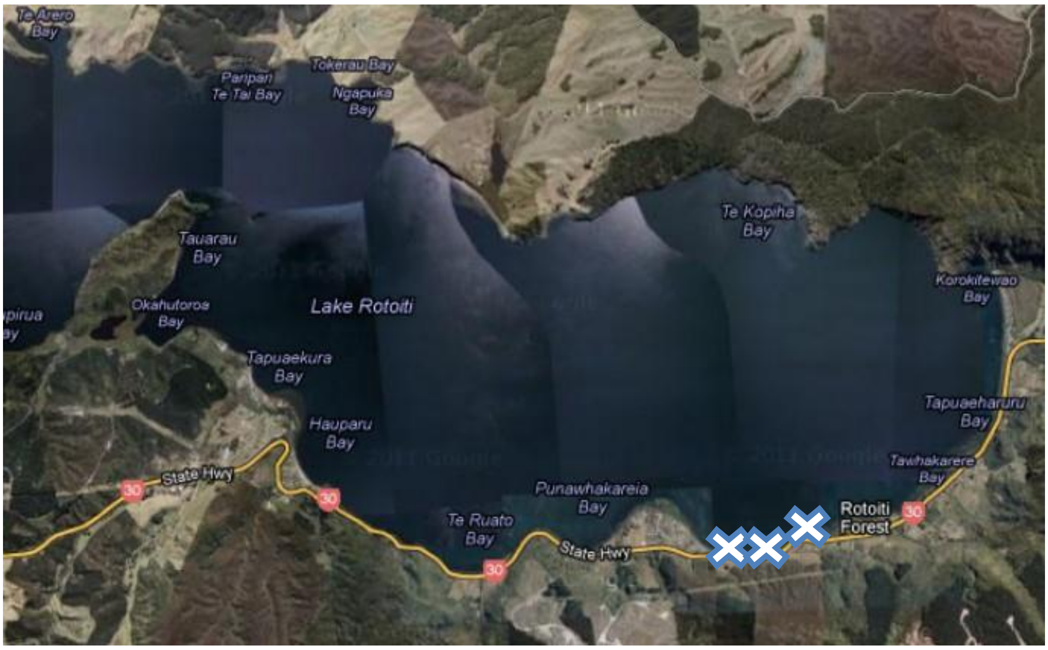

Figure 18. Lake Rotoiti (cross marks the sample sites; Google Maps, 2012).

d) Lake Rotoma (38”03’02.13” South, 176”35’07.09” East, 315 metres above sea level; Google Earth, 2012) is an oligotrophic lake with a surface area of 1100 ha and a maximum depth of 83 metres (Allan, et al., 2007; Burns, et al., 2009; Scholes, 2004) (Figure 19).

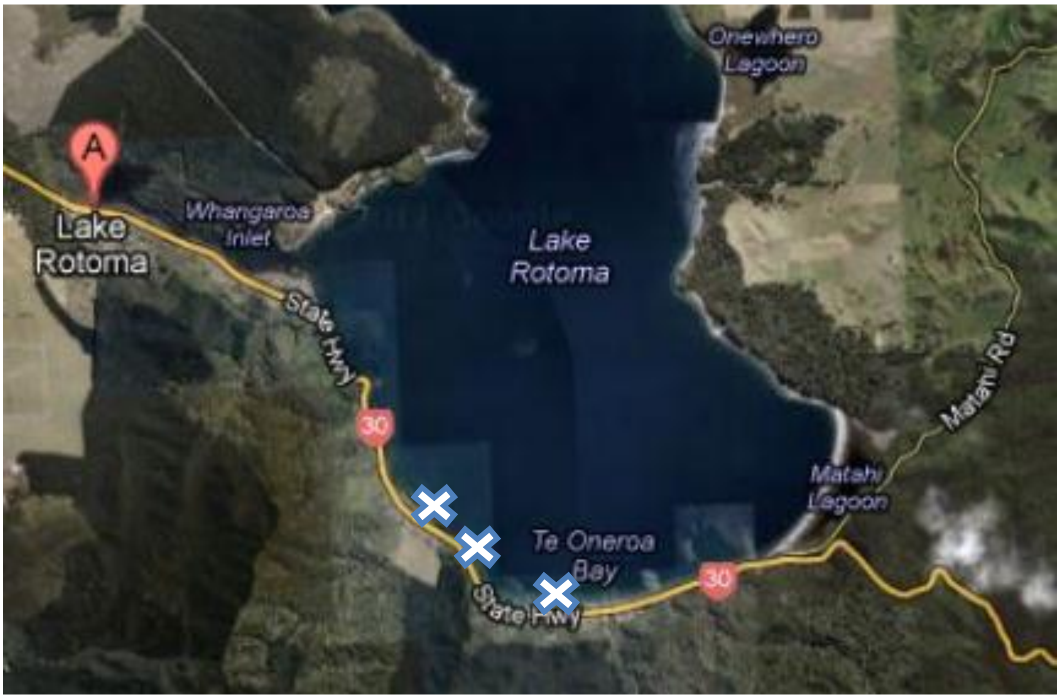

Figure 19. Lake Rotoma (cross marks the sample sites; Google Maps, 2012).

e) Lake Okataina (38”05’59.75” South, 176”25’48.88” East, 382 metres above sea level; Google Earth, 2012) is an oligotrophic lake with a surface area of 1100 ha and a maximum depth of 78.5 metres (Allan, et al., 2007; Burns, et al., 2009; Scholes, 2004) (Figure 20).

Figure 20. Lake Okataina (cross marks the sample sites; Google Maps, 2012).

2.2.3 Sampling Methods

Minnow traps (42 cm × 25 cm × 25 cm, mesh size 2 mm) were set from the banks of the lakes and rivers and were baited with marmite (Sanitarium, New Zealand) to catch common bullies. Minnow traps were set for four hours or overnight when possible. Small catfish, rudd and eels were occasionally caught. Mosquitofish and small common bullies were caught by using scoop nets swung just under the surface of the water. At least 100 mosquitofish and bullies were collected at each lake where possible. Occasionally small catfish and rudd were caught in the minnow traps. Fish were killed and placed in 50 mL conical tubes (Corning Incorporated, Mexico) or plastic bags and transported back to the laboratory for processing.

Alive and freshly killed catfish, goldfish, rudd and koi carp were obtained from Waikato River (Huntly), Lake Ohinewai and a small stream between Lake Waikare and Lake Ohinewai.

Fish were measured in the laboratory. The total length of fish was measured to the nearest 0.5 mm and the net weight of fish was measured immediately after being killed to the nearest 0.001 g. The sex of mosquitofish and common bullies was recorded. Presence of the modified anal fin, gonopodium on male mosquitofish easily distinguished male mosquitofish from the female (Figure 21; (McDowall, 1978, 2000). Male common bullies have bigger fins and blunter snout, and are darker than the female, and the outer margin of male common bullies' first dorsal fin is often orange (McDowall, 2000).

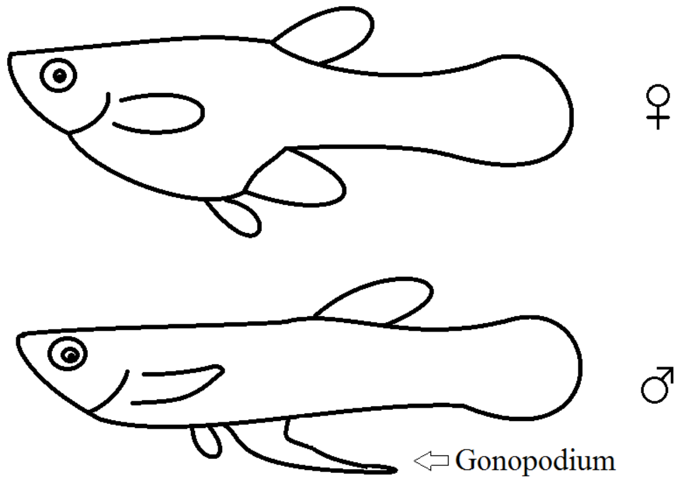

Figure 21. Diagram of male (♂) and female (♀) mosquitofish.

2.2.4 Parasite examination

Larger fishes (> 10 cm), such as koi carp, gold fish, large catfish and rudd, and a sub-sample (10%; random selected) of mosquitofish and common bullies, were examined for parasites by using the method of Hoffman (Hoffman, 1999). Dead fish were submerged in water in a dish and were examined by using a 40X dissection microscope. If the fish was large, fins were removed. Gills were removed and examined with 40X dissection microscopes and 1000X compound microscope. Viscera were removed and placed in saline under the dissection microscope and organs were teased apart with forceps. The gastrointestinal tracts of small fish were opened under the dissection microscope. For the gastrointestinal tracts of larger fish, the wall was scraped to remove the contents. The contents were then suspended in saline, shaken, and the parasites were allowed to settle in a conical or cylindrical container. The fluid was removed after five to 10 minutes, leaving the parasites on the bottom. This process was repeated until the liquid was clear. The sediment was then poured into a small petri dish to be examined under the dissection microscope for parasites.

Fish muscle tissue was teased apart carefully and was examined for parasites under a dissection microscope. The eyes and the brain were removed and examined. The head was cut lengthwise to remove the brain. The mouth and oesophagus were placed in water. The inside of the mouth and oesophagus was examined under the dissection microscope. All ecto-parasites were observed alive in chlorine-free tap water, and most internal parasites were observed in physiological saline.

Parasites found were counted for each fish and were preserved in alcohol (90%). Parasitic worm length was measured to nearest 0.5 mm. Parasites were identified following the book *Parasite of North American Freshwater Fishes* (Hoffman 1999).

2.2.4.1 Digestion Methods

A digestion method to remove fish tissue as suggested by Hoffman (1999) was used to detect metazoan parasites especially trematode and nematode larvae in mosquito fish, common bullies, small rudd and catfish (< 10 cm). The fish were digested in a 0.5% w/v solution of pepsin (United States Biochemical Corporation, Cleveland, USA) and 0.5% hydrochloric acid in water. The body cavity of the fish was cut open (individual organs were digested separately when necessary) and placed in a 50 mL conical tube (Corning, Mexico). Twenty mL of the pepsin HCl solution was added per 1 g of fish and the tissues were incubated at 37 – 39 ^{o}C for one to two hours in a water bath shaker until the tissues had completely disintegrated. Tubes were checked every 10 minutes for the presence of parasites for up to two hours. The digested materials were strained through a wire tea strainer (mesh size 1 mm) to remove bones and undigested particles. The digested tissues were allowed to stand for about 15 minutes until the parasites fell to the bottom of the tube and the supernatant was then removed. Saline (0.9%) was added to the debris until the solution was clear. The concentrated parasites were then poured into a small petri dish and were examined under the dissection microscope (80X).

2.3 Data analysis

Statistica 7 (StatSoft, Inc., 2004) was used to analyse all data in order to run statistical tests and to create graphs. Mean total length and weight, and sex ratios of sampled fishes were calculated for all lakes. Standard deviation (SD) was used as the measure of variability.

The parasite infections of sampled fish were compared locally (i.e. within lakes) and regionally (i.e. among lakes). Two parameters were used to characterise parasite infection: prevalence (proportion of fish which were infected by parasites) and mean intensity (number of parasites found / number of infected fish; (Bush, Lafferty, Lotz, & Shostak, 1997).

The number of fish caught varied between different lakes, especially for common bullies. Therefore Turkey's Honestly Significant Difference (HSD) Test was used to compare number of parasites between New Zealand native and non-indigenous freshwater fishes; fish length and weight between different lakes and regions; infected fish length and weight between different lakes; and parasite fauna between different lakes. Probability values (p) less than 0.01 were considered as statistically significant.

Kolmogorov-Smirnov Test was used to examine the normality of the data. Data that were not normally distributed were log (ln or $\log_e$) transformed before plotting.

Scatter plots were used to examine the relationship between the number of parasites harboured and the size of the fish (length and weight). Correlation coefficients (r) and coefficients of determination (r^2) were calculated by using Statistica 7 (StatSoft, Inc., 2004) to show the strength of the linear relationship; r or r^2 value equal to one indicates a perfect linear fit and r or r^2 values equal to zero means there is no linear relationship between the two variables (Brown, 2003).

Chapter 3: Results

3.1. Parasite Checklist

Metazoan parasites of the twenty non-indigenous freshwater fish species with established populations in New Zealand were recorded from literature review, which include parasite fauna of the native range, New Zealand and some other introduced ranges (Figure 22; Appendices 1-20). The recorded parasites were taxonomically diverse, and included representatives from the Phyla Cnidaria, Platyhelminthes, Nematoda, Nematomorpha, Acanthocephala, Annelida, Mollusca, Arthropoda and Chordata (Appendix 20). Parasites reported from Canada, United States of America (USA) and Mexico were included under North America.

In eight out of thirteen comparable data sets, the host fishes had greater numbers of parasite species recorded from their native range than hosts in their introduced ranges, and North America had more parasite species than the native population for the rest five (Figure 22). North America had the highest diversity of parasite fauna of most of the fishes introduced to New Zealand (Figure 22). Parasite diversity was very different in their host's native habitat and the introduced regions. For instance, *Gyrodactylus ctenopharyngodontis* was found only on New Zealand grass carp (Hine, et al., 2000). Mosquitofish has 48 species of parasite in its native habitat, North America, but no parasite species have been recorded on hosts that were introduced to Australia, and New Zealand (Fletcher & Whittington, 1998; Hine, et al., 2000; Hoffman, 1999; Lymbery, et al., 2010). Parasite diversity of grass carp was largely reduced when being introduced from China (McDowall, 1990) into North America (Hoffman, 1999), Philippines (Arthur & Lumanlan-Mayo, 1997), Bangladesh (Chandra, 2006), Latvia (Kirjušina & Vismanis, 2007) and New Zealand. Silver carp parasite diversity was reduced when they were introduced from eastern Asian (Fuller, et al., 1999) to Bangladesh, Philippines, North America and New Zealand (Figure 22). Sailfin molly, guppy and rainbow trout have all reduced their parasite diversity when being introduced into New Zealand and other regions (Figure 22).

Only eight out of the twenty introduced freshwater fish species have been recorded to have metazoan parasites in New Zealand (Figure 22; (Hine, et al., 2000). The parasite diversity of these freshwater fishes was largely reduced in New Zealand compared with their home range, except brown trout (Figure 22; Appendices 4-20). Brown trout were found to have fifteen species of parasite in New Zealand, where only seven species of parasite were found in the native Latvian population (Figure 22; (Hine, et al., 2000; Kirjušina & Vismanis, 2007).

Digeneans, trematodes and crustaceans were the most abundant fish parasites found in New Zealand freshwater fishes (Table 2) (Hine, et al., 2000). More than one third of the freshwater fish parasite species recorded on the checklist globally belonged to the phylum Platyhelminthes (Table 2, Appendices 1-21). Within the Platyhelminthes, two thirds of the parasite species belonged to the subclass Digenea (Table 2). A number of parasite genera were shared between fish species of different locations. The most common Monogeneans were gill parasites of the genera *Dactylogyrus* and *Gyrodactylus*, which can be found on mosquitofish, catfish, a few Cyprinidae and Salmonidae species in both the introduced and the native regions (Table 2, Appendices 1-21). The most common Nematoda were in the genera *Eustrongylides* and *Contracaecum*, and *Eustrongylides* were mostly recorded from mosquitofish and a few salmonids. Only a few parasitic species of Acanthocephala were found on freshwater fish, and the genus *Acanthocephalus* was the most common Acanthocephala parasitising the fish introduced to New Zealand (Table 2, Appendices 1-21).

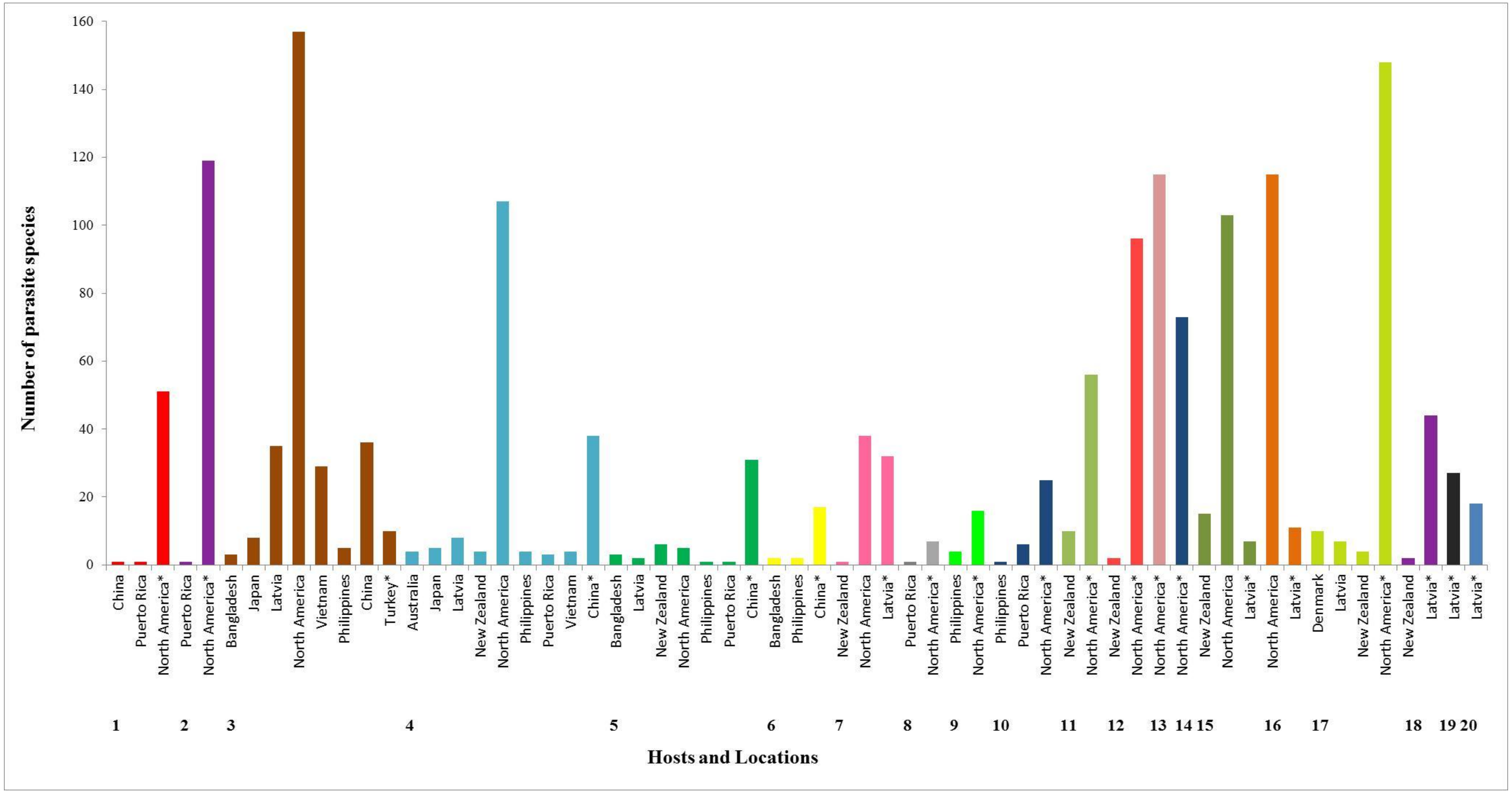

Figure 22. Parasite species diversity of different hosts over number of countries (1 = mosquitofish, 2 = catfish, 3 = koi carp, 4 = goldfish, 5 = grass carp, 6 = silver carp, 7 = tench, 8 = green swordtail, 9 = sailfin molly, 10 = guppy, 11 = quinnat salmon, 12 = sockeye salmon, 13 = American brook trout, 14 = lake trout, 15 = brown trout, 16 = Atlantic salmon, 17 = rainbow trout, 18 = perch, 19 = orfe, and 20 = rudd; location name with * refers to the native range).

Table 2. Summary of parasite species of the parasite checklist (Appendices 1-21)

Phylum	Class	Sub class/phylum	Number of parasite species
Cnidaria			1
Platyhelminthes	Trematoda	Monogenea	259
		Digenea	459
		Aspidogastrea	3
	Cestoidea		253
Nematoda			284
Nematomorpha			2
Acanthocephala			154
Annelida		Hirudinea	40
Mollusca			24
Arthropoda		Crustacea	212
		Acarina	4
Chordata		Agnatha	1

In general, the parasite diversity of freshwater fish is much lower in their introduced ranges than their native ranges. However, some parasites have been successfully established in the introduced range with their hosts (Appendices 1-20). The majority of parasites were similar between goldfish of North America and China, and between tench of Latvia and North America (Appendices 1-20). The genus *Dactylogyrus* was the most common monogenean gill parasite found on koi carp in both the native and introduced ranges, including North America (Hoffman, 1999), Asia (Chandra, 2006; Nagasawa, Urawa, & Awakur, 1987), and Europe (Kirjušina & Vismanis, 2007). *Lernaea* and *Argulus* were the most common crustaceans found on cyprinids such as koi carp and goldfish in both their native and introduced ranges (Appendices 1-20)

Some parasites were acquired at the introduced range by these hosts (Appendices 1-20). Goldfish have acquired the common New Zealand digenean trematode *Coitocaecum parvum* and tench have acquired the nematode *Eustrongylides* sp. (Hine et al., 2000). Other examples of parasites gained include catfish introduced to Puerto Rico from Canadian and the USA. They have gained a parasite, the monogenean *Cleidodiscus pricei* (Bunkley-Williams & Williams, 1994); a cestode

Bothriocephalus acheilognathi is found on grass carp in Philippines and Puerto Rico and on silver carp in Philippines (Arthur & Lumanlan-Mayo, 1997; Bunkley-Williams & Williams, 1994); and nematodes *Capillaria* sp., *Philometra* sp. and *Spiroxys* sp. on grass carp in North America (Hoffman, 1999).

