The link between floodplain inundation and whitebait food supplies in the lower Waikato River

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Abstract

Globally, many large, lowland rivers are regulated due to the construction of stopbanks and flood protection schemes. Many of these changes now govern discharge regimes and lateral floodplain interactions. These modifications, along with others, contribute to declines in many native fish, including larval Galaxiidae of whitebait. Many attempts to enhance whitebait fisheries within New Zealand have focused on restoring spawning habitat. However, no research has been aimed at understanding the dietary requirements of riverine whitebait and where they source their food from during upstream migration. Previous work has hypothesised that receding floods may introduce large-bodied zooplankton, to the river which may be important for whitebait during upstream migration. The objectives of this research were to investigate (i) the potential of zooplankton to emerge from floodplain soils following inundation, and (ii) whether certain zooplankton groups, indicative of those originating from floodplains, could be a food supply for migrating juvenile *Galaxias maculatus* in the lower Waikato River. Previous work investigating zooplankton communities in the lower Waikato River floodplain was undertaken during inundation events, but, the origin of zooplankton could not be pin pointed.

To test whether inundated floodplain areas developed zooplankton from dormant states in soils, dry soil cores were collected from native forest, scrub (predominantly *Salix* sp.) and pasture vegetation types, inside and outside of stopbanks to provide different levels of connectivity. Zooplankton emerged from submerged soil within three days of wetting and after 12 days of inundation no new taxa arose. Community composition differed between vegetation types, with larger-bodied cladocerans and copepods dominating native forested and scrub sites, and rotifers dominating pastoral sites. Connectivity did not play a statistically significant role in determining composition of zooplankton communities. Differences in zooplankton composition between sites indicate that floodplain vegetation structure has a dominant role in the development of communities of zooplankton during flooding. Differences in vegetation types were largely due to varying levels of soil moisture, canopy cover and other environmental factors.

Gut analyses indicated that juvenile *G. maculatus* feed on a wide range of aquatic and semi-aquatic organisms. Large-bodied zooplankton and insects found in the gut likely came from multiple sources. Insect presence varied over time whereas Cladocera dominance appeared to be related to flow pulses. Field diet analyses and laboratory selectivity experiments yielded similar results regarding selectivity. Feeding in the laboratory was density-dependent as more food items were consumed at lower fish densities, with no evidence of prey switching to less desirable groups at high densities.

This study has increased the understanding of potential food-web linkages between rivers and their floodplains for migrating whitebait populations. The findings of this research indicate that scrub and forested floodplains are important areas for the production and emergence of large-bodied zooplankton following inundation. Transfer of floodplain zooplankton back into the river channel could then be selected by juvenile migrating whitebait as they have shown a feeding preference for large-bodied zooplankton. As a result, management plans have the potential to be implemented to sustain food supplies for migrating whitebait species within large lowland riverine-floodplain environments.

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To my funders, Waikato Regional Council, Department of Conservation and the University of Waikato, thank you for seeing the potential in my research and me. All the help was extremely appreciated.

I will leave these pages with a classic, yet timely joke.

Where do fish keep their money?

In a river bank.

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Chapter One

General Introduction

1.1 Riverine landscapes

Riverine landscapes encompass the broad-scale patterns and processes associating fluvial systems with their biotic communities (Ward 1998), and are among the most biologically productive and diverse ecosystems worldwide (Tockner et al. 2010; Figure 1.1). Geomorphology plays an important role in maintaining connective pathways, especially between the river and its floodplain, directly and indirectly influencing biodiversity patterns within these systems (Ward 1998). Biodiversity patterns within riverine landscapes can be structured along different spatial axes: longitudinally – down the river course, laterally – off-channel areas including floodplains, vertically – aquifers, and temporally – changes over time (Ward 1998; Ward et al. 2002). Generally, lowland riverine landscapes are characterised by extensive floodplains (Tockner & Stanford 2002), high hydrological connectivity (Tockner et al. 1999; Jenkins & Boulton 2003) and controlled by a flow regime that is highly dynamic in both space and time (Poff et al. 1997; Robinson et al. 2002). Interactions between these characteristics are major factors influencing species distributions and abundances within lowland riverine environments (Robinson et al. 2002).

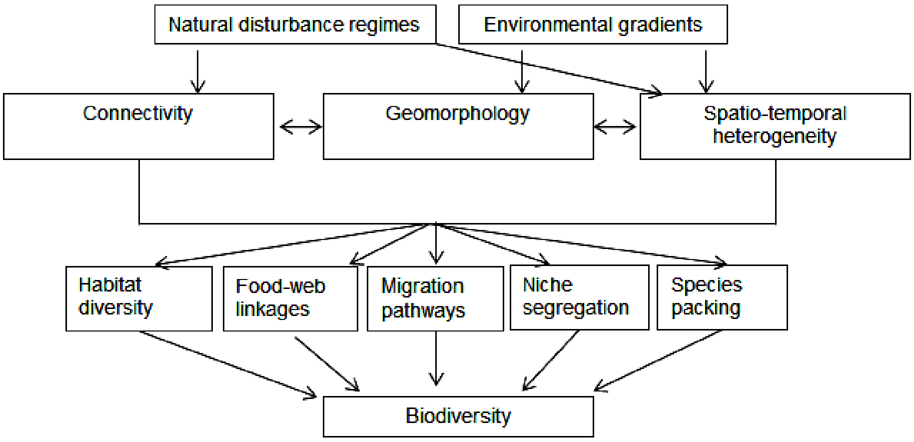

Figure 1.1: Interactions within riverine landscapes that structure biodiversity (modified from Ward 1998).

Floodplains are defined as ‘areas of low lying land that are subject to inundation by lateral overflow water from rivers or lakes with which they are associated’ (Junk & Welcomme 1990; Tockner & Stanford 2002). Globally, floodplains make up 2 x 10^6 km^2, representing an extensive resource for biotic and human use (Tockner & Stanford 2002). In Europe, around 10% of all species are restricted only to riverine floodplains (Tockner & Stanford 2002). In addition, hydrological connectivity between rivers and their floodplains is a leading factor influencing fish productivity within these systems (Ward 1998; Ward et al. 2002).

Floodplains are ecotones between aquatic and terrestrial systems, and include areas with low to high levels of water saturation, which influences the type of terrestrial vegetation present (Tockner & Stanford 2002). The flood pulse in rivers, both the expansion and contraction of water levels, is the main driver influencing connectivity within riverine floodplains (Tockner & Stanford 2002). During inundation, floodplains provide areas that have distinctive physical and chemical conditions that may act as refugia for fish, zooplankton and amphibians outside the main river channel (Opperman et al. 2010; Tockner et al. 2010). Furthermore, floodplains that interact with the river after high flows can expand to include floodplain wetlands and off-channel lakes (Robinson et al. 2002). These off-channel waterbodies range from lotic to lentic in state, and thus have varying degrees of physical and chemical conditions, depending on their spatio-temporal connection to the main river channel (Robinson et al. 2002).

Connections to floodplain wetlands and lakes increases beta diversity of riverine landscapes, due to the unique habitat conditions that create refugia, and provide riverine systems with a further supply of nutrients, organic matter and zooplankton (Robinson et al. 2002). As water extends onto the floodplain, water velocity slows and causes turbidity to decrease as suspended sediment within the water column settles, ultimately allowing greater rates of plant photosynthesis and algal production (Opperman et al. 2010). This greater plant and algal growth is then coupled with increased productivity of aquatic invertebrates and zooplankton populations, and can cause turbidity to increase once more (Opperman et al. 2010). Temperature in off-channel floodplain areas is known to have high heterogeneity compared to the main river channel, and can range from 15 - 35 ºC depending on the season and hydrological water permanence (Tockner et al. 2000). High temperatures and increased evaporation, coupled with increased nutrients fuelling algal and zooplankton growth, can cause dissolved oxygen levels to decrease rapidly (Nadai & Henry 2009).

Within large river environments, plankton can achieve high densities due to long water residence times and low flows allowing suitable time for growth, survival and reproduction (Basu & Pick 1997). Plankton distribution and abundance, however, is rarely uniform throughout a river's length (Shiel et al. 1982; Kim & Joo 2000). The factors influencing diversity and abundance of plankton include temperature, discharge, turbidity, light and nutrient concentrations (Shiel et al. 1982; Basu & Pick 1997). Temperature is a leading environmental factor that affects plankton growth and maturity (Thorp et al. 1994; Kobayashi 1997; Kobayashi et al. 1998), and has been documented to influence seasonal succession of zooplankton in the Murray River (Shiel et al. 1982).

Many studies have indicated that there is a negative relationship between discharge and plankton abundance (Shiel et al. 1982; Basu & Pick 1997; Thorp et al. 1994). Despite this, large flows increase downstream connectivity and can be highly valuable for the transfer of materials from off-channel inundated floodplain, lake and wetland systems back into the main river channel (Poff et al. 1997; Kobayashi et al. 1998). In addition, increased turbidity reduces the amount of light that can infiltrate the water column, leading to reductions in phytoplankton growth and in turn zooplankton populations (Basu & Pick 1997; Kobayashi et al. 1998). Generally, algal productivity is known to increase down the length of the river, and is attributed particularly to slower velocities and greater nutrient concentrations (Shiel et al. 1982). Thus, flow regimes are also a major driver influencing plankton dynamics and in turn the functioning of entire riverine food webs (Kobayashi et al. 1998).

Slower water velocities in off-channel areas provide refugia during high flows for fish populations. Spawning of several fish species appears linked with floods enabling offspring to grow in sheltered areas rich with food (Opperman et al. 2010; Wu et al. 2013). However, finding areas suitable for spawning can become difficult due to spatial and temporal variability in floodplain temperatures (Górski et al. 2010). Wu et al. (2013) reported that floodplain areas within the lower Waikato River, northern New Zealand, were highly used by non-native fish species to spawn and acted as nurseries for their young. Furthermore, non-native species such as koi carp rely on zooplankton as a food source during their larval stages, foraging mainly in productive floodplain areas. Therefore highlighting the potential for non-native species to displace native fish in these lateral habitats.

1.2 Ecosystem services of floodplains

Due to their dynamic and diverse landscape features, floodplains provide high recreational, economic and aesthetic values, in addition to the biodiversity functions described above. Floodplains are responsible for providing > 25% of total terrestrial ecosystem services, despite only covering 1.4% of total land area (Tockner & Stanford 2002). The main ecosystem services provided by floodplains are water supply and regulation, habitat provision for flora and fauna, nitrogen removal, flood control and productive land for agricultural use (Tockner & Stanford 2002; Dudgeon et al. 2006; Tockner et al. 2010). Overall ecosystem services can be categorised as supporting, provisioning, regulating or cultural services.

Supporting services refer to the resources provided by floodplains to promote growth and survival of diverse populations of flora and fauna (Wright 2008). Floodplains promote high biological productivity through water purification and nutrient rich soils that allow plants to flourish, and therefore they provide ideal habitats for numerous terrestrial and aquatic species (Gren et al. 1995). Habitat provision in these areas supports spawning/breeding and feeding grounds for fauna such as fish, amphibians and birds, and maintains biodiversity within the ecosystem (Wright 2008). Breakdown of the floodplain vegetation into organic matter and detritus provides a nutrient-rich addition to off-channel lakes, wetlands and back into the main river channel that supports secondary production (Wright 2008). Globally, total primary production in floodplain forests range from 750-1370 g m^2 yr^{-1} dependant on flow regime (Tockner & Stanford 2002). This net productivity influences animal production within floodplains and is shown to be 3.5 times higher than for terrestrial systems outside of floodplains (Tockner & Stanford 2002). These high heterogeneity areas provide nutrient-rich refugia for biota to inhabit and develop in, ultimately for transfer back into the main river channel as a potential food source as floodwaters subside (Robinson et al. 2002).

Provisioning services are defined as ‘products that are obtained from ecosystems’ and include food production, water for drinking and irrigation, and materials that may be used by humans (Palmer & Richardson 2009). Floodplains provide sites for aquaculture, agriculture and vegetative production (Brauman et al. 2007; Wright 2008). The food-rich, slow-flowing waters of floodplains provide areas that aid in fish productivity, which may become available for human consumption. Furthermore, floodplain land enhances agricultural production by providing wide, flat land coupled with readily available groundwater and irrigation supplies (Wright 2008). Lastly, floodplains promote the growth of multiple plant and tree species that can be used for forestry or restoration (Hughes et al. 2001; Wright 2008).

The term ‘regulating’ services refers to the benefits obtained from floodplains that are non-material, such as flood control, water purification and nutrient removal (Gren et al. 1995; Wright 2008; Palmer & Richardson 2009). Due to the nature of floods, they shape the topography of the areas they inundate. Thus, during flooding, floodplains provide a large generally flat area for floodwaters to spill out onto and be stored (Wright 2008). The transfer of water and nutrients to floodplains periodically creates a mosaic structure, which temporally connects multiple biotic pathways and environmental gradients, important for maintaining functional integrity within the riverine environment (Ward 1998). Furthermore, flood storage and terrestrial vegetation present on river-floodplain margins reduces the likelihood of erosion (Brauman et al. 2007).

Floodplains provide multiple services, including the maintenance of water quality. As floodwaters from the river extend out onto the floodplain, the suspended sediment load and organic debris is deposited on the floodplain (Brauman et al. 2007; Wright 2008). Terrestrial vegetation traps the released sediment and reduces the likelihood of erosion and the excess nutrients that are deposited can be taken up by floodplain soils, creating productive nutrient-rich land. Vegetative cover can also shade the waters, creating a habitat suitable for biota because of reduced temperatures (Wright 2008). Additionally, floodplains contribute to the regeneration of groundwater due to infiltration (Gren et al. 1995) and thus help to regulate flows in the main river during periods when there are no floods (Wright 2008).

Riverine floodplains also encapsulate cultural services, which are ones that contribute to human-wellbeing through religious, spiritual and aesthetic values (Brauman et al. 2007; Posthumus et al. 2010). Floodplain cultural services can include landscape value, recreation, education, and tourism values (Brauman et al. 2007; Posthumus et al. 2010).

1.3 Threats and stressors

Floodplains are particularly vulnerable to human pressures based on the multiple ecosystem services they provide, and generally they are located in dense populated areas. Consequently, they are one of the most exploited ecosystems on the planet (Tockner & Stanford 2002). Continued vulnerability of floodplain landscapes due to human-induced changes has been well documented (Bunn & Arthington 2002; Tockner & Stanford 2002; Tockner et al. 2010), and much research has focussed on restoring river-floodplain linkages and processes (Buijse et al. 2002; Palmer et al. 2005). The major drivers causing freshwater biodiversity loss and/or degradation of floodplain ecosystems include; habitat alteration, pollution, invasive species, altered flow regimes and overexploitation (Dudgeon et al. 1997; Poff et al. 1997; Bunn & Arthington 2002; Tockner & Stanford 2002; Figure 1.2). A combination of these multiple stressors continually shifts riverine floodplain resilience and resistance, leading to further degradation and loss of ecosystem integrity.

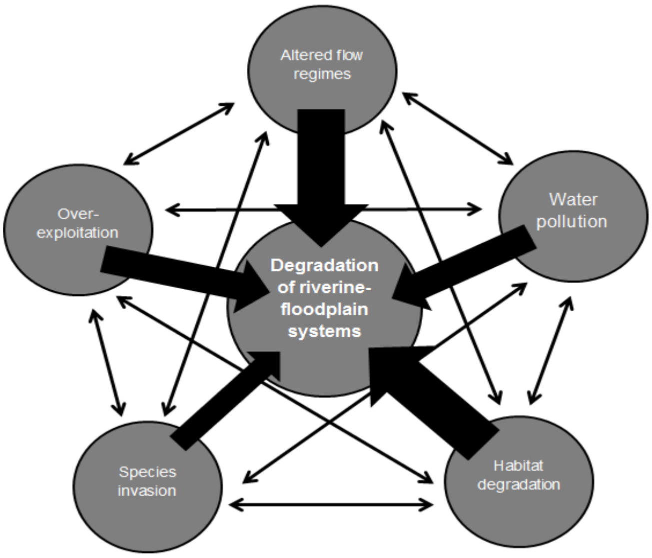

Figure 1.2: Diagrammatic representation of the five major threats and their contribution towards degradation of riverine-floodplain systems. Size of arrows indicates relative contribution towards ecosystem degradation (adapted from Dudgeon et al. 2006).

1.3.1 Habitat alteration

Habitat alteration and land-use change are the leading factors causing declines in biodiversity and ecosystem services in floodplain ecosystems. In North America, 85% of freshwater species are affected by habitat loss, with fish populations appearing the most affected (Tockner & Stanford 2002). Land-use change is the main agent of habitat loss and includes modification of the natural landscape and flow regime (Poff et al. 1997; Tockner & Stanford 2002). Alteration to the natural flow regime could be caused by construction of dams, levees and channelised canals, all of which alter natural flow pulses and affect longitudinal and lateral connectivity which is extremely important for migrating fish and other biota (Tockner et al. 1999). Disconnection of floodplains from the main river channel is a global phenomenon and is well-documented on the Danube River where 23% of floodplain areas have been disconnected due to drainage, and over 60% by river engineering works (Tockner et al. 1999).

1.3.2 Pollution

Water quality in riverine-floodplain systems is directly related to primary productivity and species diversity. Pollution in aquatic systems can be caused by increasing amounts of nutrients entering the system; for example, through the use of pesticides and herbicides due to cultivation and untreated wastewater discharge (Tockner & Stanford 2002). Increased pollutants in floodplain areas can cause deterioration of floodplain soils and groundwater sources due to infiltration of the contaminants blocking soil pores (Parkyn & Wilcock 2004). Consequently, this can cause changes in floodplain terrestrial vegetation which may have cascading effects for aquatic-terrestrial linkages (Molder & Schneider 2011). Nutrient run-off into nearby water-bodies can cause algal production to increase, leading to decreases in oxygen levels. This effect, coupled with increases in water temperature and suspended solids, create areas that are inhospitable for fauna (Sundermann et al. 2013).

1.3.3 Species invasion

Invasion of introduced species into aquatic systems is one of the biggest causes of degradation (Tockner & Stanford 2002). Introduced species are able to tolerate harsher physical and chemical conditions, which allow them to outcompete and displace native species, through greater rates of growth and reproduction (Tockner & Stanford 2002; Dudgeon et al. 2006). Already degraded systems accelerate widespread invasions of introduced species (Dudgeon et al. 2006) and removal of these species becomes increasingly difficult once established. Within the upper Parana River floodplains, non-native piranha have invaded and are causing the widespread decline of some native floodplain fish through overlap in habitat and feeding territories (Agostinho et al. 2003). Feyrer et al.

(2004) documented the Sacramento River floodplain to be dominated by introduced fish species, with < 1% of total fish sampled contributing to native populations.

1.3.4 Altered flow regimes

With increasing human population density, exploitation of aquatic resources due to water abstraction, construction of infrastructure such as dams, stopbanks and flood gates, and land conversion is causing many alterations to freshwater systems (Tockner & Stanford 2002). Many of these changes modify the hydrology, leading to altered magnitude, timing, duration, frequency and predictability of flows, and causing loss of functional integrity of river systems (Poff et al. 1997). Regulation of flow through infrastructure ultimately reduces natural flows and floods, which are highly variable both seasonally and annually. Generally, large floods are decreased and low flows increased with altered hydrology (Duncan & Woods 2004). Alteration of flow therefore influences the frequency and degree to which floodplains are inundated and thus connected to the river (Young et al. 2004). Furthermore, climate change will intensify the effects of altered flow regimes and may fundamentally cause loss of ecosystem structure and function (Palmer et al. 2009). Flood gates and stopbanks reduce the connectivity between the main river channel and its floodplain, which ultimately cause loss of resources and biotic abundances, as species cannot make optimal use of floodplain habitats and large nutrient transfers of carbon and nitrogen are lost (Young et al. 2004). However, the effect of altered flow regimes depends somewhat on river catchment geomorphology as this influences flood hydrology (Young et al. 2004). Large lowland rivers with extensive floodplains will thus be highly impacted compared to steep gradient river catchments.

1.3.5 Over-exploitation

Vertebrates such as fish, reptiles and amphibians are particularly prone to over-exploitation causing dramatic declines in population numbers due to harvesting (Dudgeon et al. 1997; Tockner & Stanford 2002). If harvesting has been continuous for a few decades, vertebrate stocks are unlikely to recover due to the increased pressures from other degradation factors such as pollution and disease (Allan et al. 2005). The majority of these species complete part or their full life-cycle in floodplains, and removing these species through harvesting can have cascading effects down the food-web and alter important trophic links between systems. Hoberg et al. (2002) demonstrated that Okavango delta floodplain supports multiple fish species that graze extensively on zooplankton originating from the terrestrial floodplains, and these trophic subsidies are linked back into the main river channel supporting other aquatic biota.

1.4 Riverine floodplains in New Zealand

Within New Zealand, aquatic systems make up around 3% of the land area, comprising 3820 lakes (Lowe & Green 1987) and over 180,000 km of river systems (Collier 1994). Many of these freshwater ecosystems have become degraded due to land-use changes, primarily from agriculture, waste water discharges, urbanisation and flood protection schemes (Mulholland 2010). Native forest cover has decreased from 75% to 23% since European settlement, leading to the majority of catchments having modified vegetation cover (McGlone 1983; Fahey et al. 2004), primarily on river-floodplains where fertile soils encourage agricultural development. Increased sediment loads and run-off resulting from forest clearance have altered the natural structure and function of riverine floodplains (Hicks & Hill 2010).

Nationally, flooding between 1976 and 2003 cost New Zealand’s economy $17 million per year through industry insurance payments (Pearson & Henderson 2004). Throughout New Zealand, flood control works in river catchments are largely implemented to protect surrounding land through stopbanks and flood gates. However, these structures have altered the extent of floodplain inundation, causing loss of connections to outer floodplains, wetlands and lakes (Beard 2010). This severing of catchment connections has caused the loss of many ecosystem services and many rivers now function in isolation from their floodplains. A number of riverine-floodplains in New Zealand can also be influenced by hydro-electric schemes that have altered the natural hydrology, such as the Waikato River which supports eight hydro-stations (Collier et al. 2010).

As has been found overseas (Gren et al. 1995; Robinson et al. 2002; Opperman et al. 2010; Tockner et al. 2010), New Zealand floodplain waterbodies can provide extremely important habitat for many native species such as waterfowl, fish (eels and galaxiids) and plankton (Beard 2010). Despite their importance, more than 90% of wetlands have been drained and over 50% of floodplains disconnected from the main river channel in the lower Waikato system alone

(Sorell & Gerbeaux 2004; Beard 2010; Mullholland 2010). Noticeable declines in many native fish populations may be linked to these alterations, due to loss of habitat, food and ecosystem structure. Despite the loss of structure and function, riverine-floodplain systems within New Zealand are still largely productive, important for habitat and food provision for native fish, birds, plants and other biota.

1.5 Whitebait fishery within New Zealand

Many native fish in New Zealand are diadromous, with larvae that spend their early lives in the sea before migrating back up rivers as juveniles (e.g. galaxiids or whitebait) (Hickford et al. 2010). Diadromous migrations allow fish to recolonize numerous catchments and a variety of inter-linked systems (McDowall 1995). Many native fish species including galaxiids are, however, particularly prone to human-induced changes because their life history involves large migrations to and from the sea to complete their life-cycles (McDowall 1995; Boubee & Ward 1997; Boubee et al. 1997). Altered flow regimes, barriers to migration and loss of habitat complexity and connectivity are thus major factors influencing fish populations in New Zealand (David & Speirs 2010; Lyon et al. 2010).

In New Zealand, there are around 13 species of native fish within the galaxiid family (Allibone & Wallis 1993), and the larvae of five of these make up the whitebait fishery; inanga (*Galaxias maculatus*), banded kokopu (*G. fasciatus*), koaro (*G. brevipinnis*), short-jaw kokopu (*G. postvectis*) and giant kokopu (*G. argenteus*) (Boubee et al. 1997; David & Speirs 2010). The whitebait catch is comprised largely of inanga (around 70 - 100%), which is predominately a lowland species and more tolerant of lower water quality and increased temperatures than the other four species (Richardson 1997; Richardson et al. 2001; Olsen et al. 2012). Banded kokopu comprise around 7 - 15% of the catch, with koaro around 0.2%; however these two species can increase up to around 30% in rivers where inanga habitat is minimal (Rowe et al. 1992). The remaining species, giant kokopu and short-jaw kokopu, contribute little in the catch (Stancliff et al. 1988). Whitebait support important commercial, cultural and recreational fisheries which are directly managed by the Department of Conservation. Although there are regulations for the methods, fishing season and the structures from which whitebait are caught, there is no limit to the amount that can be taken or who can sell it (Conservation Act 1987).

Generally, the whitebait fishery is not well monitored, and the catch data are estimated and highly variable (Hickford et al. 2010). Despite this, there is anecdotal evidence to suggest there has been a widespread decline in whitebait populations since the early 1900's. Overfishing is thought to be a major driver causing the decline, although no direct evidence exists (Hickford et al. 2010). However, changes in land use from native forest to agricultural systems, urbanisation and altered flow regimes are known to affect whitebait populations either directly (i.e. loss of spawning habitat) or indirectly through riverine connectivity (Hickford et al. 2010; Hickford & Schiel 2013). Of the whitebait species, short-jaw kokopu is classified as 'threatened', with koaro, giant kokopu and inanga classified as 'at risk', and banded kokopu classified as 'not threatened' (Goodman et al. 2013). Nevertheless, there is a clear indication that the whitebait catch has declined substantially within the Waikato River since the 1930's when catches exceeded 60 tonnes, with only around three tonnes of whitebait estimated to be caught annually at present, although records are highly variable (Baker & James 2010; NIWA 2010; Figure 1.3).

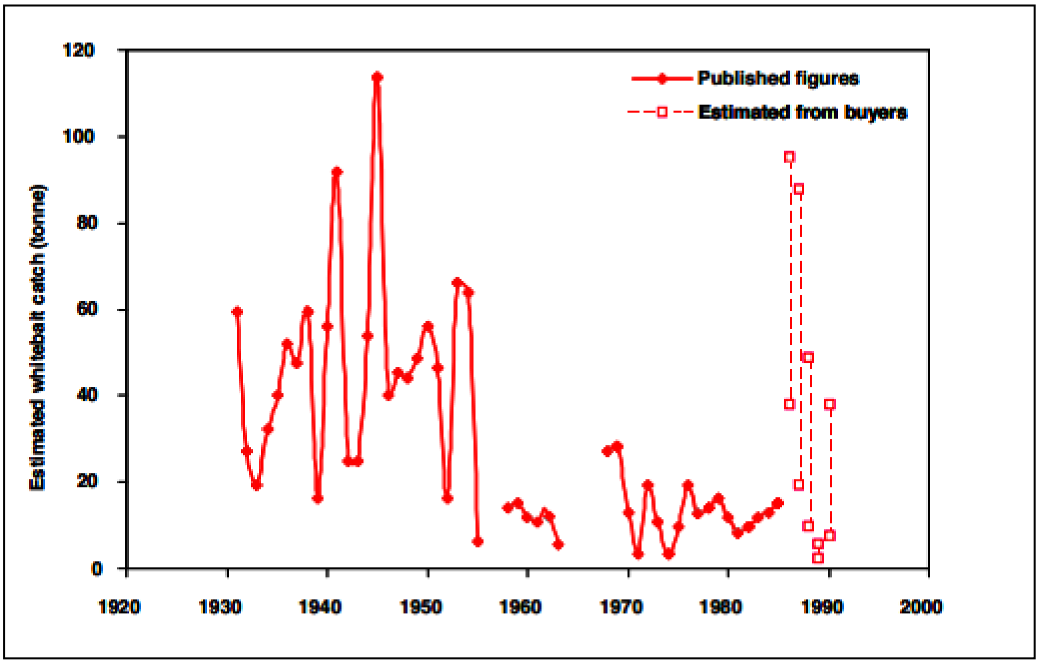

Figure 1.3: Estimated annual whitebait catch in the Waikato River (including smelt, *Retropinna retropinna*) established from Marine Department records (1931-1973), a canning factory in Auckland (1958-1963) and records from commercial buyers (1975-1990) (reproduced by permission from Baker & James 2010).