Only eight out of twenty species of non-indigenous freshwater fish in New Zealand have been reported to have parasites (Table 3), and approximately half of the native freshwater fish were found to be parasitized by metazoan parasites (Table 4). Tukey's unequal *n* HSD Test was done, which showed no significant differences on parasite numbers between the native and non-indigenous species (p = 0.62).

Table 3. Total number of parasite species of New Zealand non-indigenous freshwater fish (Hine et al., 2000)

Non-indigenous freshwater fish	Number of parasites
Goldfish (Carassius auratus)	4
Grass carp (*Ctenopharyngodon idella*)	4
Rainbow trout (*Oncorhynchus mykiss*)	3
Sockeye salmon (*Oncorhynchus nerka*)	2
Chinook salmon (*Oncorhynchus tshawytscha*)	10
Red-finned perch (*Perca fluviatilis*)	2
Brown trout (*Salmo trutta*)	15
Tench (*Tinca tinca*)	1

Table 4. Total number of parasite species of New Zealand native freshwater fish (Hine et al., 2000)

Native fish species	Number of parasite species
Shortfin eel (*Anguilla australis*)	25
Longfin eel (*Anguilla dieffenbachli*)	28
Torrentfish (*Cheimarrichthys fosteri*)	1
Giant kokopu (*Galaxias argenteus*)	1
Koaro (*Galaxias brevipinnis*)	7
Dwarf galaxias (*Galaxias divergens*)	3
Banded kokopu (*Galaxias fasciatus*)	1
Inanga (*Galaxias maculatus*)	11
Short-jawed kokopu (*Galaxias postvectis*)	1
Common river galaxias (*Galaxias vulgaris*)	2
Cran’s bully (*Gobiomorphus basalis*)	2
Upland bully (*Gobiomorphus hreviceps*)	6
Common bully (*Gobiomorphus cotidianus*)	8
Giant bully (*Gobiomorphus gobioides*)	4
Blue-gilled bully (*Gobiomorphus hubbsi*)	4
Red-finned bully (*Gobiomorphus huttoni*)	4
Brown mudfish (*Neochanna apoda*)	5
Smelt (*Retropinna retropinna*)	11

3.2 Mosquitofish (Gambusia affinis)

Due to the great loss of parasites of mosquitofish in New Zealand, it is unclear whether the parasites were all lost or whether there is a lack of such study in New Zealand. Many studies have examined and discussed the invasiveness of mosquitofish and the impacts that mosquitofish have done to New Zealand native fauna, but there were rarely studies on the parasites. In my study, 1168 mosquitofish were caught from Kiosk Pond and Lake Pupuke in the Auckland region, Lakes Ngatu, Kai-iwi, Waiparera, Wahakari and a small pond at Taharoa Domain (STD) in the Northland region, and Chapel Lake, Lakes Rotokaeo, Rotoroa, Hakanoa and Ngaroto in the Waikato region (Table 5), in order to specifically examine their parasite fauna. But no parasites were found by using digestion and dissection methods.

Mosquitofish from the Northland lakes were relatively larger than those from the Auckland and Waikato, especially those from Lakes Ngatu and Kai-iwi. Fish sampled from Lakes Kai-iwi and Ngatu had the highest mean length and weight compared with the fish from other lakes. Mosquitofish from Lake Waiparera and a small pond at Taharoa Domain had the lowest mean length and weight. Tukey's unequal *n* HSD Test showed that mosquitofish from the Auckland and Waikato regions had similar length and weight ($p > 0.01$). Mosquitofish caught from the Northland lakes were significantly larger ($p < 0.01$) than both the Auckland and Waikato lakes (Tables 5 & 6).

The number of female mosquitofish caught was three times more than that of the male in the Auckland and Northland samples, but the difference between the numbers of the male and female mosquitofish in the Waikato sample was not great (Table 6).

Table 5. Summary of mosquitofish for 12 lakes (STD = Small pond at Taharoa Domain)

Location	Sample size (n)	Length (mm) ± SD	Weight (g) ± SD	Sex ratio (F:M)
Lake Pupuke	53	24 ±4.5	0.12 ±0.07	53:1
Kiosk Pond	110	22 ±2.4	0.09 ±0.03	2:1
Lake Kai-iwi	110	32 ±4.3	0.34 ±0.15	5:1
Lake Ngatu	110	29 ±5.3	0.26 ±0.19	13:1
Lake Wahakari	37	23 ±2.8	0.08 ±0.03	2:1
Lake Waiparera	110	20 ±4.5	0.10 ±0.03	3:1
STD	110	21 ±2.8	0.10 ±0.05	5:6
Chapel Lake	110	23 ±4.3	0.13 ±0.07	1:2
Lake Rotokaeo	110	21 ±3.5	0.10 ±0.04	7:9
Lake Rotoroa	102	21 ±3.4	0.11 ±0.06	7:8
Lake Hakanoa	107	24 ±2.9	0.15 ±0.06	2:1
Lake Ngaroto	99	23 ±4.4	0.12 ±0.07	6:5

Table 6. Regional differences in mosquitofish length and weight

Region	Unequal N HSD Test (*p*)	
	Length	Weight
Waikato vs. Auckland	0.820	0.227
Waikato vs. Northland	<0.001	<0.001
Auckland vs. Northland	<0.001	<0.001

3.3 Other introduced fishes

A total of 90 (19 rudd, 27 catfish, 14 goldfish and 30 koi carp) other non-indigenous fish were caught from Lakes Ngaroto, Rotoroa, Ohinewai, the Waikato River (Huntly) and a stream between Lake Waikare and Lake Ohinewai (Table 7). No metazoan parasites were found in any of the fish.

Table 7. Summary of rudd, catfish, goldfish and koi carp sampled from five locations (SWO = stream between Lake Waikare and Lake Ohinewai; n = sample size)

Fish species	Location	n	Length (mm) ± SD	Weight (g)
Rudd	Lake Ngaroto	4	86.5 ± 21.2	10 ± 3.9
	Lake Rotoroa	8	83.8 ± 3.3	6.8 ± 0.7
	Waikato River	7	212.3 ± 17.9	176.9 ± 66.2
Catfish	Lake Ngaroto	8	154.4 ± 9.4	45.6 ± 8
	Lake Rotoroa	8	121.1 ± 5	18.3 ± 2.3
	Lake Ohinewai	1	275	263
	SWO	10	240.8 ± 7.2	159 ± 15.7
Goldfish	Lake Ohinewai	7	250 ± 7.5	211.6 ± 12
	SWO	7	195.6 ± 20	137.1 ± 35.7
Koi carp	Lake Ohinewai	18	352.2 ± 23.7	720.7 ± 163.2
	SWO	12	343.3 ± 24.4	582.1 ± 107.7

3.4 Common Bullies (*Gobiomorphus cotidianus*)

A total of 576 common bullies were caught by using scoop nets and minnow traps from Lakes Okaro and Rotorua in the Rotorua region, Lakes Kai-iwi, Ngatu, Rotokawau East and Waiparera in the Northland region, and Chapel Lake, Lake Rotoroa, Lake Hakanoa and Lake Ngaroto in the Waikato region. However, the absence of common bullies from other sample sites does not indicate that other lakes do not contain common bullies; rather, they might not be captured by the methods used. Small common bullies were generally seen and caught along the shoreline and large common bullies were caught by minnow traps further away from the shoreline (personal observation).

Twenty-five per cent of common bullies were infected by parasites. Lake Rotokawau East had the highest prevalence of 100%, while common bullies from Lake Okaro and Lake Hakanoa had detected zero infections. Lake Rotorua common bullies had the highest parasite mean intensity (number of parasites per host = 32) and Lake Ngaroto and Chapel Lake had the lowest mean parasite intensity of one (Table 8).

Female common bullies were much more abundant than the male at Lake Okaro, Lake Rotorua, Lake Kai-iwi and Lake Hakanoa. The largest common bullies were found from Lake Ngatu and Lake Rotokawau East and the smallest individuals were from the Rotorua region (Table 8).

Table 8. Summary of common bullies from 10 sampled lakes (parasite prevalence refers to the number of fish infected by parasites; mean intensity refers to the number of parasites per fish)

Location	Sample size (n)	Length (mm) ± SD	Weight (g) ± SD	Sex ratio (F:M)	Parasite prevalence (%)	Mean intensity
Lake Okaro	52	34 ± 5	0.4 ± 0.2	1:0	0	0
Lake Rotorua	42	34 ± 8	0.5 ± 0.6	9:1	97.6%	32.6
Lake Kai-iwi	44	31 ± 7	0.3 ± 0.3	4:1	25%	29.1
Lake Ngatu	89	60 ± 22	3.7 ± 4.0	1:1	38.2%	2.2
Lake Rotokawau East	12	68 ± 11	4.0 ± 1.9	1:3	100%	20.3
Lake Waiparera	36	48 ± 6	1.3 ± 0.5	2:5	30.6%	4.2
Chapel Lake	105	38 ± 8	0.6 ± 0.6	1:2	4.8%	1.2
Lake Rotoroa	10	48 ± 11	1.2 ± 1.4	2:3	70%	25.8
Lake Hakanoa	8	41 ± 8	0.7 ± 0.3	5:3	0	0
Lake Ngaroto	178	46 ± 7	1.1 ± 0.9	1:1	9.6%	0.9

The mean length and weight of Northland common bullies were significantly higher from the Waikato and Rotorua bullies. Common bullies lengths were significant greater in Waikato populations than Rotorua populations, but weights were not statistically similar (Table 9). The two lakes from the Rotorua region -- Lake Okaro and Lake Rotorua had no statistically significant differences between common bullies' length and weight. The common bullies' length from the Northland lakes was statistically different except for Lake Ngatu and Lake Rotokawau East. As for common bullies' weight of the Northland lakes, no differences were found between Lake Kai-iwi and Lake Waiparera, or between

Lake Ngatu and Lake Rotokawau East. The rest were all different from each other. In Waikato region, the common bullies were only statistically different in length between Chapel Lake and Lake Ngaroto (Appendices 22 & 23).

Table 9. Regional differences in common bullies length and weight

Region	Unequal N HSD Test (*p*)	
	Length	Weight
Waikato vs. Rotorua	<0.001	0.178
Waikato vs. Northland	<0.001	<0.001
Rotorua vs. Northland	<0.001	<0.001

3.5 Parasites of common bullies

3.5.1 Parasite summary

Two parasite species were found from common bullies: the nematode *Eustrongylides ignotus* Joegerskiold, 1909 and the trematode *Telogaster opisthorchis* MacFarlane, 1945. Both species were found as metacercaria. *Eustrongylides ignotus* were usually found in large common bullies with a length of 46 – 95 mm; common bullies with length less than 35 mm or greater than 96mm had fewer infections (Table 10). *Telogaster opisthorchis* was usually found in medium - sized common bullies with a length of 36 – 46 mm. The number of *T. opisthorchis* cysts was markedly decreased when common bullies were shorter than 36 mm or greater than 46 mm (Table 11).

Table 10. Summary of *Eustrongylides ignotus* infection of common bullies (n = number of fish collected)

Host length (mm)	n	Number of *Eustrongylides ignotus* per host (% of total fish sampled)										
		0	1	2	3	4	5	6	7	8	9	>9
21-25	24	100										
26-35	135	97.8	1.5	0.7								
36-45	203	94.6	5.4									
46-55	143	88.1	7.7	2.8	0.7					0.7		
56-65	25	68	32									
66-75	14	35.8	14.3	14.3	14.3		7.1	7.1			7.1	
76-85	19	42	15.8	15.8	10.5		5.3		5.3			5.3
86-95	3			33.3	33.3			33.3				
96-105	9		33.3	22.2	44.4							
106+	1			100								

Table 11. Summary of *Telogaster opisthorchis* infection of common bullies (n = number of fish collected)

Host length (mm)	n	Number of *T. opisthorchis* cysts per host (% of total fish sampled)											
		0	1-10	-20	-30	-40	-50	-60	-70	-80	-90	-100	100+
21-25	24	79.2	20.8										
26-35	135	83	8.9	2.2	3.7	1.5	0.7						
36-45	203	88	3.4	1.5	1.5	2.0	0.1	0.5		0.5	0.5	0.5	1.5
46-55	143	92.3	3.5	1.4	0.7	0.7	0.7						0.7
56-65	25	88	8										4
66-75	14	57.2	14.3	21.4			7.1						
76-85	19	88.5	10.5	0.5	0.5								
86-95	3	100											
96-105	9	100											
106+	1	100											

3.5.2 Parasite correlation

Data of the number of *E. ignotus* and *T. opisthorchis* cysts, and the total number of cysts were not normally distributed. Thus they have been transformed by using the natural log (ln) to determine the relationships with their hosts (Table 12).

Table 12. Summary of Kolmogorov-Smirnov Test and Coefficients of determination (r^2) of common bullies (host) and their parasites

Parasites	Kolmogorov-Smirnov Test (p)	Coefficients of determination (r^2)	
		vs. host length	vs. host weight
Number of *E. ignotus* cysts	< 0.01	0.201	0.163
Number of *T. opisthorchis* cysts	< 0.01	0.025	0.008
Length of *E. ignotus*	> 0.01	0.001	0.002
Total number of cysts	< 0.01	0.042	0.036

No relationships were found between the length and weight of common bullies and the number of *Eustrongylides ignotus* and *T. opisthorchis* cysts, and the length of *Eustrongylides ignotus*, in which the coefficients of determination r^2 were less than 0.3 (Figure 23-30). This suggested that the number and size of encysted metacercaria were not influenced by the size of the common bullies. However, slight decreases in the total number of cysts found on common bullies were seen with the increase of common bullies' length and weight (Figures 29 & 30).

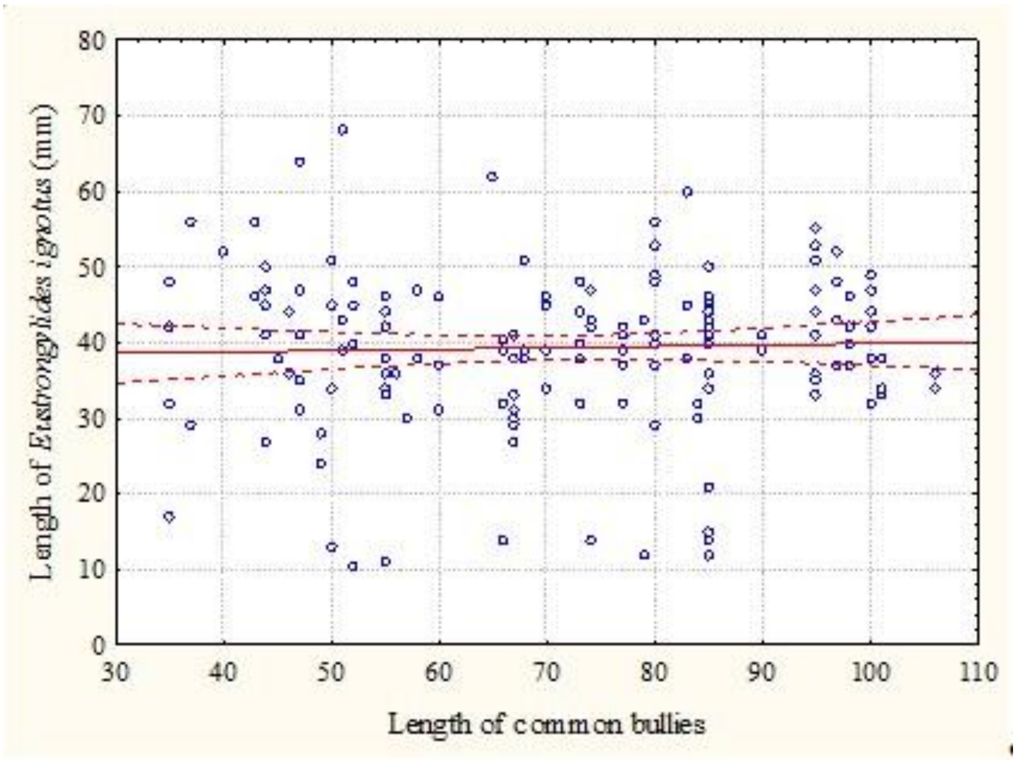

Figure 23. Scatterplot of *Eustrongylides ignotus* metacercaria length versus host length showing line of best fit and 95 % confidence interval.

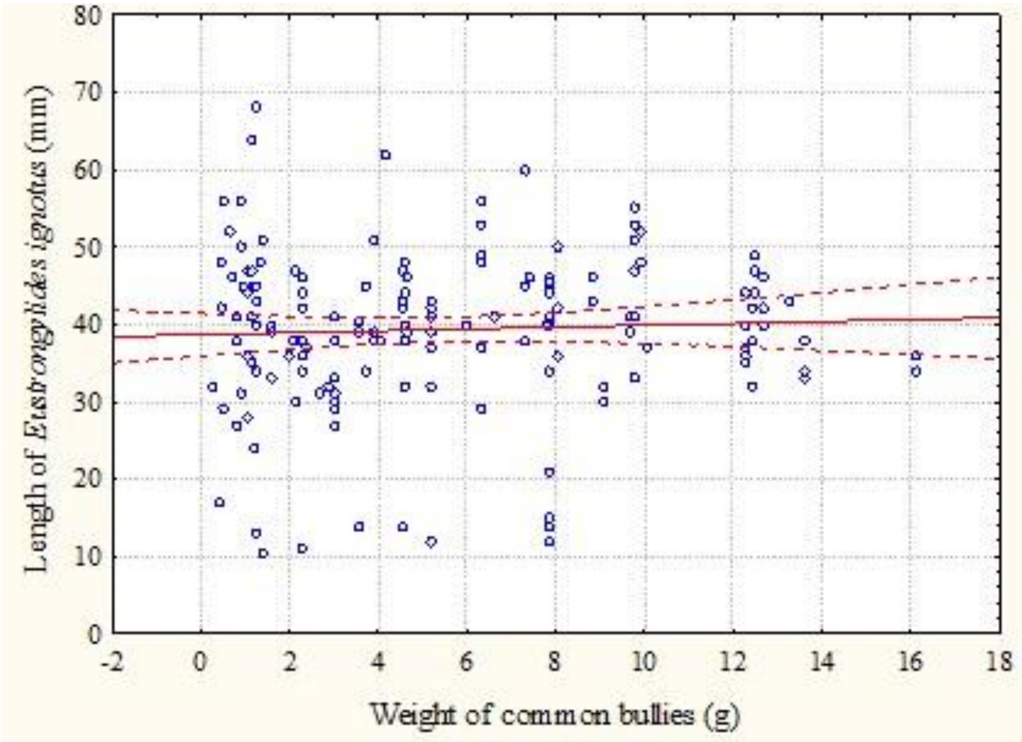

Figure 24. Scatterplot of *Eustrongylides ignotus* metacercaria length versus host weight showing line of best fit and 95% confidence interval.

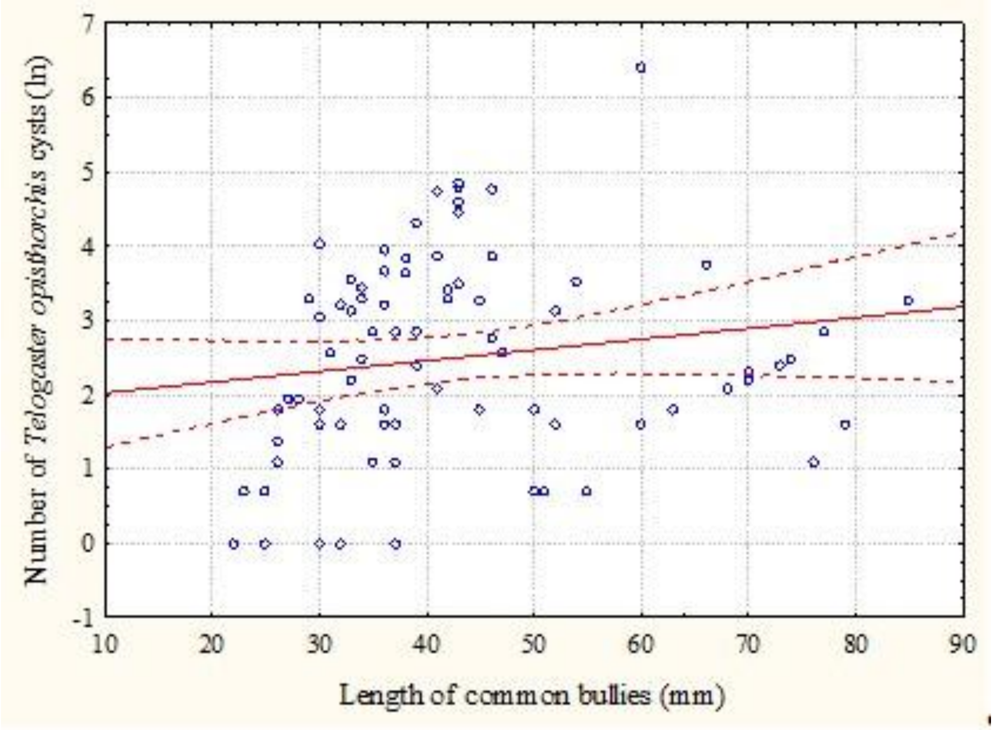

Figure 25. Scatterplot of number of *Telogaster opisthorchis* cysts versus host length showing line of best fit and 95% confidence interval.