Galaxiids spawn directly after autumn floods in bankside vegetation close to their adult habitats, especially in areas with high amounts of leafy material, apart from inanga which spawns in vegetation within tidally influenced areas along the river salt wedge (Charteris et al. 2003; Hickford & Schiel 2013). When a spring tide occurs, usually around a month later, this bankside vegetation is inundated and this triggers a hatching event. Larvae are subsequently carried out to sea, where they spend four to six months in the pelagic zone (Hickford et al. 2010; Hickford & Schiel 2013, 2014). Following large spring floods, juvenile galaxiids migrate back into estuaries and upriver as they can sense freshwater plumes (Hickford & Schiel 2014).

Whitebait predominately feed on zooplankton in their larval and juvenile stages, and this is known to be extremely important as a food source for larval fish in the days following hatching (Rowe et al. 2002; Schiemer et al. 2003). The timing of this migration is thought to coincide with the production and dispersal of large-bodied zooplankton from outer tributaries, lakes and floodplains during periods of inundation (Górski et al. 2013). Timing of migration can then be advantageous for native juvenile fish as they can capture a wide range of food sources and find suitable food-rich areas for sustaining migration (Robinson et al. 2012; Górski et al. 2013).

1.6 Objectives of thesis

The link between floodplain inundation and zooplankton food supply for migrating fish has been documented in several parts of the world (Brock et al. 2003; Ning & Nielsen 2010; Battauz et al. 2014), with studies highlighting larval galaxiid populations to show zooplankton preferences (Modenutti et al. 1993). Floodplain soils are recognised to be productive areas for dormant zooplankton populations (Brock et al. 2003; Ning & Nielsen 2010), and may be an important food source for migrating whitebait as subsiding floodwaters transfer zooplankton back into the main river channel following spring floods. However, the link between floodplain productivity and migrating galaxiid populations within New Zealand has not been established. Generally, most of the literature is primarily focused on lake and wetland ecosystems (Barriga et al. 2012; Modenutti et al. 1993; Watkins et al. 2013), with little focus on the structure and function of riverine-floodplain ecosystems. An understanding of the relationship between floodplain inundation and production of zooplankton within New Zealand is required in order understand trophic linkages between zooplankton populations and the recruitment of larval fish, including migrating galaxiid populations.

In the Waikato River catchment, less than 50% of floodplain area remains connected to the river due to construction of 242 km of stopbanks, 249 flood gates and 65 pump stations (Mulholland 2010). Coincident with the construction of the flood control scheme has been the apparent drastic decline in the whitebait fishery over the last 70 years due to multiple factors affecting river water quality and habitat quality, coupled with overfishing (Stancliff et al. 1988; Baker & James 2010). Many attempts to enhance whitebait fisheries within New Zealand have focused on restoring spawning habitat (Richardson & Taylor 2002; Hickford & Schiel 2013, 2014). However, no research has been aimed at understanding their dietary requirements and where they source their food from during upstream migration.

Górski et al. (2013) reported that more large-bodied cladocerans were found in patches of native forest trees and absent within pastoral grass sites along the Waikato River floodplain following inundation. They hypothesised that the peak in abundance of large-bodied cladocerans and copepods post-flooding may play an important role in food provision for migrating galaxiids. It is difficult to test this hypothesis as sampling was undertaken during inundation events, thus the origin of zooplankton from riverine, floodplain or other habitats cannot be pin pointed. I therefore sampled floodplain habitats during dry periods and hatched zooplankton from soils, in order to understand the origin of zooplankton found within riverine-floodplain systems. I then carried out dietary analyses and feeding experiments on juvenile inanga to determine prey preferences. Accordingly, the objectives for this thesis were to:

1. Determine the potential of floodplain soils to generate zooplankton following inundation;

2. Assess the influence of riverine-floodplain connectivity and vegetation type on zooplankton production from floodplain soils;

3. Investigate the diet and prey preferences of migrating *G. maculatus* whitebait; and

4. Determine the influence of zooplankton community composition and abundance on feeding rate and selectivity of *G. maculatus* whitebait.

It is hoped that this research can be used to develop a greater understanding of the importance of riverine-floodplain management for food-web productivity, and in turn allow management of the whitebait fishery to be directed to areas important for their growth and survival.

1.7 Outline of thesis

This thesis comprises five chapters, with the two main results chapters set out in the style of manuscripts for later submission to scientific journals. Due to this, there is some repetition throughout the thesis within the study area and methods sections. This chapter reviewed the literature on the structure and function of riverine-floodplains, globally and within New Zealand, and sets out the overall objectives of the thesis. Chapter 2 presents the study area, including catchment characteristics and site descriptions. Chapter 3 investigates the mechanisms influencing zooplankton emergence from riverine-floodplains. Chapter 4 examines the diet and feeding preferences of *Galaxias maculatus* within the Waikato River. Chapter 5, the overall discussion chapter, summarises the main findings from Chapters 3 and 4 and highlights possible management strategies to maintain the structure and function of riverine-floodplains and sustain migrating galaxiid populations.

Chapter Two

Study area – The lower Waikato River

2.1 Background

The Waikato River is New Zealand's longest river, running 442 km north from its headwaters at Lake Taupo to its outflow at Port Waikato. It drains 13% of the North Island (14,442 km^2), with an average discharge of 422 m^3/s to the sea (Brown, 2010). The river valley formed around 26,500 years ago when the Oruanui eruption at Taupo deposited large amounts of sediment on the Waikato landscape (Hicks & Hill 2010). Around 17,000 years ago the sediment supply decreased, and the river discharging from Lake Taupo cut a single channel into the deposited sediment, eventually forming the Waikato River seen today (Hicks & Hill 2010). Remaining alluvial deposits on the sides of the Waikato River formed terraces (Hicks & Hill 2010) and the base of the floodplains within the catchment. The upper catchment originates in the Taupo Volcanic Zone where pumice-dominated alluvial deposits can be found in allophanic and gley soils, particularly in the lower regions of the catchment (Collier et al. 2010).

The climate of the lower Waikato River is dominated by mild winters and moderate rainfall with a mean annual temperature of 12.5^{o}C (Collier et al. 2010). Rainfall in the area is controlled by the local topography and westerly winds which result in an average annual rainfall of 981 - 4372 mm (Collier et al. 2010). Today, the river is important for its role in hydroelectricity generation with eight hydro-stations located in the upper section of river. As well, the river provides habitat for a range of threatened species and associated fisheries (Burger et al. 2002; Collier et al. 2010). Culturally, the Waikato River is important for Waikato-Tainui through physical well-being, culture and identity (Watene-Rawhiri & Flavell 2010). Through the river settlement, Waikato-Tainui co-manage the Waikato River with the Crown and have implemented management initiatives such as the Waikato River Clean-up Trust that aims to protect the health and well-being of the river for present and future generations (Waikato River Authority 2010).

The lower Waikato River has extensive floodplains which, like other floodplains around the world, increase biodiversity values by adding a level of complexity to the physico-chemical conditions in the area (Tockner et al. 2010). During high flows, the Waikato River connects with multiple floodplain wetlands, lakes and other tributaries in the catchment. However, large floods also inundate farm land and infrastructure, and a flood protection scheme was implemented in 1961 to reduce this. The last large flood occurring before the stopbanks and other measures were implemented was recorded at Ngaruawahia in 1958 and reached around 1400 cumecs (Brown 2010). Wetlands within the catchment are part of a complex network of water systems connected to the river, which currently occupy 155 km^2 and are highly important for biodiversity, habitat provision and regulating water quality (Beard 2010). The Whangamarino wetland is of particular importance as it is one of the largest intact wetlands in New Zealand, covering 73 km^2. It is the largest wetland connected to the Waikato River, playing an important part in the flood protection scheme and providing extensive habitat for plant and bird life (Beard 2010).

2.2 Changes to the lower Waikato River

Historically, floodplains of the Waikato River were extensive and served as a linkage between the main river channel and the catchment's lakes and wetlands (Hamilton et al. 2010). Since the implementation of the flood protection scheme, approximately 50% of floodplains, shallow lakes and peat wetlands have been disconnected from the Waikato River (Collier 1994; Chapman 1996; Mulholland 2010; Figure 2.1). Flood gates, pump stations and stopbanks now regulate lateral connectivity, and without the transfer of material between the river and the floodplain many ecosystem services have been lost. Before stopbanks were constructed, inundation of lower Waikato River floodplains resulted from sustained high flows over 800 cumecs for periods > 14 days (Brown 2010). With implementation of the flood control scheme, the last flood that overtopped the stopbanks was in 2008 at around 1300 cumecs, although this level varies depending on location (Brown 2010; Waikato Regional Council 2014b). Floods that occur in the lower Waikato River at Rangiriri and Mercer will only overtop the stopbanks when the discharge exceeds 1300 cumecs (Waikato Regional Council unpubl. data; Figure 2.2).

Many floodplain lakes and wetlands have been lost or degraded due clearance and drainage of agricultural land. Lower river wetlands historically comprised 14% of the total catchment area, but this has declined to only 1% and remaining wetlands have decreased in size (Beard 2010). Overall, wetland drainage for agriculture is the major factor leading to wetland loss within the Waikato, and wetlands now exist as small isolated fragments, generally no bigger than 0.5 km^2 in area (Beard 2010). Wetland water quality has degraded over time due to increased sedimentation and run-off from surrounding land, coupled with altered flow regimes and water levels due to the flood protection scheme (Beard 2010).

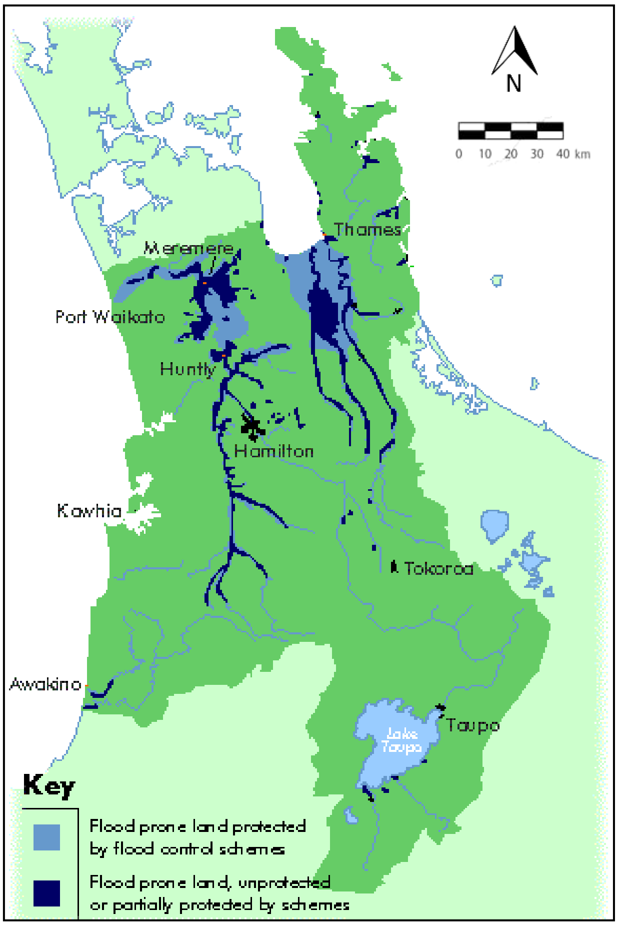

Figure 2.1: Map of the Waikato region (dark green) encapsulating the Waikato River catchment, indicating areas that are protected or partially protected by flood control schemes or unprotected from floods (Waikato Regional Council 2014a).

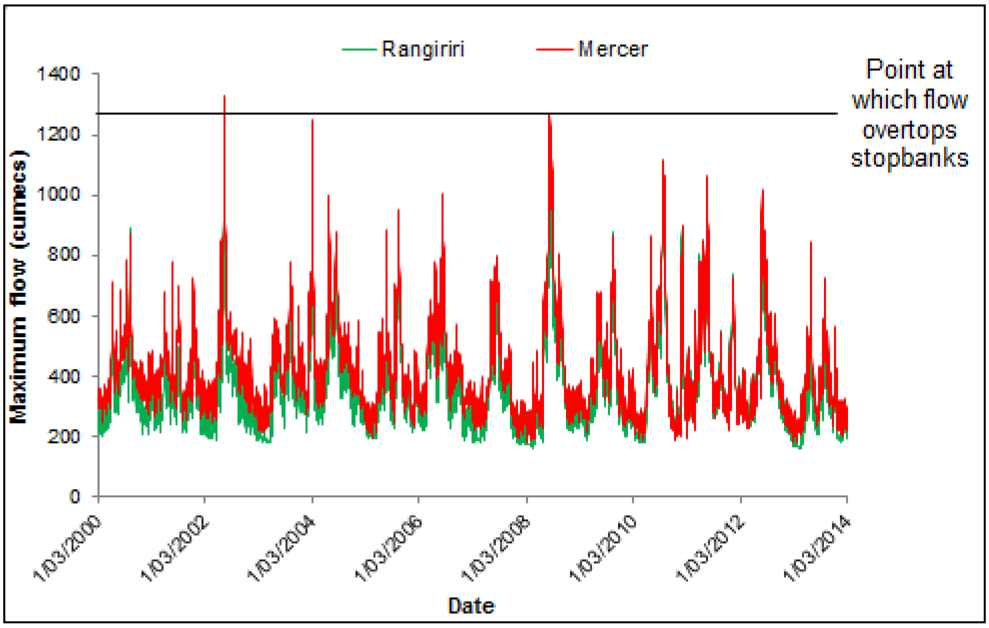

Figure 2.2: Maximum water flow in the lower Waikato River at two sites; Rangiriri and Mercer from January 2000 to January 2014. Solid line represents point at which flow overtops stop banks (Waikato Regional Council unpubl. data).

The landscape of the lower Waikato River is characterised by lowland undulating hills, 75% of which is now in agricultural development, with only 6% of the remaining catchment in native forest, 4% in planted forest and up to 17% in scrub and horticulture (Collier et al. 2010). Due to land use change, however, native forest cover within the lower catchment has decreased from 75% to 23% leading to the majority of the river catchment having modified vegetation cover (Collier 1994). Floodplain vegetation of the lower Waikato River catchment is now dominated by pastoral grasses, with remnant patches of native trees interspersed with exotic scrub and willow. Further, the lower catchment supports 2.3 million farm animals dominated by dairy cows and sheep (Collier et al. 2010). Urban areas occupy 0.6% of the catchment, mainly between Karapiro and Port Waikato, providing high aesthetic and recreational values for the regional population (Collier et al. 2010).

The lower catchment contains 49 lowland lakes, most of which are small (catchment areas of around 0.5 km^2), shallow and highly eutrophic (Hamilton et al. 2010). During 2003 - 2007, water quality of the floodplain lakes was comparable to earlier studies in the 1980's with a few exceptions (Lake Whangape, Waahi) whereby total nitrogen, phosphorus and chlorophyll *a* were relatively similar to historical values (Hamilton et al. 2010). Present-day water quality, however, has shown large reductions in water quality, mainly due to the loss of macrophyte beds (Hamilton et al. 2010). Consequently, there is a marked change in water quality from the upper reaches of the catchment, which is generally pristine, to the lower reaches where water quality is degraded due to urbanisation, pollution and land use changes for agricultural development (Vant 2010). These degradation factors have caused an increase in nitrogen into the river system of about 18% and a 6% decrease in overall water clarity (Vant 2010).

Within the Waikato River there are 12 species of non-native fish that were intentionally introduced for sports fishing from several regions of the world (Hicks et al. 2010). Invasive species such as koi carp (*Cyprinus carpio*), goldfish (*Carassius auratus*), gambusia (*Gambusia affinis*), brown bullhead catfish (*Ameiurus nebulosus*) and rudd (*Scardinius erythrophthalmus*), have caused declines in water quality and have affected many native fish species (Hicks et al. 2010). Connections to off-channel floodplain waterbodies, wetlands and lakes have facilitated the widespread invasion of many of these species, particularly in the lower reaches (Wu et al. 2013). These non-native species can out-compete native fish due to overlap in diet and habitat, and they have the ability to tolerate low water quality and higher thermal regimes (Hicks et al. 2010; Wu et al. 2013).

Within off-channel floodplain waterbodies, zooplankton assemblages are available for consumption for non-native fish such as koi carp, which rely on zooplankton as a food source during their larval stages (Wu et al. 2013). Riverine zooplankton assemblages are typically dominated by rotifers, with cladocerans and copepods in lower abundance (Shiel et al. 1982; Kobayashi 1997). This composition has been documented in the Waikato River where rotifers numerically comprise 85% of total zooplankton numbers (Burger et al. 2002). However, within the floodplain lakes of the Waikato River catchment, zooplankton communities are dominated by large Cladocera such as *Daphnia* sp. and *Bosmina* sp., and calanoid and cyclopoid copepods, zooplankton groups that are typical of other New Zealand lakes (Chapman & Green 1999).

2.3 Site selection

Nineteen sites on the lower river floodplain between Ohinewai and Meremere were selected for soil sample collection encapsulating native forest, scrub and pasture land cover types (Figure 2.3; 2.4). These three vegetation types were chosen as they are likely to exhibit different physical and chemical conditions, depending on river connectivity, and represent the range of vegetation types present today on the lower river floodplain (Plate 2.1). Generally, sites in areas of remnant native forest were comprised of kahikatea (*Dacrycarpus dacrydioides*) with smaller amounts of pukatea (*Laurelia novae-zelandiae*) and native podocarp species such as totara. One forest site, however, was dominated by *Coprosma* sp. (Table 2.1). Groundcover was a mixture of leaf litter from the surrounding trees, along with exotic annuals and various reeds and creepers such as *Persicaria* sp. Pasture sites were mainly used for grazing by dairy cows and comprised various mixtures of pastoral plants such as perennial grasses and clover with areas of dried bare ground. Scrub sites were dominated by willow (*Salix* sp.) and ground cover consisted of various grasses, night shade (*Solanum* sp.), leaf litter and large areas of bare ground.

For each vegetation type, sites were selected that were either connected or disconnected from the river based on the degree of flooding potential determined using ground elevation LiDAR (Light Detecting And Ranging) data to 1300 m elevation (usually in front of or behind stop banks) (obtained from Waikato Regional Council & NZ Aerial Mapping Ltd, 2010). Connected sites were within 17 - 320 m of the river and disconnected sites were 45 - 490 m from the river. Connected and disconnected sites and vegetation types were dispersed throughout the study area, unless sites could be nested together based on connectivity (Table 2.1).

Table 2.1: Locations and physical properties of the 19 sites located on the lower Waikato River floodplain.

Site number	X coordinate (NZTM 2000)	Y coordinate (NZTM 2000)	River connectivity	Vegetation type	Dominant vegetation	Distance from river (m)
1	17525972	37172639	Disconnected	Forest	Kahikatea	270
2	17533813	37182867	Disconnected	Forest	Kahikatea	160
3	17532434	3719489	Disconnected	Scrub	Willow	360
4	17535489	37192919	Connected	Forest	Kahikatea	320
5	17532600	37195559	Connected	Forest	Kahikatea	140
6	17533853	3720285	Disconnected	Scrub	Willow	490
7	17531163	3720342	Connected	Pasture	Pastoral grass	93
8	1753821	3720868	Disconnected	Pasture	Pastoral grass	155
9	17523811	37201414	Disconnected	Forest	Kahikatea	75
10	17562071	37253255	Connected	Forest	*Coprosma* sp.	200
11	17532536	37243699	Disconnected	Scrub	Willow	305
12	17534169	37244247	Connected	Scrub	Willow	145
13	17585075	37263495	Connected	Pasture	Pastoral grass	162
14	17585741	37263275	Disconnected	Pasture	Pastoral grass	263
15	17591271	37291711	Connected	Pasture	Pastoral grass	25
16	17592605	37291598	Disconnected	Pasture	Pastoral grass	45
17	17592739	37295650	Connected	Scrub	Willow	52
18	17595179	37305328	Connected	Scrub	Willow	125
19	17532908	37195030	Connected	Forest	Kahikatea	17

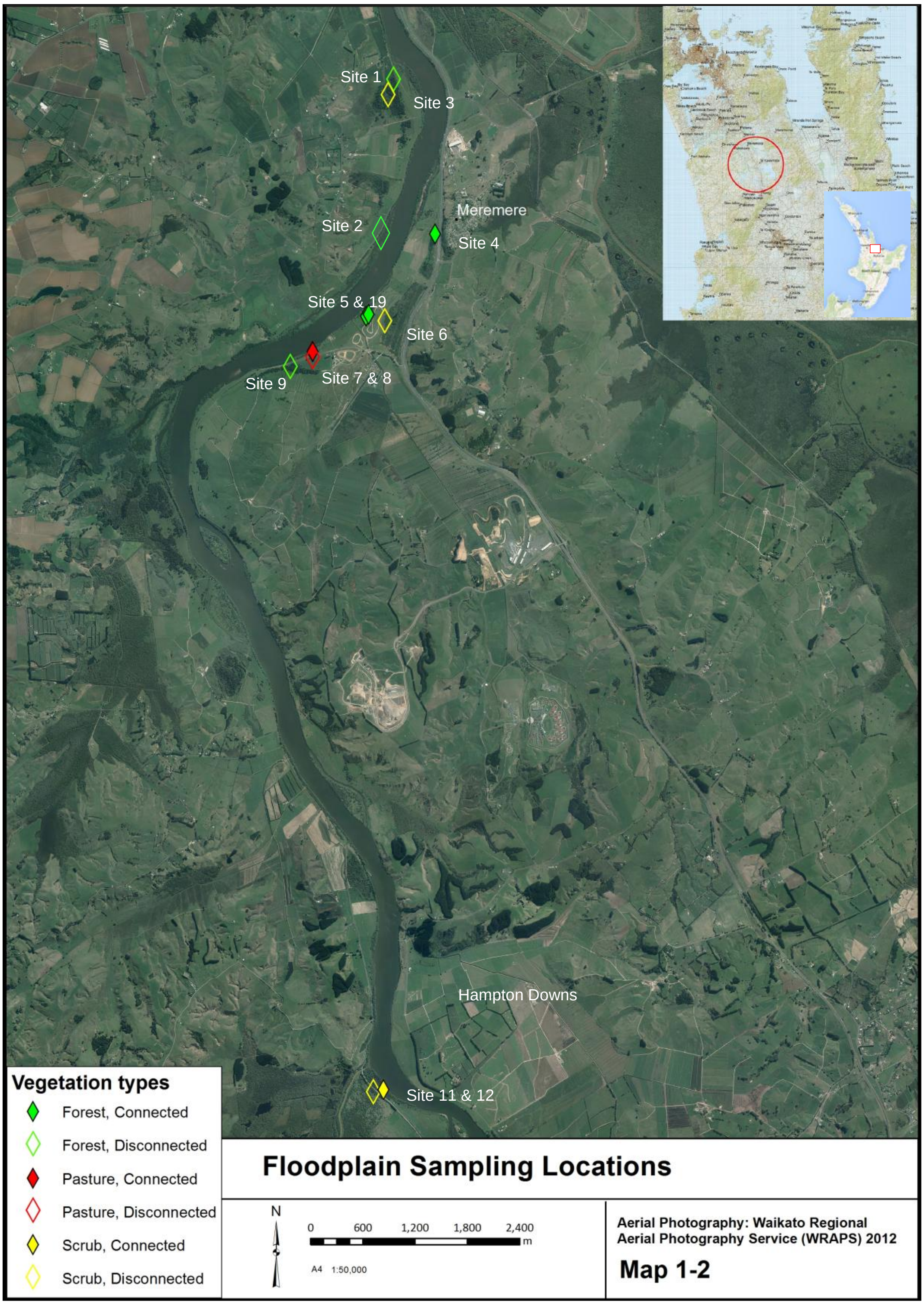

Figure 2.3: Map of 12 sites sampled on the lower Waikato River floodplain. Native forest = Green; Scrub = Yellow; Pasture = Red. Sites with closed diamonds are connected to the river and sites with open diamonds are disconnected from the river.

Figure 2.4: Map of 9 vegetation sites sampled on the upper range of the lower Waikato River floodplain, including sites 11 and 12 that are presented again for map comparison. Native forest = Green; Scrub = Yellow; Pasture = Red. Sites with closed diamonds are connected to the river and sites with open diamonds are disconnected from the river.

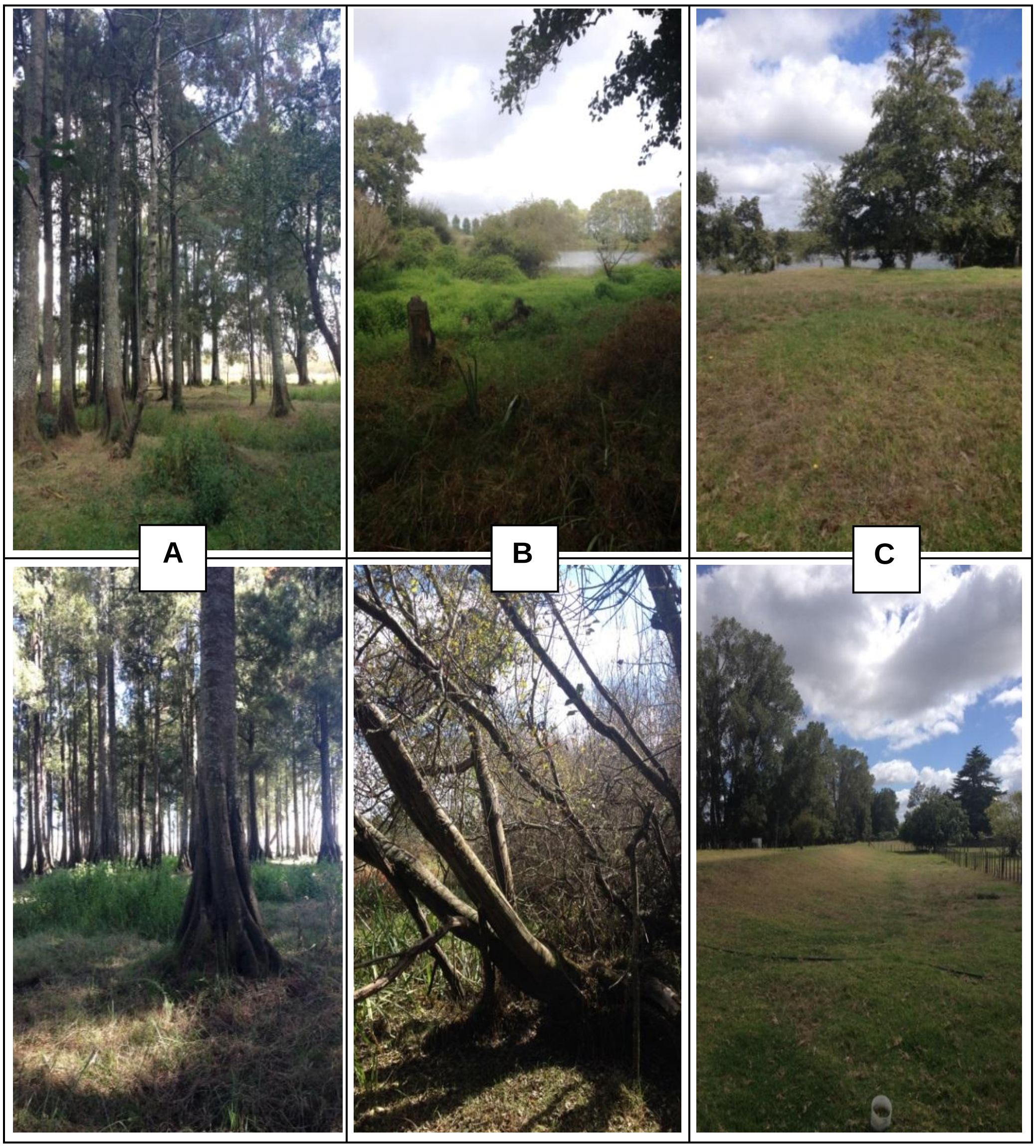

Plate 2.1: Photographic images of the three lower Waikato River floodplain sampling sites; A = Native forest, Site 9; B = Scrub, Site 6 (upper),17 (lower); C = Pasture, Site 13 (upper),14 (lower). Top images are connected sites, bottom images are disconnected sites.