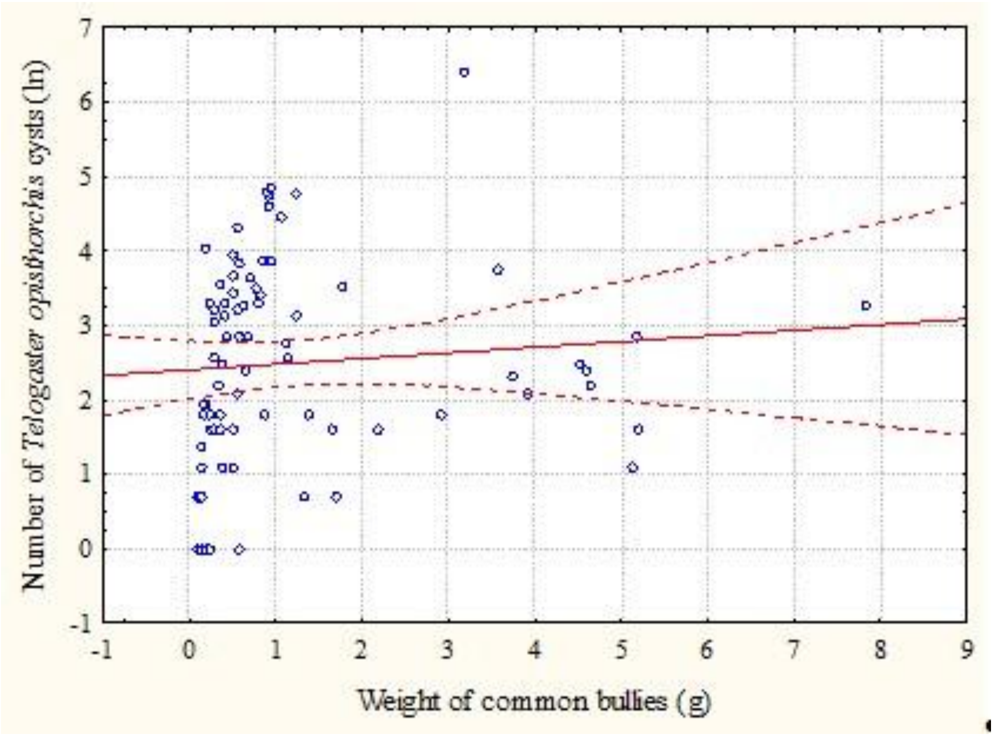

Figure 26. Scatterplot of number of *Telogaster opisthorchis* cysts versus host weight showing line of best fit and 95% confidence interval.

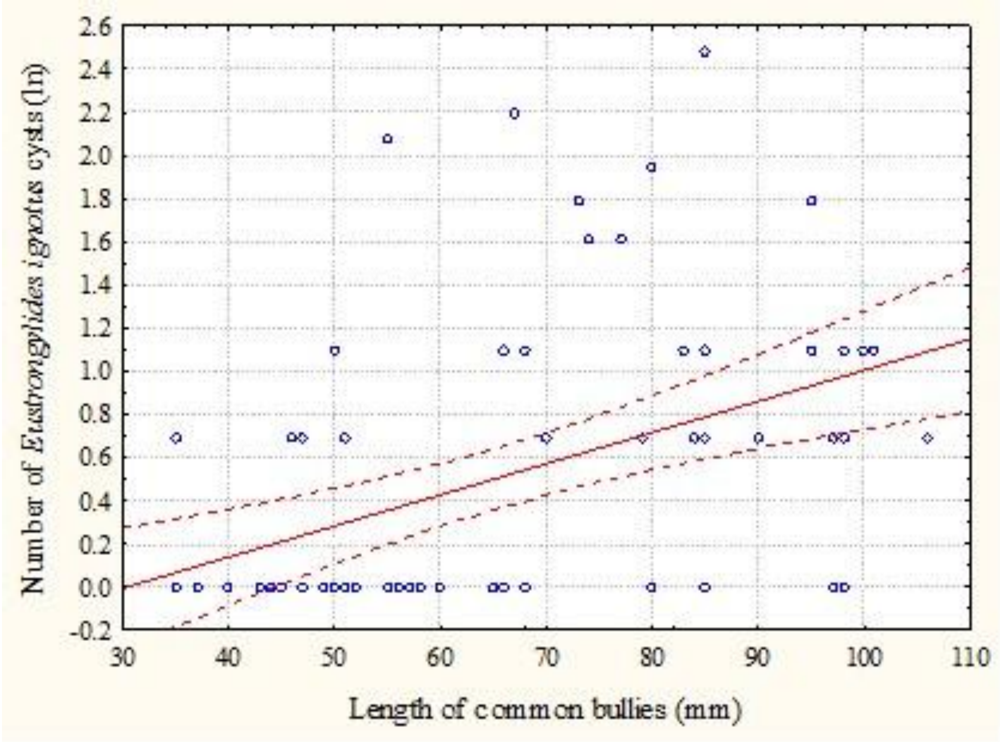

Figure 27. Scatterplot of number of *Eustrongylides ignotus* cysts versus host length showing line of best fit and 95% confidence interval.

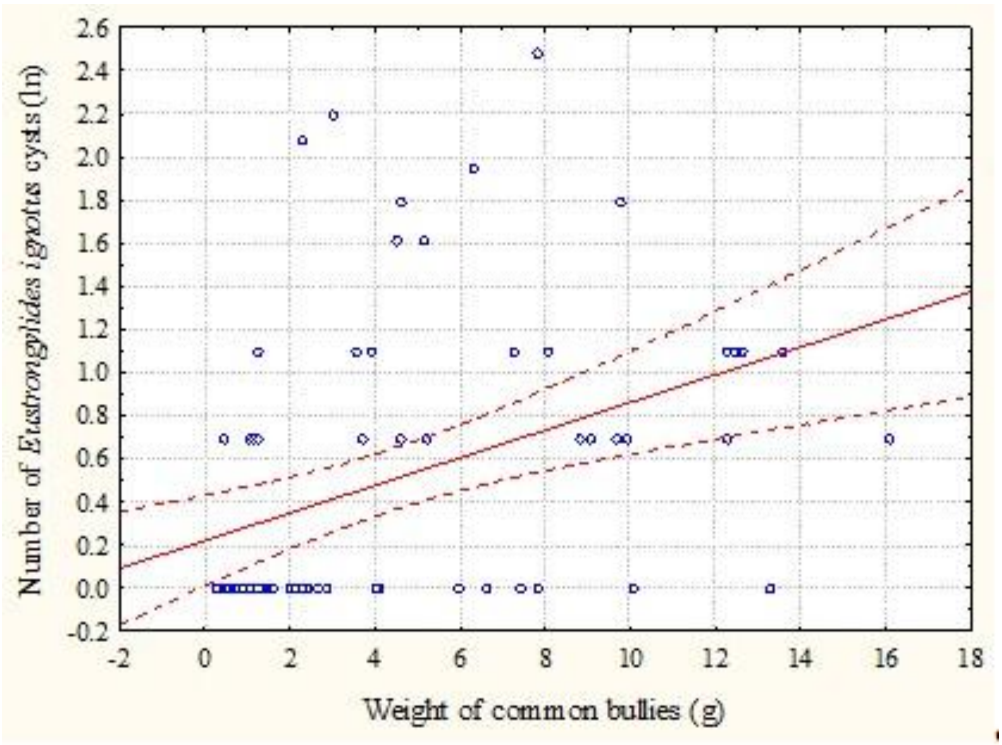

Figure 28. Scatterplot of number of *Eustrongylides ignotus* cysts versus host weight showing line of best fit and 95% confidence interval.

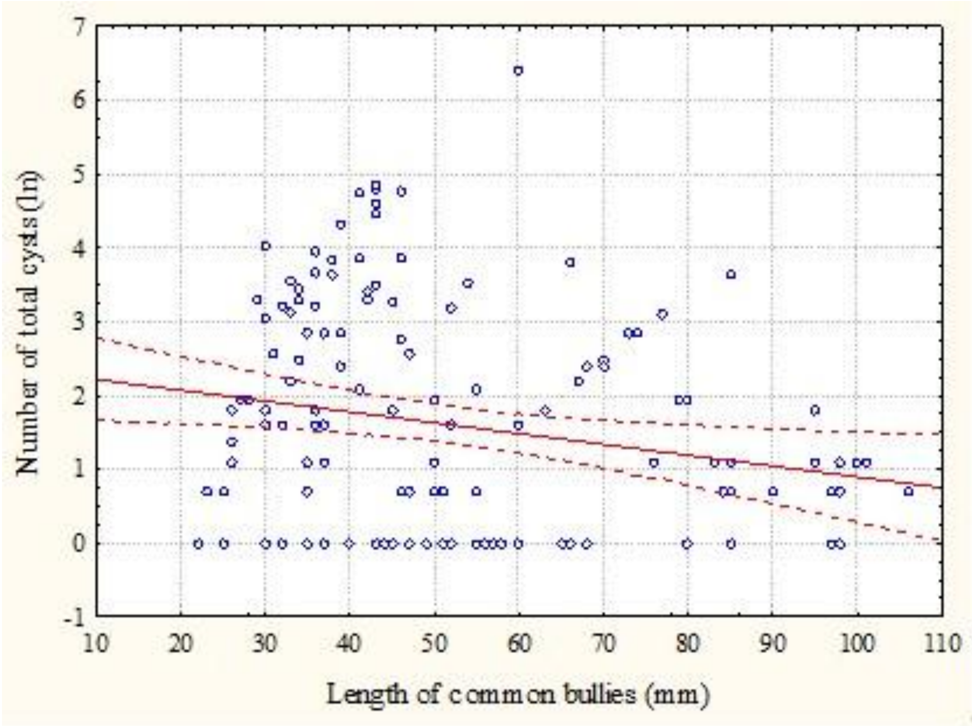

Figure 29. Scatterplot of host length versus number of total cysts showing line of best fit and 95% confidence interval.

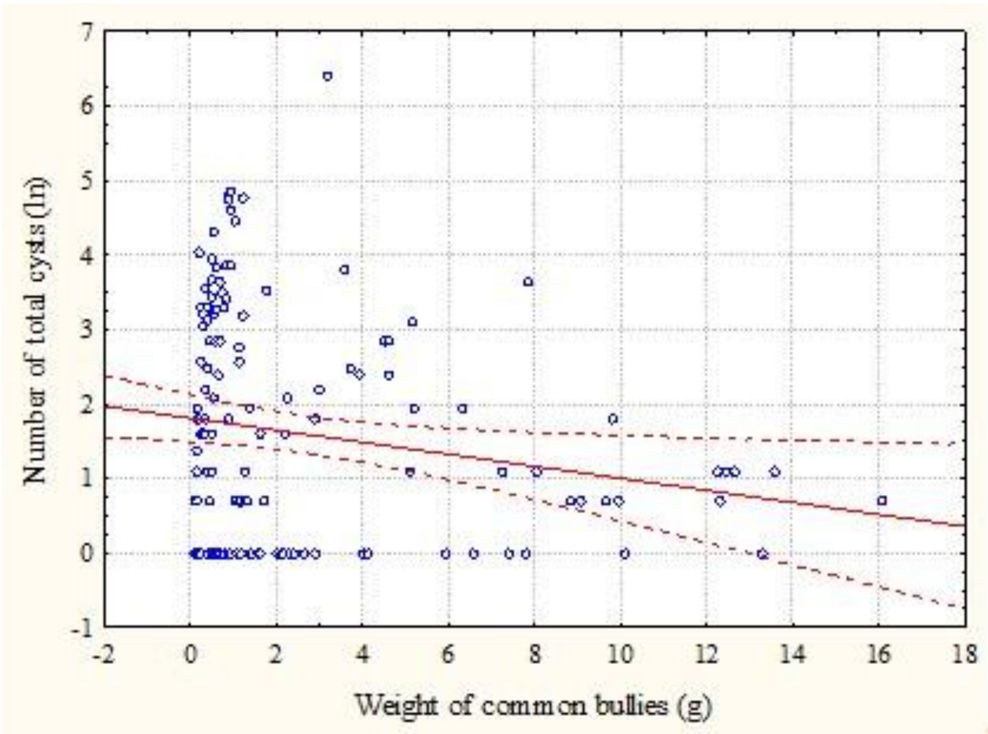

Figure 30. Scatterplot of host weight versus number of total cysts showing line of best fit and 95% confidence interval.

3.5.3 Parasite distribution among sample locations and host sexes

No geographic pattern was found in regards to parasite infections in the regions we surveyed, except for the absence of *Eustrongylides ignotus* cysts on common bullies of the Rotorua region. Both *E. ignotus* and *T. opisthorchis* cysts were found in the Waikato and Northland regions.

Infection rates of *T. opisthorchis* cysts in male and female common bullies from Lake Kai-iwi were not significantly different. *Eustrongylides ignotus* was the only parasitic species collected from bullies in Lake Ngatu and was more abundant on female hosts than the male but it was not significant. At Lakes Rotokawau and Waiparera, both *E. ignotus* cysts and *T. opisthorchis* were found. *Eustrongylides ignotus* cysts were more abundant on males than on the female for Lake Rotokawau East common bullies. At Lake Waiparera *T. opisthorchis* cysts were only found on male common bullies while *E. ignotus* cysts were mostly found on female common bullies. *Telogaster opisthorchis* was the only parasitic species of common bullies found at Lake Rotoroa and Lake Rotorua, where the cysts were more abundant on the female hosts than the male ones. *Eustrongylides ignotus* cysts on Lake Ngaroto common bullies had similar distribution among the male and female hosts (Tables 13 & 14).

Two lakes, Lake Ngatu and Lake Ngaroto, were found to have a significant difference between the male and the female host in length and weight. The female common bullies were significantly larger than the males at Lake Ngatu, while the male common bullies were significantly larger than the female at Lake Ngaroto (Tables 13 & 14). Female common bullies have relatively more parasites and greater intensity than the male at Lake Ngatu. At Lake Ngaroto, both male and female common bullies had similar parasite prevalence and intensity (Table 13).

Table 13. Summary of total parasite and parasite intensity between female and male hosts over seven lakes (E. = *Eustrongylides ignotus*; T. = *Telogaster opisthorchis*; mean ± SD for host length and weight)

	Female hosts				Male hosts			
	Total parasites (mean intensity)		Host		Total parasites (mean intensity)		Host	
Location	*E.*	*T.*	Length (mm)	Weight (g)	*E.*	*T.*	Length (mm)	Weight (g)
Lake Kai-iwi	0	182 (26)	35.9 ± 1.4	0.5 ± 0.1	0	132 (33)	36.8 ± 2.3	0.5 ± 0.1
Lake Ngatu	65 (2.6)	0	86.5 ± 3.5	8.7 ± 0.8	10 (1.1)	0	57.9 ± 2.8	2.4 ± 0.4
Lake Rotokawau East	4 (1.3)	58 (19.3)	57.3 ± 2.3	5.9 ± 0.7	38 (4.2)	121 (13.4)	72.0 ± 3.1	4.5 ± 0.6
Lake Waiparera	13 (3.3)	0	52.0 ± 1.1	1.7 ± 0.2	1 (0.1)	28 (4)	54.4 ± 2.0	1.8 ± 0.2
Lake Rotoroa	0	158 (31.6)	49.4 ± 6.8	1.6 ± 0.9	0	19 (9.5)	46.0 ± 1.0	1.0 ± 0.1
Lake Ngaroto	10 (1.4)	0	43.3 ± 1.9	0.9 ± 0.1	7 (1)	0	51.6 ± 2.1	1.4 ± 0.2
Lake Rotorua	0	1608 (47.3)	34.5 ± 1.2	0.6 ± 0.1	0	96 (24)	41.8 ± 3.2	0.9 ± 0.2

Table 14. Parasite and host difference between female and male common bullies (E. = *Eustrongylides ignotus*; T. = *Telogaster opisthorchis*; mean ± SD for host length and weight)

Location	Unequal N HSD Test (p)					Host Length (mm)		Host Weight (g)	
	T. (n)	*E.* (n)	*E.* length	Host Length	Host Weight	Male	Female	Male	Female
Lake Kai-iwi	0.83	N/A	N/A	0.76	0.74	38 ± 2	29 ± 1	0.58 ± 0.08	0.25 ± 0.04
Lake Ngatu	N/A	0.08	0.67	< 0.01	< 0.01	52 ± 2	69 ± 4	1.78 ± 0.19	5.75 ± 0.75
Lake Ngaroto	N/A	0.06	0.07	0.01	0.04	49 ± 1	42 ± 1	1.40 ± 0.12	0.81 ± 0.03
Lake Rotokawau East	0.02	0.51	0.78	0.09	0.13	72 ± 3	57 ± 6	4.50 ± 0.57	2.33 ± 0.71
Lake Rotorua	0.8	N/A	N/A	0.10	0.28	43 ± 4	33 ± 1	0.96 ± 0.27	0.48 ± 0.09

Chapter 4: Discussion

4.1 Parasite Checklist and the other non-indigenous freshwater fishes

4.1.1 Parasites loss:

Apart from brown trout, all the studied non-indigenous freshwater fish in New Zealand have lost all or most of their parasites. In New Zealand, most monogenean parasite species found on non-indigenous freshwater fish were lost compared with their native conspecifics. Monogenea is one of the most diverse groups of parasite found on fish. The most common monogeneans found on freshwater fish are *Dactylogyrus* and *Gyrodactylus* species which have been introduced worldwide with their cyprinid hosts (Bunkley-Williams & Williams, 1994). However, only three species of Monogenea have been established in New Zealand with their introduced cyprinid hosts, *Dactylogyrus ctenopharyngodonis, Gyrodactylus ctenopharyngodontis,* and *Gyrodactylus sp*. (Hine et al., 2000). Most Monogenean parasites are specialists (Sasal, Trouve, Muller-Graf, & Morand, 1999; Ziętara & Lumme, 2002). They are normally restricted to their hosts when they are introduced into other habitats (Pearson, 2005). For example, the Monogenea *Dactylogyrus bifurcatus* is specific to the fathead minnow (*Pimephales promelas*), which was lost after 20 years of establishment in Puerto Rico when fathead minnow perished (Buchmann & Bresciani, 1997).

Ninety fish (rudd, goldfish, koi carp and catfish) sampled in New Zealand lakes have shown no metazoan parasite infection. Hine et al. (2000) summarised that no parasites have been recorded for catfish, koi carp and rudd. However, four species of parasites have been recorded for goldfish: digenean *Coitocaecum parvum*, copepods *Abergasilus amplexus*, *Argulus japonicus* and *Lernaea cyprinacea* (Hine et al., 2000). This may indicate that the parasites were not present in the lakes where goldfish were caught or that parasite prevalence was very low. If freshwater fishes, ornamental fishes in particular, carry parasites which can cause server damage to infected fish population, their introductions are strictly controlled

(Pearson, 2005; Velázquez-Velázquez, González-Solís, & Salgado-Maldonado, 2011). Introduced fish species in New Zealand face a 3 - 6 week quarantine period to remove any parasites or disease agents (Pearson, 2005). In 1972, a shipment of 2,000 goldfish introduced from Hong Kong contained the parasite *Bothriocephalus acheilognathi* which was removed by quarantine (Edwards & Hine, 1974).

Grass carps have largely reduced in their parasite diversity when being introduced into New Zealand. The treatments done before releasing grass carps into the wild facilitated the reduction of parasites in New Zealand. Chemotherapeutic treatment has been done on 2000 grass carps when they were introduced into New Zealand from Hong Kong in 1971 (Edwards & Hine, 1974). External parasites *Tripartiella* sp., *Dactylogyrus ctenopharyngodonis,* and *Gyrodactylus clenopharyngodontis* were eliminated before releasing into the wild. Experimental eradications were done to remove the cestode *Bothriocephalus gowkongensis*.

No significant difffernces were found on number of parasite species between the native and introduced freshwater fishes in New Zealand. This suggests that the parasite diversity of New Zealand native freshwater fishes is not abundant. Therefore, if non-indigenous fish were introduced into New Zealand with most or all parasites lost, the New Zealand aquatic environment can hardly fill the gaps.

Parasites with complex life cycle are often lost due to the absence of suitable hosts in the introduced ranges (Bunkley-Williams & Williams, 1994; MacLeod et al., 2010; Torchin et al., 2003; Torchin & Mitchell, 2004). In New Zealand, the introduced aquatic invertebrates were less successful in establishment and spread than fish species, and only a small proportion of aquatic invertebrates in New Zealand are non-indigenous (Champion et al., 2002). Therefore the likelihood that introduced parasites will find a suitable first intermediate host is reduced. Most parasites of Digenea, Nematoda and Cestoidea have not established in New Zealand due to the missing of suitable hosts (Pearson, 2005).A study of Danish farmed rainbow trout has shown an absence of the previously prevalent parasite *Myxobolus cerebralis*due to the prevention of the intermediate hosts of *M. cerebralis* from reaching the rainbow trout fry An aniskid marine nematode went extinct from Denmark’s farmed rainbow trout due to the change of fish food from marine fish offal which was infected with anisakid larvae was no longer fed to the rainbow trout to dry pellets. Therefore *M. cerebralis* can no longer access the second intermediate host rainbow trout populations. Furthermore, the Cestoidea, *Triaenophorus nodulosus* was absent in farmed rainbow trout as the definite host of this Cestoidea, pike (*Esox lucius*) were not present in the farm, therefore copepod entering the trout farm rarely contain *T. nodulosus* larvae (Buchmann & Bresciani, 1997).