For the study of inanga diet and feeding, two sites were selected in the lower reaches of the Waikato River. The sites, Tuakau and Mercer, were located 11 km apart in order to encapsulate potential spatial differences in whitebait and zooplankton populations (Figure 2.5). The sites are located around 30 to 41 km, respectively, from the mouth of the Waikato River, at Port Waikato (Plate 2.2). Tuakau has an average river level of 1.8 m, although this site is highly influenced by tidal phases with the water level reaching around 3.8 m during high tide (Waikato Regional Council unpubl. data). Discharge, however, is not monitored at Tuakau. Water quality in the lower reaches of the river around Tuakau is degraded, with total nitrogen, phosphorus, water clarity and biological oxygen demand having significantly lower average values compared to the upper reaches of the catchment (Vant 2010). Floodplain vegetation in the Tuakau area consists of remnant patches of kahikatea forest along with other indigenous vegetation, exotic willow and pastoral grasses interspersed along the river banks and floodplains (Burge 2014). Mercer has an average river level of 2.3 m and is partially affected by tidal phases, although not extensively (Waikato Regional Council unpubl. data). The discharge at Mercer is 422 cumecs and the area is very susceptible to large floods (Brown 2010). The river discharge at Mercer during the course of whitebait collections is shown in Figure 2.6. Water quality at Mercer is analogous to Tuakau with increased total nitrogen, phosphorus and decreased water clarity compared to upper regions of the catchment (Vant 2010). Riparian vegetation at Mercer is dominated by exotic scrub and willow species surrounded by intensive pastoral development.

Figure 2.5: Map of the two whitebait sampling locations, Mercer and Tuakau, on the lower Waikato River.

Plate 2.2: Photographic images of the two whitebaiting sites on the lower Waikato River. A = Mercer, B = Tuakau. Top images are looking upstream, bottom images are looking downstream.

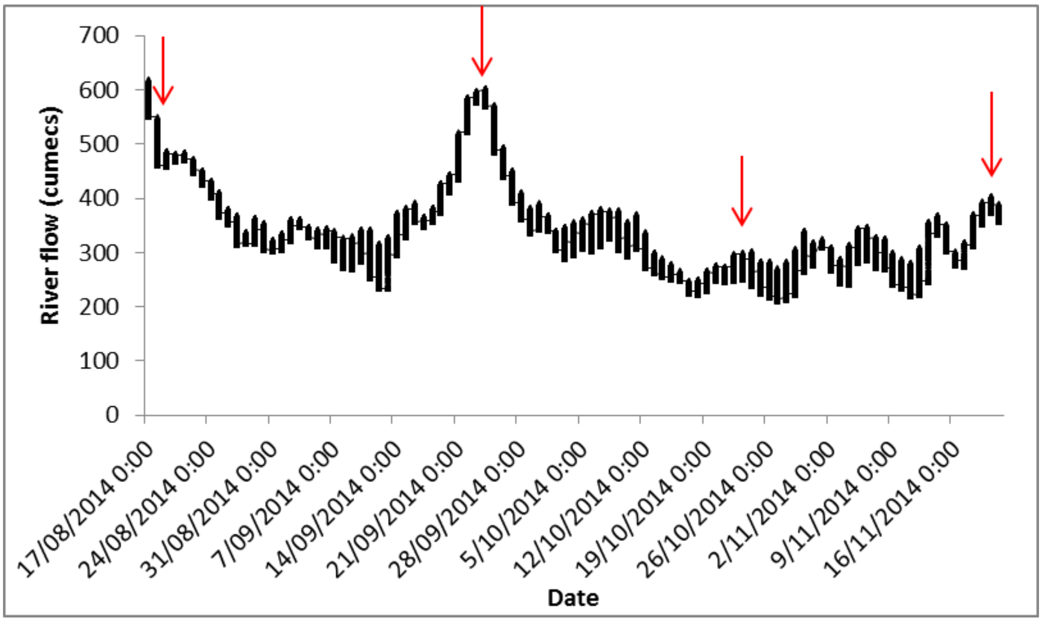

Figure 2.6: Hydrograph of the Waikato River at the Mercer site during whitebait sampling from August to November 2014. Arrows indicate when sampling was undertaken. (Waikato Regional Council 2014b).

Chapter Three

Zooplankton emergence following inundation of floodplain soils: Does vegetation type and riverine connectivity influence community composition?

3.1 Introduction

Floods are a key determinant of the structure of aquatic plant and animal communities in rivers (Bornette et al. 2001; Górski et al. 2013). Most rivers have floodplains of various extents and during floods water can extend out onto these low-lying areas (Bornette et al. 2001; Leyer 2005; Tockner et al. 2010). Low gradient, lowland rivers, in particular, typically have extensive floodplains that are important for energy transfer to the main channel when inundated, and these transfers can ultimately make a significant contribution to aquatic invertebrate and fish production (Junk et al. 1989; Tockner et al. 1999; Tockner et al. 2010).

Flow regimes influence productivity, species abundances and biodiversity in stream and river-floodplain ecosystems (Poff et al. 1997; Tockner et al. 2000). In particular, flow variability plays an important role in the dynamics of river-floodplain systems as this leads to inundation and the consequent flooding influences and maintains biodiversity by producing a mosaic of physical conditions that support different species assemblages (Poff et al. 1997). Low and high discharge events in rivers act on both temporal (across seasons) and spatial (across landscape) scales, and effects from flow on the river are dependent on the topography and local geology of the area (Bornette et al. 2001; Leyer 2005). Due to regular wet and dry cycles, lateral areas alongside rivers experience large fluctuations in productivity leading to the development of more diverse microfaunal species assemblages than less variable habitats (Tockner et al. 1999; Havel et al. 2000; Jenkins & Boulton 2003).

The Flood Pulse Concept is widely accepted in river ecology (Junk et al. 1989), with recent modifications to include temperate, lowland floodplains (Tockner et al.

2000). Tockner et al. (2000) explained the significance of smaller flow pulses to river ecosystem function; these pulses, no matter how small, generate spatial heterogeneity in aquatic and terrestrial habitats that are characteristic of riverine floodplains. Hydrological connectivity between the main river channel and lateral floodplain areas is the major driver generating such heterogeneity in floodplains. The extent and duration of the flood pulse in rivers determines the degree of connectivity between these areas and therefore the extent of nutrient and biotic exchange (Tockner et al. 2000). Each flood pulse will have a specific individual effect on floodplain ecosystems. Many riverine species have life-cycles adapted to flood regimes with larger flows allowing longer aquatic-terrestrial connections and thus greater use of floodplain resources (Tockner et al. 2000).

The extensive loss of floodplain areas is a global phenomenon (Watkins et al. 2013; Wu et al. 2013), with the consequent loss of ecosystem services such as sequestration of nutrients, flood control, and maintenance of water quality and habitat for wildlife (Tockner et al. 2010). Over the past few decades, the majority of large, lowland rivers have become regulated by construction of flood gates, stopbanks, dams and flood protection schemes which govern discharge regimes and therefore floodplain interactions (Buijse et al. 2002). Among the other factors contributing to the degradation of river-floodplain systems, alteration of land-use for urban development and agriculture is the single most influential factor affecting loss of species and habitat complexity (Tockner & Stanford 2002). In Europe and North America, for example, over 70% of natural floodplains have been modified through dams, reservoirs and water abstraction, and consequently they have been degraded to the point that they are no longer functionally viable (Tockner et al. 2010). In Japan, floodplains contain 50% of the human population and 75% of economic assets, and modification these floodplains has resulted in substantial loss of ecosystem functions (Yoshimura et al. 2005; Nakamura et al. 2006).

Seasonally, flood pulses are highest in winter due to additional rainfall and/or snowmelt and lowest during the summer months when there is increased evaporation and water abstraction, and reduced rainfall (Junk et al. 1989; Poff et al. 1997; Leyer 2005). To tolerate the variable physical and chemical conditions in floodplains, some organisms such as zooplankton have evolved life-history strategies that enable them to survive periodic drying (Schroder 2001; Gyllstrom & Hansson 2004; Lumban Touran 2012). This is achieved through the production of diapausing stages that remain in a state of dormancy in floodplain sediments until favourable environmental conditions arise (Brendonck & De Meester 2003; Battauz et al. 2014). As a favourable strategy to increase chances of survival, dormant stages must be produced before floodplains are dry so they can survive the terrestrial phase and emerge once inundated (Schroder 2001). If the egg bank is not exhausted after a wetting event, accumulation of these resting stages can lead to a long-lived egg bank in floodplain soils that can remain viable for many years (Brock et al. 2003; Ning & Nielsen 2010; Battauz et al. 2014).

Water residence time (WRT) is the crucial factor determining the structure and diversity of zooplankton communities that develop in inundated floodplain areas, with communities shifting from rotifer to crustacean dominance within a number of weeks (Pace et al. 1992). Hydrological connectivity between the river and these lateral areas can then provide a continuous supply of newly-hatched zooplankton to the river and provide food for riverine biota such as migrating juvenile fish (Ning & Nielsen 2010). The emergence dynamics of the dormant zooplankton stages, however, are influenced by the life history of the species and the characteristics of the floodplain habitat (Brock et al. 2003; Battauz et al. 2014).

Vegetation structure of lateral riverine areas and associated floodplains are directly linked to flow variability and hydrological connectivity (Leyer 2005). Once propagules have been deposited or established from resting seed banks, growth in floodplain areas is reliant on site specific conditions and competition between biota (Brock et al. 2003; Leyer 2005). Both zooplankton and seed egg banks display similar dormancy characteristics and thus lead to a continuous and diverse species pool within floodplain sediments (Brock et al. 2003). Changes in land use from native forest to grazing pastoral land, however, can alter soil properties, reducing productivity. Such changes reduce the diversity and abundance of floodplain biota (Opperman et al. 2010), that may be important for energy transfer back into the main river channel.

3.1.1 Study objectives and aims

The objective of this study was to assess the potential of floodplain soils to hatch out zooplankton when inundated and to investigate whether river connectivity or floodplain vegetation type influences zooplankton community composition. Górski et al. (2013) examined zooplankton composition in lateral floodplain areas during inundation of different vegetation types along the Waikato River, and found different zooplankton groups in different floodplain vegetation types. Notably, large-bodied cladocerans were abundant in patches of native forest trees and absent within pastoral grass sites. However, their results were correlational, and it is unclear whether the zooplankton encountered entered the floodplain from the river or developed from dormant eggs in the soil.

Here, I quantify the abundance and composition of zooplankton emerging from egg banks in floodplain soils among different vegetation types and with different levels of connectivity with the lower Waikato River. Based on findings elsewhere (Modenutti et al. 1993), floodplain areas are expected to act as zooplankton “nurseries” until favourable conditions arise, such as inundation, allowing zooplankton to emerge and recede back into the river as floodwaters subside, potentially acting as a food source for diadromous fish (Górski et al. 2013).

It has been documented that *Galaxias maculatus* present in a South American landlocked lake preferentially consume large-bodied copepods and cladocerans (Modenutti et al. 1993), and similar preferences may occur within New Zealand *Galaxias* riverine populations. I tested the following hypotheses:

1. Floodplain vegetation type will influence the composition and abundance of emerging zooplankton communities due to differences in soil conditions mediated by vegetation cover;

2. The level of connectivity between the floodplain and the main river channel will influence zooplankton community composition and abundance, linked with the probability of inundation.

I collected soil cores from floodplain areas with three types of vegetation cover (native forest, scrub and pasture), inside or outside stopbanks, and inundated these cores in the laboratory to determine potential sources of zooplankton during flooding.

3.2 Methods

3.2.1 Study area

The Waikato River is the longest river in New Zealand running for 442 km from its headwaters at Lake Taupo, in a northerly direction to its outflow to the Tasman Sea at Port Waikato (Brown 2010). My study was conducted in the lower reaches of the Waikato River, where floodplains are generally extensive and the land use is predominately pastoral with patches of remnant native vegetation or exotic scrub (Górski et al. 2013). For more details on the study area, see Chapter 2.

Floodplain soil cores were collected from three different floodplain vegetation types; native forest, pasture and scrub. Generally, native forested sites were dominated by kahikatea (*Dacrycarpus dacrydioides)* with smaller amounts of pukatea (*Laurelia novae-zelandiae*) and lesser amounts of *Coprosma* species. The soil surface was a mixture of leaf litter from the surrounding trees, and ground cover by exotic annuals, various reeds and grasses. Some patches of native forest were also open to grazing by cattle. Pasture sites were mainly used for grazing by dairy cows and comprised various mixtures of pastoral grasses with areas of dried bare ground. Scrub sites were dominated by willow (*Salix* sp.) and ground cover consisted of various grasses, night shade (*Solanum* sp.), leaf litter and large amounts of bare, dried ground. For each vegetation type, sites were selected that were either connected or disconnected from the river based on the degree of flooding potential determined using remote sensing Light Detecting And Ranging data (LIDAR) and stopbank position (i.e. in front of or behind stopbanks).

3.2.2 Soil sampling

Soil cores were collected from 17 to 20 March 2014 when the floodplains had been dry for an extended period of time. The last rain event was one week prior to sampling where an average of 1.2 mm fell; however, this was not sufficient to moisten the soil (NIWA 2014). Six 10 cm diameter core samples were taken at each vegetation/connectivity type to account for spatial variability at each site. Each vegetation/connectivity type was replicated three times, except forest which was replicated four times to encapsulate variability in the vegetation present at each forested site, making a total of 19 sites. Cores were taken to a soil depth of 7 cm, a depth known to capture the majority of zooplankton resting stages (Brendonck & De Meester 2003). Corers were pushed into the ground using a mallet, until the top of the corer was at ground level. Each core was then lifted out of the ground and a flat slice was placed underneath to prevent any soil falling out. Each core was collected at least 15 m in from the edge of each forest and scrub site to compensate for any edge effects. Excess groundcover vegetation was removed from the surface of each core which was then placed in a 1 L container to preserve sediment structure for transport back to the laboratory in a cooler. One additional sediment core was collected at each site to determine soil properties. This core was sealed in a labelled plastic bag to prevent evaporation.

3.2.3 Environmental data and soil analyses

Vegetation composition was recorded at each site within a 5 m^2 area by giving each species present a percentage composition value relative to all species at the site. Canopy cover was assessed using a spherical densitometer (Model A, Wildco, USA), which involved taking four measurements at north, south, east and west orientations to get an overall percentage estimate of cover (Strickler 1959). Ground cover was estimated using a percentage scale and involved scoring percentages of rock, bare ground, vegetation or leaf litter at each core site. Lastly, soil and air temperature were recorded for each core using a multi-thermometer logger (ATP; ST-9258) in order to assess potential variability between sites. Soil temperature was taken at the depth of the core and air temperature was taken approximately 1.4 m above ground height.

The 19 sediment samples collected from each site were analysed to quantify properties of the sediment that may differ between vegetation types using standard methods from Brix (2008). Soil moisture was determined by placing known weights of fresh soil (5 - 10 g), measured to the nearest 0.001 g, into pre-weighed crucibles and drying them in an oven at 105 ºC for eight hours. Soil samples were then reweighed and soil moisture was calculated as:

Equation 3.1:

$$\text{Soil moisture (\%)} = \frac{B - C}{C - A} \times 100$$

Where:
A: Weight of porcelain crucible
B: Weight of porcelain crucible + fresh soil sample
C: Weight of porcelain crucible + sample after drying at 105ºC

The organic matter content of the soil was calculated in order to understand the amount of water and nutrients within the soil, which are important for viability of the soil and the egg banks (Boulton & Lloyd 1992). Organic matter was measured as the ash-free dry weight of the soil. Firstly air-dried soil was weighed and placed in a muffle furnace at 450 ºC for 12 hours overnight. The soil was then reweighed and organic matter content calculated as:

Equation 3.2:

$$\text{Organic matter content, LOI (Loss On Ignition) (\%)} = \frac{C - D}{C - A} \times 100$$

Where letters A and C are the same as Equation 3.1;
D: Weight of porcelain crucible + sample after burning at 450ºC

3.2.4 Incubation experimental design and processing

In the laboratory, the incubation experiment was initiated by placing Waikato River water over the top of each core in individual plastic 1 L containers to promote hatching. River water had been filtered through a 0.5 µm GF/C Whatman glass fibre filter paper to mimic natural conditions while excluding waterborne zooplankton; six containers filled with only filtered river water served as controls. The amount of water added to each container ranged from 600 to 715 mL; the water level was marked on each container so additional water could be added regularly if necessary to maintain this level. Each container was covered with cling wrap to minimise evaporation and prevent contamination among samples. Samples were incubated at 20°C/12ºC coupled with a 12:12 light/dark cycle to mimic natural light and temperature conditions based on local meteorological data (NIWA 2014).

On days 3, 7, 12, 17, 23, 30 and 39, around 50 mL of water was pipetted out of each container and combined for each site (the exact volume of water extracted was recorded). This volume was used as it allowed some water to be left within the container and therefore enabled continuous development of zooplankton. The combined sample was filtered through a 40 µm mesh and preserved in 90% ethanol. After each sampling the containers were replaced with new filtered river water to the original level. The pipette was rinsed thoroughly between samplings to prevent cross-contamination between the sites. To minimise position effects in the incubation fridges all treatments were arranged randomly after each sampling. Later, each preserved sample was checked for hatched zooplankton at 25x magnification under an Olympus SZ60 stereo zoom microscope. Hatched zooplankton were identified to the lowest possible taxonomic level and the presence of other invertebrate taxa, generally nematodes, oligochaetes and mites, were recorded.

3.2.5 Data analysis

Factorial ANOVAs, run in STATISTICA (v 11; StatSoft, Oklahoma, USA), were used to analyse differences between vegetation type and connectivity and environmental variables, zooplankton taxon richness, density and abundance. If there were differences between factors, a Tukey's post-hoc test was used to examine pairwise differences. Pearson correlations between zooplankton species abundances and environmental variables were used to explore relationships between factors and zooplankton abundances. Correlation analyses, run in STATISTICA, were used to test whether any zooplankton taxa were correlated with the environmental factors measured. Analyses were based on average zooplankton species abundances against environmental factors measured. All data were tested for normality using expected normal histograms and Lilliefors test. If data were found to be non-normal, the data were log transformed.

Primer 6 (v 6.1.15; Plymouth Marine Laboratory, Ivybridge, UK) was used to create multidimensional scaling (MDS) ordinations using zooplankton community abundance data calculated as numbers of individuals per litre. Two-dimensional MDS plots, based on the Bray-Curtis distance matrix, were used to evaluate patterns in zooplankton community composition for the three vegetation types and two levels of connectivity. Relative distance between the points represents the relative dissimilarities in community composition between the sites. Points that are closer together in community composition are more similar and points that are further away from one another are more dissimilar (in ordination space). Abundance data were log (x+1) transformed prior to analysis to reduce the influence of high taxa abundances. Zooplankton community composition and potential associations with environmental factors were assessed using vector overlays. Permutational multivariate analysis of variance (PERMANOVA; McArdle & Anderson 2001) was used to determine the differences in zooplankton communities between different floodplain vegetation types and levels of connectivity (connected vs. disconnected) to the Waikato River (i.e., sites positioned in front of or behind stopbanks). PERMANOVA is an analysis of variance on data based on resemblance measures (Bray-Curtis) using randomisation measures. Results were obtained using 9999 permutations under a reduced model. Pair-wise tests were conducted on factors with effects $P < 0.05$ to determine which pairs of categories had significant differences in community composition.

Distance-based linear models (DistLM) were used to test which predictor variables best explained the dissimilarities between zooplankton community composition and environmental factors measured. Step-wise DistLM adds a single variable at each step then assesses whether removing or adding variables improves the overall model until no further improvements are needed. The selection criterion for the DitsLM, R^2, denotes the proportion of variation that is explained by the cumulative fit of the predictor variables. All variables used were log (X+1) transformed. Each predictor variable in the DistLM has a corresponding P-value, R^2 value and cumulative R^2 value. Each run of the DistLM analysis included 9999 permutations and corresponding marginal tests.

3.3 Results

3.3.1 Environmental conditions

Canopy cover was highest at the forested sites with around 90% cover, followed by scrub sites with 75% cover (Figure 3.1). The pastoral sites were relatively open and had significantly less canopy cover compared to forest and scrub sites (ANOVA P < 0.001) (Figure 3.1). Ground cover was heavily dominated by grass (97%) in the pastoral sites whereas both forest and scrub sites had a mixture of grass, leaf litter, bare ground and various wetland plants such as *Juncus* sp. and *Ludwigia palustris* (Figure 3.1). Types of ground cover found in the pastoral sites were significantly different from vegetation present at the forest and scrub sites (P < 0.001) (Figure 3.1).

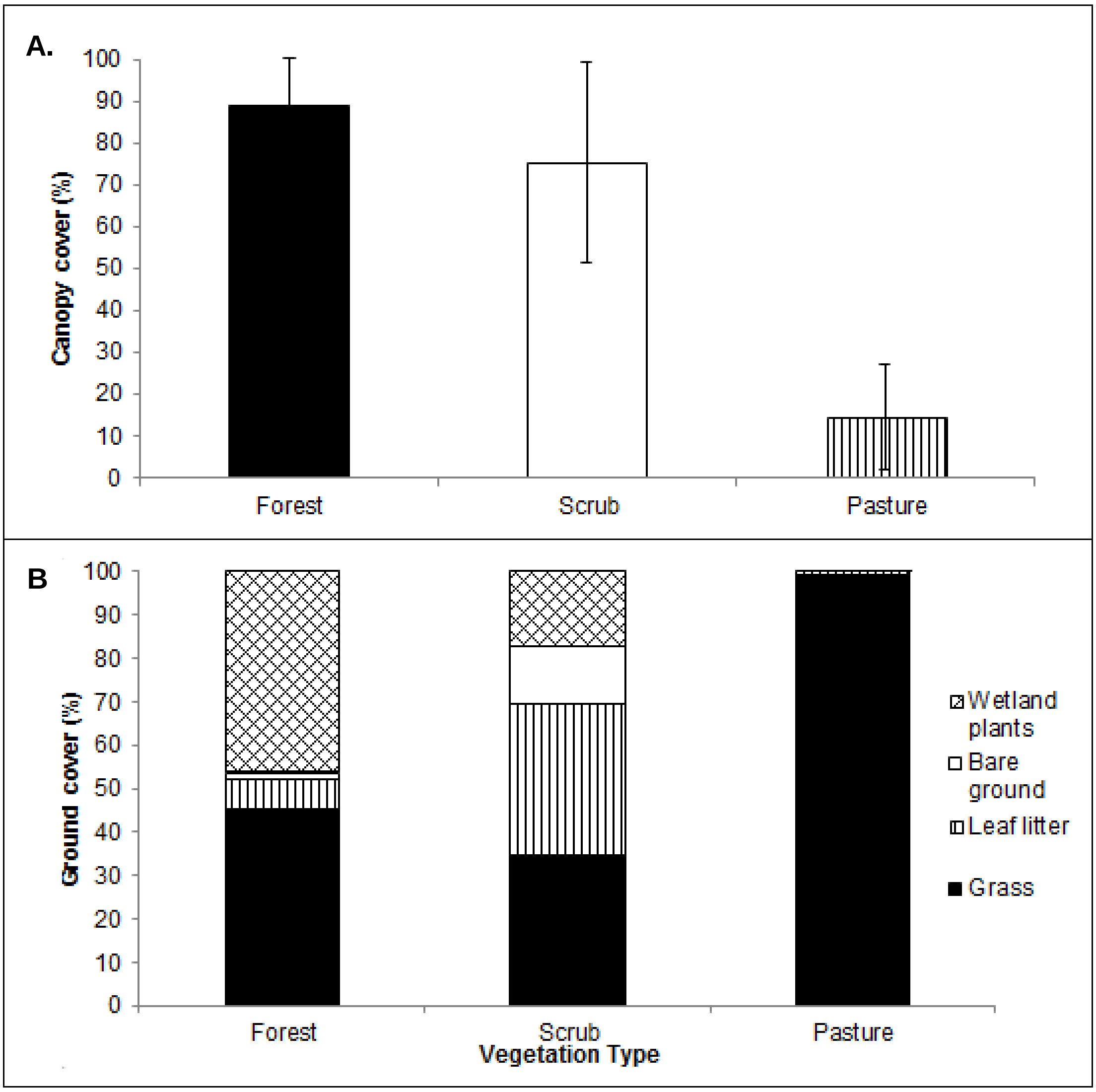

Figure 3.1: Overhead canopy cover for A) and ground cover B) (mean ± SE; n =12,9,9 for forest, scrub and pasture vegetation types, respectively) at sampling sites on the lower Waikato River floodplain.

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Forest and scrub air temperatures were around 21 - 22 °C whereas pasture sites were around 3 °C higher on average (Figure 3.2). Soil and air temperatures were significantly different between pastoral compared to forest and scrub sites (Table 3.1). However, there was no difference in either temperature between forest and scrub sites ($P > 0.05$; Table 3.1). Soil temperatures were 1 - 2 °C lower than air temperatures on average (Figure 3.2).

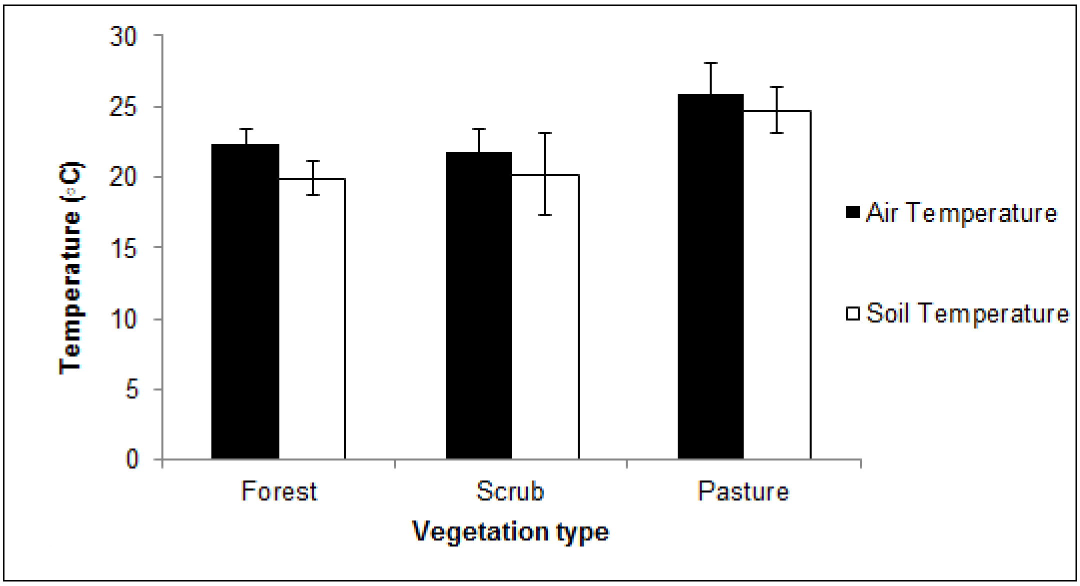

Figure 3.2: Air and soil temperatures averaged across the three cores taken at each site (mean ± SE; n = 12,9,9 for forest, scrub and pasture vegetation types, respectively) at sampling sites on the lower Waikato River floodplain.

Table 3.1: Summary of ANOVA results for (A) air temperature, (B) soil temperature, (C) canopy cover and (D) ground cover composition measured at each core sampling site for the three vegetation types on the lower Waikato floodplain; SS, sums of squares, df, degrees of freedom, MS, mean squares, F, F values, P, probability value.