Most fish parasites were specialists in New Zealand aquatic habitats infecting one or two hosts (Hine et al., 2000); the chances that the non-indigenous freshwater fish to harbour native parasites thus reduced. The establishment of Monogenea and other parasites with direct life cycle are regulated by the transmission efficiency (Bunkley-Williams & Williams, 1994). Variations in water temperature (Buchmann & Bresciani, 1997; LoBue & Bell, 1993; Rubio-Godoy & Tinsley, 2008; Yao & Nie, 2004) and current speed (Guégan, Lambert, Lévêque, Combes, & Euzet, 1992) can reduce the transmission efficiency of monogenean parasite. Therefore environmental differences between the native range and introduced range can result in the extinction of fish parasites.

Introducing young fish may not be a major factor in explaining the reduced parasite fauna of New Zealand non-indigenous freshwater fish. The grass carps introduced from Hong Kong as mentioned earlier, into New Zealand were all juveniles, which have four species of parasites that were introduced with them (Edwards & Hine, 1974). Some parasites use young fish as their intermediate host. Monogenea *Dactylogyrus* and Asian fish tapeworm *Bothriocephalus acheilognathi* were found infecting and causing mortality in young carps and many other juvenile fishes (Abdullah, 2008; Salgado-Maldonado & Pineda-Lopez, 2003). Juvenile fishes may be easier to infect than the adult, since the juvenile do not have fully developed immune defences against the parasites (Šimková et al., 2008).

4.1.2 Parasite gain and persistence:

Non-indigenous freshwater fish were found to harbour new parasites in the introduced ranges, which have been found for few New Zealand species. Generalist parasites are more likely to infect introduced fishes than specialists (Keane & Crawley, 2002; Torchin et al., 2002). This is because that the specialist parasites have adapted to the specific features including behaviour, anatomy and physiology of their hosts and a sudden change of hosts will cause mortality of the parasites (Sasal et al., 1999). A number of New Zealand fish parasites are generalists which infect both native and introduced freshwater fishes (Hewitt & Hine, 1972; Hine et al., 2000). The nematode *Eustrongylides ignotus* are generalist, which infect tench, rainbow trout and many other native fishes. The nematode *Hysterothylacium* sp. were found on 54 fishes including brown trout, rainbow trout and chinook salmon. Copepode *Abergasilus amplexus* were found on perch and some other native fishes (Hine et al., 2000).

Host preference and the ability to change hosts can strongly influence the successfulness of parasite invasion. Generalist parasites are more likely to establish in the introduced range than the specialists (Keane & Crawley, 2002). Unlike specialist parasites, generalists are not restricted by the specific features of their hosts (Sasal et al., 1999). Generalist parasites may be able to transfer to native hosts when the introduced host population are insufficient to carry their parasite reproduction (Keane & Crawley, 2002; Torchin et al., 2002). However, New Zealand freshwater fauna have largely escaped from the effect of the introduced parasites. Champion et al. (2002) have suggested that no parasites were associated with the introduction of freshwater fishes.

4.1.3 Parasite impacts

Releases from parasitic infections are very likely to facilitate the invasiveness of non-indigenous fish. Partly because the impacts that parasites can pose on them. The majority of parasites have been reported to cause physical damage to their host species and mortality when being heavily infected. The freshwater fish louse, *Argulus foliaceus* is a common parasitic crustacean found on freshwater fish. *A. foliaceus* feeds on host blood by piercing the skin of their hosts and injecting a toxin. Heavy infestations have been reported to cause serious damage to the skin (Alaş, Öktener, & Solak, 2010; Öktener, Ali, Gustinelli, & Fioravanti, 2006). Monogeneans, such as *Gyrodactylis salaris* and *G, derjavini,* cause epithelial disruption that can result in secondary infection by bacteria, which can cause serious impact on fish physical health. Species of *Dactylogyrus* have been reported to cause great damage to the gill filaments of carps (Abdullah, 2008; Buchmann & Bresciani, 1997). The tapeworm, *Bothriocephalus acheilognathi* can cause severe damage to the intestines of their fish hosts, such as reducing intestinal functioning and enzyme release, thus reducing the host's growth and reproductive capacity. Muscular fatigue, decreased haemoglobin content and secondary bacterial infections are all associated with *B. acheilognathi* infection.

4.2 Mosquitofish (*Gambusia affinis*)

4.2.1 Mosquitofish distribution

Mosquitofish were present in twelve out of the nineteen sampled lakes; Lake Pupuke, Kiosk Pond (Auckland Domain), Lakes Kai-iwi, Ngatu, Wahakari, Waiparera, a small pond at Taharoa Domain, Chapel Lake, and Lakes Rotokaeo, Rotoroa, Hakanoa and Ngaroto. The lakes in which mosquitofish were found are eutrophic or hypertrophic (Ball et al., 2009; Duggan & Barnes, 2005; Edwards et al., 2010; Hicks et al., 2001; Spiller & Forsyth, 1970; Wells & Champion, 2010), except Lake Kai-iwi and Lake Ngatu, which are considered mesotrophic to eutrophic (Northland Regional Council, 2008). Vegetation was present in the littoral zone of all sample sites.

No mosquitofish were caught in the lakes of the Rotorua region. However, mosquitofish have been reported from Ohau Channel, linking Lake Rotorua and Lake Rotoiti (Brijs, Hicks, & Bell, 2008) and Lake Tarawera (Leusch, 2004). The littoral zone of Ohau Channel consists of submerged macrophytes such as pondweed (*Potamogeton crispus*) and parrot's feather (*Myriophyllum aquaticum*; Brijs et al., 2008), which were rarely seen at the sample sites of Lake Rotorua and some other Rotorua lakes. The absence of mosquitofish at these sample sites may thus be due to mosquitofish preferring vegetation that can act as shelter (Ling & Willis, 2005). The absence of mosquitofish at Lake Okataina and Lake Rotoma may be due to the low primary productivity of these oligotrophic lakes (Parliamentary Commissioner for the Environment, 2006). Alternatively, the introduction of mosquitofish into the Rotorua region is relatively recent compared with the introduction into the Northland and Auckland regions (Brijs et al., 2008; McDowall, 1978). As such, mosquitofish are not likely to have yet established wide populations in the Rotorua lakes.

Mosquitofish were significantly larger in Northland lakes compared with lakes of the Waikato and Auckland regions. Mosquitofish were collected in the same period of the year for most of the lakes. Mosquitofish were collected in spring (September 2011) from Auckland region, Northland region and Rotorua region, and in autumn, winter and spring (between May to September 2011) from Waikato region. This size difference could be because Northland has better environmental conditions than Waikato and Auckland for the growth and reproduction of the mosquitofish. For example, Northland lakes have higher average water temperatures than Auckland, Rotorua and Waikato lakes. Since mosquitofish reduce reproduction when temperature decreases, they are normally absent from the lakes when the summer water temperature drops below 20 ℃ (Baker et al., 2004).

The sex ratio of female to male mosquitofish caught was 2:1 in seven of the twelve lakes where mosquitofish were sampled. It has been suggested that male mosquitofish are less adapted than the female to seasonal environmental variations, such as temperature fluctuations, which may cause increased mortality of males (Pan, Su, & Zheng, 1980). Small lakes are expected to have greater seasonal variations than large lakes (Fee, Hecky, Kasian & Cruikshank, 1996). My results seemly support this hypothesis as more male mosquitofish than the female were found in large lakes such as Lake Ngatu and Lake Wahakari, and more females than the male were found in small lakes such as Chapel Lake and the small pond at Taharoa Domain. Additionally, male mosquitofish have been reported to be more aggressive than the female and intraspecific competition between males could cause higher mortality rates (Pan et al., 1980). Greater interspecific competition in larger lakes may explain greater proportions of males in these lakes.

4.2.2 Lost parasites

I found no parasites associated with New Zealand mosquitofish. The majority of the parasites infecting mosquitofish in its native range are metazoans (Hoffman, 1999). More than 40 species of metazoan parasites have been recorded from mosquitofish in North America, including mosquitofish of native Central America population (Hoffman, 1999), the mosquitofish's native habitat, while the digenean trematode *Centrocestus formosanus* has been reported from China (Zeng et al., 2005) and *Echinochasmus donaldsoni* from Puerto (Bunkley-Williams & Williams, 1994) (Appendix 1).

The average length of mosquitofish sampled in New Zealand was 24 mm, with the largest mosquitofish reaching 47 mm. Adult female mosquitofish from Louisiana, USA, examined by Brock and Font (2009) were between 20 to 30 mm in length and were infected by eight species of parasites. The prevalence of five of these parasites found on mosquitofish was greater than 67% (Brock & Font, 2009). Mosquitofish, which harbour Asian tapeworm *Bothriocephalus acheilognathi* in North Carolina, have a length between 26 to 39 mm (Granath & Esch, 1983). Mosquitofish found in China have a length of 14 to 46 mm, and were infected by the digenean trematode *Centrocestus formosanus* (Pan et al., 1980). The sizes of New Zealand mosquitofish I collected were similar to other regions where mosquitofish are infested by parasites. Therefore, the size of mosquitofish examined during this study does not explain the lack of parasites recorded from New Zealand mosquitofish. The different methods used to examine mosquitofish for parasites (digestion versus dissection) may explain the non-detection of parasites in New Zealand mosquitofish. However, for most of the mosquitofish I examined I used a digestion method, which was different to the above studies as they used a dissection method. The digestion method I used was designed to detect tematode and nematode larvae (Hoffman, 1999). A sub-sample (10% of total fish sampled) of mosquitofish caught were examined by using dissection method to ensure that no parasites were lost due to the use of digestion method. And because these are major parasites of mosquitofish elsewhere, I would have collected them if they were present.

There are three hypotheses to explain the absence of parasites from mosquitofish in New Zealand: missing the boat, sinking with the boat and lost overbroad (Bunkley-Williams & Williams, 1994; MacLeod et al., 2010; Torchin et al., 2003; Torchin et al., 2002; Torchin & Mitchell, 2004). Missing the boat suggests that the introduced individuals were free from parasties prior to arrival in New Zealand (MacLeod et al., 2010; Paterson & Gray, 1997; Paterson et al., 1999). Lost overboard suggests that parasites may arrive with their hosts to a new range but the parasites cannot establish due to the lack of suitable hosts to complete their life cycle, or the parasites' population size is too small to establish in the new range (MacLeod et al., 2010). Sinking with the boat suggests that the parasites species and their hosts both failed to eatablish in the new habitatas due to the influence of the population bottlebeck or population fragmentation (Torchin et al., 2003). Sinking with the boat is not relevant for New Zealand mosquitofish, as mosquitofish have established widely in New Zealand (McDowall, 1978).

4.2.2.1 Missing the boat

There are only two recorded attempts to have introduced mosquitofish into New Zealand (McDowall, 1978). The first introduction was from Sydney in 1930. However, all mosquitofish arriving from Sydney died before they could be released. The second introduction, from Hawaii, was successful, which was later released into the wild (McDowall, 1978). Mosquitofish were introduced to Hawaii from the mainland of North America (Font, 2003, 2007). Thus mosquitofish were introduced into New Zealand from other introduced ranges rather than from their native habitat, which likely increased the probability of mosquitofish parasites missing the boat.

The parasite fauna of Hawaiian mosquitofish is reduced compared with mosquitofish from their native North America (more than 40 species of parasites recorded) (Hoffman, 1999). For example, parasite species such as *Ascocotyle ampullacea*, *Ascocotyle mcintoshi*, *Phagicola diminuta*, *Phagicola* sp., *Echinochasmus swartzi*, *Posthodiplostomum minimum*, and *Glossocercus* sp. found on mosquitofish in Louisiana, USA (Brock & Font, 2009), were not found in Hawaii (Font & Tate, 1994). None of the Hawaiian mosquitofish were reported by be heavily infected with parasites (Font, 2003, 2007; Font & Tate, 1994). Thus the parasites of mosquitofish in New Zealand may have "missed the boat" particularly due to it being a two-step process.

The Hawaiian Islands are extremely isolated with only five native freshwater fish species (Font & Tate, 1994). The introduction of Poecilid fishes including guppy (*Poecilia reticulata*), short-tail molly (*Poecilia mexicana*), green swordtail (*Xiphophorus helleri*) and mosquitofish (*Gambusia affinis*) into Hawaii have resulted in the establishment of some helminthic parasites in Hawaii (Font & Tate, 1994), including *Ascocotyle tenuicollis, Centrocestus formosanus* and *Bothriocephalus acheilognathi* (Font, 2007). The trematode *Ascocotyle tenuicollis* were found on the conus arteriosus of mosquitofish in Hawaii (Font, 2007). These helminthic parasites have broad host specificity, and have been found to infect native Hawaiian gobioid fishes (Font, 2003, 2007). *Ascocotyle tenuicollis* and *B. acheilognathi* have been found on mosquitofish in North America (Hoffman, 1999), and *C. formosanus* were found on mosquitofish in China (Zeng et al., 2005). These parasites have not been found on New Zealand freshwater fishes, including the mosquitofish (Hine et al., 2000), but the key intermediate hosts and definitive hosts of *C. formosanus* and *B. acheilognathi* are known from New Zealand (Pearson, 2005). Consequently, if these parasites were introduced into New Zealand with mosquitofish, they were very likely to have established and spread through the New Zealand freshwater fish fauna. It is likely that the mosquitofish introduced into New Zealand were free from parasites. That is, they missed the boat.

4.2.2.2 Lost overboard

Parasites may arrive with their host to the new range but subsequently go extinct (be lost overboard) because of the absence of suitable additional hosts (MacLeod et al., 2010; Torchin et al., 2002, 2003; Torchin & Mitchell, 2004). Although a number of relatives of these fish-eating birds from North America are present in New Zealand, including species of herons (Pearson, 2005; Wells & Champion, 2010), it appears that many of these bird species in New Zealand are not suitable hosts for most of the parasites found on mosquitofish and suggests that the parasites could have arrived with the introduction of mosquitofish, but failed to establish due to the missing of suitable hosts.

A survey done in Bayou Traverse, a waterway in the LaBranche wetlands of south-eastern Louisiana, USA, found that eight species of parasites infected thirty female mosquitofish (Brock & Font, 2009). The parasite species include: *Ascocotyle ampullacea*, *A. mcintoshi*, *A. tenuicollis*, *Phagicola diminuta*, *Phagicola* sp., *Echinochasmus swartzi*, *Posthodiplostomum minimum*, and *Glossocercus* sp. All of these parasites were found as encysting metacercariae; thus, additional hosts are crucial for parasites to complete their life cycle (Brock & Font, 2009).

The reason these parasites are missed from New Zealand mosquitofish could be that suitable hosts are absent. For example, the raccoon (*Procyon lotor*) is the definitive host of, *Ascocotyle. ampullacea* (Brock & Font, 2009). There is no ecological equivalent of the racoon in New Zealand. Similarly the definitive hosts of *Ascocotyle tenuicollis*, found on mosquitofish in Hawaii, are wading birds such as American bittern *Botaurus lentiginosus*, little blue heron, and tricolor heron (*Hydranassa tricolor ruficollis*) (Brock & Font, 2009; Font & Tate, 1994). Although a number of relatives of these fish-eating birds from North America are present in New Zealand, including species of herons (Pearson, 2005; Wells & Champion, 2010) it appears that many of these bird species in New Zealand are not suitable hosts for most of the parasites found on mosquitofish and suggests that the parasites could have arrived with the introduction of mosquitofish, but failed to establish due to the missing of suitable hosts.

Even when suitable additional hosts are present in New Zealand, the hosts may have limited distributions (Pearson, 2005). For example, the trematode *Ascocotyle tenuicollis* infecting mosquitofish in Hawaii uses the snail *Melanoides tuberculata* as the first intermediate host (Font, 2007). *Melanoides tuberculata* is only known in New Zealand from geothermal waters and home aquaria (Duggan, 2002, 2010), and thus is unlikely to transmit parasites to mosquitofish.

It is possible that some parasites were introduced into New Zealand with mosquitofish, but the parasite population size was too small to be reproduced sustainably. However it is more likely that missing the boat explains the absence of parasites from mosquitofish in New Zealand.

4.2.3 Parasite spillback

Parasite spillback was not observed in New Zealand mosquitofish. Parasite spillback is the acquisition of parasites by introduced species from native hosts in the new region (Kelly et al., 2009). Mosquitofish were found to harbour new parasite species after being introduced to China. Since the introduction of the mosquitofish in 1927 from Manila to Shanghai, mosquitofish have acquired the Asian trematode *Centrocestus formosanus*. Mosquitofish act as the second intermediate host, which transport *C. formosanus* larva to their definitive host, the Chinese water snake, *Enhydris chinensis* (Chen et al., 2008). Therefore, mosquitofish can acquire new parasites in their introduced ranges if they are suitable intermediate hosts of the parasite and can be eaten by the definitive hosts.

Among the reported parasites of mosquitofish, two species have been recorded from other New Zealand freshwater fishes: *Eustrongylides ignotus* and *Proteocephalus* sp. (Hewitt & Hine, 1972; Hine et al., 2000). In New Zealand, *Eustrongylides ignotus* metacercaria has been found on longfin eels, *Anguilla dieffenbachii*, shortfin eels, *A. australis* (Hine, 1978), inanga *Galaxias maculatus*, upland and giant bullies (family Gobiidae), tench, flounders (family Pleuronectidae), rainbow trout, brown trout, and sockeye salmon (Hewitt & Hine, 1972; Hine et al., 2000). The cestode *Proteocephalus* sp. larvae (proteocephalid plerocercoid) were found in the intestines or body cavities of New Zealand shortfin and longfin eels (Hine et al., 2000). As the two parasites found on mosquitofish in North America are found on New Zealand freshwater fishes, some barriers may be preventing these parasites from infecting New Zealand mosquitofish.

The nematode *Eustrongylides ignotus* has been found in more than 50% of mosquitofish in North America (Deaton, 2009). In New Zealand, *Eustrongylides ignotus* was found from common bullies (*Gobiomorphus cotidianus*) throughout my study. As common bullies were frequently caught in the same lakes as mosquitofish, it is interesting to speculate why *Eustrongylides ignotus* infect common bullies but not mosquitofish in New Zealand. Differences in the feeding behaviour of the two hosts may explain why bully parasites have not switched to mosquitofish. Mosquitofish are diurnal feeders (Capps et al., 2009), and *Eustrongylides ignotus* in New Zealand use eels (longfin and shortfin) as their definitive hosts. Both common bullies and eels are nocturnal feeders (Bisazza et al., 1999; Jellyman, 1989; Macfarlane, 1952) and studies of stomach contents of shortfin and longfin eels have found common bullies (Chisnall, 2000; Jellyman, 1989). Differences in the active periods of mosquitofish and eels may mean that mosquitofish are rarely eaten by eels, and *E. ignotus* which infect mosquitofish will not able to complete their life cycle. Thus there may be selection pressure for *E. ignotus* to avoid using mosquitofish as hosts.

However, mosquitofish not being part of the eel's diet does not answer why *Eustrongylides ignotus* do not infect mosquitofish. Mosquitofish and common bullies share the same habitat. They occupy the littoral zone of lakes, and as they are of similar sizes they likely feed on similar sized zooplankton and invertebrates (Champion et al., 2002). With over a thousand individuals of mosquitofish examined, it is very likely that some individuals had ingested oligochaetes infected with *E. ignotus* larvae. The result of non-parasitic infection on mosquitofish suggests that the mosquitofish and common bullies must have some dietary differences. Mosquitofish mainly feed on planktons (Mansfield & Mcardle, 1998), while common bullies prey more on larger invertebrates including oligochaetes (Sagar & Eldon, 1983). The mosquitofish in northern Waikato region have a major dietary composition of zooplankton, terrestrial fauna and large invertebrates such as Cladocera, Copepoda and Chironomidae (Mansfield & Mcardle, 1998). The amphipod, *Paracalliope fluviatilis* dominated the diet of juvenile common bullies in Lake Waihola, New Zealand (Wilhelm et al., 2007). A small number of oligochaetes were eaten by common bullies in Rakaia River, New Zealand (Sagar & Eldon, 1983). Invertebrates such as copepods, snails, chironomids, and isopods were found in common bullies stomach content (Wilhelm et al., 2007). The dietary composition of mosquitofish and common bullies may vary at the sampled lakes thus resulted in the distinct parasite fauna.

Another possible reason for the absence of *E. ignotus* may be the physical constraints. Adult common bullies can grow up to twice the size of adult mosquitofish (McDowall, 2000). My results showed that common bullies less than 35 mm in total length were not infected by *Eustrongylides ignotus* and *Telogaster opisthorchis* cysts. This suggests that common bullies < 35 mm do not ingest the gastropod *Potamopyrgus antipodarum* which is the host of *T. opisthorchis* larvae and oligochaetes which contain *E. ignotus* larvae. As more than 98% of the mosquitofish caught were less than 35mm in length, it is likely that mosquitofish were free from *E. ignotus* infection because mosquitofish can rarely ingest the first intermediate host of *E. ignotus*.