	SS	df	MS	F	P
A. Air temperature					
Intercept	40976.11	1	40976.11	14580.19	< 0.01
Vegetation Type	249.89	2	124.95	44.46	< 0.001
Error	205.16	73	2.81		
B. Soil temperature					
Intercept	35286.84	1	35286.84	8969.28	< 0.01
Vegetation Type	362.09	2	181.04	46.018	< 0.01
Error	287.20	73	3.93		
C. Canopy cover					
Intercept	233468.60	1	233468.60	636.03	< 0.01
Vegetation Type	57633.60	2	28816.8	78.51	< 0.01
Error	26796.10	73	367.1		
D. Ground cover					
Grass					
Intercept	261387.90	1	261387.90	221.97	< 0.01
Vegetation Type	55640.50	2	27820.20	23.62	< 0.01
Error	85957.90	73	1177.50		
Leaf litter					
Intercept	13540.19	1	13540.19	34.66	< 0.01
Vegetation Type	13389.81	2	6694.91	17.14	< 0.01
Error	28514.14	73	390.60		
Bare ground					
Intercept	1526.85	1	1526.85	9.89	< 0.01
Vegetation Type	1794.64	2	897.32	5.81	< 0.05
Error	11272.47	73	154.42		
Wetland plants					
Intercept	10483.40	1	10483.4	22.26	< 0.01
Vegetation Type	9840.00	2	4920.00	10.44	< 0.01
Error	34384.67	73	471.62		

Soil moisture averaged close to 50% in scrub sites compared to around 34% in forested and pastoral sites but these differences were not statistically significant (P > 0.05) (Figure 3.3). Organic matter content ranged from 1.5 - 2.5% on average and was not significantly different between vegetation types (P > 0.05) (Figure 3.3).

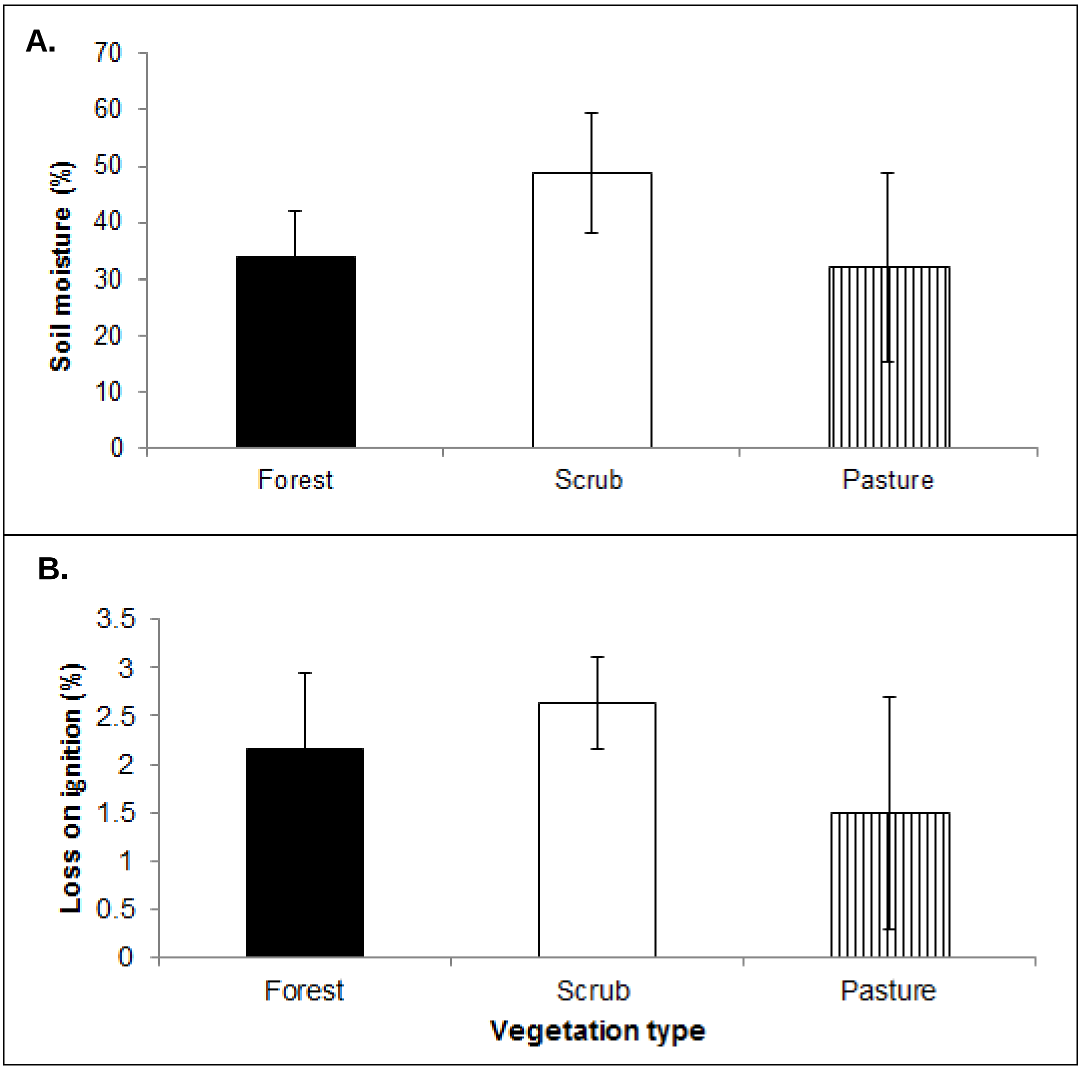

Figure 3.3: Soil moisture (A) and organic matter content (B) (mean ± SE, n = 12, 9, 9 for forest, scrub and pasture vegetation types, respectively) on the lower Waikato River floodplain.

3.3.2 Dissolved oxygen

Over the 39 day incubation period, dissolved oxygen levels in water overlying soil cores steadily decreased over time and were similar between different vegetation types (Figure 3.4). The water-only control showed the same pattern over time but maintained a much higher DO saturation (by around 20 - 30%) than the soil samples (Figure 3.4).

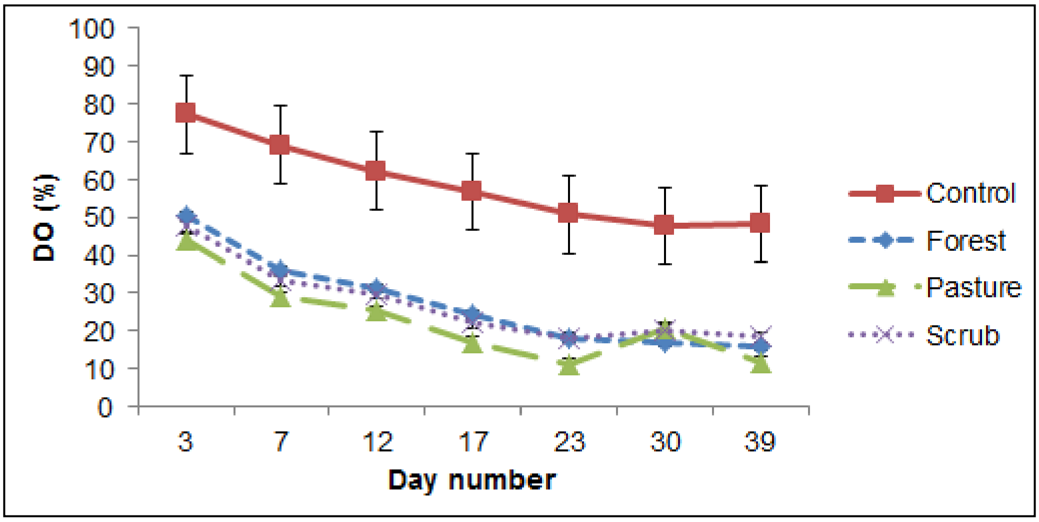

Figure 3.4: Dissolved oxygen saturation (mean ± SE; n = 6,12,9,9 for control, forest, scrub and pasture treatments, respectively) from day three to day 39 incubations for controls (filtered river water only) and soil cores from three lower Waikato River vegetation types.

3.3.3 Taxon richness

Zooplankton taxon richness (i.e. number of taxa appearing over the full incubation period) was low in all vegetation types and similar for both connected and disconnected floodplain samples (Figure 3.6). Richness was lowest in pasture cores and highest in scrub disconnected cores. Mean taxon richness for forested sites ranged from 2.5 - 4.0 taxa and from 3.0 - 4.5 taxa at scrub sites, with pastoral sites having fewer taxa (~1.5 - 2.0) on average (Figure 3.5). However, the differences between vegetation types and connectivity levels were not statistically significant ($P > 0.05$) (Figure 3.5).

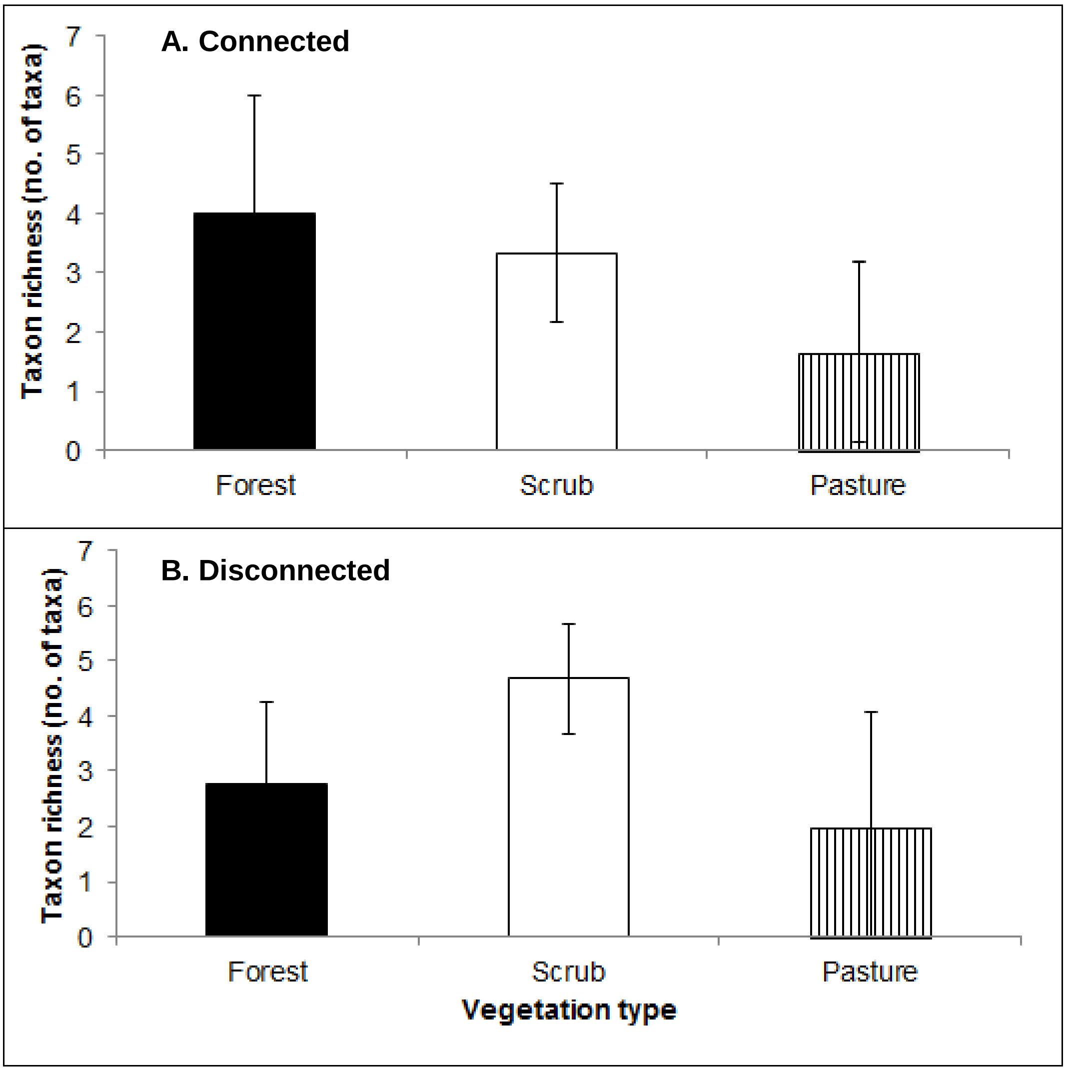

Figure 3.5: Taxon richness (mean ±SE, n = 12,9,9 for forest, scrub and pasture vegetation types, respectively) in incubated soil cores for A) connected and B) disconnected sites on the lower Waikato River floodplain over a 39 day period.

Mean taxon richness over the incubation period generally decreased steadily for all vegetation types, with forest peaking at 2 taxa at day 12 for connected sites and an average of 2.5 taxa for disconnected sites (Figure 3.6). Pastoral sites had lower numbers of taxa at both levels of connectivity over the incubation time than forested and scrub sites which were significantly different to pastoral sites at days 3 and 12 compared to day 23 and beyond ($F_{(2,6)}$ = 4.95, $P < 0.01$) (Figure 3.6). Connectivity had no effect on the taxon richness between cores ($P > 0.05$). However, vegetation type affected taxon richness ($F_{(1,2)}$ = 9.79, $P < 0.05$) (Figure 3.6). No taxa were present in pasture disconnected sites from day 23 of the incubation onwards (Figure 3.6).

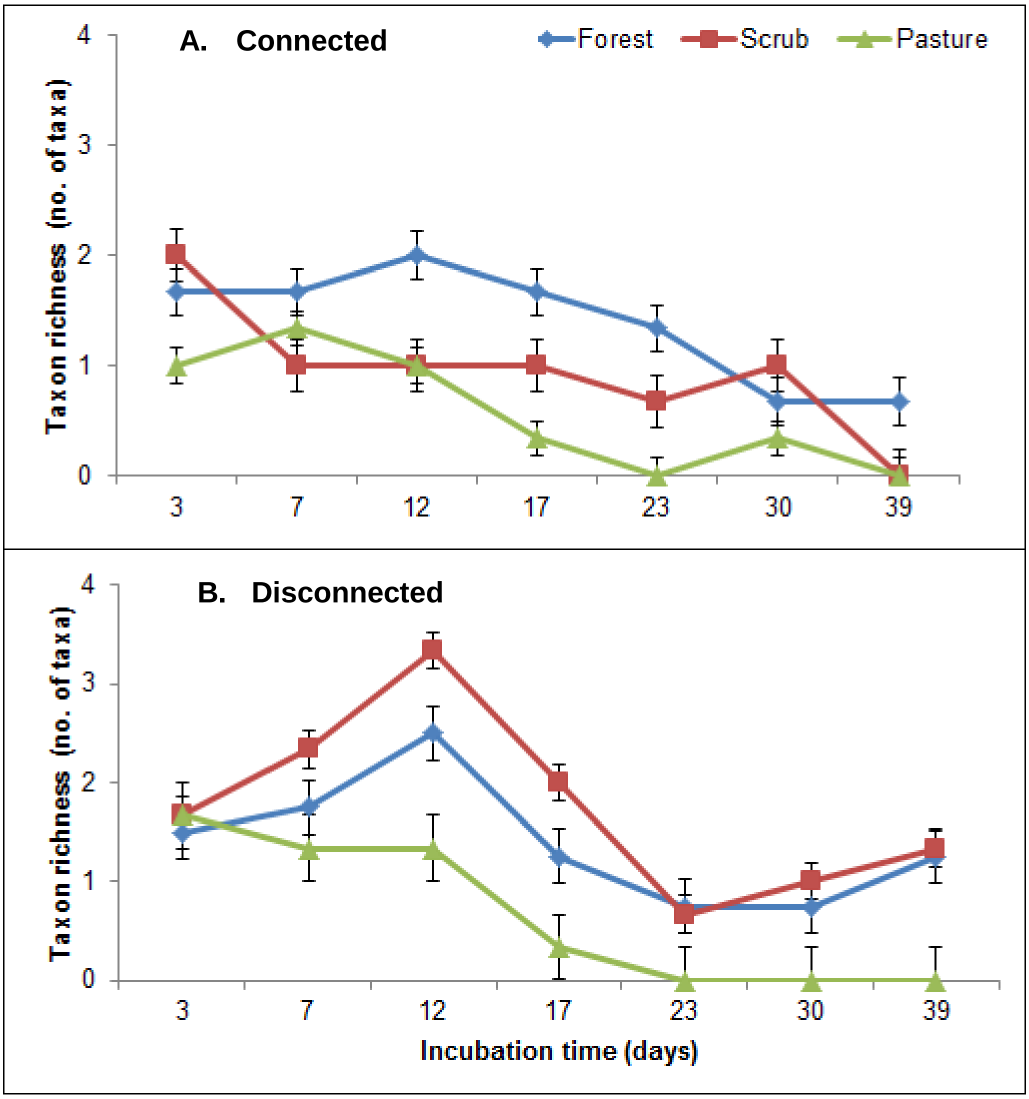

Figure 3.6: Taxon richness (mean ± SE; n = 12,9,9 for forest, scrub and pasture vegetation types, respectively) at each sampling day for incubated soil samples on A) connected and B) disconnected sites on the lower Waikato River floodplain.

3.3.4 Zooplankton density

At connected sites, the number of individual zooplankton hatching varied over the sampling period, and was highest at day three and day 12 before steadily decreasing over time (Figure 3.7). Day three was characterised only by high numbers of rotifers at all sites. However, at day 12 rotifers, cladocerans and ostracods were highly abundant at scrub and forested sites for both connected and disconnected sites. The pastoral sites had low zooplankton densities from day 12 onwards, whereas forested sites in general and disconnected scrub sites had more persistent emergence of zooplankton over time (Figure 3.7; Table 3.2).

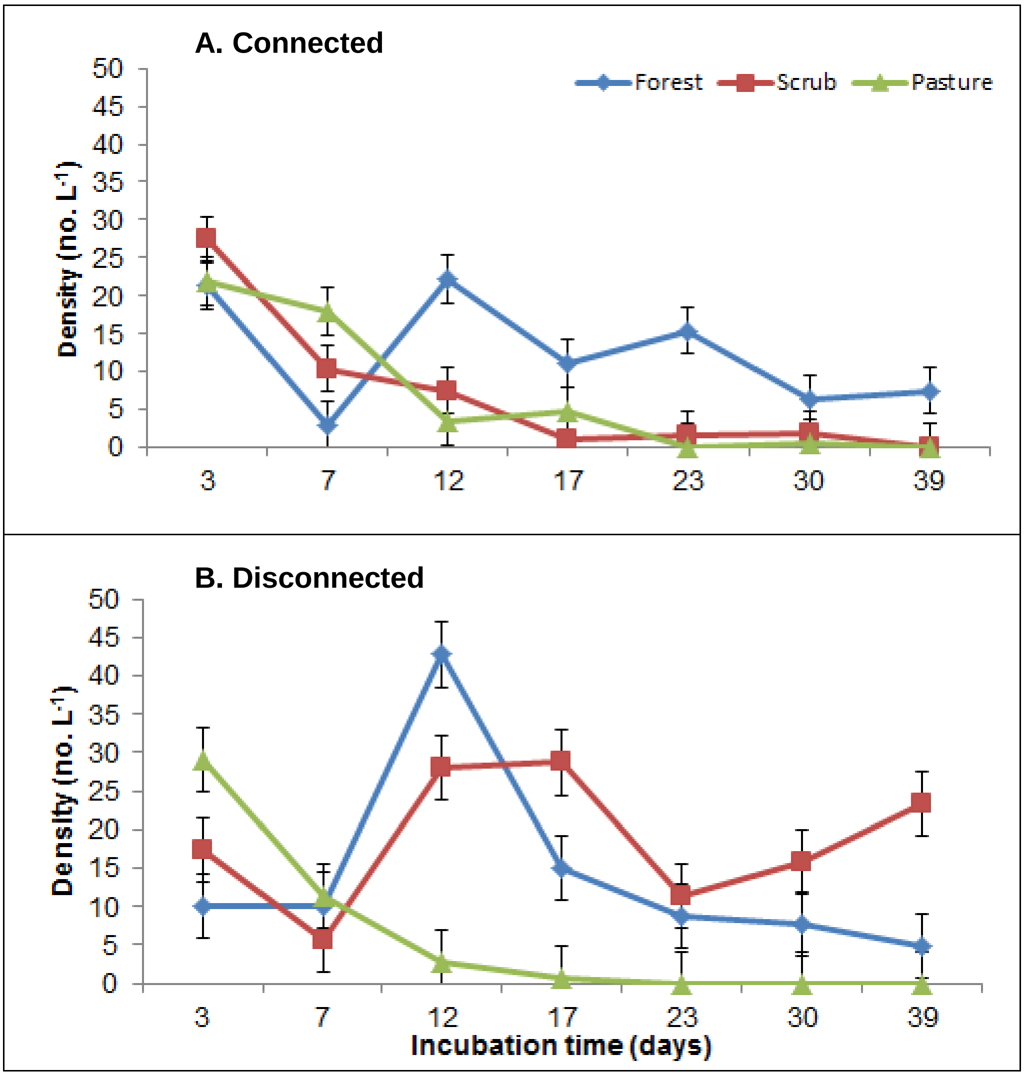

Figure 3.7: Zooplankton densities (mean ± SE; n = 12,9,9 for forest, scrub, pasture, respectively) hatching over time for incubated soil cores for A) connected and B) disconnected sites on the lower Waikato River floodplain.

Average zooplankton densities combined over all sampling days were dominated by rotifers for each of the vegetation types (average ~11 ind. L^{-1}), except for forested disconnected sites where rotifers were generally absent (Figure 3.8). Cladoceran densities were highest in scrub disconnected cores (~2 ind L^{-1}), whereas copepod densities were highest in both scrub and forested floodplain habitats (~2 ind. L^{-1}) (Figure 3.8). However, these differences were not statistically significant ($P > 0.05$). Zooplankton assemblages in pastoral soil cores contained no cladocerans or copepods, supporting only rotifers (Figure 3.8). Zooplankton densities between vegetation types were only significantly different for the copepods *Diacylops bicuspidatus* and *Bryocamptus pygmaeus* ($P < 0.05$) between scrub and pasture and forest and pasture, reflecting the absence of copepods in pastoral sites (Figure 3.8).

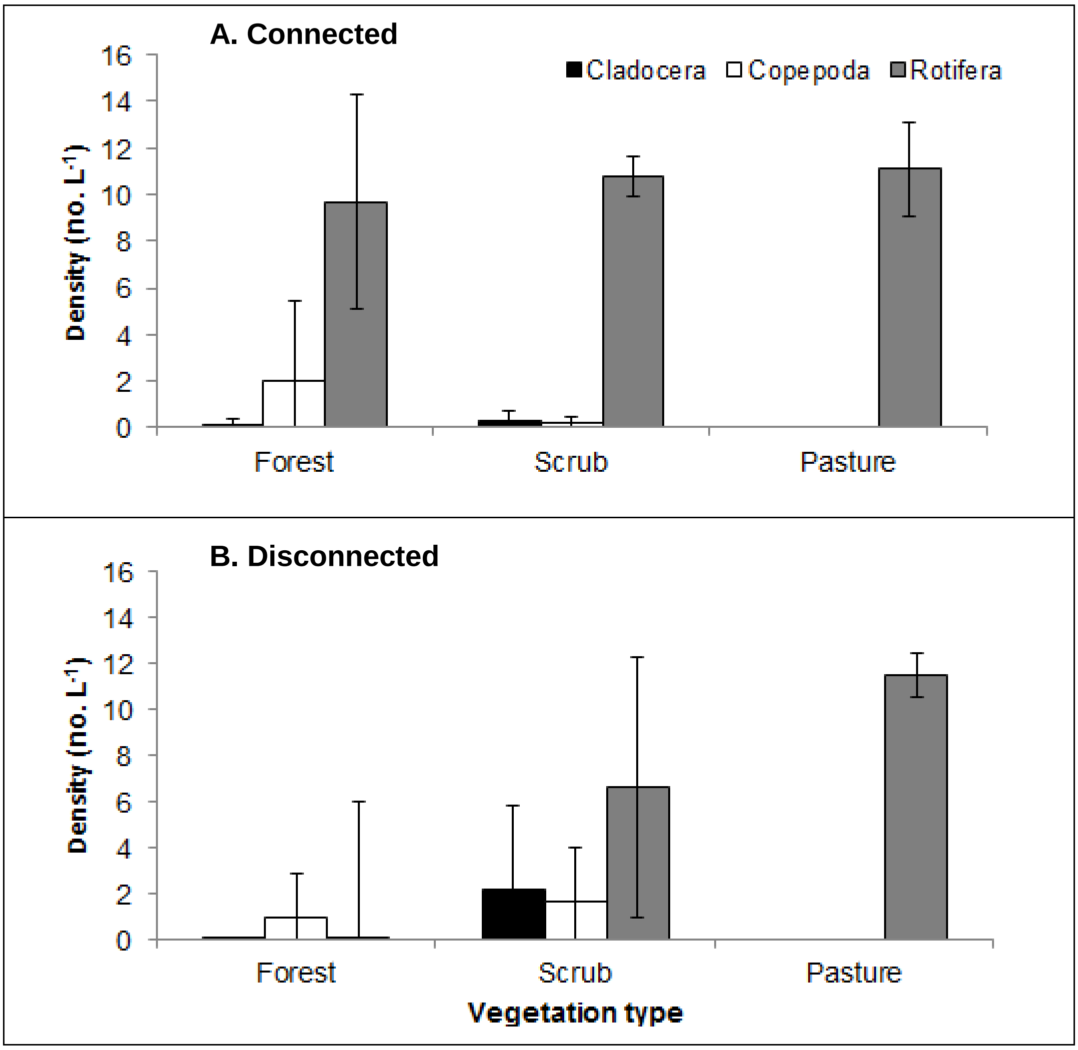

Figure 3.8: Zooplankton densities from soil cores for each of the major groups averaged over all sampling days (mean ± SE; n = 12,9,9 for forest, scrub and pasture vegetation types, respectively) on A) connected and B) disconnected sites on the lower Waikato River floodplain.

Table 3.2: Summary of ANOVA results for zooplankton density for inundated soil cores over a 39 day period for the three vegetation types on the lower Waikato floodplain; SS, sums of squares, df, degrees of freedom, MS, mean squares, F, F values, P, probability value.

Connected	**SS**	**df**	**MS**	**F**	**P**
Vegetation type	134.55	2	67.27	1.81	> 0.05
Day	954.85	6	159.14	4.27	< 0.05
Disconnected					
Vegetation type	546.24	2	273.12	2.40	> 0.05
Day	796.11	6	132.68	1.17	> 0.05

Correlation analysis based on average zooplankton species abundances against environmental factors measured indicated that the most common and abundant taxon over the incubation time, bdelloid rotifers, were influenced by canopy cover ($P < 0.05$, $r^2 = 0.25$, $n = 19$), air temperature ($P < 0.05$, $r^2 = 0.22$, $n = 19$) and soil temperature ($P < 0.01$, $r^2 = 0.43$, $n = 19$). Further, *Synchaeta oblonga* were highly correlated with canopy cover ($P < 0.05$, $r^2 = 0.29$, $n =19$) whereas ostracods were influenced only by soil moisture ($P < 0.05$, $r^2 = 0.21$, $n = 19$). The remainder of the taxa, including *Bryocamptus pygmaeus*, *Diacylops bicuspidatus*, *Saycia cooki* and *Epiphanes brachionus*, were not statistically correlated with any environmental factors ($P > 0.05$).

Only 73% variation in the zooplankton community composition was accounted for in the DistLM using environmental variables, suggesting that the environmental factors measured may play an important role in observed zooplankton community composition. Soil moisture was the only environmental variable that was individually significant, accounting for 16% of the variation among the soil cores. Remaining variables explained less than 14% variation. All variables were included in the most parsimonious model (Table 3.3).

Table 3.3: DISTLM analysis of the cumulative effect of environmental variables on zooplankton community composition in incubated soil cores for each of the three vegetation types on the lower Waikato River floodplain. Significant P value shown in bold. LOI = Loss on ignition.

Variable	Pseudo-F	P	Proportion	Cumulative R^2
Distance from river (m)	0.545	0.617	0.031	0.031
Canopy cover (%)	2.405	0.087	0.127	0.158
Air temperature (˚C)	1.441	0.234	0.074	0.232
Soil temperature (˚C)	3.034	0.070	0.137	0.368
Soil moisture (%)	4.474	**0.026**	0.162	0.530
Organic matter content (LOI %)	2.035	0.139	0.068	0.598
Grass (%)	0.417	0.745	0.015	0.613
Leaf litter (%)	0.522	0.662	0.019	0.632
Bare ground (%)	0.500	0.662	0.019	0.651
Wetland plants (%)	2.236	0.118	0.076	0.728

3.3.5 Zooplankton community composition

Zooplankton community composition showed heterogeneity in relation to vegetation type (Figure 3.9; Table 3.4). Community composition was significantly different between forest and pasture sites, and between and scrub and pasture sites ($P < 0.05$). However, levels of connectivity did not have any effect on zooplankton community composition ($P > 0.05$) (Table 3.4). Composition between sampling days was also significantly different ($P < 0.05$).