However, *E. ignotus* can omit the first intermediate host by developing from its first stage larvae to fourth stage larvae in second intermediate hosts that have ingested the eggs of *E. ignotus* (Coyner, Spalding, & Forrester, 2003). In laboratory conditions, eastern mosquitofish (*Gambusia holbrooki*) were fed with the eggs of *E. ignotus* and successfully infected with *E. ignotus* (Coyner et al., 2003). Thus, if mosquitofish (*Gambusia affinis*) ingest the eggs of *E. ignotus*, they will very likely to be infected with *E. ignotus* suggesting that feeding preference of mosquitofish at the sampled lakes may explain the absence of *E. ignotus* from mosquitofish.

Lernaea cyprinacea was reported as a generalist species which infects the congeneric eastern mosquitofish (*Gambusia holbrooki*) in Australian waters (Hassan, 2008; Lymbery et al., 2010). *Lernaea cyprinacea* have been found on gold fish and grass carp in New Zealand, but not on mosquitofish (Hine et al., 2000). Mosquitofish and goldfish have been found to co-exist in many New Zealand lakes (Brijs et al., 2008; Hicks et al., 2001). This suggests parasites can transmit between mosquitofish and carps. It is possible that mosquitofish occupy habitats with poor environmental conditions that carps cannot tolerate (Champion et al., 2002; McDowall, 1978). It could also be due to the fact that mosquitofish occupy littoral zone of the lakes or rivers (Chen et al., 2008; McDowall, 1978; Pan et al., 1980), while carp prefer deeper habitats (Koehn, 2004; McDowall, 1978). However, the most likely explanation is that *L. cyprinacea* has an extremely low abundance with limited distribution, which was rarely found on grass carps in New Zealand (Edwards & Hine, 1974), and thus they are less likely to transmit to mosquitofish.

4.2.4 Mosquitofish invasiveness

The absence of parasites from mosquitofish in New Zealand may facilitate the invasiveness of mosquitofish. Parasites of mosquitofish are reported to have significant adverse impacts on the fitness of individuals. For example, the presence of the nematode *E. ignotus* was found to reduce fecundity of female mosquitofish and increase exposure of mosquitofish to the predators in Oklahoma, USA (Deaton, 2011). Survivorship of mosquitofish from North Carolina, USA, was reduced by the infection of Asian tapeworm *Bothriocephalus acheilognathi* (Granath & Esch, 1983). Therefore, by lacking parasite infestations, mosquitofish in New Zealand likely have greater competitive abilities due to having faster individual and population growth rates, higher survival rate, higher fecundity, and are better avoiding predators than their conspecifics in their native range.

Other factors also contribute to mosquitofish becoming invasive. Mosquitofish have a high tolerance for surviving harsh conditions, including large fluctuations in water temperature, dissolved oxygen concentrations and the pollution (Brock & Font, 2009; Ling, 2001, 2004). The high feeding rate and feeding intensity of the mosquitofish (Chen et al., 2008) allow them to outcompete native species. Since they are aggressive predators, they have been reported to consume more invertebrates than their own weight in a day in China (Baker et al., 2004; Pan et al., 1980), prey on the eggs and fry of native New Zealand galaxiids fishes and attack adult mudfish (genus *Neochanna*) and some other large fishes in New Zealand (Barrier & Hicks, 1994; Ling, 2001). Mosquitofish have early maturation (reach maturity in about 40 days), internal fertilisation, and multiple reproductions in each season, and they can therefore establish quickly in habitats to which they are introduced and utilize empty niches. Mosquitofish are live-bearing fish which may increase survival of eggs (Rowe & Graynoth, 2002). Female mosquitofish can also retain viable sperm over winter. Therefore, their populations can build up during summer even in the absence of males (Baker et al., 2004; Chen et al., 2008; Langerhans, 2009; Pan et al., 1980). However, Ling (2004) suggested that the extreme aggressive competition or predation may be lake specific as the New Zealand native fish such as inanga and some other dune lake galaxiads can co-exist with mosquitofish in many Northland dune lakes, without the native fish being driven to the extinction.

4.3 Common bullies (*Gobiomorphus cotidianus*)

4.3.1 Parasites found

The nematode *Eustrongylides ignotus* and the trematode *Telogaster opisthorchis* were found from common bullies. *Eustrongylides ignotus* are red roundworms with a length up to 60 mm, coiled inside an encysting membrane (McDowall, 1978). *Eustrongylides ignotus* are found in the body cavity of common bullies by attaching to the abdominal and visceral walls. *Telogaster opisthorchis* have small (1 mm in diameter) clear to white cysts found under the skin of hosts and inside their musculature as described by (Macfarlane, 1945). *Eustrongylides ignotus* have not been reported from common bullies previously (Hine et al., 2000). *Eustrongylides ignotus* have been reported on shortfin eel, longfin eel, inanga (*Galaxias maculatus*), upland bully (*Gohiomorphus breviceps*), giant bully (*Gobiomorphus gobioides*), rainbow trout (*Oncorhynchus mykiss*), sockeye salmon (*Oncorhynchus nerka*), brown trout (*Salmo trutta*) and tench (*Tinca tinca*; (Hine et al., 2000).

Eustrongylides ignotus has a complex life cycle with four developmental stages to grow from eggs to sexually mature adults. *Eustrongylides ignotus* usually requires two intermediate hosts in orders to be sufficiently developed to infect their definitive hosts, fish-eating birds (Friend & Franson, 1999). The first intermediate hosts are oligochaetes, *Limnodrilus hoffmeisteri*. *Eustrongylides ignotus* is not host specific. A variety of freshwater fish act as the second intermediate hosts: this includes the families Anguillidae, Centrarchidae, Cottidae, Cyprinidae, Ictaluridae, Moronidae, Poecilidae and Salmonidae (Roffe, 1988). Some amphibians and reptiles have also been reported to host *E. ignotus* larvae and act as transporters in North America (Barros, Tortelly, Pinto, & Gomes, 2004; Coyner et al., 2003; Measures, 1988). Black crappie (*Pomoxis nigromaculatus*), largemouth bass (*Micropterus salmoides*) and warmouth (*Lepomis gulosus*), which ingest the second intermediate hosts, have been reported to act as vectors to the definitive hosts in Florida, USA (Coyner et al., 2003). Adult *E. ignotus* have been found infecting shags (*Phalacrocorax* spp.) in New Zealand (Hine, 1978).

The trematode *Telogaster opisthorchis* belongs to the family Cryptogonimidae. *Telogaster opisthorchis* use shortfin eels (*Anguilla australis*) and longfin eels (*A. dieffenbachii*) as their definitive hosts (Hine, 1978). *Telogaster opisthorchis* use the gastropod *Potamopyrgus antipodarum* as their first intermediate host (Hine, 1978). New Zealand freshwater fish, giant bully (*Gobiomorphus gobioides*) and koaro (*Galaxias brevipinnis*) were reported to host *T. opisthorchis* metacercaria (Macfarlane, 1952). *Telogaster opisthorchis* has been reported on number of fishes in New Zealand, including shortfin and longfin eels, koaro, dwarf galaxias (*Galaxias divergens*), banded kokopu (*Galaxias fasciatus*), inanga (*Galaxias maculatus*), short-jawed kokopu (*Galaxias postvectis*), common river galaxias (*Galaxias vulgaris*), upland bully (*Gobiomorphus breviceps*), common bully (*Gobiomorphus cotidianus*), blue-gilled bully (*Gobiomorphus hubbsi*), red-finned bully (*Gobiomorphus huttoni*), brown mudfish (*Neochanna apoda*), smelt (*Retropinna retropinna*) and brown trout (*Salmo trutta*) (Hine et al., 2000).

4.3.2 Host size and parasite abundance

My results showed no correlations between the size of the common bullies sampled and the length of *Eustrongylides ignotus* cysts, or the total number of *E. ignotus* and *T. opisthorchis* cysts. However, the parasite intensities were greater for medium to large common bullies. Female common bullies were significantly larger with relatively more parasite infections than the male at Lake Ngatu. Larger hosts generally harbour more and larger parasites than smaller hosts (Sasal et al., 1999). Larger hosts provide more surface area for the attachment (Buchmann & Bresciani, 1997) and more resources with more space which can promote parasite growth (Macfarlane, 1952; Sasal et al., 1999).

Numbers of encysted metacercariae of *E. ignotus* and *T. opisthorchis* were higher in larger common bullies. For example, common bullies with a total length of less than 35 mm contained no cysts. Larger common bullies feed more than smaller ones, potentially increasing the probability of ingesting infected invertebrates. A greater period of their lives also leads to a greater probability being infected by parasites. As discussed above, common bullies that are less than 35 mm will have difficulties ingesting the gastropod *P. antipodarum* infected by *T. opisthorchis* larvae or oligochaetes which contain *Eustrongylides ignotus* larvae. (Macfarlane, 1952) has found the freshwater eels in the Heathcote, Selwyn and Cass Rivers and Lake Sarah, New Zealand with a length less than 35 - 40 cm were not infected with *T. opisthorchis*. He suggested that *P. antipodarum* less than 2 cm long which can be eaten by small eels (< 30 cm long) rarely harbour *T. opisthorchis* metacercariae. *Potamopyrgus antipodarum* that do contain *T. opisthorchis* metacercaria are typically larger than 2 cm, and these snails are rarely eaten by eels that are less than 35 cm. Also larval common bullies with total length less than 18 mm are planktonic and feed on zooplankton rather than infected gastropods and oligochaetes (Rowe, 1999).

On average, more *Eustrongylides ignotus* cysts were found on larger common bullies than *T. opisthorchis* cysts, which further suggest differences in the feeding behaviour of larger and smaller hosts. Also the first intermediate hosts of *Eustrongylides ignotus* may be larger than that of *T. opisthorchis*. Nevertheless, larger hosts have the potential to host more parasites than the smaller ones.

A decrease in cyst intensity was found, when the total length of common bullies exceeds 96 mm for *Eustrongylides ignotus* cysts and 46 mms for *T. opisthorchis* cysts (Tables 15, 16). Despite that the increased body size of common bullies leading to a change of dietary composition, it results a reduction of parasite larvae intake and parasite harbouring. A more functional immune defence against parasite infections seemed more likely. The immune defence of the hosting fish can also affect the intensity of parasite infections. Boerlage, Graat, Verreth, & de Jong, (2011) suggested larger mature fishes will have more developed immune systems against parasitic infection than the smaller immature ones. They found the fish size and attack rate of gill parasites were negatively correlated with the size of koi carp. Small koi carp have more metacercaria than the medium and large ones. Buchmann and Brosciani (1997) found a similar result in farmed rainbow trout. Mitchell, Goodwin, Salmon and Brandt (2002) discovered a decrease of *Centrocestus formosanus* cysts after 50 days of experimental infection on channel catfish, *Ictalurus punctatus* and sunshine bass *Morone* sp. However, the immune defence of the common bullies on the parasitic infection of *Eustrongylides ignotus* and *T. opisthorchis* has not been well investigated, thus this is likely to happen but may not definitely happen.

4.3.3 Parasite distribution

Common bullies were parasitized in eight of the lakes sampled. There were differences in the parasite fauna in some of the lakes. *Telogaster opisthorchis* was the only parasite species found at Lake Rotorua, Lake Kai-iwi, and Lake Rotoroa. *Eustrongylides ignotus* was the only parasite species found at Chapel Lake, Lake Ngatu and Lake Ngaroto. Both *Eustrongylides ignotus* and *T. opisthorchis* were found at Lake Rotokawau East and Lake Waiparera.

The differences in the parasite fauna of bullies in the different lakes is possibly explained by differences in the distribution and presence of the intermediate hosts and definitive hosts of the parasite species. Although the invertebrate, fish and fish-eating bird species of the sample lakes were not examined, published records give an insight to factors preventing parasites completing their life cycles. For example, shags (*Phalacrocorax* spp.) and abundant invertebrate species have been recorded from Lake Ngatu but there are no records of the snail *P. antipodarum,* which may explain the absence of *T. opisthorchis* from common bullies in this lake, as *P. antipodarum* is the first intermediate host of *T. opisthorchis* (Ball et al., 2009; Wells & Champion, 2010). Shortfin and longfin eels and *P. antipodarum* are present in Lake Waiparera which coincides with *Eustrongylides ignotus* and *T. opisthorchis* infection of common bullies (Ball et al., 2009; Wells & Champion, 2010). Likewise the presence of *Eustrongylides ignotus* in bullies from Chapel Lake coincided with the presence of short-finned eel and shag (Hicks & Bryant, 2002). However, the absence of *T. opisthorchis* on common bullies of Lake Ngaroto, when both eels and *P. antipodarum* were present in August (Hicks et al., 2001), seemingly contradicts this hypothesis.

Parasites showed a preference for host sex at four sampled lakes. More *E. ignotus* and *T. opisthorchis* cysts were found on female common bullies than the male at Lakes Waiparera, Rotoroa and Rotorua. As Lake Rotorua, female common bullies caught were significantly more than the male. *Telogaster opisthorchis* cysts were found only on male common bullies at Lake Waiparera, which twice as many male common bullies as the female were found. Common bullies caught from Lakes Ngatu and Ngaroto showed no differences between the number of the female and male or the number of parasite found on different sexes. According to

Poulin (1996) and Edwards and Heather (2003), one sex will contain more parasites than the other as a result of variations in morphological, physiological and behavioural aspects. Common bullies are territorial and male common bullies are very aggressive (McDowall, 1978, 2000). Territorialism and social interactions will allow one sex to be more dominant than the other. Dominancy allows the individual to gain access to more food resources, which leads to a higher probability of ingesting infected prey (Maher & Lott, 2000).

4.4 Conclusion

My study shows that the non-indigenous freshwater fish fauna of New Zealand have had a loss or reduction in their parasite fauna. “Missing the boat” and “lost over boat” are the major contributors to the loss of parasites. Parasites with complex life cycles have likely been lost from their non-indigenous freshwater fish hosts when being introduced into New Zealand, due to the absence of the additional host required. Therefore, “lost over board” may provide one good explanation for the reduction in parasites from New Zealand non-indigenous freshwater fishes. On the other hand, parasites of mosquitofish introduced into New Zealand may have missed the boat. Mosquitofish were introduced to Hawaii before they were introduced into New Zealand. The parasite fauna of Hawaiian mosquitofish is known to have been reduced, and appears to have been further reduced on their introduction to New Zealand. No parasites were found on mosquitofish at their first release sites in New Zealand, and it seems likely based on my results that mosquitofish introduced from Hawaii to New Zealand may have been parasite free. My study supports part of the parasite release hypothesis, as the fish species have lost their parasites when being introduced into geographically different habitats, while native species harbour more parasites than the introduced species within the same habitats. Even though parasites can pose great impacts on both the physiology and behaviour of their fish hosts, the lack of parasites cannot explain their invasion success on its own. However, I believe this loss may be a contributing factor, in addition to favourable resource availability and physical environment (Ling, 2004).

The introduced mosquitofish were found to have fewer parasites than their native competitor common bullies living in the same freshwater lakes of New Zealand. The trematodes *Eustrongylides ignotus* and *Telogaster opisthorchis* cysts were found on common bullies but not on mosquitofish. Mosquitofish are free from the impact of parasite spillback, which is very likely due to the dietary composition differences between common bullies and mosquitofish. There were no relationships found between the number of trematode cysts and the size of common bullies. However, these parasitic cysts were found to have higher proportions infecting medium to large sized common bullies than smaller ones. The size range of common bullies can result in dietary differences with age, which may lead to the difference in parasite infection between the juvenile and adult common bullies. The parasite fauna showed differences between sampled lakes, which may be due to the difference invertebrate communities and final hosts present at different lakes. The presence of parasite larvae and the dietary preference of fish species are very important in determining the parasite fauna of these fish.

For future studies on non-indigenous freshwater fishes, experimental infections of parasites will provide useful information as they will show to what extent the parasite can influence their fish hosts. Investigations on the dietary composition of common bullies and mosquitofish from the same habitats, expanding the sample locations to cover streams and rivers, using alternative methods and greater investigation of other non-indigenous fish species will provide invaluable data.

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Appendices:

Appendix 1.Parasites of mosquitofish (*Gambusia affinis*) recorded in the literature

Location	Phylum/subphylum	Parasite species	Reference
North America	Monogenea	*Gyrodactylus gambusiae*	(Brock & Font, 2009; Hoffman, 1999; Salgado-Maldonado, 2008)
		Haplocleidus sp.	
		Salsuginis bahamianus	
		S. seculus	
	Digenea	*Allacanthochasmus* sp.	
		Ascocotyle ampullacia	
		A. leighi	
		A. mcintoshi	
		A. tenuicollis	
		Bolbophorus confusus	
		Crassiphiala bulboglossa	
		Crepidostomum sp.	
		Diplostomulum scheuringi	
		Diplostomulum sp.	
		Echinochasmus pelecani	
		E. swartzi	
		Heterophyes aequalis	
		Macroderoides spiniferus	
		Nanophyetus salmincola	

	Neascus sp.
	Ornithodiplostomum ptycocheilus
	Paramacroderoides echinus
	Phagicola diminutus
	Phagicola sp.
	Phyllodistomum sp.
	Plagioporus sinitsini
	Posthodiplostomum minimum
	Prohemistomulum expeditum
	Rhipdocotyle papillosa
	Szidatia joyeuxi
	Tetracotyle sp.
Cestoidea	*Bothriocephlaus acheilognathi*
	Glossocercus sp.
	Ophiovalipora sp.
	Proteocephalus sp.
Nematoda	*Camallanus oxycephalus*
	Camallanus sp.
	Contracaecum spiculigerum
	Eustrongylides ignotus
	Rhabdochona canadensis
	R. kidderi
	Rhabdochona sp.
	Spinitectus carolini

		Spiroxys sp.	
	Acanthocephala	*Leptorhynchoides thecatus*	
		Neoechinorhynchus cylindratus	
		Octospiniferoides chandleri	
	Crustacea	*Ergasilus funduli*	
		Lernaea catostomi	
		L. cyprinacea	
		Sebekia mississippiensis	
China	Digenea	*Centrocestus formosanus*	(Zeng et al., 2005)
Puerto Rica	Digenea	*Echinochasmus donaldsoni*	(Bunkley-Williams & Williams, 1994)

Appendix 2. Parasites of catfish (*Ameiurus nebulosus*) recorded in the literature

Location	Phylum/subphylum	Parasite species	Reference
Puerto Rica	Monogenea	*Cleidodiscus pricei*	(Bunkley-Williams & Williams, 1994)
North America	Monogenea	*Gyrodactylus fairporti*	(Hoffman, 1999; McDonald & Margolis, 1995)
		G. nebulosus	
		Haplocleidus sp.	
		Ligictaluridus floridanus	
		L. longus	
		L. monticellii	
		L. pricei	
	Digenea	*Acetodextra amiuri*	
		Allocreadium ictaluri	
		Alloglossidium corti	
		A. geminus	
		A. geminus	
		Apophallus venustus	
		Azygia acuta	
		A. angusticauda	
		Bucephalus elegans	
		Centrovarium lobotes	
		Clinostomum complanatum	
		Crepidostomum cooperi	
		C. cornutum	
		C. ictaluri	
		Diplostomulum scheuringi	
		D. spathaceum	
		Diplostomulum sp.	

	Echinochasmus donaldsoni
	Euparyphium melis
	Glossidium geminum
	Homalometron armatum
	Hysteromorpha triloba
	Lepidauchen sp.
	Macroderoides spiniferus
	Megalonia ictaluri
	Megathylacoides intermedia
	Microphallus opacus
	Neascus sp.
	Petasiger nitidus
	Phyllodistomum americanum
	P. folium
	P. hunter
	P. staffordi
	P. superbum
	Plagiorchis ameiurensis
	P. corti
	Polylekithum ictaluri
	Posthodiplostomum minimum
	Rhipidocotyle sp.
	Tetracotyle sp.
	Vietosoma parvum
Cestoidea	*Bothriocephalus claviceps*

	B. cuspidatus
	Corallobothrium fimbriatum
	C. intermedium
	C. parafimbriatum
	C. parvum
	C. perplexus
	Corallotaenia minutia
	Haplobothrium globuliforme
	Proteocephalus ambloplitis
	P. pearsei
	P. stizostethi
	Proteocephalus sp.
Nematoda	*Camallanus oxycephalus*
	Camallanus sp.
	Capillaria sp.
	Contracaecum brachyurum
	C. spiculigerum
	Contracaecum sp.
	Contracaecum sp.
	Cucullanus cotylophora
	Cystidicoloides prevosti
	Dacnitoides robusta
	Dichelyne cotylophora
	D. robusta
	Dioctophyme renale

	Eustrongyloides sp.
	Metabronema prevosti
	Rhabdochona cascadilla
	Rhabdochona sp.
	Spinitectus carolini
	S. gracilis
	Spinitectus sp.
	Spiroxys contortus
	Spiroxys sp.
Acanthocephala	*Acanthocephalus dirus*
	Echinorhynchus salmonis
	E. thecatus
	Echinorhynchus sp.
	Fessisentis tichiganensis
	Leptorhynchoides thecatus
	L. thecatus
	Neoechinorhynchus cylindratum
	N. rutili
	Pilum pilum
	Pomphorhynchus bulbocolli
	P. bulbocolli
Hirudinea	*Actinobdella inequiannulata*
	Desserobdlla phalera
	Illinobdella moorei
	I. richardsoni

	Illinobdella sp.
	Myzobdella lugubris
	Piscicola punctate
	Piscicolaria sp.
Mollusca	*Glochidia* sp.
	Unionidae *gen*. sp.
Crustacea	*Actheres pimelodi*
	Argulus americanus
	A. appendiculosus
	A. flavescens
	A. maculosus
	Ergasilus arthrosis
	E. clupeidarum
	E. cyprinacea
	E. elegans
	E. megaceros
	Lernaea cyprinacea
	L. pomotides
	L. tortua
	L. variabilis

Appendix 3. Parasites of koi carp (*Cyprinus carpio*) recorded in the literature

Location	Phylum/subphylum	Parasite species	Reference
Bangladesh	Monogenea	*Dactylogyrus* sp.	(Arthur & Ahmed, 2002)
	Digenea	Digenea *gen*. sp.	
	Acanthocephala	*Pallisentis* sp.	
Japan	Monogenea	*Dactylogyrus extensus*	(Nagasawa, Awakura, & Urawa, 1989)
		D. falciformis	
		Eudipolzoon nipponicum	
		Gyrodactylus kherulensis	
	Digenea	*Posthodiplostomum sp.*	
	Cestoidea	*Bothriocephalus acheilognathi*	
	Crustacea	*Lernaea cyprinacea*	
		Argulus japonicus	
Latvia	Monogenea	*Dactylogyrus achmerowi*	(Kirjušina & Vismanis, 2007)
		D. anchoratus	
		D. extensus	
		D. minutus	
		D. vastator	
		Diplozoon paradoxum	
		Diplozoon sp.	
		Eudiplozoon nipponicum	
		Gyrodactylus katarineri	
		G. medius	
	Digenea	*Bucephalus polymorphus*	
		Diplostomum	

	spathacem
	Ichthyocotylurus plathycephalus
	Posthodiplostomum cuticola
	Sanguinicola inermis
	Tetracotyle sp.
	Tylodelphys clavata
Cestoidea	*Archigetes brachyurus*
	Bothriocephalus acheilognathi
	Caryophyllaeus fimbriceps
	C. laticeps
	Khawia sinensis
	Ligula intestinalis
	Neogryporhynchus cheilancristrotus
	Paradilepis scolecina
	Valipora campylancristrota
Nematoda	*Contracaecum micropapillatum*
	Nematoda *gen*. sp.
	Philometroides cyprinid
	Shulmanella petruschewskii
Acanthocephala	*Acanthocephalus anguillae*
	A. lucii
Hirudinea	*Piscicola geometra*
Mollusca	*Unio tumidus*
Crustacea	*Argulus foliaceus*

Turkey	Monogenea	*Dactylogyrus. Anchoratus*	(Tekin-Özan, Kir, & Barlas, 2008)
		D. extensus	
		D. minutus	
		Dactylogyrus sp.	
	Cestoidea	*Bothriocephalus acheilognathi*	
		Caryophyllaeus laticeps	
		Ligula intestinalis	
	Acanthocephala	*Neochinorhynchus rutili*	
	Crustacea	*Argulus foliaceus*	
		Ergasilus sieboldi	
Viet Nam	Monogenea	Dactylogyridae *gen*. sp.	(Arthur & Te, 2006)
		Dactylogyrus achmerowi	
		D. anchoratus	
		D. extensis	
		D. falciformis	
		D. minutus	
		Dactylogyrus sp.	
		Gyrodactylus medius	
		Gyrodactylus sp.	
		Paradiplozoon doi	
	Digenea	*Allocreadium isoporum*	
		Centrocestus formosanus	
		Centrocestus sp.	
		Stephanostomum sp.	
	Cestoidea	*Diphyllobothrium* sp.	
		Khawia sinensis	

	Nematoda	*Camallanus truncatus*	
		Cucullanus cyprini	
		Philometra sp.	
	Acanthocephala	*Brentisentis cyprini*	
		Dendronucleata dogieli	
	Mollusca	Unionidae gen. sp.	
	Crustacea	*Argulus foliaceus*	
		Argulus sp.	
		Lernaea cyprinacea	
		Lernaea sp.	
		Paraergasilus brevidigitus	
		P. medius	
		Paraergasilus sp.	
Philippines	Monogenea	*Dactylogyrus* sp.	(Arthur & Lumanlan-Mayo, 1997)
		Gyrodactylus sp.	
		Monogenea *gen*. sp.	
	Crustacea	*Argulus* sp.	
		Lernaea sp.	
North America	Monogenea	*Dactylogyrus achmerovi*	(de León, García-Prieto, León-Règagnon, & Choudhury, 2000; Hoffman, 1999)
		D. anchoratus	
		D. auriculatus	
		D. biwaensis	
		D. crassus	
		D. cryptomerus	
		D. cyprini	
		D. difformis	
		D. dujardianus	

	D. extensus
	D. falcatus
	D. falciformis
	D. fallax
	D. formosus
	D. lopuchinae
	D. minutus
	D. mollis
	D. nipponicum
	D. solidus
	D. takahaskii
	D. vastator
	D. wegeneri
	Diplozoon nipponicum
	Gyrodactylus fairporti
	G. gracilis
	G. katherineri
	G. medius
	G. nagibinae
	G. shulmani
	G. sprostonae
	G. stankovici
	Pseudoacolpenteron pavlovskii
Aspidogastrea	*Aspidogaster amurensis*
	A. ejimai
	A. limacoides
Digenea	*Allocreadium carparum*
	A. isosporum
	Apharyngostrigea cornu
	Aponurus tshugunovi

Apophallus venustu

Ascocotyle coleostoma

Asymphylodora japonica

A. kubanicum

Bolbophorus confuses

Bucephalus polymorphis

Bunoderina luciopercae

Clinostomum complanatum

Clonorchis sinensis

Crepidostomum cooperi

Crepidostomum sp.

Diplostomulum clavatum

D. flexicaudum

D. scheuringi

D. spathaceum

Diplostomulum sp.

Echinochasmus perfoliatus

Exorchis oviformis

Haplorchis taickui

Hysteromorpha triloba

Metagonimus katsuradae

M. yokogawai

Metorchis orientalis

Neascus sp.

Neodiplostomum perlatum

	Opisthorchis felineus
	Ornithodiplostomum ptychocheilus
	Phyllodistomum dogieli
	P. elongatum
	Plagiocirrus primus
	Posthodiplostomum cuticola
	P. minimum
	Sanguinicola armata
	S. inermis
	Sphaerostoma bramae
	Tetracotyle echinata
	T. sogdiana
Cestoidea	*Archigetes iowensis*
	Atracolytocestus huronensis
	Biacetabulum appendiculatum
	Bothriocephalus acheilognathi
	Caryophyllaeus fimbriceps
	C. laticeps
	C. terebrans
	Caryophylleaus sp.
	Corallobothrium sp.
	Cysticercus Paradilepsis scolecina
	C. Gryporhynchus cheilancristrotus
	Digramma interrupta
	Dilepis sp.

	Khawia iowensis
	K. japonicus
	K. sinensis
	Ligula intestinalis
	Triaenophorus nodulosus
Nematoda	*Anisakis* sp.
	Camallanus ancyllodirus
	Capillaria catenata
	C. patzcuarensis
	Contracaecum squali
	Cucullanus cyprinid
	C. dogieli
	Eustrongylides excisus
	Eustrongylides ignotus
	Goezia nankingensis
	Philometra cyprini
	P. lusiana
	P. sanguinea
	Philometroides cyprini
	Porrocaecum reticulatum
	Pseudocapillaria brevispicula
	Raphidascaris acus
	Rhabdochona cascadilla
	Spinitectus carolini
	S. gracilis
	Spiroxys sp.
Acanthocephala	*Acanthocephalus alabamensis*
	A. anguillae

	A. dirus
	A. lucii
	Corynosoma strumosum
	Fessisentis fessus
	Leptorhynchoides thecatus
	Neoechinorhynchus cylindratus
	N. rutilis
	Paracanthocephalus curtus
	P. tenuirostris
	Pomphorhnychus bulbocolli
	P. laevis
	Pseudoechinorhynchus clavula
Hirudinea	*Hemiclepsis marginate*
	Piscicola geometra
	Placobdella montifera
	Trachelobdella sinensis
Mollusca	*Glochidia* sp.
Crustacea	*Argulus appendiculatus*
	A. biramosus
	A. catostomi
	A. coregoni
	A. flavescens
	A. foliaceus
	A. japonicus
	Caligus lacustris
	C. orientalis

		Ergasilus arthrosis	
		E. briani	
		E. caeruleus	
		E. elegans	
		E. esocina	
		E. sieboldi	
		Lamproglena pulchella	
		Lernaea cyprinacea	
		Neoergasilus japonicus	
		N. longispinus	
		Paraergasilus brevidigitus	
		P. longidigitus	
		Synergasilus undulatus	
		Tracheliastes polycolpus	
China	Monogenea	*Ancylodiscoides* sp.	(Guo, Liu, & Huhebatour, 1994; Jin et al., 1993; Jin, Liu, & Zeng, 1993; Li & Zhang, 1992; Xie et al., 2000; Xu, Sun, Han, Li, & Liu, 2001; Yao & Nie, 2004)
		Eudiplozoon nipponicum	
		Dactylogyrus anchoratus	
		D. extensus	
		D. minutus	
		D. vastator	
		D. achmerowi	
		D. solidus	
		Dactylogyrus sp.	
		Gyrodactylus paralatus	
		G. gei	
		G. sprostonae	
	Digenea	*Aspidogaster*	

	amurensis
	Allocreadium
	hypophthalmichydis
	Diplostomulum
	hupehensis
	D. niedashui
	Diplostomulum sp.
	Orienlotrema japonica
Cestoidea	*Bothriocephalus*
	opsarichthydi
	Caryophyllaeus
	brachialis
	C. minutus
	Gryporhynchus sp.
	Khawia cyprinid
	K. japonensis
	K. sinensis
	Ligula sp.
	Tsengia
	neimongkuensis
Nematoda	*Cucullanus cyprini*
	Philometra cyprini
Acanthocephala	*Hebesoma violentum*
	Rhadinorhynchus
	cyprini
	Neoechinorhynchus
	austral
Crustacea	*Lernaea cyprinacea*
	Argulus chinensis
	A. japonicus
	A. ellipticaudatus

Appendix 4. Parasites of goldfish (*Carassius auratus*) recorded in the literature

Location	Phylum/subphylum	Parasite species	Reference
New Zealand	Digenea	*Coitocaecum parvum*	(Hine et al., 2000)
	Crustacea	*Abergasilus amplexus*	
		Argulus japonicus	
		Lernaea cyprinacea	
Japan	Monogenea	*Eudiplozoon nipponicum*	(Nagasawa et al., 1989)
		Gyrodactylus sp.	
	Digenea	*Posthodiplostomum sp.*	
	Cestoidea	*Digramma interrupta*	
	Crustacea	*Neoergasilus japonicus*	
Latvia	Monogenea	*Dactylogyrus anchoratus*	(Kirjušina & Vismanis, 2007)
		D. inexpectatus	
		Gyrodactylus katharineri	
		G. longoacuminatus	
		G. medius	
	Digenea	*Ichthyocotylurus plathycephalus*	
	Hirudinea	*Piscicola geometra*	
	Crustacea	*Argulus foliaceus*	
Viet Nam	Monogenea	Dactylogyridae *gen.* sp.	(Arthur & Te, 2006)
		Dactylogyrus intermedius	
		Paradiplozoon doi	
	Crustacea	*Lernaea cyprinacea*	
Australia	Monogenea	*Dactylogyrus* sp.	(Fletcher & Whittington, 1998)
		Gyrodactylus kobayashii	
		Gyrodactylus sp.	
	Crustacea	*Lernaea cyprinacea*	
Philippines	Monogenea	*Dactylogyrus* sp.	(Arthur & Lumanlan-Mayo, 1997)
		Gyrodactylus sp.	
	Digenea	Digenea *gen.* sp.	

	Crustacea	*Lernaea cyprinacea*	
Puerto Rica	Monogenea	*Dactylogyrus anchoratus*	(Bunkley-Williams & Williams, 1994)
	Crustacea	*Argulus japonicus*	
		Lernaea cyprinacea	
North America	Monogenea	*Dactylogyrus anchoratus*	(Hoffman, 1999)
		D. arquatus	
		D. auriculatus	
		D. baueri	
		D. crassus	
		D. cryptomeres	
		D. dogieli	
		D. dujardinianus	
		D. dulkeiti	
		D. extensus	
		D. folax	
		D. formosus	
		D. hypothalmichthys	
		D. inexpectatus	
		D. intermedius	
		D. laymani	
		D. minutus	
		D. nobilis	
		D. skryabini	
		D. suchengtaii	
		D. vastator	
		D. wegeneri	
		D. wuhuensis	
		D. yinwenyin	
		Diplozoon minutus	
		D. nipponicum	
		D. nobilis	
		D. skrjabini	

	D. suchengtaii
	D. vastator
	D. wegeneri
	D. wuhensis
	D. yinwenyin
	Gyrodactylus anchoratus
	G. carassii
	G. chinensis
	G. elegans muelleri
	G. gurleyi
	G. katharineri
	G. kobayashii
	G. medius
	G. mutabilitas
	G. schulmani
	G. sprostonae
Digenea	*Allocreadium isoporum*
	A. transversale
	Asymphylodora markewitschi
	A. tincae
	Bucephalopsis clara
	Bucephalus polymorphus
	Clinostomum complanatum
	Clonorchis sinensis
	Cotylurus pileatus
	Cyathocotyle orientalis
	Diplostomulum clavatum
	D. paradoxum
	D. spathaceum
	Hysteromorpha triloba
	Metagoniums katsuradai
	M. yokogawai

	Metorchis orientalis
	Nanophyetes salmincola
	Opisthorchis felineus
	Paracoenogonimus ovatus
	Phyllodistomum elongatum
	P. folium
	Posthodiplostomum cuticola
	Sanguinicola lungensis
Cestoidea	*Caryophyllaeus laticeps*
	Cysticercus of *Paradilepis scolecina*
	Cysticerns of *Gryporhynchus pusillum*
	Digramma interrupta
	Khawia parva
	K. rossitensis
	Triaenophorus nodulosus
Nematoda	*Agamospirura* sp.
	Capillaria brevispicula
	Contracaecum squalii
	Philometra carassii
	P. sanguinea
	Raphidascaris acus
Acanthocephala	*Acanthocephalorhynchoides ussuriensis*
	Acanthocephalus anguillae
	A. jacksoni
	Neoechinorhynchus rutili
	Neoechinorhynchus sp.
	Paracanthocephalus tenuirostris
	Pomphorhynchus bulbocolli

		P. laevis	
	Hirudinea	*Piscicola geometra*	
		Trachelobdella sinensis	
	Mollusca	Unionidae *gen. sp.*	
	Crustacea	*Argulus ernsti*	
		A. foliaceus	
		A. japonicus	
		A. lunatus	
		A. trilineatus	
		Ergasilus briani	
		E. sieboldi	
		Lamproglena carassii	
		Lernaea barilii	
		L. cyprinacea	
		Neoergasilus longispinosus	
		Paraergasilus brevidigitus	
		P. longidigitus	
		Sinergasilus undulatus	
	Acarina	Hydrachnellae *gen.* sp.	
China	Monogenea	*Dactylogyrus anchoratus*	(Guo et al., 1994; Jin, Dai et al., 1993; Li & Zhang, 1992; Xu et al., 2001; Yao & Nie, 2004)
		D. arcuatus	
		D. formosus	
		D. inexpectatus	
		D. intermedius	
		D. vastator	
		Diplozoon paradoxum	
		Gyrodactylus sprostonae	
		G. gei	
		G. elegans sinensis	
	Digenea	*Asymphylodora markewitschi*	
		A. japonica	
		Carassotrema koreanum	

	C. schistorchis
	Diplostomulum hupehensis
	D. niedashui
	Diplostomulum sp.
	Dollfustrema sp.
	Phyllodistomum
	(Catoptroides) carassii
Cestoidea	*Caryophyllaeus*
	brachycollis
	Digramma
	Digramma sp.
	Gryporhynchus sp.
	Khawia japonensis
	Ligula sp.
	Senga sp.
Nematoda	*Anisakis (A) simpler*
	Contracaecum sp.
	Philometra carassii
	Philometra sp.
Hirudinea	*Hemiclepsis* sp.
Crustacea	*Lernaea cyprinacea*
	Argulus japonicus
	Neoergasilus japonicus
	Sinergasilus major
	S. undulatus
	Paraergasilus brividigitus
	P. longdigitus

Appendix 5. Parasites of grass carp (*Ctenopharyngodon idella*) recorded in the literature

Location	Phylum/subphylum	Parasite species	Reference
Bangladesh	Monogenea	*Dactylogyrus* sp.	(Arthur & Ahmed, 2002)
	Crustacea	*Argulus* sp.	
		Lernaea sp.	
Latvia	Digenea	*Diplostomum spathaceum*	(Kirjušina & Vismanis, 2007)
New Zealand	Monogenea	*Dactylogyrus ctenopharyngodonis*	(Hine et al., 2000)
		Gyrodactylus ctenopharyngodontis	
	Cestoidea	*Bothriocephalus gowkongensis*	
	Crustacea	*Lernaea cyprinacea*	
North America	Monogenea	*Cotyluris communis*	(Hoffman, 1999)
	Cestoidea	*Bothriocephalus acheilognathi*	
	Nematoda	*Capillaria* sp.	
		Philometra sp.	
		Spiroxys sp.	
Philippines	Cestoidea	*Bothriocephalus acheilognathi*	(Arthur & Lumanlan-Mayo, 1997)
Puerto Rica	Cestoidea	*Bothriocephalus acheilognathi*	(Bunkley-Williams & Williams, 1994)
China	Monogenea	*Amurotrema dombrovskajae*	(Guo et al., 1994; Jin, Dai et al., 1993; Li & Zhang, 1992; Xu et al., 2001; Yao & Nie, 2004)
		Balantidium ctenopharyngodoni	
		Carassotrema koreanum	
		C. ptrorchis	

	Capillaria sp.
	Dactylogyrus ctenopharyngodonis
	D. hypophthalmichthys
	D. lamellatus
	D. mantschuricus
	D. magnihamatus
	D. nobilis
	D. primaries
	D. yinwenyingae
	Diplozoon sp.
	Gyrodactylus ctenopharyngodonis
	Lamproglena chinensis
	Pseudorhipidocotyle elopichthys
Digenea	*Diplostomulum hupehensis*
	D. niedashui
	Diplostomulum sp.
Cestoidea	*Bothriocephalus gowkongensis*
	B. opsariichthydis
	Bulanticlium ctenopharyngodoni
	Carassotrema koreanum
	Orienlotrema japonica
	Sinergasilus major
	Sinoichthyonema ctenopharyngodoni

Crustacea	*Argulus ellipticaudatus*
	A. yuji
	Hebesoma violentum
	Lernaea ctenopharyngodontis

Appendix 6. Parasites of silver carp (*Hypophthalmichthys molitrix*) recorded in the literature

Location	Phylum/subphylum	Parasite species	Reference
Bangladesh	Monogenea	*Dactylogyrus* sp.	(Arthur & Ahmed, 2002)
	Crustacea	*Lernaea* sp.	
Philippines	Cestoidea	*Bothriocephalus acheilognathi*	(Arthur & Lumanlan-Mayo, 1997)
	Crustacea	*Lernaea* sp.	
China	Monogenea	*Dactylogyrus hypophthalmichthys*	(Guo et al., 1994; Li & Zhang, 1992; Xu et al., 2001; Yao & Nie, 2004)
		D. suchengtaii	
	Digenea	*Allocreadium hypophthalmichthydis*	
		Carassotrema megapharyngus	
		Diplostomulum hupensis	
		D. niedashui	
		Diplostomulum sp.	
	Cestoidea	*Caryophyllaeus brachycollis*	
		Contracaecum sp.	
		Gryporhynchus sp.	
	Acanthocephala	*Neoechinorhynchus rutili*	
		Acanthosentis similis	
	Crustacea	*Lernaea cyprinacea*	
		L. polymorpha	
		Argulus japonicus	
		Sinergasilus polycopus	
		S. undulatus	

Appendix 7. Parasites of tench (*Tinca tinca*) recorded in the literature

Location	Phylum/subphylum	Parasite species	Reference
North America	Monogenea	*Dactylogyrus macracanthus*	(Hoffman, 1999)
		D. monocornis	
		D. similis	
		Diplozoon paradoxum	
	Digenea	*Allocreadium isoporum*	
		Asymphylodora kubanicum	
		A. tincae	
		Cotylurus pileatus	
		Crowcrocoecum skjabini	
		Diplostomulum clavatum	
		D. spathaceum	
		Hysteromorpha triloba	
		Neodiplostomulum pseudattenuatum	
		Opisthorchis felineus	
		Paracoenogonimus ovatus	
		Phyllodistomum elongatum	
		Sanguinicola armata	
		S. inermis	
		Sphaerostoma bramae	
	Nematoda	*Anisakis* sp.	
		Contracaecum squalii	
		Desmidocercella sp.	
		Raphidascaris acus	
		Skrjabillanus tincae	
	Acanthocephala	*Acanthocephalus anguillae*	
		A. lucii	
		Corynosoma smerine	