The copepods *Diacylops bicuspidatus* and *Bryocamptus pygmaeus*, and the cladoceran *Saycia cooki* were characteristic of sites with more wetland plant ground cover and higher soil moisture when comparing zooplankton community composition across all sites (Figure 3.9). Four sites (10, 11, 12 and 19; Figure 2.3; 2.4), displayed a dissimilar zooplankton community composition compared to the other 15 sites, and all had native forest or scrub vegetation types. These sites had a high percentage of ground cover by wetland plants (40 - 100%) and had, on average, higher soil moisture content than the other sites (~44% compared to ~33% at the other sites). Sites 10, 12 and 19 were connected and site 11 was disconnected to the river; however, connectivity played no role in zooplankton composition over any of the sites (Table 3.4).

The rotifer *Synchaeta oblonga* tended to be characteristic of sites with higher canopy cover, organic matter content and bare ground (Figure 3.9). Rotifers such as bdelloids tended to dominate sites characterised by high grass cover, and high soil and air temperatures, as measured in the majority of the pastoral sites (Figure 3.9).

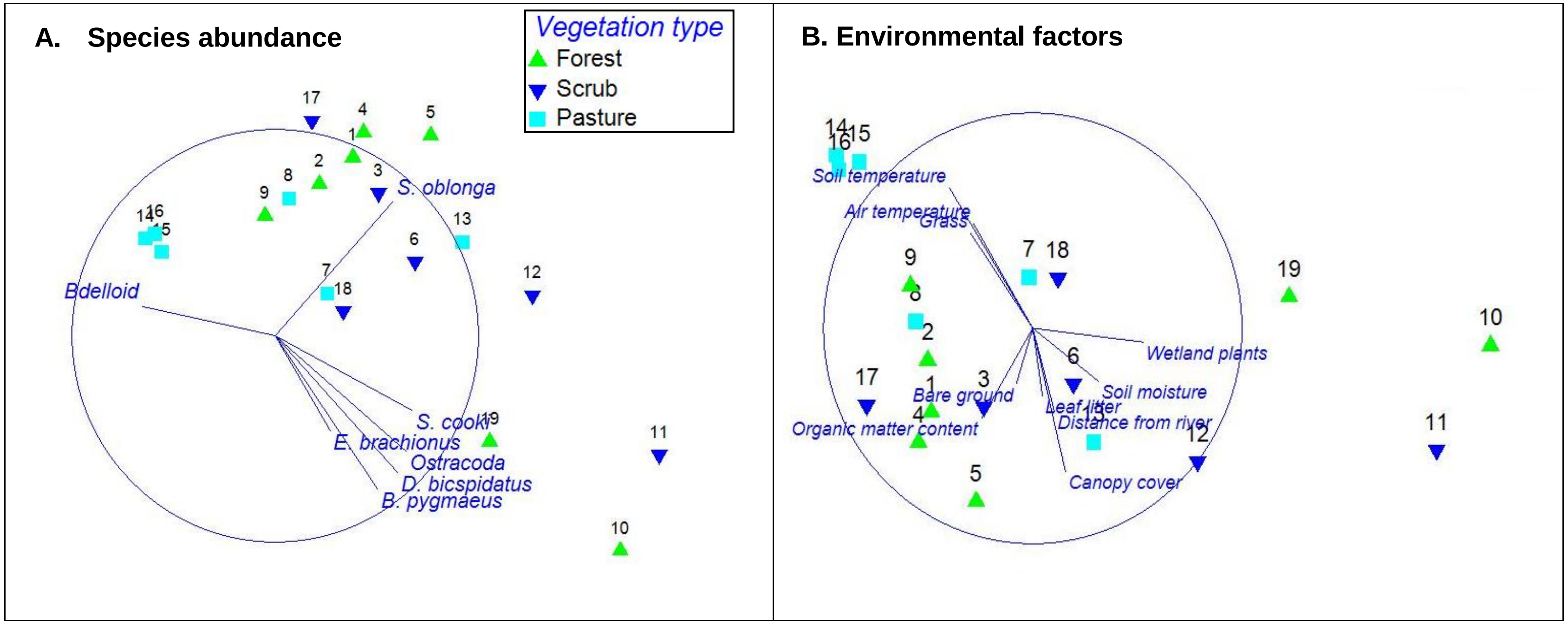

Figure 3.9: Multi-dimensional scaling plot (based on Bray Curtis dissimilarities) of zooplankton community abundance data combined for incubated soil cores from three vegetation types on the lower Waikato River floodplain. A) Zooplankton species abundance (no. of individuals L^{-1}) vector overlay combined for all incubation days for each of the 19 sites; B) Zooplankton species abundance (no. of individuals L^{-1}) overlaid with environmental factors measured. The density data used for the analysis were log (x+1) transformed.

Table 3.4: PERMANOVA results conducted on zooplankton density data for samples in inundated soil cores from the lower Waikato River floodplain; df, degrees of freedom, SS, sums of squares (obtained using 9999 permutations of residuals under a reduced model), Pseudo-F, F value, P, probability value.

Source	df	SS	Pseudo-F	P
Day number	2	7844.5	2.059	< 0.05
Vegetation type	2	10087	2.648	< 0.05
Connectivity	1	693.5	0.364	> 0.05
Residual	51	97149		

3.4 Discussion

3.4.1 Role of vegetation type and connectivity

Observed differences in zooplankton composition between sites suggest that vegetation structure plays a pivotal role on zooplankton communities generated from lower Waikato River floodplain soils during inundation. Native forest remnants and scrub patches, in particular, appeared to provide conditions suitable for large-bodied cladocerans and copepods to emerge. This finding confirms that inundated soils can produce emergent zooplankton from dormant egg banks and supports the hypothesis that floodplain vegetation type will influence the composition and abundance of emerging zooplankton communities. However, position inside or outside of stopbanks had no effect on zooplankton community composition, which did not support the hypothesis that levels of riverine connectivity will affect floodplain zooplankton communities hatching from egg banks. However, this may be due to the floodplain being dry for several years, with the last notable flood occurring in 2008. This might not have been a sufficient dry period to see differences in the two connectivity sites. Another possible explanation for the lack of differences in zooplankton communities between areas, may be due to the connected (i.e. inside of stopbanks) floodplain sites undergoing frequent wetting and drying events which could mean that the egg bank does not have ample time to develop.

Zooplankton emerged within three days of inundation from the floodplain soil cores and densities peaked between days three and 12 for all vegetation and connectivity types, before steadily decreasing over time. Composition over this time period was initially characterised by rotifers, and then increasing abundances of copepods and cladocerans. These larger-bodied zooplankton were found to have persistent emergence over the incubation time period, although densities remained low. A large-bodied cladoceran, *Saycia cooki*, was found during the hatching period in low densities from scrub and forested floodplain sites. Its presence is particularly important as it is extremely rare, to date only known from a limited number of temporary water bodies in Australia and New Zealand (Frey 1971).

The number of zooplankton emerging in this study was similar to the study by Battauz et al. (2014) carried out on dry floodplain sediments of the middle Parana River, Argentina, in which numerous rotifers hatched within the first 7 days followed by cladocerans later in the incubation period. Ning & Nielsen (2010) documented bdelloids to be the most dominant rotifer taxa and Ostracoda, Chydoridae and *Daphnia* as common crustacean taxa, in riverine and floodplain soils of the Broken River, Australia, in accordance with the findings of this study. Bdelloids are highly abundant as they are resistant to desiccation and can therefore survive long-lasting dry periods in floodplain soils, (Jenkins & Boulton 2003), and were abundant at pastoral sites in which other species appear unable to survive.

Rotifers were the most abundant zooplankton group to hatch out of the inundated soil cores over the incubation period. Rotifers have short generation times and so can multiply quickly and dominate zooplankton populations in New Zealand, especially in rivers (Burger et al. 2002), whereas flowing water is not suitable habitat for the development of larger-bodied zooplankton (Lair 2006). Crustacean zooplankton are known to have longer development times compared with rotifers and thus crustacean emergence exhibits a lag between floodplain inundation and increasing abundance (Lair 2006; Górski et al. 2013). Further, larger crustaceans are more efficient at feeding and evading capture, allowing them to out-compete rotifers in off-channel habitats and increase in abundance following inundation (James et al. 2008; Górski et al. 2013). However, in my laboratory setting, rotifers were the dominant emerged taxa over cladocerans and copepods, where overall emergent numbers remained low.

All emergent taxa were habitat specific in floodplain vegetation, with rotifers dominating pastoral sites, and cladocerans and copepods only found in scrub and forested floodplain sites. This result signifies that different types of floodplain vegetation have an important role in supporting taxon specific zooplankton communities. On the river Rhine floodplain, the structure of arthropod communities was directly related to land use, whereas the floodplain plant composition was influenced more by flooding attributes (Schipper et al. 2014). This result supports the finding in my study that both the structure and composition of floodplain vegetation, as influenced by physico-chemical conditions, affect the observed zooplankton communities found on the lower Waikato River floodplain. The removal of forested and scrub floodplain areas could then have a major impact on observed zooplankton community structure and diversity. Large-bodied taxa such as the cladoceran, *S. cooki*, would become absent due to limited favourable habitat, while rotifers such as bdelloids would become highly abundant as they can be resilient in areas that remain dry for long periods of time (Jenkins & Boulton 2003).

It is well documented that frequent flow pulses extending onto floodplains can promote species diversity (Bayley 1995; Tockner et al. 2000). However, it is less understood at what stage species diversity and abundance peaks. As the majority of the zooplankton species emerged in large densities by day 12, optimal inundation time for lowland riverine floodplains maybe around 12 days to maximise productivity of zooplankton from terrestrial soils. Generally, large floods in the lower Waikato are sustained for a 14 day period on average, although they occur only intermittently, with the last large floods occurring in 1995, 1998 and 2008 (Brown 2010). Floodwater permanence in the lower Waikato may be extended if floodwaters overtop the stopbanks (~1300 cumecs) as they may prevent water drawback into the river.

3.4.2 Role of physico-chemical factors

Both biotic and abiotic factors, such as inter-annual flow variability and temperature, are underlying factors moderating zooplankton populations in wetland areas, tributaries and lakes (Brendonck & De Meester 2003). However, river floodplains are influenced by abiotic and biotic factors independent of the main channel, and therefore are more susceptible to the effects of receding floodwaters (Thomaz et al. 2006; Ning & Nielsen 2010), such as changes in physico-chemical conditions within the soils and the overlying waters. These conditions exhibited in riverine floodplains are likely to affect factors influencing the emergence of dormant eggs in the soil by affecting sediment mixing and dispersal (Hairston et al. 1995), both of which are cues for zooplankton hatching (Brendonck & De Meester 2003; Ning & Nielsen 2010).

Soil moisture was the most significant environmental variable affecting zooplankton structure and composition. Soil moisture is linked with vegetation type as pastoral sites were a lot drier than forested and scrub sites, likely explaining differences in the diversity of zooplankton assemblages between vegetation types. Frisch (2002) found that terrestrial soils with higher soil moisture content increased survival through droughts of zooplankton eggs (especially for copepods), and water porous soils can therefore act as a refuge in seasonally inundated areas.

Measured air and soil temperatures were similar for forest and scrub sites. However, pastoral sites had both air and soil temperatures higher than the other vegetation types. These factors, nonetheless, were only measured once during core sampling and conditions are likely to change both seasonally and diurnally on the lower Waikato River floodplain. With increasing temperatures due to changes in land use from native forest to open areas, soil quality and biological activity is quickly decreased leading to large unproductive areas (Islam & Weil 2000), leading to the potential loss of floodplain biota.

Dissolved oxygen levels significantly decreased over the soil core incubation period. Declining dissolved oxygen is characteristic of temporary ponds, wetlands and floodplains globally due to increasing evaporation and minimal flow (Nadai & Henry 2009). Low dissolved oxygen levels can influence juvenile growth, time until maturity and egg clutch size of cladoceran (Hanazato & Dodson 1995) and copepod (Stalder & Marcus 1997) zooplankton populations. Low dissolved oxygen levels recorded in this study may have influenced the degree of zooplankton hatching and resulted in mortality, potentially underrepresenting the hatching community.

3.4.3 Ecological significance

The simulated nature of the incubation potentially could have led to an under-estimation of zooplankton abundance and composition for the floodplain vegetation types sampled. However, simulated incubation techniques are commonly used to explore dormant egg communities (Havel et al. 2000; Schroder 2001; Ning & Nielsen 2010; Battauz et al. 2014), as they allow hatching, identification and counting to be assessed in a controlled environment. Consequently, specific hatching cues cannot be replicated for all species within the community and therefore likely under-represent certain factors affecting the dormant zooplankton community (Ning & Nielsen 2010).

Many studies have documented zooplankton community composition and dynamics in lake and wetland ecosystems (Hairston et al. 1995; Havel et al. 2000; Jeppesen et al. 2000; Lumban Toruan 2012; Watkins et al. 2013). However, there has been less focus on zooplankton ecology in rivers and the interactions with their floodplains (Thorp et al. 1994). Within riverine environments, high zooplankton abundance and diversity are important due to their food provision for juvenile fish (Burger et al. 2002; Thorp & Casper 2002). Rotifer, cladoceran and copepod abundance is generally higher in the lateral areas of the main channel, as water velocity is slower, providing a refuge for zooplankton populations (Baranyi et al. 2002; Saunders & William 1988). Maintaining connectivity between the main channel and lateral areas is vital to ensure the viability of populations and species in riverine environments, including macrophytes (Bornette et al. 2001), fish and zooplankton (Amoros & Bornette 2002).

It has been proposed that rising flood pulses transport large amounts of highly productive material and biota between waterbodies and off-channel areas (Junk et al. 1989; Jenkins & Boulton 2003). Generally, increasing distance from the river decreases the likelihood of floodplain inundation, suggesting that loss of connectivity caused by flood control reduces transfer to floodplains of nutrients, sediment, and zooplankton that can survive for extended periods as dormant stages. Diverse species assemblages produced in inundated floodplains could potentially supply the river with an abundant food source, enhancing productivity and supporting native biota (Boulton & Lloyd 1992). The magnitude of flooding can determine the distance taxa are transported back from the floodplain to the river and between habitats (Jenkins & Boulton 2003). The ability of hatched zooplankton to drain back into the river is highly unlikely if floodwaters are detained behind stopbanks. Therefore, there may be a constant food source loss from these largely disconnected areas for fish in the Waikato River such as juvenile whitebait. As highlighted in this study, seasonal inundation of floodplain areas allows dormant zooplankton to emerge and this may facilitate energy transfer back into the main river channel.

Though little to no research has been undertaken on emerging zooplankton from inundated floodplain soils, my findings show similar results to studies around the globe. This study allowed the role of floodplain egg bank communities to be assessed and therefore widen our understanding of zooplankton egg banks to include riverine floodplain areas. Overall, this study suggests that floodplain vegetation type plays a key role influencing the structure and composition of zooplankton communities in floodplain areas whereas connectivity to the river did not have any influence on these populations, at least within the time since last flood that over-topped stopbanks (2008). Longer term disconnection may have an effect on floodplain communities, however, the conversion of floodplain land use from native forest and scrub to pastoral land thus has the potential to reduce diversity and structure of floodplain zooplankton populations. Maintaining hydrological connectivity and vegetative heterogeneity may therefore promote the growth of diverse zooplankton communities, particularly for large-bodied cladocerans and copepods, however this result was not found in this study. Annual whitebait migrations up the Waikato River historically may have coincided with receding floodwaters with large-bodied zooplankton carried from the floodplains back into the main channel, thus providing a survival advantage for whitebait in the early stages of their migration (Górski et al. 2013). Floodplain integrity may therefore play an important role in supporting productivity and biodiversity within this large lowland river-floodplain system.

Chapter Four

Diet and feeding preferences of *Galaxias maculatus* in the lower Waikato River

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4.1 Introduction

4.1.1 Large river food-webs

River-floodplain systems encompass lentic (still water) and lotic (running water) environments, with productivity derived from within the river itself through primary production (i.e. autochthonous production) or from terrestrial inputs derived from vegetated headwaters, riparian margins and tributary outflows into the river (i.e. allochthonous production) (Shiel et al. 1982; Thorp et al. 1998; Pingram et al. 2012). Large river productivity, however, is generally dependant on autochthonous production, although the importance differs between river areas and season (Pingram et al. 2014). Multiple factors govern the flow of carbon through aquatic food webs in large rivers (Pingram et al. 2012). Generally, spatial heterogeneity influences patch dynamics of food resources which can affect predator-prey interactions (Winemiller & Jepsen 1998; Fauchald & Tveraa 2006). Some aspects of habitat and water quality change seasonally, and physical disturbance caused by floods also affects species interactions and community dynamics within rivers and streams (Winemiller & Jepsen 1998; Taylor & Warren 2001).

Fish communities are significant drivers of trophic structure within aquatic food-webs through predation on a number of aquatic groups, ranging from small fish to macro-invertebrates and zooplankton (Holmlund & Hammer 1999). Fish communities are strongly structured along the length of rivers by levels of longitudinal and lateral connectivity and climbing ability. Movement on both regional and local scales is generally attributed to changes in physical and chemical conditions, resource availability, competition, predation and reproduction (Winemiller & Jepsen 1998; Rolls et al. 2013). Few freshwater fish species complete their life-cycle within a single habitat patch (Rolls et al. 2013), and large fish movements are driven by the need to find suitable habitat patches that are food-rich and lacking predators (Winemiller & Jepsen 1998; Opperman et al. 2010; Wu et al. 2013). Food abundance in riverine systems is thus a major factor determining fish population densities and species composition within riverine environments (Grenouillet et al. 2002).

4.1.2 Role of zooplankton in riverine food-webs

Large temperate, lowland river systems provide complex and heterogeneous environments for plankton production which in turn can influence food-web dynamics. Zooplankton are extremely important in riverine food-webs because of their high abundances, and their role in recycling and transferring nutrients and carbon (Kobayashi et al. 1998; Burger et al. 2002). Zooplankton communities in large temperate rivers are typically dominated by small rotifer species with comparatively lower abundance of cladocerans and juvenile copepods (Shiel et al. 1982; Kobayashi 1997; Kobayashi et al. 1998; Burger et al. 2002). Rotifers are smaller in size, and they can easily out-compete the other zooplankton groups as they have a shorter generation time and are less likely to be physically damaged through downstream transport in high flows (Kobayashi 1997; Burger et al. 2002). In contrast, both copepods and cladocerans have multiple stages which require a set of specific environmental and physiological conditions to enable growth and reproduction.

Transfer downstream typically occurs too quickly to allow substantial growth of large-bodied copepods and cladocerans in short river systems (Viroux 2002). However, they may be able to develop in areas of the river that have slower water velocities and low turbidity levels, such as lateral floodplain areas, slack-waters and off-channel tributaries (Kobayashi 1997; Casper & Thorp 2007). These areas have contrasting biological, physical and chemical conditions to those of the flowing channel of the river, providing suitable areas for the development of large zooplankton (Burger et al. 2002; Casper & Thorp 2007). A combination of lotic and lentic environments thus contributes to the composition and abundance of a heterogeneous riverine zooplankton community.

Riverine fish can significantly affect zooplankton populations through predation, especially in their juvenile stages (DeVries et al. 1998; Barriga et al. 2012). Thus, larval fish prey mainly on zooplankton while adult fish are more likely to select larger prey items as gape size increases with fish size (Mayer & Wahl 1997), resulting in an ontogenetic diet shift (Wu & Culver 1992). Fish are primarily visual predators and their ability to select prey items depends on light availability, water clarity and characteristics of their prey that influence ease of capture (Robertis et al. 2003). Important characteristics enabling zooplankton to evade capture include swimming speed and their morphology, such as shape and structural adaptations in the form of spines (Mayer & Wahl 1997). Rotifers are typically evasive swimmers, possess spines and other less palatable adaptations and are extremely small in size, causing fish to avoid predation on these taxa (Preston et al. 1999). Copepods are known to have a streamlined body, a small average size and fast swimming speeds allowing them to escape fish predation (Mayer & Wahl 1997; Sheppard et al. 2011), while cladocerans are relatively large and move slowly, and are therefore frequently preyed upon where they occur in high numbers (Sheppard et al. 2011). Generally planktivorous fish feed selectively and prey on the largest plankton that can be ingested, thus directing zooplankton community structure towards smaller taxa and smaller individuals (Mayer & Wahl 1997). Therefore, the diet of juvenile fish may lead to dietary divergence between larger zooplankton taxa such as copepods and cladocerans and smaller zooplankton such as rotifers.

4.1.3 Prey selectivity by juvenile fish

A multitude of factors governs prey selectivity among fish taxa, limiting the ability to make worldwide comparisons. Most of the literature has focused on planktivorous fish within brackish waters (Mehner & Thiel 1999) and lake systems (Modenutti et al. 1993; Mayer & Wahl 1997; Sheppard et al. 2011; Barriga et al. 2012), with limited knowledge on the feeding selectivity of juvenile fish within riverine environments. The ability of a fish to selectively choose its prey is advantageous as this can enable fish to maximise energy intake, leading to optimal growth, reproduction and survival (Mayer & Wahl 1997). Although certain prey sizes, species and densities can lead to maximal growth, not all prey assemblages will, depending on the energetic requirements of the fish (Mayer & Wahl 1997). The Optimal Diet Model can be used to explain prey choice by a predator as it predicts low profitability prey items, or small prey, should be avoided when larger, more profitable prey items are present (Stephens et al. 2007). However, in situations with high fish densities, food availability may be limited and may lead to competitive interactions for the remaining resources, resulting in density-dependent growth (Rose et al. 2001; Amunsden et al. 2007).

Worldwide, many riverine fish populations are highly susceptible to anthropogenic changes which alter ecosystem structure and function and therefore affect the structure of fish communities (Bunn & Arthington 2002; Tockner et al. 2010; Rolls et al. 2013). Altered flow regimes, barriers to migration and loss of habitat complexity and connectivity are thus major factors influencing fish populations and are the major drivers causing declines in many fish populations. The loss of fish species within riverine food-webs due to human disturbance can alter predator-prey interactions between fish and zooplankton, leading to reduced phytoplankton growth and nutrients available for primary production (Holmlund & Hammer 1999).

4.1.4 New Zealand diadromous galaxiids

Many Southern Hemisphere rivers experience large seasonal influxes of juvenile Galaxiidae which become populous in lakes, waterways and large rivers. In New Zealand, there are five migratory species of native galaxiid fish whose larvae make up the whitebait fishery, which is regarded highly important for cultural, recreational and commercial purposes (David & Speirs 2010). All five species are diadromous and complete large seasonal migrations to and from the sea, although landlocked populations of some species can occur. Four out of five of these species are classified as 'in decline' due to barriers to migration, altered flow regimes, pollution, and the impacts of non-native species (David & Speirs 2010). The majority of the whitebait catch consists of *Galaxias maculatus*, known locally as inanga, which has an extremely wide distribution within the Southern Hemisphere, including New Zealand, Australia, Lord Howe and Chatham Islands, Chile, Argentina and the Falkland Islands (Barriga et al. 2012).

When inanga return from the sea, they are around 40 - 55 mm in total length (McDowall et al. 1994). Due to their small gape size it is thought that zooplankton is an important food source during their upstream migration (Rowe et al. 2002). Modenutti et al. (1993) examined the selective feeding of *G. maculatus* on zooplankton within a South Andes lake, and found that the juvenile fish selected mostly planktonic prey, with prey size selection increasing with fish size. However, that study was conducted on a landlocked population of *G. maculatus.* Only one study in New Zealand has looked at the feeding of multiple migrating juvenile riverine fish in relation to the effects of turbidity (Rowe & Dean 1998). However, I am not aware of any published research that has quantified diets of juvenile migratory fish in New Zealand. Knowledge of the diet and feeding of migrating galaxiid larvae within New Zealand is pertinent in order to manage the fishery and ensure availability of suitable food resources to sustain upstream migration.

4.1.5 Study objectives and aims

The aim of this chapter is to quantify the diet and feeding preferences of *Galaxias maculatus* from the Waikato River. Based on findings elsewhere on juvenile walleye, a small planktivorous fish (Mayer & Wahl 1997), juvenile galaxiids are expected to select zooplankton based on prey size and morphology due to gape size limitations. I tested the following hypotheses:

1. Migrating inanga selectively feed on larger zooplankton prey such as cladoceran taxa due to the profitability of larger zooplankton as prey items;

2. Migrating inanga will become less selective on their zooplankton prey when housed in high densities which cause a density-dependent shift towards less preferred rotifer prey.

The diet and feeding of *G. maculatus* was assessed using a combination of field analyses and laboratory experiments to determine consumption rates and prey selection. Field analyses were conducted at two differing sites in the Waikato River that encapsulate spatial differences in zooplankton populations, allowing changes in the diet of *G. maculatus* to be assessed as they moved up the river over a distance of around 11 km. Laboratory experiments focused on calculating feeding rates of inanga and measuring selectivity.

4.2 Methods

4.2.1 Sampling sites

Field sampling was conducted on the lower reaches of the Waikato River at two sites; Mercer, which is downstream of the Mangatawhiri River and Whangamarino River outlets, and Tuakau, 11 km downstream of Mercer with no nearby upstream tributary outlets. These sites were selected because they were thought likely to have different zooplankton communities due to the inputs of tributaries draining wetlands, and therefore provide a wider range of zooplankton types for larval whitebait to feed on during upstream migration. Corresponding zooplankton samples were taken from these sites on the main river to assess diversity and abundances available for whitebait consumption. For further details on the study sites, see Chapter 2.

4.2.2 Field collections

Zooplankton and whitebait samples were collected monthly for gut contents analysis during November 2013 and from August - November 2014. Inanga were collected for the feeding experiment from 17 - 28 October 2014. Physico-chemical measurements were taken in the main river channel at the Mercer and Tuakau sites during each monthly visit from August to November 2014, as water quality differences could influence zooplankton community composition at each site. Variables measured were temperature, conductivity and dissolved oxygen saturation using a YSI Pro2030 meter.

Whitebait were captured using a double-winged fine-mesh (1.5 mm) fyke net that was set for up to four hours or until the required amount of whitebait was caught. A minimum of 20 inanga was taken from each of the two sites per month for gut content analysis. Once caught, inanga for gut contents were anaesthetised in a ice slurry to halt the digestion process, and then transferred into a labelled container with 90% ethanol to be taken back to the laboratory. In addition, 150 inanga were collected at the Mercer site for the feeding experiment. These inanga were placed in aerated capture bins with freshwater and taken back alive to the laboratory where permanent housing tanks were set up.

The riverine zooplankton community was sampled at each collection site concurrently with collection of fish for gut analysis to compare potential prey composition with whitebait diet. Zooplankton samples were collected within 5 m of the shoreline just below the surface by filtering 40 L of water through a 40 µm mesh net, following Górski et al. (2013). Once filtered, any material retained on the net was preserved in 90% ethanol and returned to the laboratory for identification.

4.2.3 Laboratory analyses

The riverine zooplankton community was analysed by thoroughly mixing the water samples, sieving each sample through a 40 µm mesh and then examining 5 mL subsamples on a gridded perspex tray under an Olympus SZ60 stereo microscope at 25x magnification. Zooplankton were counted and identified to the lowest level practical (genus) to determine relative proportions of each zooplankton taxon. A minimum of 300 individuals was counted as this is an adequate sample size to provide a representative inference of community composition (De Meester et al. 2007).