		C. strumosum	
		Echinorhynchus sp.	
		Neoechinorhynchus crassus	
		N. rutile	
	Hirudinea	*Piscicola geometra*	
	Crustacea	*Argulus foliaceus*	
		Ergasilus briani	
		E. sieboldi	
		Lernaea cyprinacea	
		L. esocina	
New Zealand	Nematoda	*Eustrongylides* (*ignotus*?)	(Hine et al., 2000)
Latvia	Monogenea	*Dactylogyrus macracanthus*	(Kirjušina & Vismanis, 2007)
		D. tincae	
		Diplozoon paradoxum	
		Gyrodactylus elegans	
		G. medius	
	Digenea	*Allocreadium isoporum*	
		Asymphylodora tincae	
		Bucephalus polymorphus	
		Diplostomulum sp.	
		Diplostomum spathaceum	
		Hysteromorpha triloba	
		Ichthyocotylurus plathycephalus	
		Paracoenogonimus ovatus	
		Phyllodistomum elongatum	
		Posthodiplostomum brevicaudatum	
		Tylodelphys clavata	
	Cestoidea	*Caryophyllaeus laticeps*	

	Neogryporhynchus cheilancristrotus
	Paradilepis scolicina
	Valipora campylancristrota
Nematoda	*Nematoda gen. sp.*
	Raphidascaris acus
	Skrjabillanus tincae
Acanthocephala	*Acanthocephalus anguillae*
	A. lucii
	Corynosoma semerme
Hirudinea	*Piscicola geometra*
Mollusca	*Anodonta cygnea*
	Unionidae *gen*. sp.
Crustacea	*Argulus foliaceus*
	Ergasilus briani
	E. sieboldi

Appendix 8. Parasites of orfe (ide) (*Leuciscus idus*) recorded in the literature

Location	Phylum/subphylum	Parasite species	Reference
Latvia	Monogenea	*Dactylogyrus fallax*	(Kirjušina & Vismanis, 2007)
		D. ramulosus	
		D. similis	
		D. tube	
		D. yinwenyingae	
		Dactylogyrus sp.	
		Gyrodactylus prostate	
		Paradiplozoon alburni	
	Digenea	*Allocreadium isoporum*	
		Diplostomum spathaceum	
		Ichthyocotylurus platycephalus	
		Paracoenogonimus ovatus	
		Plagioporus angusticolle	
		Posthodiplostomum cuticola	
		Sphaerostomum bramae	
		Tylodelphys clavata	
	Cestoidea	*Caryophyllaeides fenica*	
	Nematoda	*Cucullanus heterochrous*	
		Pseudocapillaria tomentosa	
		Raphidascaris acus	
	Acanthocephala	*Acanthocephalus anguillae*	
		Corynosoma semerme	
		Pomphorhynchus laevis	
	Crustacea	*Ergasilus briani*	
		E. sieboldi	
		Lamproglena pulchella	
		Tracheliastes polycolpus	

Appendix 9. Parasites of rudd (*Scardinius erythrophthalmus*) recorded in the literature

Location	Phylum/subphylum	Parasite species	Reference
Latvia	Monogenea	*Dactylogyrus crucifer*	(Kirjušina & Vismanis, 2007)
		D. difformis	
		D. difformoides	
		D. fallax	
		D. izjumovae	
		D. simitis	
		Diplozoon paradoxum	
	Cestoidea	*Caryophyllaeides fenica*	
	Nematoda	*Desmidocercella numidica*	
		Nematoda *gen.* sp.	
		Raphidascaris acus	
	Acanthocephala	*Acanthocephalus anguillae*	
		Corynosoma semerme	
	Hirudinea	*Piscicola geometra*	
	Mollusca	*Anodonta cygnea*	
		Unionidae *gen*. sp.	
	Crustacea	*Argulus foliaceus*	
		Ergasilus seiboldi	

Appendix 10. Parasites of green swordtail (*Xiphophorus helleri*) recorded in the literature

Location	Phylum/subphylum	Parasite species	Reference
Puerto Rica	Crustacea	*Lironeca symmetrica*	(Bunkley-Williams & Williams, 1994)
North America	Monogenea	*Dactylogyrus intermedius*	(Hoffman, 1999; Salgado-Maldonado, 2008)
		D. mizellei	
	Digenea	*Saccocoelioides* cf. *sogandaresi*	
	Nematoda	*Rhabdochona xiphophori*	
	Crustacea	*Vanamea symmetrica*	
		V. symmetrica	
		Sebekia mississippiensis	

Appendix 11. Parasites of sailfin molly (*Poecilia latipinna*) recorded in the literature

Location	Phylum/subphylum	Parasite species	Reference
Philippines	Digenea	*Procerovum calderoni* *P. varium* *Transversotrema patialense*	(Arthur & Lumanlan-Mayo, 1997)
	Nematoda	Anisakidae *gen*. sp.	
North America	Monogenea	*Gyrodactylus* sp.	(Hoffman, 1999)
	Digenea	*Ascocotyle angrense* *A. chandleri* *A. leighi* *A. mcintoshi* *A. megalocephala* *A. tenuicollis* *Echinochasmus donaldsoni* *Parascocotyle diminuta* *Phagicola macrostomus* *Posthodiplostomum minimum* *Pseudoascocotyle molliensicola* *Saccocoelioides sogandaresi*	
	Nematoda	*Capillaria cyprinodonticola*	
	Crustacea	*Ergasilus funduli* *Vanamea symmetrica*	

Appendix 12. Parasites of guppy (*Poecilia reticulata*) recorded in the literature

Location	Phylum/subphylum	Parasite species	Reference
Philippines	Nematoda	*Aonchotheca philippinensis*	(Arthur & Lumanlan-Mayo, 1997)
Puerto Rica	Digenea	*Neogogatea pandionis*	(Bunkley-Williams & Williams, 1994)
		Posthodiplostomum minimum	
	Cestoidea	*Bothriocephalus acheilognathi*	
		Ophiovalipora minuta	
	Nematoda	*Camallanus cotti*	
		Eustrongylides ignotus	
North America	Monogenea	*Ancyrocephalus dyki*	(Hoffman, 1999; Salgado-Maldonado, 2008)
		Azygia Sebago	
		Gussevia minuta	
		Gyrodactylus bullatarudis	
		G. medius	
		Urocleidoides reticulatus	
	Digenea	*Ascocotyle paratenuicollis*	
		Bolbophorus confusus	
		Cercaria udoi	
		Clinostomum complanatum	
		Echinochasmus donaldsoni	

	E. zubedakhaname
	Guaicaipuris pseudoconicilia
	Plagioporus sinitsini
	Posthodiplostomum minimum
	Ribeiroia marina
	R. ondatrae
	Stephanoprora denticulate
	S. paradenticulata
Cestoidea	*Bothriocephalus acheilognathi*
	Haplobothrium globuliforme
Nematoda	*Contracaecum multipapillatum*
	C. spiculigerum
Crustacea	*Lernaea cyprinacea*
	L. hesaragattensis

Appendix 13. Parasites of chinook salmon (*Oncorhynchus tshawytscha*) recorded in the literature

Location	Phylum/subphylum	Parasite species	Reference
North America	Monogenea	*Octomacrum lanceatum*	(Hoffman, 1999; McDonald & Margolis, 1995)
	Digenea	*Brachyphallus crenatus*	
		Bucephalopsis gracilensis	
		Crepidostomum farionis	
		Deropegus aspina	
		D. varicus	
		Dipostomum baeri bucculentum	
		Genolinea oncorhynchi	
		Lampritrema miescheri	
		Lecithaster gibbosus	
		Nanophyetus salmincola	
		Neascus sp.	
		Plagioporus shawi	
		Podocotyle sp.	
		Syncoelium katuwo	
		Tubulovesicula Lindbergh	
	Cestoidea	*Bothriocephalus* sp.	
		Diphyllobothrium ditremum	
		Eubothrium crassum	
		E. salvelini	
		Gilqunea squali	
		Hepatoxylon trichuri	
		Nybelinia surmenicola	
		Pelichnibothrium speciosum	
		Phyllobothrium salmonis	

	Proteocephalus parallacticus
Nematoda	*Anisakis* sp.
	Capillaria salvelini
	Contracaecum aduncum
	C. spiculigerum
	Contracaecum sp.
	Cucullanus truttae
	Cystidicola farionis
	Haplonema sp.
	Philonema oncorhynchi
	Phocanema sp.
	Rhaphidascaris sp.
	Salvelinema walker
	Spinitectus gracilis
	Thynnascaris sp.
Acanthocephala	*Acanthocephalus dirus*
	Echinorhynchus gadi
	E. salmonis
	Neoechinorhynchus tumidus
	Rhadinorhynchus trachuri
Hirudinea	*Piscicola salmositica*
Mollusca	of *Anodonta*
Crustacea	*Argulus* sp.
	Bomolochus sp.
	Elthusa vulgaris
	Ergasilus nerkae
	Lepeophtheirus salmonis
	Lernaea cyprinacea
	Salmincola beani
	S. californiensis
	S. falculata

New Zealand	Digenea	*Derogenes varicus*	(Hine et al., 2000)
		Lecithocladium seriolellae	
		Parahemiurus sp.	
		Tubulovesicula angusticauda	
	Cestoidea	*Tetraphyllidean* (*Phyllobothrium* sp.?)	
		Unidentified trypanorhynch	
	Nematoda	*Hedruris spinigera*	
		Hysterothylacium (syn. *Contracaecum*) sp.	
	Crustacea	*Paeonodes nemaformis*	
		Cirolana sp. (syn. *Nerocila* sp.?)	

Appendix 14. Parasites of sockeye salmon (*Oncorhynchus nerka*) recorded in the literature

Location	Phylum/subphylum	Parasite species	Reference
North America	Monogenea	*Gyrodactylus nerkae*	(Hoffman, 1999; McDonald & Margolis, 1995)
		G. strelkowi	
		Gyrodactylus sp.	
		Tetraonchus alaskensis	
	Digenea	*Brachyphallus crenatus*	
		Bucephaloides basargini	
		Crepidostomum farionis	
		Derogenes varicus	
		Diplostomulum spathaceum	
		Diplostomulum sp.	
		Genolinea laticauda	
		Hemiurus levinseni	
		Lampritrema nipponicum	
		Lecithaster gibbosus	
		L. salmonis	
		Lecithophyllum anteroporum	
		L. botryophorum	
		Parahemiurus merus	
		Phyllodistomum umblae	
		Plagioporus shawi	
		Podocotyle shawi	
		Pronoprymna umblae	
		Prosorhynchoides	

	basargini
	Syncoelium filiferum
	S. katuwo
	Tetracotyle intermedia
	Tetracotyle sp.
	Tubulovesicula lindberghi
Cestoidea	*Bothriomonas sturionis*
	Cyathocephalus truncates
	Dilepidae sp.
	Diphyllobothrium cordiceps
	D. dendriticum
	D. latum
	D. ursi
	Diplocotyle olriki
	Eubothrium crissum
	Nybelinia surmenicola
	Pelichnibothrium speciosum
	Phyllobothrium caudatum
	Proteocephalus arcticus
	P. exiguus
	P. laruei
	Schistocephalus Sp.
	Scolex pleuronectis
	Triaenophorus crassus
	T. nodulosus
Nematoda	*Anisakis* sp.
	Ascarophis sebastodis

	Capillaria catenata
	Capillaria sp.
	Contracaecum aduncum
	C. spiculigerum
	Contracaecum sp.
	Cystidicola farionis
	Cystidicoloides ephemeridarum
	Dacnitis truttae
	Philonema agubernaculum
	P. oncorhynchi
	Phocanema sp.
	Rhabdochona cascadilla
	R. kisutchi
	Rhabdochona sp.
	Salvelinema salmonicola
	Spinitectus gracilis
	Terranova sp.
	Thomnix catenata
Acanthocephala	*Acanthocephalus aculeatus*
	A. dirus
	Bolbosoma caenoforme
	Corynosomum semerme
	C. strumosum
	C. villosum
	Echinorhynchus gadi
	E. salmonis

		Leptorhynchoides thecatus	
		Neoechinorhynchus pungitius	
		N. rutili	
		N. tumidum	
		Pomphorhynchus bulbocolli	
		Rhadinorhynchus trachuri	
	Hirudinea	*Piscicola salmositica*	
	Mollusca	of *Anodonta*	
	Crustacea	*Caligus clemensi*	
		Ergasilus auritus	
		E. caeruleus	
		E. nerkae	
		E. tergidus	
		Lepeophtheirus salmonis	
		Lernaeopoda falculata	
		Salmincola californiensis	
		S. carpionis	
		S. edwardsi	
		S. falculata	
		Salmincola sp.	
	Acarina	*Hydrachna* sp.	
New Zealand	Nematoda	*Eustrongylides* (*ignotus*?)	(Hine et al., 2000)
	Crustacea	*Caligus longicaudatus*	

Appendix 15. Parasites of American brook trout (*Salvelinus fontinalis*) recorded in the literature

Location	Phylum/subphylum	Parasite species	Reference
North America	Monogenea	*Discocotyle sagittata*	(Hoffman, 1999; McDonald & Margolis, 1995)
		D. salmonis	
		Gyrodactylus avalonia	
		G. colemanensis	
		G. elegans B. of Meuller	
		G. medius	
		Tetraonchus monenreron	
		T. variabilis	
	Digenea	*Allocreadium lobatum*	
		Apophallus brevis	
		A. imperator	
		Apophallus sp.	
		Azygia angusticauda	
		A. longa	
		Bolbophorus confuses	
		Brachyphallus crenatus	
		Bunodera luciopercae	
		Clinostomum complanatum	
		Cotylurus erraticus	
		Crepidostomum cooperi	
		C. cornutum	
		C. farionis	
		C. fausti	
		C. transmarinum	
		Crepidostomum sp.	

	Diplostomulum scheuringi
	D. spathaceum
	Diplostomulum sp.
	Nanophyetus salmincola
	Neascus sp.
	Phyllodistomum lachancei
	P. limnosa
	P. superbum
	P. umblae
	Phyllodistomum sp.
	Pleurogenes sp.
	Podocotyle atomon
	Posthodiplostomum minimum
	Ptychogonimus fontanus
	Sanguinicola fontinalis
	Tetracotyle intermedia
	Tetracotyle sp.
Cestoidea	*Bothriomonas sturionis*
	Cyathocephalus truncates
	Diphyllobothrium cordiceps
	D. dendriticum
	D. ditremum
	Diphyocephalus sp.
	Diplocotyle olrikii
	Eubothrium crissum
	E. salvelini
	Glaridacris carasiomi

	Ligula intestinalis
	Proteocephalus ambloplitis
	P. arcticus
	P. parallacticus
	P. pinguis
	P. pinguis
	P. pusillus
	P. salmonidicola
	P. tumidicollus
	Proteocephalus sp.
	Schistocephalus solidus
	Triaenophorus crassus
Nematoda	*Anisakis* sp.
	Bulbodacnitis globosa
	B. scotti
	Capillaria bakeri
	C. salvelini
	Contracaecum spiculigerum
	Contracaecum sp.
	Contracaecum sp.
	Cystidicola farionis
	C. stigmatura
	Cystidicoloides ephemeridarum
	Hepaticola bakeri
	Philonema agubernaculum
	P. onchorhynchi
	Rhabdochona canadense
	R. cascadilla

	R. laurentianus
	R. milleri
	R. ovifilamenta
	Rhabdochona sp.
	Rhaphidascaris alius
	R. laurentianus
	Spinitectus gracilis
	Thynnascaris brachyuran
	Truttaedacnitis truttae
	Truttaedacnitis sp.
Acanthocephala	*Acanthocephalus anguillae*
	A. dirus
	Echinorhynchus gadi
	E. lateralis
	E. salmonis
	Leptorhynchoides thecatus
	L. thecatus
	Neoechinorhynchus sp.
	N. rutile
	Pomphorhynchus bulbocolli
Nematomorpha	*Chorodes* sp.
Hirudinea	*Haemopis grandis*
	Macrobdella decora
	Piscicola punctate
Crustacea	*Argulus canadensis*
	A. coregoni
	A. stizostethi
	Caligus elongates
	Ergasilus auritus
	E. caeruleus

E. luciopercarum
Lepeophtheirus salmonis
Salmincola carpionis
S. edwardsii
S. exsanguinata

Appendix 16. Parasites of lake trout (*Salvelinus namaycush*) recorded in the literature

Location	Phylum/subphylum	Parasite species	Reference
North America	Monogenea	*Discocotyle sagittata*	(Hoffman, 1999)
		Gyrodactylus "elegans"	
	Digenea	*Apophallus brevis*	
		Apophallus sp.	
		Azygia angusticauda	
		A. longa	
		Brachyphallus crenatus	
		Bunodera luciopercae	
		Clinostomum complanatum	
		Crepidostomum cooperi	
		C. farionis	
		C. metoecus	
		Diplostomulum scheuringi	
		D. spathaceum	
		Diplostomulum sp.	
		Nanophyetus salmincola	
		Phyllodistomum lachance	
		Phyllodistomum sp.	
	Cestoidea	*Abothrium crassum*	
		Bothriocephalus cuspidatus	
		Bothriocephalus sp.	
		Cyathocephalus truncates	
		Diphyllobothrium dendriticum	
		D. ditremum	
		D. latum	
		Eubothrium crassum	
		E. salvelini	
		Proteocephalus ambloplitis	
		P. parallacticus	

	P. pusillus
	P. salvelini
	P. tumidocollus
	Proteocephalus sp.
	Schistocephalus solidus
	Triaenophorus crassus
	T. nodulosus
Nematoda	*Bulbodacnitis scotti*
	Capillaria salvelini
	Cystidicola critivomeri
	C. farionis
	C. stigmatura
	Cystidicoloides ephemeridarum
	Eustrongylides ignotus
	Philonema agubernaculum
	P. oncorhynchi
	Philonema sp.
	Rhaphidascaris acus
	Thynnascaris adunca
	T. brachyuran
	Truttaedacnitis truttae
Acanthocephala	*Acanthocephalus dirus*
	Echinorhynchus coregoni
	E. lateralis
	E. leidyi
	E. salmonis
	E. salvelini
	Leptorhynchoides thecatus
	Neoechinorhynchus rutili
	Neoechinorhynchus sp.
	Pomphorhynchus bulbocollis
Hirudinea	*Nephelopsis obscura*

	Piscicola milneri
Crustacea	*Actheres coregoni*
	Argulus canadense
	A. coregoni
	Ergasilus auritus
	E. confuses
	E. nerkae
	Salmincola californiensis
	S. edwardsii
	S. siscowet
	Salmincola sp.
Agnatha	*Petromyzon marinus*

Appendix 17. Parasites of brown trout (*Salmo trutta*) recorded in the literature

Location	Phylum/subphylum	Parasite species	Reference
Latvia	Digenea	*Diplostomum spathaceum*	(Kirjušina & Vismanis, 2007)
	Cestoidea	*Cyathocephalus truncates*	
		Eubothrium crassum	
		Proteocephalus longicollis	
	Nematoda	*Cucullanus truttae*	
	Acanthocephala	*Echinorhynchus truttae*	
	Mollusca	*Unio pictorum*	
North America	Monogenea	*Discocotyle sagittata*	(Hoffman, 1999)
		D. salmonis	
		Gyrodactylus elegans B. of Mueller	
		G. salaries	
		G. salmonis	
		Gyrodactylus sp.	
	Digenea	*Allocreadium lobatum*	
		Apophallus brevis	
		Azygia longa	
		A. luci	
		A. robusta	
		Bolbophorus confusus	
		Brachyphallus crenatus	
		Bunocotyle cingulata	
		Bunodera lucioperca	
		Coitocaecum spp.	
		Crepidostomum cooperi	
		C. farionis	
		C. metoecus	
		Diplostomulum scheuringi	
		D. spathaceum	
		D. truttae	

	Hemiurus communis
	Nanophyetus salmincola
	Neascus sp.
	Nicolla timoni
	Phyllodistomum megalorchis
	P. simile
	Plagioporus stefanski
	Pseudochaetosoma
	salmonicola
	Sphaerostoma globiporum
	S. majus
	S. salmonis
	Tetracotyle intermedia
	Tubulovesicula lindbergi
	Tylodelphys clavata
Cestoidea	*Cyathocephalus truncate*
	Diphyllobothrium dendriticum
	D. ditremum
	D. latum
	D. norvegicum
	Diphyllobothrium sp.
	Eubothrium crassum
	E. salvelini
	Proteocephalus longicollis
	E. salvelini
	Proteocephalus longicollis
	P. neglectus
	P. parallacticus
	P. pinguis
	Proteocephalus sp.
	Triaenophorus nodulosus
Nematoda	*Ascarophus skrjabini*
	Bulbodacnitis globosa
	B. scotti

	Camallanus oxycephalus
	Capillaria salvelini
	Cephalobus
	Contracaecum aduncum
	Contracaecum sp.
	Contracaecum sp.
	Cucullanus globosus
	C. truttae
	Cystidicola farionis
	Cystidicoloides
	ephemeridarum
	Eustrongylides tubifex
	Eustrongylides ignotus
	Exocoitocaecum wisnieskii
	Metabronema canadense
	M. harwoodi
	M. salvelini
	Philonema agubernaculum
	Raphidascaris acus
	Rhabdochona denudate
	R. filamentosa
	Spinitectus carolini
	S. gracilis
	Sterliadochona savini
	Truttaedacnitis sp.
Acanthocephala	*Acanthocephalus anguillae*
	A. dirus
	A. lucii
	Corynosoma strumosum
	Dentitruncus truttae
	Echinorhynchus clavula
	E. gadi
	E. lateralis
	E. truttae

		Neoechinorhynchus rutili	
		Pomphorhynchus bulbocolli	
		Pseudoenchinorhynchus clavula	
	Hirudinea	*Acanthobdella peledina*	
		Piscicola geometra	
	Mollusca	*Anodonta anatine*	
		Glochidia sp.	
	Crustacea	*Argulus coregoni*	
		A. foliaceus	
		Ergasilus sieboldi	
		Ergasilus sp.	
		Lepeophtheirus salmonis	
		Lernaea cruciata	
		L. esocina	
		Salmincola salmonea	
New Zealand	Digenea	*Coitocaecum parvum* (syn. *Coitocaecum anspidis*)	(Hine et al., 2000)
		Derogenes varicus	
		Lecithocladium magnacetabulum	
		Lecithocladium seriolellae	
		Telogaster opisthorchis	
	Cestoidea	*Pelichnobothrium* sp.	
	Nematoda	*Cucullanus antipodeus*	
		Eustrongylides	
		Hedruris spinigera	
		Hysterothylacium (syn. *Thynnascaris*) *aduncum*	
		Hysterothylacium (syn. *Thynnascaris*) sp.	
	Acanthocephala	*Corynosoma* sp.	
		Corynosoma sp.	
	Crustacea	*Nerocila orbignyi*	

Appendix 18. Parasites of Atlantic salmon (*Salmo salar*) recorded in the literature

Location	Phylum/subphylum	Parasite species	Reference
Latvia	Digenea	*Brachyphallus crenatus*	(Kirjušina & Vismanis, 2007)
	Cestoidea	*Diphyllobothrium dendriticum*	
		D. ditremum	
		Eubothrium crassum	
	Nematoda	*Cucullanus truttae*	
		Goezia sp.	
		Hysterothylacium aduncum	
		Pseudoterranova decipiens	
		Raphidascaris acus	
	Acanthocephala	*Echinorhynchus gadi*	
		E. salmonis	
North America	Monogenea	*Discocotyle sagittata*	(Hoffman, 1999)
		D. salmonis	
		D. sybillae	
		Gyrodactyloides bychowskii	
		Gyrodactylus salaries	
		G. salmonis	
		Gyrodactylus sp.	
	Digenea	*Aphanurus balticus*	
		Apophallus brevis	
		Azygia longa	
		A. lucii	
		A. Sebago	
		A. tereticollis	
		Brachyphallus crenatus	
		Bucephalus polymorphus	
		Bunocotyle cingulata	

	Bunodera luciopercae
	Clinostomum complanatum
	Crepidostomum cooperi
	C. farionis
	C. metoecus
	Derogenes varicus
	Diplostomulum scheuringi
	D. spathaceum
	Diplostomulum sp.
	Distomum appendiculatum
	D. reflexum
	D. varicum
	Hemiurus crenatus
	H. levinseni
	H. lukei
	H. ocreatus
	Lampritrema miescheri
	Lecisthaster bothryophorus
	L. confusus
	L. gibbosus
	Nanophyetes salmincola
	Neohemiurus
	Phyllodistomum lachancei
	P. luminosa
	Podocotyle atomon
	P. simples
	Tetracotyle sp.
Cestoidea	*Bothriocephalus osmeri*
	B. proboscideus
	B. solidus
	Bothriomonas sturionis

	Cyathocephalus truncates
	Diphyllobothrium dendriticum
	D. latum
	D. norvegicum
	Eubothrium crissum
	E. salvelini
	Hepatoxylon trichiuri
	Leuckartia sp.
	Pelichnibothrium sp.
	Proteocephalus pusillus
	Proteocephalus sp.
	Schistocephalus dimorphis
	Scolex pleuronectis
	S. polymorphus
	Stenobothrium appendiculum
	Tentacularia coryphaenae
	Tetrabothrium minimum
	Tetrarhynchobothrium bicolor
	Tetrahynchus grossus
	T. solidus
	Triaenophorus crassus
	Triaenophorus nodulosus
Nematoda	*Agomonema capsularia*
	A. commune
	Anisakis simplex
	Camallanus lacustris
	C. oxycephalus
	Capillaria salvelini
	Cucullanus elegans
	C. serratus
	C. truttae

	Cystidicola stigmatura
	Cystidicoloides ephemeridarum
	Exocoitocaecum wisniewskii
	Philonema agubernaculum
	Raphidascaris acus
	Thynnascaris adunca
Acanthocephala	*Acanthocephalus anguillae*
	A. lucii
	Bolbosoma heteracanthis
	Echinorhynchus acus
	E. gadi
	E. lateralis
	E. salmonis
	E. truttae
	Echinorhynchus sp.
	Leptorhynchoides thecatus
	Neoechinorhynchus cylindratum
	N. rutile
	Pomphorhynchus bulbocolli
	P. laevis
	Pseudoechinorhynchus clavula
Hirudinea	*Cystobranchus respirans*
	Piscicola geometra
	P. milneri
	P. punctate
Mollusca	*Margaritifera margaritifera*

Crustacea	*Argulus canadense*
	A. coregoni
	A. stizostethi
	Lepeophtheirus pollachii
	L. salmonis
	L. strömii
	Salmincola extumescens
	S. falculata
	S. salmoneus
Acarina	*Hydrachna* sp.
	Trhypochthoniellus sp.

Appendix 19. Parasites of rainbow trout (*Oncorhynchus mykiss*) recorded in the literature

Location	Phylum/ subphylum	Parasite species	Reference
Demark	Monogenea	*Gyrodactylus salaris*	(Buchmann & Bresciani, 1997)
		G. derjavini	
	Digenea	*Diplostomum spathaceum*	
		Tylodelphys clavata	
	Cestoidea	*Eubothrium crassum*	
		Proteocephalus exiguus	
		P. longicollis	
		Proteocephalus sp.	
		Triaenophorus nodulosus	
	Crustacea	*Argulus foliaceus*	
Latvia	Monogenea	*Diplozoon* sp.	(Kirjušina & Vismanis, 2007)
		Gyrodactylus truttae	
	Digenea	*Diplostomulum* sp.	
		Diplostomum spathaceum	
	Cestoidea	*Triaenophorus nodulosus*	
	Nematoda	*Cystidicola farionis*	
		Hysterothylacium aduncum	
North America	Cnidaria	*Hydra* sp.	(Hoffman, 1999; McDonald & Margolis, 1995)
	Monogenea	*Discocotyle sagittata*	
		D. salmonis	
		Gyrodactylus avalonia	
		G. brevis	
		G. colemanensis	
		G. elegans	
		G. salaries (E)	
		G. salmonis	
		Gyrodactylus sp.	
		Tetraonchus alaskensis	
	Digenea	*Allocreadium lobatum*	

	Apatemon gracilis
	Aponurus sp.
	Apophallus brevis
	A. donicus
	Azygia longa
	Bolbophorus confusus
	Bunodera luciopercae
	Clinostomum complanatum
	Cotylurus erraticus
	Crepidostomum cooperi
	C. cornutum
	C. farionis
	C. laureatum
	Derogenes aspina
	Diplostomulum mordax
	D. scheuringi
	D. spathaceum
	Diplostomulum sp.
	Distomulum oregonensis
	Echinochasmus milvi
	Exocoitocaecum wisnienskii
	Nanophyetus salmincola
	Neascus sp.
	Phyllodistomum lachancei
	Phyllodistomum sp.
	Plagioporus angusticole
	P. shawi
	Pseudochaetosoma sp.
	Sanguinicola alseae
	S. idahoensis
	Sanguinicola sp.
Cestoidea	*Abothrium crassum*
	Bothriocephalus cuspidatus
	Cyathocephalus truncates

	Diphyllobothrium dendriticum
	D. ditremum
	D. latum
	Diphyllobothrium sp.
	Eubothrium crassum
	E. salvelini
	Ligula intestinalis
	Phyllobothrium sp.
	Proteocephalus ambloplitis
	P. longicollis
	P. pinguis
	P. salmonidicola
	P. tumidicollis
	Proteocephalus sp.
	Schistocephalus sp.
	Triaenophorus crassus
	T. nodulosus
Nematoda	*Anisakis* sp.
	Ascarophis skryabini
	Bulbodacnitis ampullastoma
	B. globosa
	B. occidentalis
	B. truttae
	Camallanus oxycephalus
	Capillaria bakeri
	C. eupomotis
	Contracaecum spiculigerum
	Cucullanus globosus
	C. occidentalis
	C. truttae
	Cystidicola farionis
	C. stigmatura
	Cystidicoloides ephemeridarum
	C. tenuissima

	Dacnitis truttae
	Eustrongylides tubifex
	Eustrongylides ignotus
	Goezia ascaroides
	Haplonema hamulatum
	Hepaticola bakeri
	Metabronema salvelini
	Philometra sp.
	Philonema agubernaculum
	P. angusticole
	P. oncorhynchi
	Philonema sp.
	Raphidascaris acus
	Rhabdochona cascadilla
	R. denudate
	R. kisutch
	R. milleri
	Spinitectus carolini
	S. gordoni
	S. gracilis
	Sterliadochona pedispicule
	S. tenuissima
	Truttaedacnitis truttae
Acanthocephala	*Acanthocephalus acerbus*
	A. anguillae
	A. dirus
	A. jacksoni
	A. minor
	A. opsarichthydi
	Leptorhynchoides thecatus
	Metecchinorhyynchoides lateralis
	M. leidyi
	M. salmonis
	M. thecatus

	M. truttae
	Neoechinorhynchus rutili
	Pomphorhynchus bulbocolli
	P. laevis
	Pseudorhadinorhynchus sanguaiensis
	Rhadinorhynchus sp.
	Tetrarhynchus sp.
Nematomorpha	*Chorodes* sp.
Hirudinea	*Batracobdella xenoica*
	Illinobdella sp.
	Piscicola geometra
	P. punctata
	P. salmositica
Mollusca	*Glochidia* sp. of *Margarita margaritifera*
	Pisidium variable
Crustacea	*Argulus coregoni*
	A. japonicas
	A. pugettensis
	Caligus clemensi
	C. elongatus
	Ergasilus caeruleus
	E. nerkae
	E. sieboldi
	Lepeophtheirus salmonis
	Lernaea cyprinacea
	L. esocina
	Lernaeopeda bicauliculata
	Salmincola beani
	S. bicauliculata
	S. californiensis
	S. edwardsii
	S. tiddi

	Arthropoda	Unidentified mite	
New Zealand	Nematoda	*Eustrongylides* (*ignotus?*)	(Hine et al., 2000)
		Hysterothylacium (syn. *Contracaecum*) sp.	
	Crustacea	*Ligula intestinalis*	
	Mollusca	*Hyridella* sp. glochidia	

Appendix 20. Parasites of red-finned perch (*Perca fluviatilis*) recorded in the literature

Location	Phylum/subphylum	Parasite species	Reference
New Zealand	Nematoda	*Hedruris spinigera*	(Hine et al., 2000)
	Copepoda	*Abergasilus amplexus*	
Latvia	Monogenea	*Ancyrocephalus percae*	(Kirjušina & Vismanis, 2007)
		Dactylogyrus sp.	
	Digenea	*Azgia lucii*	
		Bucephalus polymorphus	
		Bunodera luciopercae	
		Diplostomulum sp.	
		Diplostomum spathaceum	
		Ichthyocotylurus pileatus	
		I. platycephalus	
		I. variegatus	
		Neodiplostomulum sp.	
		Phyllodistomum angulatum	
		P. pseudofolium	
		Paracoenogonimus ovatus	
		Posthodiplostomum brevicaudatum	
		P. cuticola	
		Rhipidocotyle campanula	
		Tylodelphys clavata	
	Cestoidea	*Cyathocephalus truncates*	
		Diphyllobothrium latum	
		Ligula intestinalis	
		Proteocephalus percae	
		Triaenophorus nodulosus	
	Nematoda	*Anguilicola crassus*	
		Camallanus lacustris	
		C. truncatus	

	Desmidocercella numidica
	Desmidocercella sp.
	Eustrongylides ignotus
	Hysterothylacium aduncum
	Nematoda *gen*. sp.
	Raphidascaris acus
Acanthocephala	*Acanthocephalus lucii*
	Corynosoma semerme
Hirudinea	*Hemiclepsis marginata*
	Piscicola geometra
Mollusca	*Anodonta cygnea*
	Pseudanadonta kletti
	Unio pictorum
	Unionidae *gen*. sp.
Crustacea	*Achtheres percarum*
	Argulus foliaceus
	Ergasilus sieboldi
	Lernaea esocina

Appendix 21. Parasite checklist of 17 fish species over seven countries

(Location: AUS=Australia; BAN=Bangladesh; JAP=Japan; LAT=Latvia; VN=Vietnam; PHI=Philippine; TUR=Turkey; DEN=Denmark; NA=North America; NZ=New Zealand; CHN=China; PR=Puerto Rico; Fish: Mos.=Mosquitofish; Cat.=Catfish; Koi.=Koi carp; Gol.=Goldfish; Gra.=Grass carp; Sil.=Silver carp; Ten.=Tench; Gre.=Green swordtail; Sai.=Sailfin molly; Gup.=Guppy; Qui=Quinnat salmon; Soc.=Sockeye salmon; Ame.=American brook trout; Lak.=Lake trout; Bro.=Brown trout; Ata.=Atlantic salmon; Rai.=Rainbow trout, Orf.=Orfe; Rud.=Rudd; Per.=Perch; Parasite species: Cnid.= Cnidaria; Mon.=Monogenea; Dig.=Digenea; Aspid.= Aspidogastrea; Ces.=Cestoidea; Nem.=Nematomorpha; Acant.=Acanthocephala Moll.=Mollusca; Acari.=Acarina Art.=Arthropoda)

		Cnid.	Platyhelminthes				Nematoda	Nem.	Acant.	Annelida	Moll.	Arthropoda		Chordata	Art.	Total
			Trematoda			Ces.										
Host	Location		Mon.	Dig.	Aspid.					Hirudinea		Crustacea	Acari.	Agnatha		
Mos.	NA	0	4	27	0	4	9	0	3	0	0	4	0	0	0	51
	CHN	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
	PR	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Cat.	NA	0	7	41	0	13	22	0	12	8	2	14	0	0	0	119
	PR	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Koi.	BAN	0	1	1	0	0	0	0	1	0	0	0	0	0	0	3
	JAP	0	4	1	0	1	0	0	0	0	0	2	0	0	0	8

	LAT	0	10	7	0	9	4	0	2	1	1	1	0	0	0	35
	VN	0	10	4	0	2	3	0	2	0	1	7	0	0	0	29
	PHI	0	3	0	0	2	0	0	0	0	0	0	0	0	0	5
	NA	0	32	41	3	18	21	0	14	4	1	23	0	0	0	157
	CHN	0	12	6	0	9	2	0	3	0	0	4	0	0	0	36
	TUR	0	4	0	0	3	0	0	1	0	0	2	0	0	0	10
Gol.	NZ	0	0	1	0	0	0	0	0	0	0	3	0	0	0	4
	JAP	0	2	1	0	1	0	0	0	0	0	1	0	0	0	5
	LAT	0	5	1	0	0	0	0	0	1	0	1	0	0	0	8
	VN	0	3	0	0	0	0	0	0	0	0	1	0	0	0	4
	AUS	0	3	0	0	0	0	0	0	0	0	1	0	0	0	4
	PR	0	1	0	0	0	0	0	0	0	0	2	0	0	0	3
	PHI	0	2	1	0	0	0	0	0	0	0	1	0	0	0	4
	NA	0	44	24	0	7	6	0	8	2	1	14	1	0	0	107
	CHN	0	10	9	0	7	4	0	0	1	0	7	0	0	0	38
Gra.	BAN	0	1	0	0	0	0	0	0	0	0	2	0	0	0	3
	LAT	0	0	0	0	1	0	0	0	0	0	1	0	0	0	2
	NZ	0	2	0	0	1	3	0	0	0	0	0	0	0	0	6
	NA	0	1	0	0	1	3	0	0	0	0	0	0	0	0	5

	PHI	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
	PR	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
	CHN	0	17	3	0	7	0	0	0	0	0	4	0	0	0	31
Sil.	BAN	0	1	0	0	0	0	0	0	0	0	1	0	0	0	2
	PHI	0	0	0	0	1	0	0	0	0	0	1	0	0	0	2
	CHN	0	2	5	0	3	0	0	2	0	0	5	0	0	0	17
Ten.	NA	0	4	16	0	0	5	0	7	1	0	5	0	0	0	38
	NZ	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
	LAT	0	5	11	0	4	3	0	3	1	2	3	0	0	0	32
Orf.	LAT	0	8	8	0	1	3	0	3	0	0	4	0	0	0	27
Rud.	LAT	0	7	0	0	1	3	0	2	1	2	2	0	0	0	18
Gre.	NA	0	2	1	0	0	1	0	0	0	0	3	0	0	0	7
	PR	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Sai.	PHI	0	0	3	0	0	1	0	0	0	0	0	0	0	0	4
	NA	0	1	12	0	0	1	0	0	0	0	2	0	0	0	16
Gup.	PHI	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
	PR	0	0	2	0	2	2	0	0	0	0	0	0	0	0	6
	NA	0	6	13	0	2	2	0	0	0	0	2	0	0	0	25

Chi.	NA	0	1	15	0	10	14	0	5	1	1	9	0	0	0	56
	NZ	0	0	4	0	2	2	0	0	0	0	2	0	0	0	10
Soc.	NA	0	4	24	0	19	20	0	14	1	1	12	1	0	0	96
	NZ	0	0	0	0	0	1	0	0	0	0	1	0	0	0	2
Ame.	NA	0	8	34	0	22	26	1	10	3	0	11	0	0	0	115
Lak.	NA	0	2	16	0	18	14	0	10	2	0	10	0	1	0	73
Bro.	LAT	0	0	1	0	3	1	0	1	0	1	0	0	0	0	7
	NA	0	6	30	0	16	27	0	12	2	2	8	0	0	0	103
	NZ	0	0	5	0	1	5	0	2	0	0	2	0	0	0	15
Atl.	LAT	0	0	1	0	3	5	0	2	0	0	0	0	0	0	11
	NA	0	7	36	0	26	15	0	15	4	1	9	2	0	0	115
Rai.	LAT	0	2	2	0	1	2	0	0	0	0	0	0	0	0	7
	NA	1	10	32	0	20	40	1	18	5	3	17	0	0	1	148
	NZ	0	0	0	0	0	2	0	0	0	1	1	0	0	0	4
	DEN	0	2	2	0	5	0	0	0	0	0	1	0	0	0	10
Per.	NZ	0	0	0	0	0	1	0	0	0	0	1	0	0	0	2
	LAT	0	2	16	0	5	9	0	2	2	4	4	0	0	0	44
Total		1	259	459	3	253	284	2	154	40	24	212	4	1	1	1697

Appendix 22.Tukey's unequal N HSD (Honestly Significant Difference) Test for common bullies' length of 10 lakes (marked are significantly differences $p < 0.01$)

	Tukey's unequal *n* HSD Test (p)									
Lake	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}
Lake Okaro {1}		1	0.961	> 0.01	> 0.01	> 0.01	0.448	0.105	0.92	> 0.01
Lake Rotorua {2}	1		0.93	> 0.01	> 0.01	> 0.01	0.713	0.128	0.94	> 0.01
Lake Kai-iwi {3}	0.961	0.93		> 0.01	> 0.01	> 0.01	0.033	0.016	0.624	> 0.01
Lake Ngatu {4}	> 0.01	> 0.01	> 0.01		0.722	> 0.01	> 0.01	0.209	0.016	> 0.01
Lake Rotokawau East {5}	> 0.01	> 0.01	> 0.01	0.722		> 0.01	> 0.01	> 0.01	> 0.01	> 0.01
Lake Waiparera {6}	> 0.01	> 0.01	> 0.01	> 0.01	> 0.01		> 0.01	1	0.949	1
Chaple Lake {7}	0.448	0.713	0.033	> 0.01	> 0.01	> 0.01		0.646	1	> 0.01
Lake Rotoroa {8}	0.105	0.128	0.016	0.209	> 0.01	1	0.646		0.077	1
Lake Hakanoa {9}	0.92	0.94	0.624	0.016	> 0.01	0.949	1	0.077		1
Lake Ngaroto {10}	> 0.01	> 0.01	> 0.01	> 0.01	> 0.01	1	> 0.01	1	1	

Appendix 23.Tukey's unequal *n* HSD (Honestly Significant Difference) Test for common bullies' weight of 10 lakes (marked are significantly differences $p < 0.01$)

	Tukey's unequal *n* HSD Test (p)									
Lake	{1}	{2}	{3}	{4}	{5}	{6}	{7}	{8}	{9}	{10}
Lake Okaro {1}		1	1	> 0.01	> 0.01	0.44	1	1	1	0.46
Lake Rotorua {2}	1		1	> 0.01	> 0.01	0.73	1	1	1	0.88
Lake Kai-iwi {3}	1	1		> 0.01	> 0.01	0.37	1	1	1	0.51
Lake Ngatu {4}	> 0.01	> 0.01	> 0.01		1	> 0.01	> 0.01	0.05	0.02	> 0.01
Lake Rotokawau East {5}	> 0.01	> 0.01	> 0.01	1		> 0.01	> 0.01	0.01	0.006	> 0.01
Lake Waiparera {6}	0.443	0.725	0.37	> 0.01	> 0.01		0.87	1	1	1
Chapel Lake {7}	1	1	1	> 0.01	> 0.01	0.87		1	1	0.61
Lake Rotoroa {8}	1	1	1	0.045	0.01	1	1		1	1
Lake Hakanoa {9}	1	1	1	0.021	> 0.01	1	1	1		1
Lake Ngaroto {10}	0.46	0.88	0.51	> 0.01	> 0.01	1	0.61	1	1	