On return to the laboratory, inanga were identified based on keys from Richardson & McDowall (2013). Identified inanga were then measured to obtain total length (mm) and weighed to the nearest milligram. Using an Olympus SZ60 stereo zoom microscope at 25x magnification, the stomachs of individual fish were dissected and isolated from the intestinal tract and other viscera. The stomach was then slit down the longitudinal axis and the contents were flushed into a glass perspex tray using 90% ethanol. A gut fullness index (GFI), ranging from 1 (0% full) to 5 (100% full), was assigned to each fish, and fish with GFI ≥ 2 were used for gut contents analysis. Fine forceps were used to capture any remaining contents, to ensure all material was removed. Total gut contents were placed onto a glass slide with 70% glycerol to prevent the material from drying out, and a cover slip was placed over the top. The entire contents of the slide were identified and counted using a compound microscope at 40x magnification. Zooplankton observed in the gut were identified to genera (see Appendix 1), and placed in the three main zooplankton groups of Cladocera, Copepoda or Rotifera for analysis. Any other invertebrate groups were identified to the lowest practical taxonomic level.

Comparisons between the main river channel and the gut contents of inanga were made with an electivity index calculated following Ivlev (1961):

Equation 4.1: $E_i = (r_i - p_i)/(r_i + p_i)$

Where the electivity index (E_i) is calculated for a given prey item in its environment (p_i) as compared to its presence in the gut (r_i). For the purposes of my study, food selectivity is inferred for index results +0.2 and above, and food avoidance for index results -0.2 and below. Between -0.2 and +0.2, no preference of the food item is inferred.

4.2.4 Laboratory feeding experiments

Whitebait were housed in the laboratory in 30 cm x 30 cm x 30 cm glass tanks equipped with an aerated freshwater system and filled with 18 L of 90% de-chlorinated freshwater mixed with 10% seawater to minimise fungal infections such as white spot. Fish were kept in constant temperature rooms set at 16 ºC, an optimum temperature for native fish survival (Richardson et al. 1994), with a natural low light regime of 12-hour light, 12-hour dark. Each tank was lined at the bottom with black polythene to mimic natural substrate cover and lined between each tank to minimise disruption and stress.

4.2.4.1 Feeding rate

Prior to the feeding rate experiment, the fish were acclimated for five days and fed once a day on a mixture of live aquarium cultured *Daphnia carinata* mixed with rotifers collected from a nearby campus lake using a 40 µm mesh net. To ensure that inanga were fed equal zooplankton biomass between tanks and treatments, a sub-sample was preserved in 90% ethanol and zooplankton were counted and identified to the lowest level practical using an Olympus SZ60 stereo zoom microscope at 20x magnification. Zooplankton biomass was calculated using the method of Lauridsen et al. (2005), and resulting data were used to administer equal amounts of zooplankton, comprising the natural prey assemblage of the lake and live cultured *D. carinata*, between inanga treatments.

After acclimation, fish were starved for 36 hours before testing as Rowe & Dean (1998) indicated that this is the time needed to eliminate prey from the gut from *G. maculatus*. To calculate feeding rate, ten fish were placed into each of the nine tanks and the fish were given calculated densities of zooplankton mixtures based on differing zooplankton taxon biomass between prey collections (~50 ind L^{-1} for *Daphnia* and ~250 ind L^{-1} for rotifers) throughout the trial, and left for three time periods to feed: 30 minutes, two hours or six hours, each replicated three times. Three tanks containing just the zooplankton mixture served as controls. After these times, each tank was thoroughly mixed and 5 L was sub-sampled, passed through a 40 µm sieve, and the retained zooplankton identified and counted using an Olympus SZ60 stereo microscope at 25 x magnification to calculate consumption rate over time. The results from this experiment provided the basis for determining optimal zooplankton concentrations for subsequent feeding selectivity experiments.

4.2.4.2 Feeding selectivity

Prior to testing, fish underwent the same preparation as in the feeding rate experiment (i.e. acclimation and starvation periods). Inanga used in this experiment were randomised from the original pool used in the feeding rate experiment, along with others that weren't used in the first experiment but had undergone the same feeding regime. Three fish densities were used (10, 15 or 20 fish per tank) to assess whether there was any density-dependent prey switching. Each density group was replicated three times for a total of nine tanks. Three tanks containing the calculated zooplankton mixture and no fish served as controls. To assess the feeding selectivity of inanga, each tank was inoculated with ~50 ind L^{-1} of live *D. carinata* (large zooplankton) and ~250 ind L^{-1} of live rotifers/copepod nauplii (small zooplankton) based on consumption recorded from the feeding rate experiment to ensure there was sufficient resources so that fish did not become food limited over the duration of the experiment. Fish were fed once a day over a three-day period.

At the end of each day, the fish from each tank were temporarily placed in bucket of cold de-chlorinated water while the entire tank water (18 L) was sieved through a 40 µm mesh. The sample was then preserved in 90% ethanol for later identification of zooplankton. Each tank was then refilled to the original level with cold de-chlorinated water, the fish were placed back into their original tanks for continued monitoring, and fed again as described earlier. At the end of the third day, fish were euthanised with a lethal dose of 2-phenoxyethanol and preserved in 90% ethanol. Zooplankton in each sample taken over the three-day period were counted and identified to the lowest level practical as described earlier. Results were used to give an overall value for selectivity for each of the three fish density groups.

4.2.5 Data analysis

4.2.5.1 Gut contents

Physico-chemical data were normally distributed, as confirmed using expected normal histograms and Lilliefors test. Thus, two-way factorial ANOVA was used to analyse differences between months and sites. If a significant effect was detected, a Tukey's post-hoc test was used to determine differences between factors.

Non-parametric Mann-Whitney tests were used to assess differences in the electivity index of zooplankton groups and other invertebrate taxa across months and between sites to test the null hypothesis that the median of all taxa was equal given non-normally distributed data (Sawilowsky 1990). Data were untransformed for this analysis as it is assumed that these data follows no specific distribution (McKnight & Najab 2010).

To calculate total length vs. dry weight relationship, a linear model and a natural log model were investigated. Multiple regression was used to explore relationships between the proportion of taxa items in the gut of *G. maculatus* and total length and dry weight of fish, to assess whether diet shifted with increasing size.

4.2.5.2 Feeding rate

Two-way factorial ANOVA was used to assess differences in zooplankton abundance and functional groups over time for fish + zooplankton treatments and zooplankton only controls. A Tukey's post-hoc test was used to analyse pair-wise differences where a significant effect was detected. All data were log transformed prior to analysis and tested for normality using normal histograms and Lilliefors test.

4.2.5.3 Feeding selectivity

Repeated measures ANOVA was used to assess (i) differences between treatments (based on differing fish densities against the zooplankton control) for zooplankton abundance of the main groups, for three consecutive sampling days, and (ii) differences in electivity index of zooplankton across fish density treatments. Where a significant effect was found, Tukey's post-hoc test was used to analyse pairwise differences for treatment type and sampling day. Data were log transformed prior to analysis and tested for normality using normal histograms and Lilliefors test.

4.3 Results

4.3.1 Physico-chemical conditions

Spot measurements of specific conductivity range from 117.3 - 169.2 µS/cm (Table 4.1) values were lowest in August and highest in October when the river flows were at their highest. Dissolved oxygen and specific conductivity during November 2013 were within the range recorded in 2014, but spot water temperature was higher than the following year (Table 4.1). Physico-chemical parameters were significantly different between months only for specific conductivity (ANOVA, $F_{(1,3)} = 21.98$, $P < 0.01$) when post-hoc tests indicated differences between August and October, November (2013 and 2014). There was no difference in physico-chemical parameters measured between the two sites, Tuakau and Mercer (ANOVA; $P > 0.05$).

Table 4.1: Physico-chemical parameters measured at two sites, Tuakau and Mercer, during November 2013 and from August to November 2014.

Site	Month	Temperature (^{0}C)	Specific conductivity (µS/cm)	Dissolved oxygen (%)
Mercer	November-13	19.8	156.9	101.3
	August-14	11.4	117.3	106.4
	September-14	14.3	147.6	96.3
	October-14	16.8	169.2	97.8
	November-14	16.8	149.1	85.7
Tuakau	November-13	20.7	160.1	116.7
	August-14	11.4	120.7	109.2
	September-14	14.5	140.6	107
	October-14	16.9	158.0	96.0
	November-14	16.8	158.0	82.8

4.3.2 *Galaxias maculatus* diet

G. maculatus collected at the two sites ranged in length from 35 mm to 59 mm (Figure 4.1). Dry weight increased with increasing length, and ranged from 0.08 g to 0.90 g (Figure 4.1). A natural log length-weight relationship was compared with as linear relationship however there was no improvement in the R^2 value which may be due to the narrow size range of fish measured.

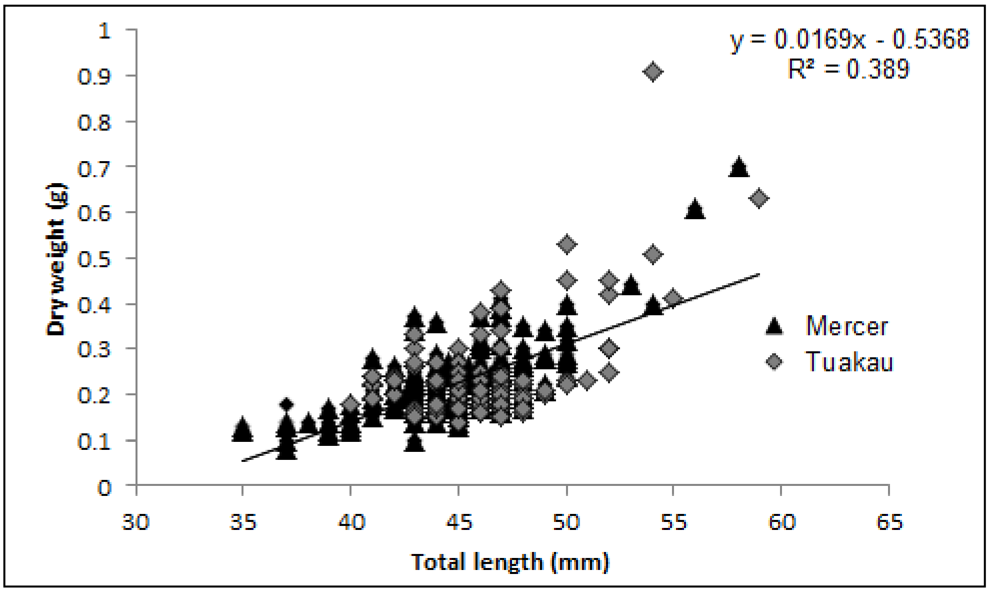

Figure 4.1: Total length vs. dry weight linear relationship for *G. maculatus* collected in November 2013 and on four occasions from August to November 2014 at two locations; Mercer (mean length: 44.91 ± 0.21 mm; mean weight: 0.23 ± 0.01 g) and Tuakau on the lower Waikato River (mean length: 46.19 ± 0.28 mm; mean weight: 0.24 ± 0.10 g) (n = 344).

Table 4.2: Comparison of gut fullness and contents measured during November 2013 and on four occasions from August to November 2014 for *G. maculatus* collected at two sites, Tuakau and Mercer, on the lower Waikato River. n = sample size; SE = standard error of the mean. Only individuals with stomachs that had a GFI ≥ 2 were used to assess total individuals in the gut.

	Tuakau						Mercer					
	Nov-13	**Aug-14**	**Sep-14**	**Oct-14**	**Nov-14**	**Overall mean**	**Nov-13**	**Aug-14**	**Sep-14**	**Oct-14**	**Nov-14**	**Overall mean**
Gut fullness index	1.84	4.20	2.32	1.58	2.44	2.48	2.26	1.47	2.15	2.71	2.39	2.20
n	16	15	25	33	25		48	56	20	24	28	
SE	0.16	0.20	0.29	0.17	0.32	0.46	0.18	0.09	0.29	0.30	0.24	0.20
Total individuals in gut	20	156	35	46	44	60.2	53	42	16	301	22	86.8
n	12	15	15	12	15		32	21	11	19	19	
SE	0.03	0.17	0.04	0.09	0.07	24.39	0.02	0.03	0.03	0.46	0.02	53.96
No. Cladocera	4	3	5	34	0	10.5	3	12	2	291	2	62
SE	0.09	0.05	0.07	0.44	0.00	6.26	0.02	0.08	0.04	2.16	0.02	57.28
No. Copepoda	0	0	5	0	0	1	0	12	1	0	1	2.8
SE	0	0	0.11	0	0	1	0	0.13	0.03	0	0.02	2.31
No. Saldidae	10	5	14	1	1	6.2	20	2	5	5	4	7.2
SE	0.24	0.21	0.41	0.08	0.07	2.56	0.15	0.07	0.37	0.10	0.12	3.25
No. Chironomidae	0	138	0	0	5	28.6	1	0	2	1	8	2.4
SE	0	1.37	0	0	0.21	27.37	0.03	0	0.12	0.05	0.16	1.44
No. Nematoda	0	1	0	0	0	0.2	1	0	0	0	0	0.2
SE	0	0.05	0	0	0	0.2	0.03	0	0	0	0	0.2
No. Trichoptera	0	0	5	0	0	1	3	6	1	4	2	3.2
SE	0	0	0.08	0	0	1	0.03	0.12	0.05	0.06	0.05	0.86

On a percentage composition basis, the gut contents of *G. maculatus* analysed in August were dominated by cladocerans (42%) and copepods (34%) at Mercer (Figure 4.2A), whereas chironomids dominated the composition in August at Tuakau (Figure 4.2B). Gut composition during September was relatively similar between sites with Saldidae dominant (~50%), and Trichoptera, Cladocera and Copepoda also present, along with chironomids at Mercer. Cladocera heavily dominated diet during October at around 97% for both sites, with Saldidae, Trichoptera and chironomids present in low numbers at Mercer; of those taxa only Saldidae was present at Tuakau (Figure 4.2). Chironomids were dominant at Mercer and Tuakau during November 2014 (50% and 62%, respectively), followed by Saldidae, Cladocera and Copepoda at Mercer (10 - 30%), and Saldidae and Trichoptera present at Tuakau (12 - 25%). Gut content composition was similar between November 2013 and 2014, with chironomids, Cladocera and Saldidae, dominating the contents for Tuakau and chironomids, Saldidae and Trichoptera dominating the contents for Mercer in both years (Figure 4.2). Overall, across all dates and sites combined the most abundant prey item was Cladocera (31%), followed by Chironomidae (28%) and Saldidae (25%).

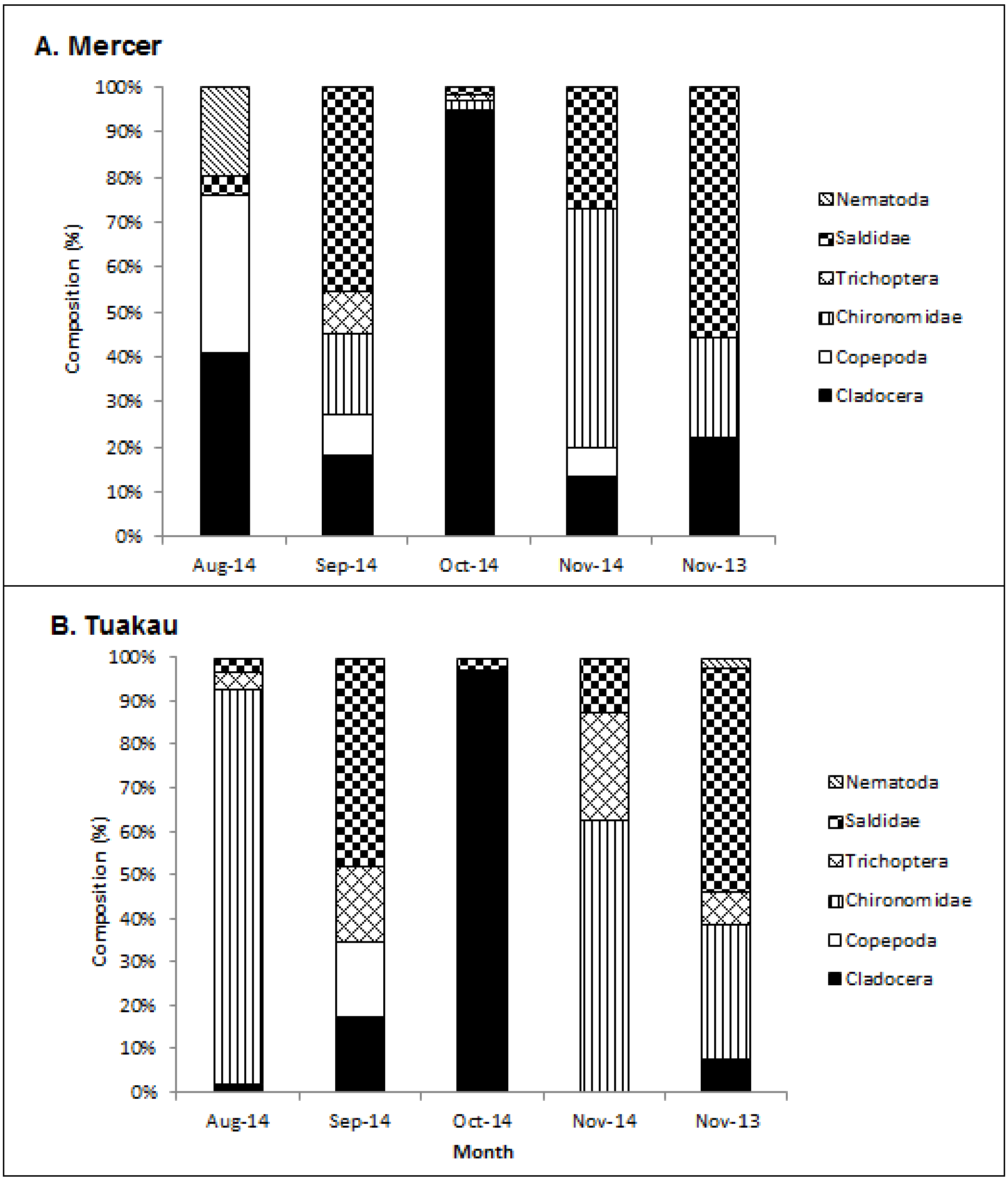

Figure 4.2: Percent composition of taxa found in the gut of *G. maculatus* for A) Mercer and B) Tuakau sites during the months of August to November 2014 and November 2013 on the lower Waikato River. November 2013 is presented at the end of this graph, and graphs hereafter, to enable direct comparison with November 2014.

Three food items of differing sizes and importance found in the gut of *G. maculatus* were selected to assess whether fish size (and by inference gape size) influenced diet. The percentage of Saldidae and Copepoda in the gut of *G. maculatus* was not related to fish length. Cladocera were ingested mostly by juveniles ranging from 42 - 50 mm but there was considerable variability among fish (Figure 4.3).

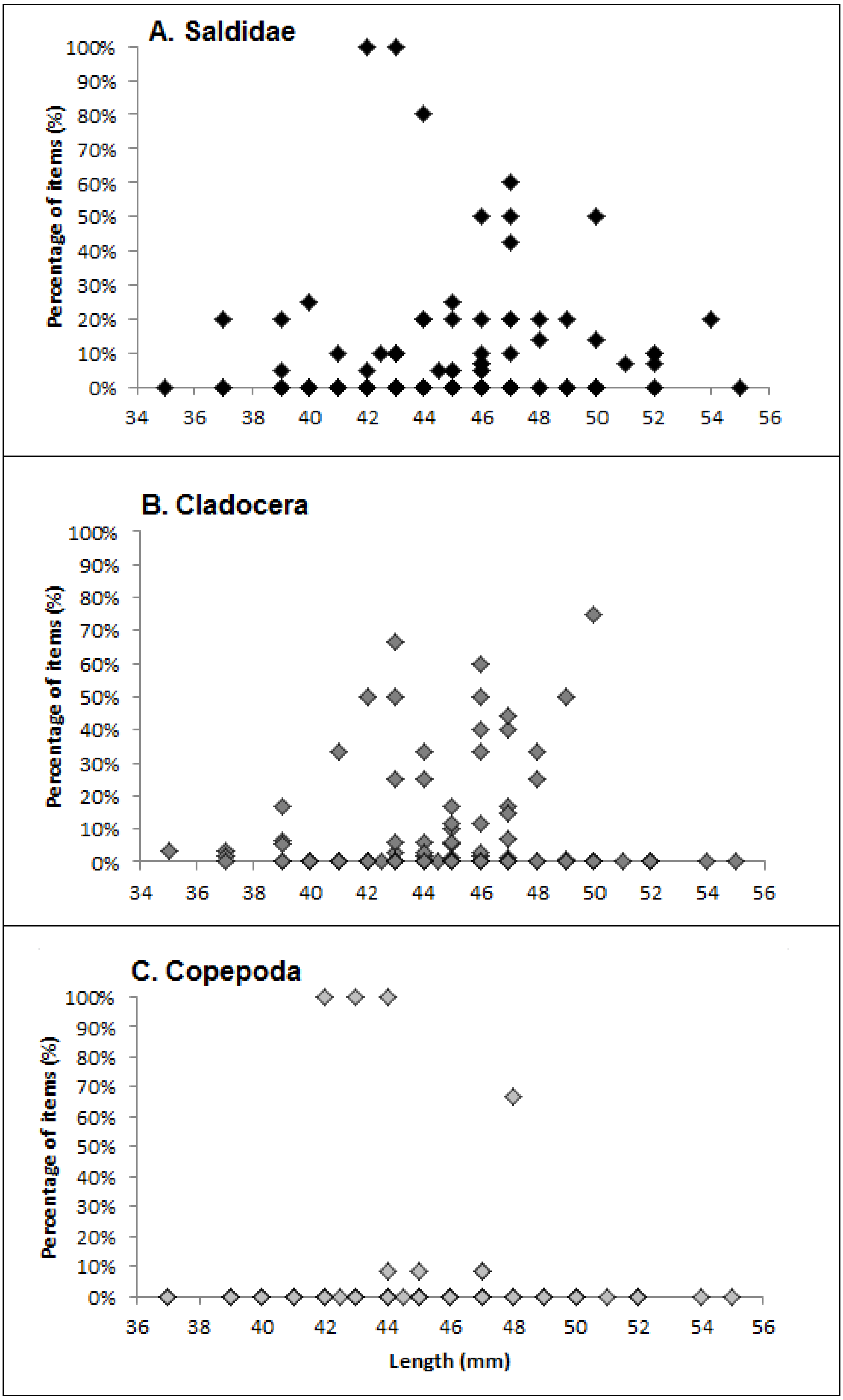

Figure 4.3: Multiple regression analyses of the percentage of three frequently-ingested items in the gut against length of *G. maculatus* (n = 170). Lines represent linear regressions (R^2 = 0.002 - 0.03).

Because food abundance was measured by taking plankton tow samples of the water column, and littoral or benthic environments were not sampled, Ivlev's Electivity Index results are shown here only for taxa known to use the water column (see Appendix 2 for further breakdown of electivity). Ivlev's Electivity Index for *G. maculatus* juveniles showed preference towards consuming Cladocera at both sites during 3 - 4 of the five months sampled (Figure 4.4). In September, avoidance of Cladocera was inferred at Mercer and no preference was evident at Tuakau. Rotifera were highly avoided during all months at both sites, whereas Copepoda were either avoided or not preferred, except during September at Tuakau when they were a selected prey item (Figure 4.4).

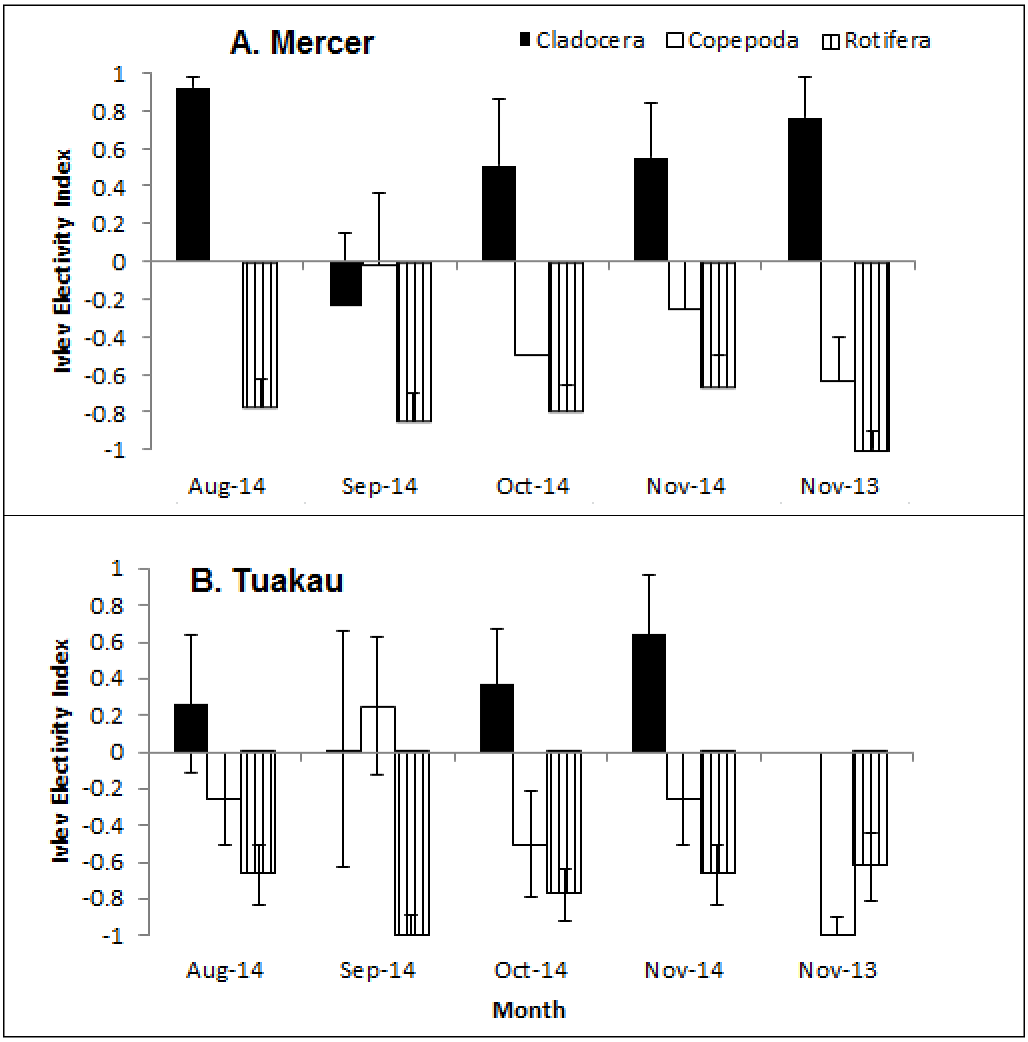

Figure 4.4: Overall Ivlev Electivity Index for *G. maculatus*, based on the three major zooplankton groups for A) Mercer and B) Tuakau sites during November 2013 and August to November 2014 on the lower Waikato River (Mean ± SE, n = 12-15 and 11-21, respectively, for Mercer and Tuakau). Values of 0.2 to 1 = food item selection, -0.19 to 0.19 = no preference, and -0.2 to -1 = food item avoidance.

4.3.3 Feeding experiments

4.3.3.1 Feeding rate

The number of zooplankton remaining in experimental tanks relative to controls after the three experimental periods was used to infer feeding by *G. maculatus*. The number of total zooplankton remaining decreased over the three time periods for all treatments, and was higher in the zooplankton only control than the treatments containing *G. maculatus* (Figure 4.5A). The number of zooplankton remaining was significantly different between the time periods of 0.5 and six hours (two-way ANOVA, $P < 0.05$). However, there was no difference in the number of total zooplankton remaining between tanks with and without fish (Table 4.3; Figure 4.5A).

The number of Cladocera remaining decreased for the treatments containing fish over the three time periods, whereas numbers in the zooplankton only controls remained relatively stable over time (Figure 4.5B). There was a significant difference between treatments (two-way ANOVA; $P < 0.05$). However, there was no difference between time periods for the number of Cladocera remaining (Table 4.5; Figure 4.5B).

The number of Copepoda remaining in tanks decreased over the three time periods for both treatments, with the zooplankton only controls maintaining higher copepod densities than the treatments containing fish (Figure 4.5C). The number of remaining Copepoda was significantly different between the time periods of 0.5 and six hours (two-way ANOVA; $P < 0.05$). However, there was no difference between treatments (Table 4.3; Figure 4.5C).

The number of Rotifera remaining decreased over the three time periods for both treatments (Figure 4.5D). There was a statistically significant difference between the time periods of 0.5 and two hours, and 0.5 and six hours (two-way ANOVA; $P < 0.01$) but there was no difference between treatments (Table 4.3; Figure 4.5B).

Overall, based on the ~80 individuals L^{-1} of *Daphnia carinata* and ~400 individuals L^{-1} of rotifers placed into all tanks at the start of the experiment and the numbers remaining after six hours, it is estimated that *G. maculatus* consumed three zooplankton (mainly *Daphnia*) per hour per fish on average. This feeding rate was used as a basis to determine food supply required for the feeding selectivity experiment.

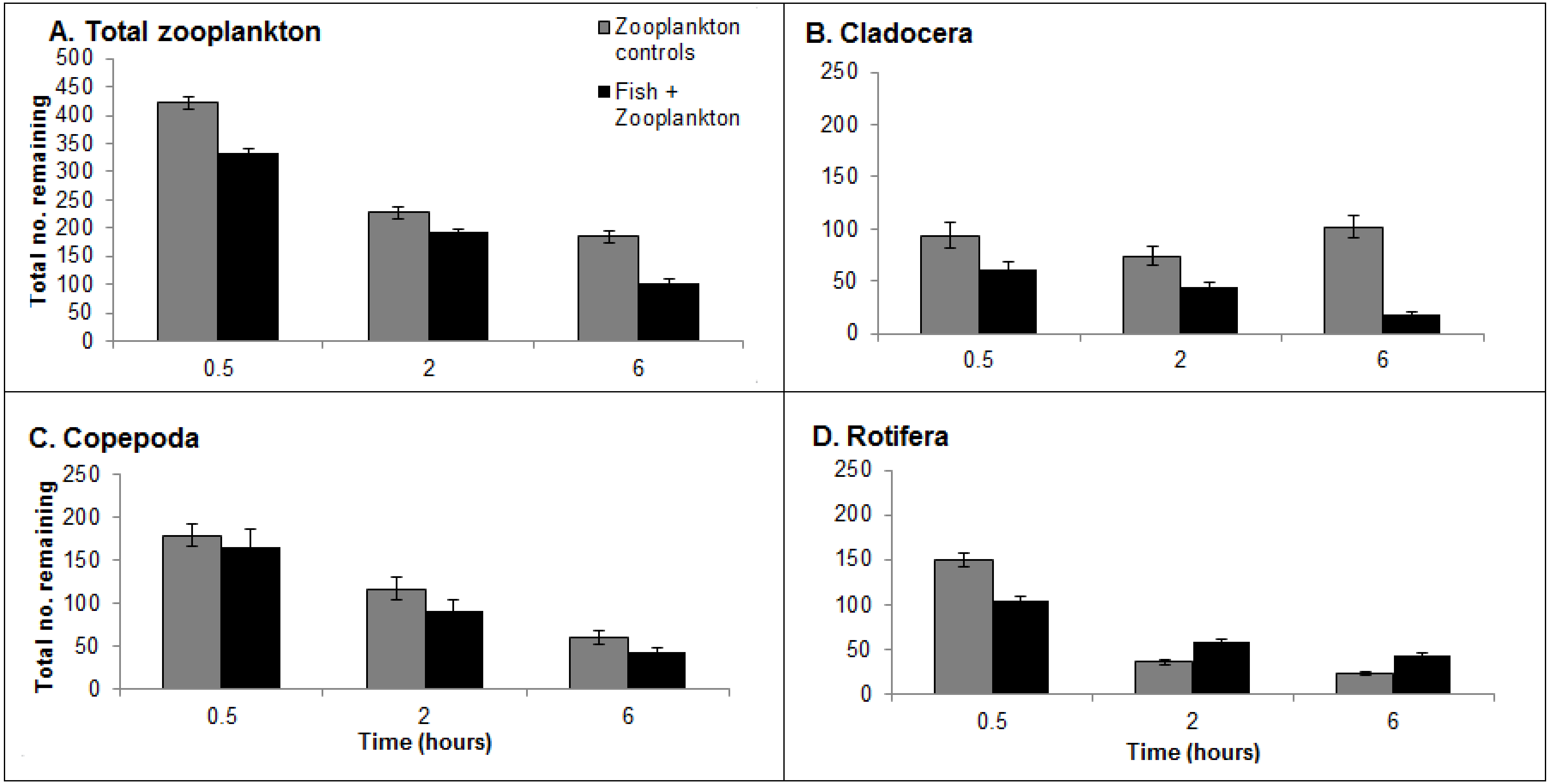

Figure 4.5: The number of individuals remaining (mean ± SE, n = 18) for A) total zooplankton, B) Cladocera, C) Copepoda and D) Rotifera over three time periods for two treatments; zooplankton only controls and tanks containing 10 *G. maculatus*.

Table 4.3: Summary of two-way factorial ANOVA results for total zooplankton, Cladocera, Copepoda and Rotifera measured over three time periods for treatments containing *G. maculatus* and zooplankton only controls; SS, sums of squares, df, degrees of freedom, MS, mean squares, F, F value, P, P value.

Total zooplankton	**SS**	**df**	**MS**	**F**	**P**
Intercept	102001.4	1	102001.4	81.0	< 0.01
Treatment	264.5	1	264.5	0.2	> 0.05
Time	10990.8	2	5495.4	4.4	< 0.05
Treatment*Time	1417.0	2	708.5	0.6	> 0.05
Error	15107.3	12	1258.9		
Cladocera					
Intercept	8022.2	1	8022.2	62.3	< 0.01
Treatment	854.2	1	854.2	6.6	< 0.05
Time	51.4	2	25.7	0.2	> 0.05
Treatment*Time	482.1	2	241.1	1.9	> 0.05
Error	1546.0	12	128.8		
Copepoda					
Intercept	20066.7	1	20066.7	66.4	< 0.01
Treatment	29.4	1	29.4	0.1	> 0.05
Time	3019.4	2	1509.7	5.0	< 0.05
Treatment*Time	916.8	2	458.4	1.5	> 0.05
Error	3628.7	12	302.4		
Rotifera					
Intercept	7770.9	1	7770.9	52.0	< 0.01
Treatment	56.9	1	56.9	0.4	> 0.05
Time	2060.4	2	1030.2	6.9	< 0.01
Treatment*Time	107.1	2	53.6	0.4	> 0.05
Error	1794.7	12	149.6		

4.3.3.2 Feeding selectivity

The total number of zooplankton remaining, was highest for Rotifera (59 - 205 individuals) and lowest for Cladocera (0 - 49 individuals) after feeding by *G. maculatus* over the three day period (Figure 4.6). The number of zooplankton remaining was higher in the zooplankton only controls compared to the fish treatments throughout the experiment (Figure 4.6). Cladocera were largely reduced in all feeding treatments, suggesting high levels of predation, whereas copepods were consumed at similar rates throughout all fish density treatments (Figure 4.6). Rotifers were consumed at higher levels in the higher density fish tanks for day one, however, there was not a similar pattern in the following days (Figure 4.6). The numbers of Rotifera, Cladocera and Copepoda remaining were significantly different between the control and medium fish density tanks and control and high density tanks (repeated measures ANOVA; Tukey's post-hoc test; $P < 0.05$). However, there was no difference between the controls and low density *G. maculatus* tanks. There was no difference between days ($P > 0.05$; Table 4.4).

To derive the number of zooplankton consumed per fish per day, the numbers remaining in the treatments with fish were subtracted from the zooplankton only controls. The number of zooplankton consumed per fish per day was highest at low fish densities (4 - 12 individuals per day) and lowest in the high density fish treatment (3 - 4 individuals per day). This increase in feeding rate compared to the last experiment may be due to the time allowed to feed (i.e. 0.5 – 6 hours vs. 12 hours).

The number of zooplankton consumed per fish per day for each of the three major zooplankton groups was highest for rotifers (~3 - 13 individuals), except on day two in the low density treatment when cladocerans were the major group consumed (Figure 4.7). Differences in zooplankton consumption may be due to the densities of these groups that were available, i.e. higher densities of rotifers than cladocerans, as equal biomasses were placed into the tanks. Zooplankton selected for consumption were not different between the fish density treatments (repeated measures ANOVA; $P > 0.05$; Figure 4.7) and the feeding duration had no effect on the type of zooplankton consumed ($P > 0.05$; Figure 4.7).

Ivlev's Electivity Index for *G. maculatus* indicated a preference for Cladocera through all treatments and either no preference or food avoidance for rotifers and copepods as food items (Table 4.5). However, there was no statistical difference in electivity between the zooplankton groups and fish density treatments (repeated measures ANOVA; P >0.05).

Table 4.4: Summary of repeated measures ANOVA results for Cladocera, Copepoda, Rotifera and all experimental days combined, measured over a three day period for treatments containing Low, Medium and High *G. maculatus* densities and the zooplankton only controls; SS, sums of squares, df, degrees of freedom, MS, mean squares, F, F value, P, P value.

Cladocera	**SS**	**df**	**MS**	**F**	**P**
Day	31.17	2	15.583	0.016	>0.05
Treatment	8423.25	3	2807.75	239.66	<0.01
Copepoda					
Day	404.26	2	202.13	0.23	>0.05
Treatment	7111.58	3	2370.53	15.99	<0.01
Rotifera					
Day	776.8	2	388.42	0.02	>0.05
Treatment	142997.3	3	47665.78	155.49	<0.01
All days combined					
Day	299.28	2	149.64	0.038	>0.05
Treatment	34125.73	3	11375.24	102.47	<0.01

Table 4.5: Ivlev's Electivity Index calculated for the three *G. maculatus* density treatments for all days combined for Rotifera, Cladocera and Copepoda; Low - 10 fish per tank, Medium - 15 fish, High - 20 fish. Values of 0.2 to 1 = food item selection, -0.19 to 0.19 = no preference and -0.2 to -1 = food item avoidance. Treatments with inferred food item selection are highlighted in bold, and those avoided are italicised.

	Low	**Medium**	**High**
Rotifera	*-0.26*	-0.03	0.00
Cladocera	**0.51**	**0.41**	**0.63**
Copepoda	-0.16	*-0.30*	-0.02

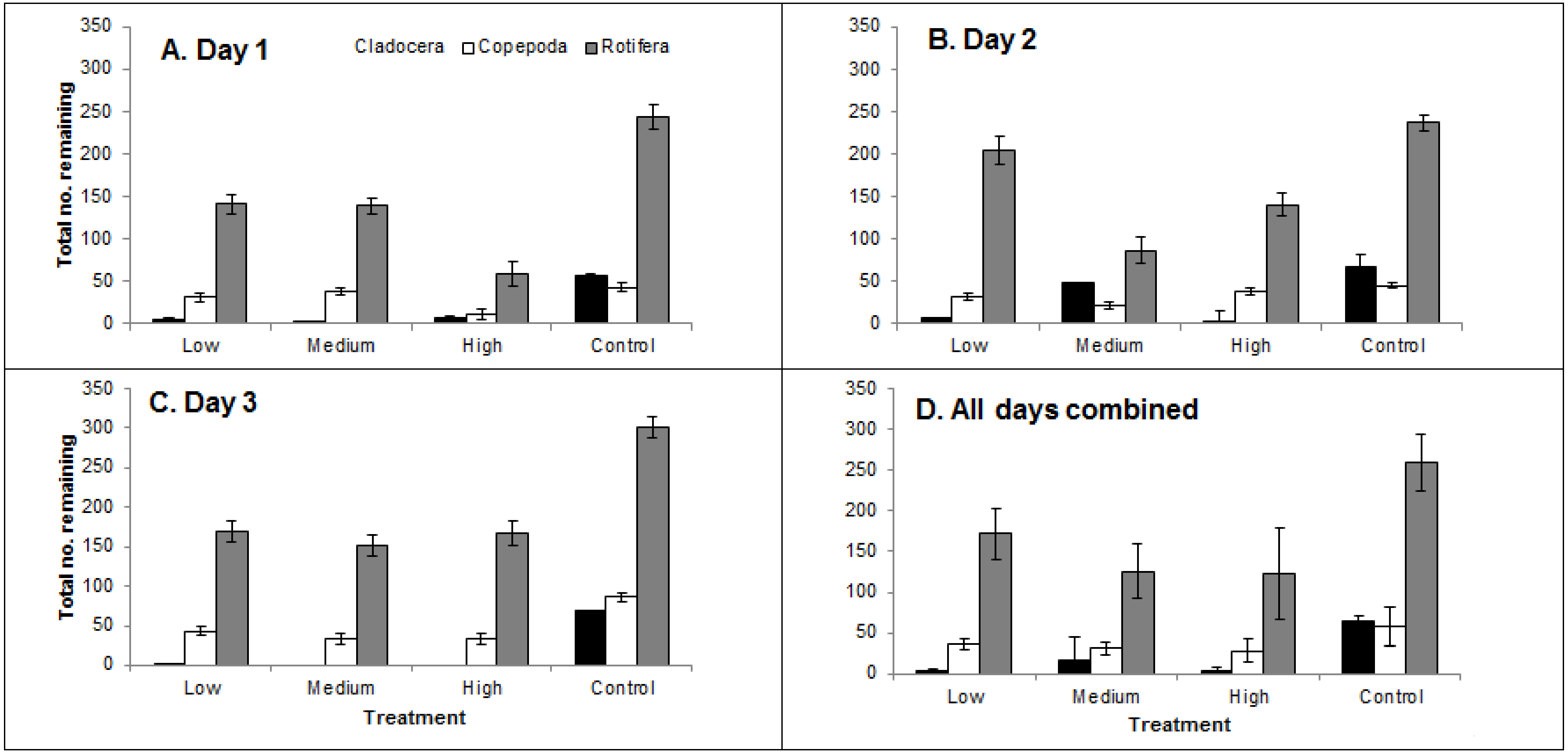

Figure 4.6: The total number of individuals of the major zooplankton groups; Cladocera, Copepoda and Rotifera remaining after A) day one of feeding, B) day two of feeding, C) day three of feeding and D) average of all feeding days combined for the Control (no fish) and Low (10 fish), Medium (15 fish) and High (20 fish) *G. maculatus* densities. (Mean ±SE, n = 12).

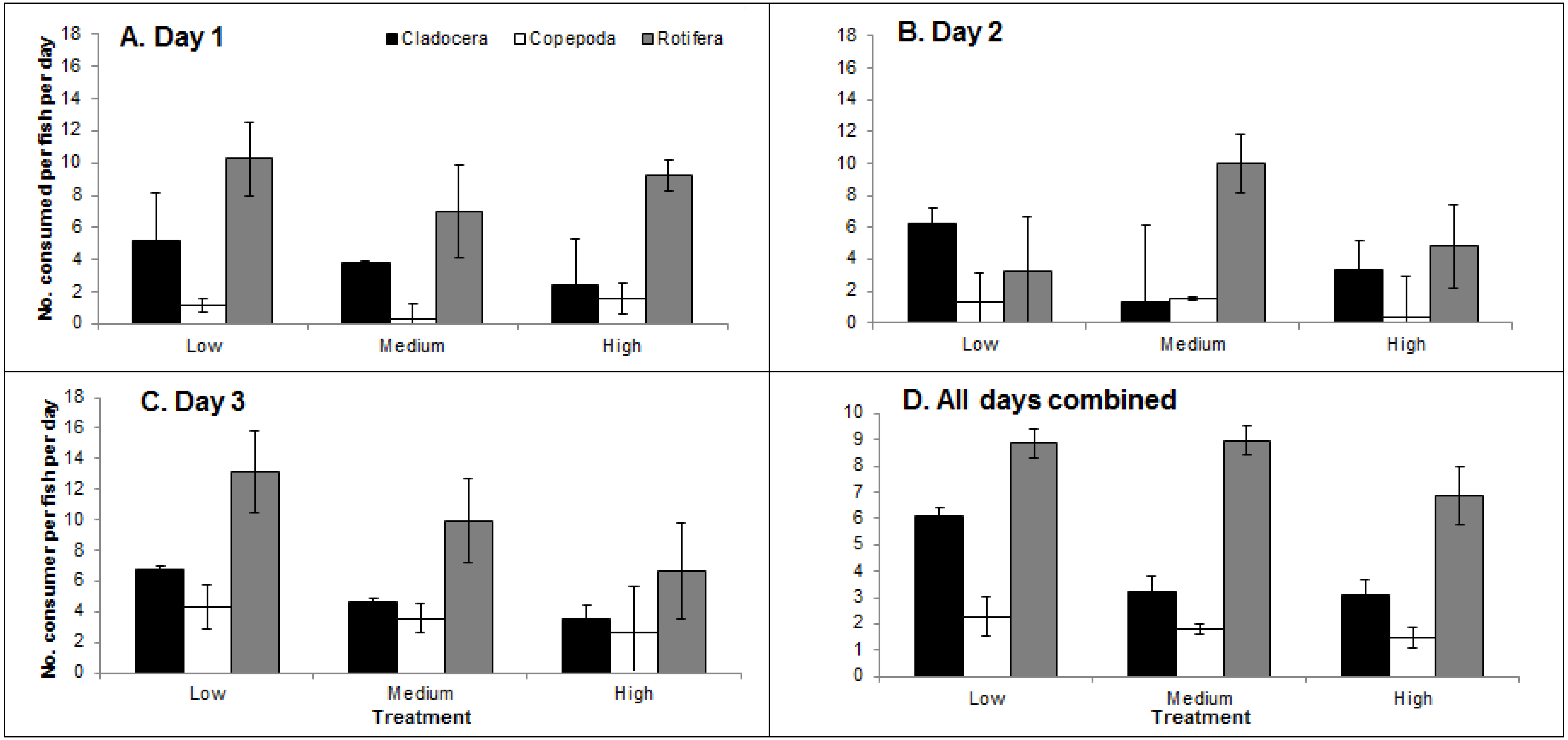

Figure 4.7: The number of zooplankton individuals consumed per fish per day for Cladocera, Copepoda and Rotifera after A) day one of feeding, B) day two of feeding, C) day three of feeding and D) average of all feeding days for Low (10 fish), Medium (15 fish) and High (20 fish*) G. maculatus* densities. (Mean ±SE, n = 9)

4.4 Discussion

4.4.1 Diet and prey preferences of migrating inanga

Juvenile *G. maculatus* showed an opportunistic diet, with a broad range of taxa consumed in different proportions over time. There were similarities in the composition of taxa consumed between sites on most dates, suggesting that local habitat characteristics strongly influenced the availability of food supplies for juvenile inanga in the lower Waikato River. Generally Cladocera and chironomids made up high proportions of the diet at Mercer, the upper site in the Waikato River. Other taxa such as Trichoptera made up significant proportions of the diet at Tuakau, the lower site, with Saldidae present in high numbers at both sites. Further, there was some consistency in diet between years (November 2013 and 2014) which may indicate inter-annual consistency in patterns of zooplankton composition and abundance (specifically Cladocera), and insect dominance by Saldidae and Chironomidae in littoral habitats of this part of the Waikato River.

Multiple physico-chemical parameters were measured monthly, with spot measurements of temperature and specific conductivity increasing over the sampling year as expected, whereas dissolved oxygen levels were close to saturation on most dates, although physico-chemical sampling was very limited. Values for dissolved oxygen, temperature and conductivity are consistent with other findings within the Waikato River, with nutrients such as nitrogen, phosphorus and *E. coli* values adding to other water quality variables that are important for measurement (Vant 2010). Although I detected no difference between months or sites in the physico-chemical parameters measured, changes in water quality can ultimately affect the survival and abundance of riverine biota such as zooplankton (Shiel et al. 1982; Basu & Pick 1997).

While water quality was similar between sites and thus unlikely to influence community composition between the sites I sampled, some observed differences in the composition of prey taxa between sites may be due to the local habitat characteristics. For example, Mercer has off-channel tributary inflows from nearby wetlands such as the Whangamarino and Opuatia wetlands, along with floodplain lakes, bringing in a supply of large-bodied cladocerans for consumption (Górski et al. 2013). These off-channel habitats provide zooplankton with optimal physical and chemical conditions that promote growth and reproduction, and allow communities to reach high densities (Shiel et al. 1982; Burger et al. 2002). At Tuakau, there are no nearby inflows to the river and supplies of large-bodied cladocerans potentially originate from upstream tributary inputs near Mercer, as well as from off-channel lakes, side arms and river edge habitats, which may have drifted down the river towards lower sites. At both sites, chironomids, Trichoptera and Saldidae in the gut of *G. maculatus* are thought to be of littoral origin (Collier & Lill 2008), suggesting that *G. maculatus* can feed from a wide range of habitats. Collier & Lill (2008) found chironomids to increase in relative abundance in the river around tributary junctions which suggests that these lateral areas may have an important role in supplying the river with diverse species assemblages. Insect taxa found in guts at Mercer are also likely to be of littoral or benthic origin. In support of this, Rowe et al. (2002) stated that other species of juvenile galaxiid such as koaro can forage on both aquatic and terrestrial organisms, dependant on the fish's location within the aquatic system.

Selectivity was relatively similar at different times of the year, which is likely due to the availability of riverine plankton populations and their response to changing water conditions such as temperature and discharge. Although prey selection by juvenile fish is largely dependent on their gape size (DeVries et al. 1998; Barriga et al. 2012), observed proportions of Saldidae, Cladocera and Copepoda, the taxa that were most frequently ingested, were highly variable in relation to total *G. maculatus* length. This may reflect consistent feeding preferences across all juvenile sizes sampled, irrespective of prey size, although Saldidae are bigger taxa than large-bodied zooplankton. Fish are highly visual predators and their ability to locate prey is an important aspect of their foraging ability (Robertis et al. 2003), but prey size does not appear to be a leading factor influencing selectivity for juvenile whitebait, as found for other species elsewhere (Zaret & Kerfoot 1975). This may be due to the small size range of inanga sampled, or maybe because there was a lack of size variation within the prey.

Cladocera were highly selected for in the diet of *G. maculatus* reflecting the high proportion found in guts compared to the environment. This result, nonetheless, is assuming that the zooplankton samples taken from the river adequately reflected the availability of food throughout the feeding habitats for inanga. Littoral and benthic habitats were not sampled to assess prey availability so inferences about prey selectivity can most reliably be made for zooplankton available in the water column. In contrast, Copepoda were neither selected nor avoided, while Rotifera were absent from the guts of *G. maculatus* and therefore highly avoided at both sites. Sutela & Huusko (2000) stated that different zooplankton such as copepods, cladocerans and rotifers have varying levels of resistance to digestion and that rotifers are generally digested rapidly, which may lead to biased diet estimates, since rotifers may be consumed but not detected. However, as *G. maculatus* were placed on ice once caught to halt the digestion process, any rotifers, if present would have been identifiable based on their trophi or lorica (hard parts) that resist digestion.

In terms of selectivity for zooplankton, the preference for large-bodied cladocerans within the lower Waikato River may be due to the prey's inability to evade capture. Large-bodied cladocerans are easily sighted as they are relatively large and exhibit a conspicuous swimming movement, and are thus frequently preyed upon (Sheppard et al. 2011). In contrast, copepods have a streamlined body and fast escape speeds with irregular trajectories, while rotifers are small in size and possess adaptations such as spines to prevent consumption (Mayer & Wahl 1997; Preston et al. 1999; Sheppard et al. 2011). Consequently, Cladocera may have had a more positive electivity index partly because of their inability to evade capture by *G. maculatus* compared to copepods or rotifer taxa. In addition, they are large profitable food items due to their high levels of polyunsaturated fatty acids (Persson & Vrede 2006).

The results of this study are in accordance with other studies examining the diet of juvenile *G. maculatus* (Modenutti et al. 1993) and for juvenile fish within lakes (Mayer & Wahl 1997; Barriga et al. 2012). However, no previous diet analyses have been undertaken on riverine populations of juvenile *G. maculatus*. Nunn et al. (2007) also showed that cladocerans were positively selected for irrespective of size by juveniles of four riverine-floodplain fish species; European chub (*Leuciscus cephalus*), yellow perch (*Perca fluviatilis*), roach (*Rutilus rutilus*) and dace (*Leuciscus leuciscus*). Electivity indices of rainbow smelt (*Osmerus mordax*) also showed a clear preference for cladocerans such as *Daphnia* sp. within lake environments (Sheppard et al. 2011).

Flow variations likely had an influence on the proportions of taxa found in the guts of inanga over time. During October there were high proportions of cladocerans, such as *Bosmina* sp., *Daphnia* sp. and Chydoridae found within the guts of *G. maculatus* from both sites, particularly from Mercer which is located downstream of wetland and tributary inflows. Corresponding to this increase in the gut, a high flow pulse was recorded in the river around the time of October sampling (Waikato Regional Council 2014b). Seasonal flow variation influences the composition and abundance of zooplankton taxa within the main river channel as flow pulses determine flushing of floodplain wetlands and lakes, and the level of connectivity with floodplain areas (Amoros & Bornette 2002; Górski et al. 2013). Some Cladocera taxa may have originated from wetland and lake tributary inflows into the river during this flow pulse. Despite this, certain species of Cladocera can develop in slow-flowing marginal areas (Hamilton & Duggan 2010). The presence of these taxa such as *Bosmina* sp., *Daphnia* sp., and also Chydoridae within the river plankton samples and the gut of *G. maculatus,* suggest that whitebait are generally feeding along the edge habitats of the Waikato River as these taxa generally inhabit slow flowing areas.

As demonstrated in Chapter 3, inundation of floodplain soils can initiate hatching by zooplankton, including some cladocerans. Large flow pulses therefore can bring in supplies of zooplankton from floodplains and other off-channel areas such as lakes, back waters and river edge habitats. Between periods of high flows and for areas of the river without tributary inflows, foraging appears directed towards semi-aquatic, benthic and littoral prey. The diet of migrating fish such as *G. maculatus* may therefore be partly dependent on these flow pulses delivering supplies of large-bodied zooplankton as a food source during peak migration periods. This interpretation supports the conclusion of Górski et al. (2013) that whitebait migrations may be linked with the timing of spring floods partly in response to food availability.

4.4.2 Feeding rates and selectivity

Laboratory feeding experiments enabled environmental variation and food resource supply to be controlled and thus allow more definitive conclusions about prey selectivity to be made. *G. maculatus* juveniles fed on zooplankton within a laboratory setting and selectivity mimicked that of the field diet analyses. Juvenile fish fed at a higher rate on Cladocera taxa as the numbers remaining in tanks were lower than that of the controls which did not change over the experimental period. There was no difference between the numbers of copepods remaining between treatments and thus no evidence of feeding selectivity, as found in the field sampling. However, treatments with fish had more rotifers remaining than the control, possibly due to a combination of factors. The loss of rotifers in the controls may have been due to the lack of food within the tanks, unsuitable conditions such as low temperature (experimental room set at 16ºC for optimal *G.*

maculatus survival) and physical abrasion on the smaller zooplankton from the larger *Daphnia*. Rotifers can be killed by *Daphnia* through abrasion from their filtering mouthparts and limbs, and can also be ingested once damaged (Stemberger & Gilbert 1987). Within tanks with fish, *Daphnia* would be selectively preyed upon first, reducing the degree of physical abrasion on rotifers by *Daphnia*. Therefore, rotifers can maintain higher densities in settings with fish present, compared to those without fish.

The density of *G. maculatus* in the laboratory experimental tanks influenced the amount of zooplankton consumed. More zooplankton were consumed in the low density fish treatments on a daily basis whereas consumption was lowest for the higher fish density treatments. Food availability may be limited at higher fish densities, and this can cause competitive interactions for the remaining resources (Amunsden et al. 2007), leading to density-dependent growth (Rose et al. 2001). Conspecifics at the same stage of development, such as migrating inanga, have the same foraging and growth requirements (Rose et al. 2001), and if their energetic requirements are not met, reduced growth and fecundity, and increased mortality, are likely to result (Amunsden et al. 2007). Keeley (2001) found steelhead trout (*Oncorhynchus mykiss*) to display density-dependent growth as stocking densities increased, leading to greater mortality due to limited food resources.

In my study, the amount of zooplankton consumed was low for the first two days of the experiment which may infer satiation as there was an abundant food resource, as proposed for juvenile chinook salmon (*Oncorhynchus tshawytscha)* feeding in a California River and floodplain by Jeffres et al. (2008). Consumption of whitebait subsequently increased after the third day, which may be due to the time taken to evacuate prey from the gut of native juvenile fish, as previously discussed (Rowe & Dean 1998). As biomass of zooplankton was calculated before zooplankton taxa were supplementary fed into the tanks, the densities placed into the tanks were substantially higher for rotifers than for cladocerans and copepods. Therefore, the finding that the number of zooplankton consumed was highest for rotifers and lowest for cladocerans can be explained primarily by numerical differences.

Rotifer taxa were found to have the highest number of individuals remaining (54%) and Cladocera had the lowest number (12%), once again indicating avoidance of

Rotifera and selectivity of Cladocera. The electivity index for the laboratory feeding selectivity experiment for all fish density treatments was positive for Cladocera, negative for Rotifera and inconsistent for Copepoda, showing similarities to the gut contents analyses. External factors that may influence selectivity in the field were able to be controlled in a laboratory environment and reaching the same conclusions indicates that dietary patterns observed in the field are driven by prey selectivity. However, as the tanks were only 18 L and the experimental room had a natural light regime, capture of zooplankton taxa would likely have been easier in the laboratory setting than in the Waikato River itself, due to lack of currents and turbidity (Shiel et al. 1982; Basu & Pick 1997; Rowe & Dean 1998).

4.4.3 Ecological significance

Results of this study were in accordance with the Optimal Diet Model (Stephens et al. 2007) whereby juvenile inanga preferentially consume large-bodied zooplankton over smaller copepods and rotifers, as larger prey types are more profitable and require less effort to capture and ingest. *Bosmina* sp., *Daphnia* sp. and Chydoridae were the particular cladocerans that were found in the guts of *G. maculatus*. Generally, *Bosmina* sp. are derived from within the river itself as they are largely planktonic, with *Daphnia* sp. originating in lakes (Hamilton & Duggan 2010). Chydoridae, however, are typically plant- or bottom-dwelling species and are commonly associated with edge habitats of large rivers (Hamilton & Duggan 2010; Chapman et al. 2011). Lake tributaries may then be extremely important in facilitating transfer of *Daphnia* sp. (and potentially other species not found during sampling) to the river as a food supply for juvenile fish. Furthermore, inundated near shore floodplains, wetlands and off-channel areas may serve as important environments for the production of large-bodied cladocerans which flourish in slow flowing edge habitats. The ability of zooplankton taxa to reproduce and grow at high numbers, especially in backwater areas with slow velocities, can supply the river with diverse species assemblages that increase productivity whilst supporting native biota (Boulton & Lloyd 1992), although backwater areas were not sampled during this research.

Prey selection by fish confers a natural advantage as energy intake can be maximised and lead to optimal growth, survival and reproduction (Mayer & Wahl 1997), allowing an increase in the recruitment of fish populations and potentially helping to sustain upstream migrations. Juvenile inanga were found to consume cladocerans and copepods even in high density situations without switching prey to the more abundant rotifers in the experimental tanks. As juvenile inanga did not prey switch, this may suggest that cladocerans are an optimal food source as switching prey to rotifers would not confer a greater advantage in densely-stocked environments. Therefore, high abundances of large-bodied cladocerans in riverine-floodplain environments appear important to support growth and migration of juvenile inanga and potentially other whitebait species.

Although there have been some international studies on feeding selectivity of juvenile *G. maculatus* in lakes (Modenutti et al. 1993; Rowe & Dean 1998), no published research that I am aware of has been undertaken in New Zealand in rivers on this topic. This study allowed the preference of juvenile *G. maculatus* in a large lowland river to be assessed and therefore widen feeding selectivity knowledge to include a diadromous galaxiid population. Overall, this study suggests that cladoceran taxa are highly important as a food source for migrating whitebait populations, which was shown both in a natural environment and a laboratory setting. Slow water velocity areas of the river, and nearby lake and wetland areas, can support abundant zooplankton assemblages within rivers (Burger et al. 2002), and high densities of these zooplankton taxa may be extremely important for the nutrition of juvenile inanga in the main river channel itself. Górski (2012) found lake and wetland areas in the Waikato River catchment, such as Lake Whangape and Whangamarino wetland outflows, to be of particular importance for delivering high amounts of large-bodied cladocerans and copepods to the main river. Maintaining connectivity with these lentic environments can therefore promote the growth of zooplankton communities and potentially help sustain whitebait migrations within lowland river environments. Understanding the feeding preferences of *G. maculatus* populations enables management to be directed to actions that promote the abundance and diversity of large-bodied zooplankton taxa, such as restoring connectivity to off-channel scrub and native forest floodplain areas (Chapter 3).

Chapter Five

General discussion

The overall aim of this thesis was to investigate the potential of inundated floodplain soils to produce zooplankton and to assess whether hatched zooplankton could act as a food supply for migrating juvenile *Galaxias maculatus* in the lower Waikato River. Previous floodplain zooplankton work carried out by Górski et al. (2013) was undertaken during inundation events on the lower Waikato River floodplain, and led to hypotheses about the sources of zooplankton and their potential importance to migrating whitebait. Annual migrations of whitebait up the Waikato River are thought to coincide with receding floodwaters that could provide them with abundant, large-bodied cladocerans and copepods that help fuel upstream migration (Górski et al. 2013). Górski et al. (2013) suggested that high flow pulses influence riverine-floodplain connectivity and govern zooplankton community composition within the Waikato River. However, as this sampling was undertaken during inundation, the origin of large-bodied zooplankton could not be pin pointed and remained a matter of speculation.

Although there have been studies documenting the importance of floodplain soils in generating zooplankton and their transfer back into main waterbodies for fish (Jenkins & Boulton 2003; James et al. 2008), only one study has looked at the feeding preferences of galaxiids and they were lake-dwelling (Modenutti et al. 1993). Generally, overseas literature has focused on lake and wetland ecosystems (Modenutti et al. 1993; Barriga et al. 2012; Watkins et al. 2013), with little research undertaken on the structure and function of riverine-floodplain ecosystems. Understanding food-web linkages within the lower Waikato River and its floodplain may help in managing the whitebait fishery which is thought to be in steady decline (Hickford et al. 2010). To investigate the key linkages, I firstly investigated the potential of floodplain soils to generate zooplankton following inundation, and the influence of riverine-floodplain vegetation type and connectivity on zooplankton production (Chapter 3). Secondly, I investigated the diet and feeding preferences of juvenile *G. maculatus* in the lower Waikato River (Chapter 4). Inundated floodplain soils that support the production of zooplankton that are highly favoured by juvenile whitebait could have implications for the management of the whitebait fishery through protection of important floodplain areas that facilitate zooplankton generation following large spring floods.

5.1 Generation of zooplankton from floodplain soils

To address the first aspect of the study, I incubated soil cores taken from three different types of floodplain vegetation (native forest, scrub and pasture) and two levels of connectivity to the lower Waikato River (connected or disconnected). The artificial nature of the incubation may have led to an underestimation of the sampled zooplankton communities, due to potential underrepresentation of species-specific hatching cues (Ning & Nielsen 2010). Despite this, it is a commonly used technique to assess dormant egg banks as hatching and identification can be undertaken in a controlled environment. Very little research has been done in New Zealand and this study increases the limited knowledge on zooplankton egg banks within floodplain soils.

Once incubated, zooplankton were able to emerge within three days of inundation, suggesting that temporary inundation can generate zooplankton from floodplain soils with the potential to facilitate transfer back into the river. Zooplankton densities peaked after 12 days which may indicate that a flood with permanence of around 12 days would be optimal for hatching of dormant zooplankton communities within the floodplain soils. Heterogeneity in floodplain vegetation structure and its correlated habitat characteristics appeared important to promote the growth of assemblages that are characterised by particular groups of species. Thus, different vegetation types were characterised by different zooplankton communities, with rotifers dominating pastoral sites (although present in all vegetation types), and cladocerans and copepods only found in scrub and forested floodplain sites. This result suggests that different types of floodplain vegetation play an important role in structuring zooplankton communities that emerge from soils following inundation.

Overall, rotifers were the most abundant zooplankton group that emerged from the inundated soil cores, and bdelloids were the only taxon present in pastoral habitats, reflecting the ability of these species to avoid desiccation and withstand extended dry periods in floodplain soils (Jenkins & Boulton 2003). After rotifer emergence from the soil cores, large-bodied copepods and a cladoceran emerged and displayed more persistent emergence over time, although in low densities. Overall, these large-bodied zooplankton are known to exhibit longer development times compared to rotifers, explaining why there was a lag between soil core inundation and crustacean emergence (Lair 2006; Górski et al. 2013). The emerged large-bodied cladoceran, *Saycia cooki*, is rarely encountered (Frey 1971), and was found to emerge from scrub and forested floodplain habitats which indicates the importance of these vegetation types for supporting specific assemblages of zooplankton during inundation. The loss of scrub and forested floodplains due to conversion for pastoral land would potentially cause the loss of this species and enhance smaller species such as rotifers, and ultimately could affect the structure and diversity of zooplankton assemblages that are transferred back into the main river channel as floods subside. Protecting remnant patches of scrub and forest floodplain vegetation is therefore potentially important for biodiversity purposes.

Soil moisture was linked with floodplain vegetation type and was the most significant factor associated with zooplankton community composition on the lower Waikato River floodplain. Soil moisture was low for pastoral sites and higher in scrub and forested sites which may partly explain the differences in zooplankton communities between floodplain vegetation types. The higher levels of soil moisture found at scrub and forest sites enhance survival of dormant zooplankton eggs, especially through periods of drought (Frisch 2002). Canopy cover was lowest for pastoral sites, while air and soil temperatures were higher at these sites. Dissolved oxygen significantly decreased over the incubation period for all soil cores and did not differ among vegetation types. Growth, development and egg clutch size of cladocerans and copepods can be highly impacted by low dissolved oxygen levels (Hanazato & Dodson 1995; Stalder & Marcus 1997), which may be decreased in open habitats following inundation. Low dissolved oxygen levels are characteristic of temporary floodplain waterbodies and wetlands due to increased evaporation and minimal flow (Nadai & Henry 2009).

Frequent flows that extend onto floodplains are extremely important in order to promote species diversity (Bayley 1995; Tockner et al. 2000), and increase the size of dormant egg banks (Havel 2000). With increasing distance from the river the likelihood of floodplain inundation decreases causing loss of floodplain connectivity, although this is dependent on elevation. In a non-regulated, pre-human state with the absence of stopbanks and more intact scrub and floodplain forested areas, the number of zooplankton hatching out of these floodplain sites would have been greatly increased. Stopbanks and areas disconnected from the river can prevent zooplankton, once hatched, from draining back into the river to support juvenile fish and higher trophic levels (Boulton & Lloyd 1992). However, riverine-floodplain connectivity did not have a statistically significant effect on zooplankton community composition or taxon richness and abundance on lower Waikato River floodplain soil cores. This may be because there was not a long enough dry period to see differences in the two connectivity sites. Furthermore, connected (i.e. inside of stopbanks) floodplain sites undergo frequent wetting and drying events which could mean that the egg bank does not have ample time to develop.

5.2 Diet and feeding selectivity of juvenile *Galaxias maculatus*

Fish are primarily visual predators and rely on their ability to locate prey, irrespective of prey size (Zaret & Kerfoot 1975). Juvenile *G. maculatus* had an opportunistic diet and fed on a wide range of invertebrate groups when in the natural river environment. Gut contents analyses showed differences in consumption of zooplankton and insect taxa between sites, likely due to differences in local habitat characteristics. Large-bodied cladocerans were more prevalent in the gut at the upper site at Mercer along with the semi-aquatic hemipteran Saldidae. In contrast, Tuakau, the lower site, had high proportions of chironomids and Trichoptera, which are thought to have been of littoral or benthic origin.

G. maculatus larvae from both sites were largely similar in diet composition on most dates, with diet variability occurring over time. Feeding selectivity between years (November 2013 and 2014) for the field analyses showed similarities, which may indicate seasonally consistent patterns of prey abundance and diversity in the Waikato River. Peaks of cladocerans were noted at both field sampling sites during October 2014 and led to almost exclusive consumption of cladocera by *G. maculatus*. This was found to be correlated with a high flow pulse that was recorded within the Waikato River. This large peak of Cladocera may have washed in from lake and wetland tributaries during the high flow pulse, lending support to the hypothesis of Górski et al. (2013). Large seasonal pulses influence the structure and composition of zooplankton communities as high flows increase connectivity to off-channel waterbodies (Amoros & Bornette 2002). Inputs from floodplain wetland and lake tributaries are prevalent around the Mercer sampling site which may account for differences in taxa composition of the diet. These off-channel areas can be extremely important in facilitating transfer of nutrients and food such as invertebrates and zooplankton for biota such as juvenile fish (Boulton & Lloyd 1992). Tockner et al. (2000) stated that riverine-floodplains are contracting and expanding systems, dependant on flow pulses, which cause a shift in aquatic and terrestrial habitats leading to high habitat heterogeneity. This habitat heterogeneity is largely dependent on hydrological connectivity and influences transfer of organic matter and biota (Tockner et al. 2000). Based on how the lower Waikato River floodplain responded to the high flow pulse during October 2014, by increasing availability of food supplies back into the main river channel, these findings are in accordance with the Flood Pulse Concept as modified by Tockner et al. (2000).

Due to their large size, large-bodied cladocerans may be of high importance as a profitable food item for riverine biota such as juvenile whitebait. The finding that *G. maculatus* capture large-bodied cladocerans in a laboratory setting as well as in field samples is in accordance with overseas studies, although these have only been done on populations of juvenile fish in lakes (Modenutti et al. 1993; Mayer & Wahl 1997; Sheppard et al. 2011). The main cladocerans found the gut of *G. maculatus* were *Bosmina* sp., *Daphnia* sp. and Chydoridae. Generally, *Bosmina* sp. are derived from lakes or within the river as they are largely planktonic, with *Daphnia* sp. originating in lakes (Hamilton & Duggan 2010). Chydoridae, however, are typically plant- or bottom-dwelling species (Hamilton & Duggan 2010; Chapman et al. 2011), and are commonly associated with edge habitats of large rivers, irrespective of off-channel floodplain and tributary areas. Therefore the cladocerans found in the gut of *G. maculatus* likely did not originate from floodplain soils.

The abundance of zooplankton food items in riverine environments enables juvenile fish to be highly selective on their prey. The prevalence of cladocerans in the diet of *G. maculatus* is thought to be due to their inability to evade predation as they are large in size and have a conspicuous pattern of movement (Sheppard et al. 2011). In addition, they are highly profitable prey items due to their large size (Mayer & Wahl 1997) and high levels of polyunsaturated fatty acids (Persson & Vrede 2006), explaining the positive electivity index for the *G. maculatus* diet. Other studies have also observed prey selection on cladocerans related to growth advantages for juvenile fish such as yellow perch (Mills et al. 1989). Copepoda were neither preferred nor avoided in the diet of *G. maculatus*, possibly because they are able to evade capture due to fast escape speeds, which influence the search and capture time of predators (Preston et al. 1999; Stephens et al. 2007). Rotifera are small, less profitable prey items, and this may account for the high level of avoidance of this prey type compared to the other zooplankton taxa. Collectively, these results support The Optimal Diet Model (Stephens et al. 2007).

The laboratory experiments were highly valuable in understanding the diet of juvenile whitebait as they allowed factors such as predation, turbidity and prey availability, which may all influence selectivity, to be controlled. Large-bodied cladocerans were consistently their preferred prey choice, with copepods fed on in medium densities, and rotifers avoided by *G. maculatus*. The densities of *G. maculatus* within the experimental tanks were found to influence the amount of zooplankton consumed. Low fish densities resulted in higher amounts of zooplankton being consumed compared to the high fish density treatments in which zooplankton consumption was low. Feeding within the laboratory therefore exhibited density-dependence as more zooplankton could be consumed at low *G. maculatus* densities. This result may suggest that whitebait which migrate early, or in smaller shoals may have a feeding (and potentially a growth) advantage over the main pulse of migrating juveniles. Despite the effect of density-dependence, prey-switching did not occur in tanks with higher fish densities. Large-bodied cladocerans therefore represent an optimal prey choice, potentially leading to greater growth and providing survival advantages over other prey assemblages. Maintaining adequate populations of these zooplankton taxa, either from floodplain or riverine sources, may be important for supporting migrating whitebait in large river systems. Knowledge of food-web interactions between predators such as *G. maculatus* and their zooplankton prey within riverine environments allows for a better understanding of the factors important for sustaining the whitebait fishery.

5.3 Management implications

Floodplain vegetation structure was identified as a significant factor influencing the zooplankton communities sampled on the lower Waikato River floodplain. Within my sampled sites, soil from native forest remnants and areas of scrub were particularly important in providing conditions suitable for emergence of large-bodied cladocerans and copepods, while pastoral floodplains only produced rotifer communities. Scrub and forest remaining in floodplain areas should be protected from land use conversion, drainage or further disconnection.

These changes may promote further production of zooplankton communities that potentially play a pivotal role for higher trophic levels. Juvenile *G. maculatus* were found to largely prey on large-bodied cladocerans which may be produced in areas of inundated floodplains with scrub and forest land cover. Removing scrub and forested floodplains may lead to reductions of large-bodied zooplankton and enhance smaller species, such as rotifers that are not selected by *G. maculatus*. Protection of these remnant vegetated patches or new native riparian plantings may be extremely beneficial for preserving egg banks of large zooplankton. In addition, cladocerans preferentially consumed by larval fish may originate within slow-flowing areas of the river, such as side-arms, or the wider floodplain including connected lakes and wetlands. Therefore protection of edge habitats, including backwaters and side-arms, as well as larger floodplain water bodies, for example through planting to sustain heterogeneity, may be extremely important to promote the growth and survival of these taxa at high abundances. Understanding the key taxa that *G. maculatus* prey upon could therefore be highly advantageous to implementing management protocols that support these food supplies.

5.4 Future work

This thesis has increased understanding of the link between zooplankton emergence within inundated floodplain areas and food supply for migrating juvenile *G. maculatus* in the lower Waikato River. My research is the first comprehensive study in New Zealand looking at the ability of inundated floodplains to produce zooplankton and the potential of *G. maculatus* whitebait to select and feed upon zooplankton, some of which could originate from floodplain areas during inundation. However, only riverine-floodplains were sampled whereas previous research by Górski et al. (2013) included zooplankton sampling in lakes, wetlands and other tributary inflows. Future research should encapsulate off-channel areas such as wetlands and lakes to assess whether these sediments can produce large-bodied zooplankton and whether zooplankton originating there, are preferentially fed on by migrating juvenile whitebait. In order to gain a better insight into whitebait feeding, selectivity on zooplankton and the importance of floodplain areas, replicate studies should be carried out on other large lowland rivers and whitebait populations within New Zealand to see whether similar patterns arise. Furthermore, this study was temporally limited as the Waikato River floodplain had remained dry for many years prior to sampling. Thus further studies should be undertaken over multiple years to increase the understanding of the link between riverine whitebait populations and nutrient and food supplies from their floodplains, especially over time following inundation events. In addition, future studies should aim to encapsulate the feeding preferences of the other four migrating whitebait species to inform more broad scale management plans that encompass the whole fishery. Lastly, further research could be carried out to investigate whether juvenile whitebait and juvenile non-native fish have an overlap in diet and potentially compete for resources, either temporally or spatially within the lower Waikato River floodplain system, due to the widespread distribution of non-native fish species in northern New Zealand.

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Appendices

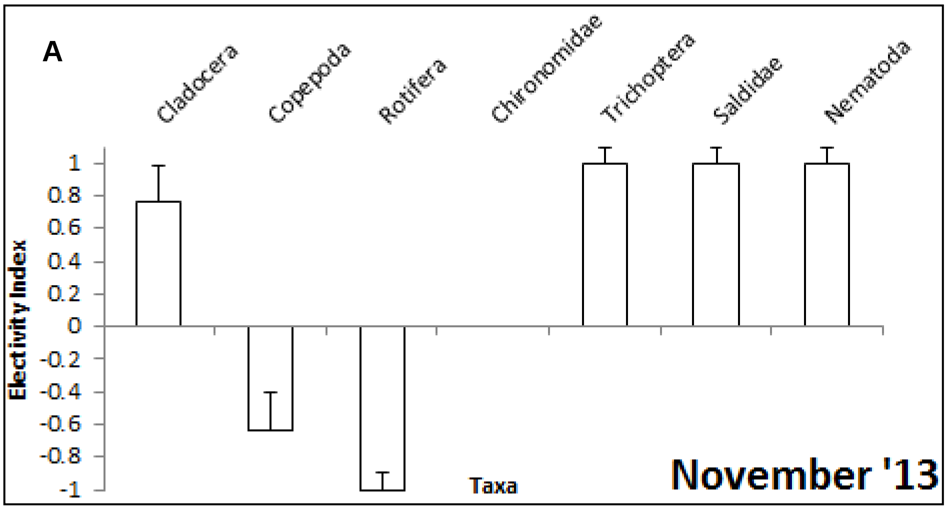
Appendix 1: Taxa found in the gut of *G. maculatus* by site and date in the lower Waikato River.

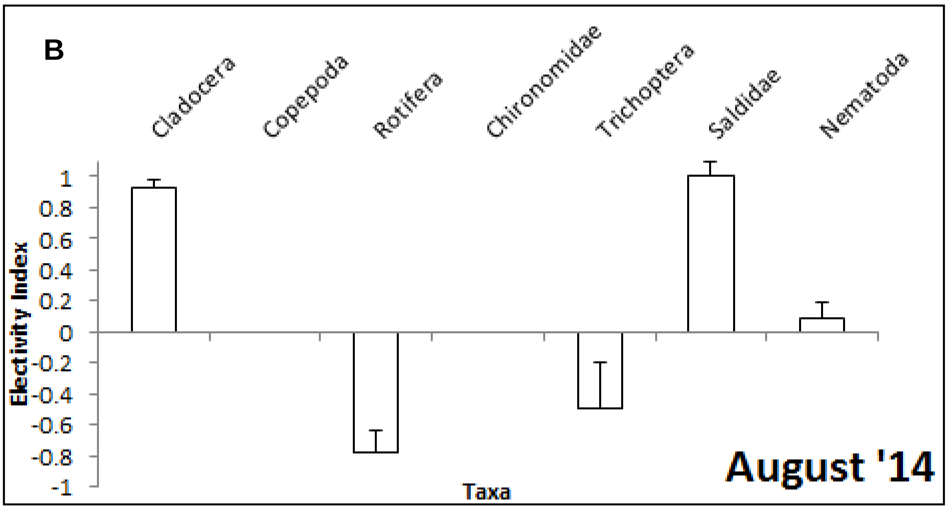
Site: Mercer

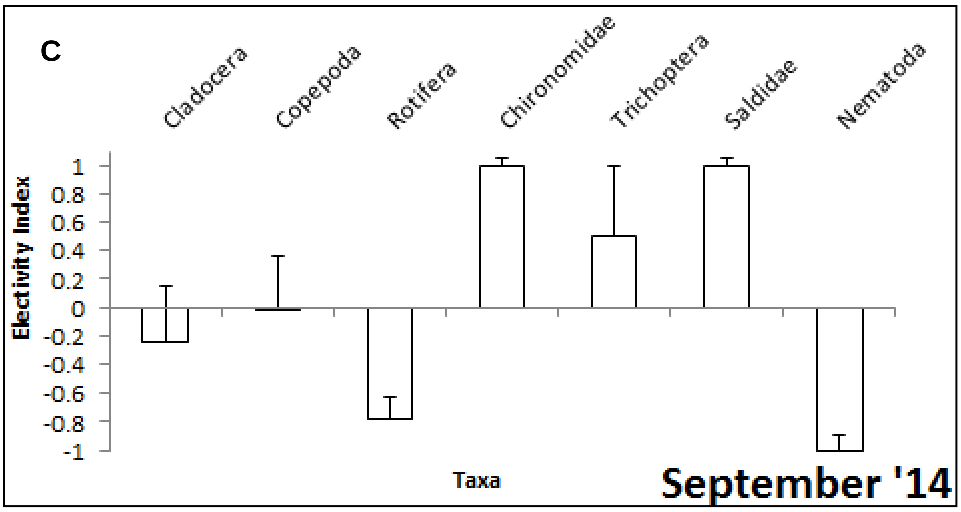
Date	**20/11/2013**	**19/08/2014**	**23/09/2014**	**23/10/2014**	**19/11/2014**
Species					
Bosmina sp.	1	4	1	251	1
Daphnia sp.	2	7	0	39	1
Chydoridae	0	1	0	1	0
Cyclopoid Copepoda	3	0	0	0	0
Harpaticoid Copepoda	3	0	0	0	1
Calanoid Copepoda	0	12	1	0	0
Unknown Insecta	11	14	4	0	7
Chironomidae	12	0	2	1	8
Nematoda	1	1	0	0	0
Bryozoan (statocyst)	1	0	0	0	0
Amphipoda	0	0	0	0	0
Ostracoda	1	1	0	0	0
Trichoptera	3	0	1	4	0
Arachnida	1	0	0	0	0
Saldidae	20	2	5	5	4

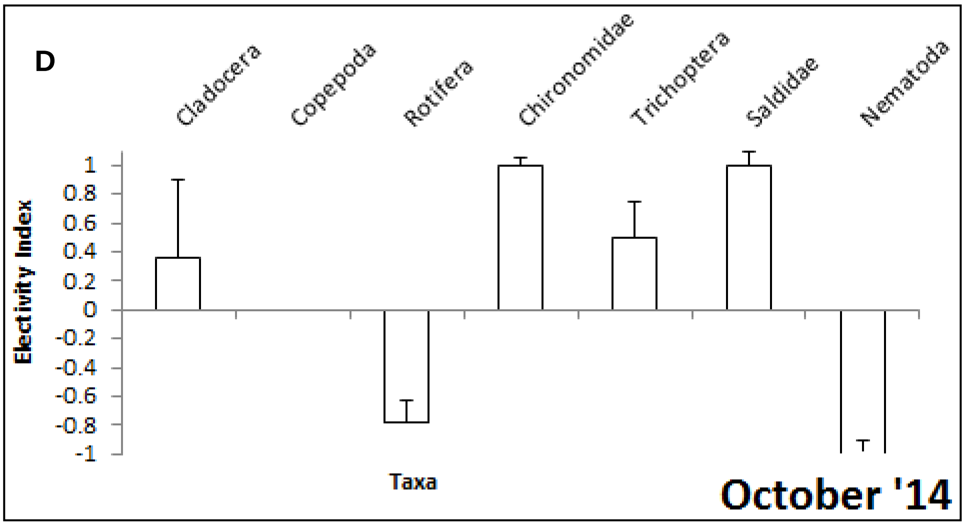
Site: Tuakau					
Date	**20/11/2013**	**27/08/2014**	**23/09/2014**	**23/10/2014**	**19/11/2014**
Species					
Bosmina sp.	4	1	5	8	0
Daphnia sp.	0	0	1	26	0
Chydoridae	0	2	0	0	0
Cyclopoid Copepoda	4	0	0	0	0
Harpaticoid Copepoda	4	0	0	0	0
Calanoid Copepoda	0	0	5	0	0
Unknown Insecta	0	2	7	10	6
Chironomidae	0	138	0	0	5
Nematoda	2	0	0	0	0
Bryozoan (statocyst)	4	0	0	0	0
Amphipoda	0	2	0	1	0
Ostracoda	0	0	0	0	0
Trichoptera	0	6	5	0	2
Arachnida	0	0	0	0	0
Saldidae	10	5	14	1	1

Appendix 2: Ivlev Electivity Index for *G. maculatus*, for all invertebrate groups for sampling during November 2013, August - November 2014, for Mercer (A - E) and Tuakau (F - J) sites on the lower Waikato River (Mean ± SE, n = 12-15 and 11-21, respectively). Values of 0.2 to 1.- = food item selection, -0.19 to 0.19 = no preference and -0.2 to-1 = food item avoidance. November 2013 is presented at the end of the graph to enable direct comparison with November 2014.






C
Cladocera
Copepoda
Rotifera
Chironomidae
Trichoptera
Saldidae
Nematoda
Electivity Index
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
Taxa
September '14


D
Cladocera
Copepoda
Rotifera
Chironomidae
Trichoptera
Saldidae
Nematoda
Electivity Index
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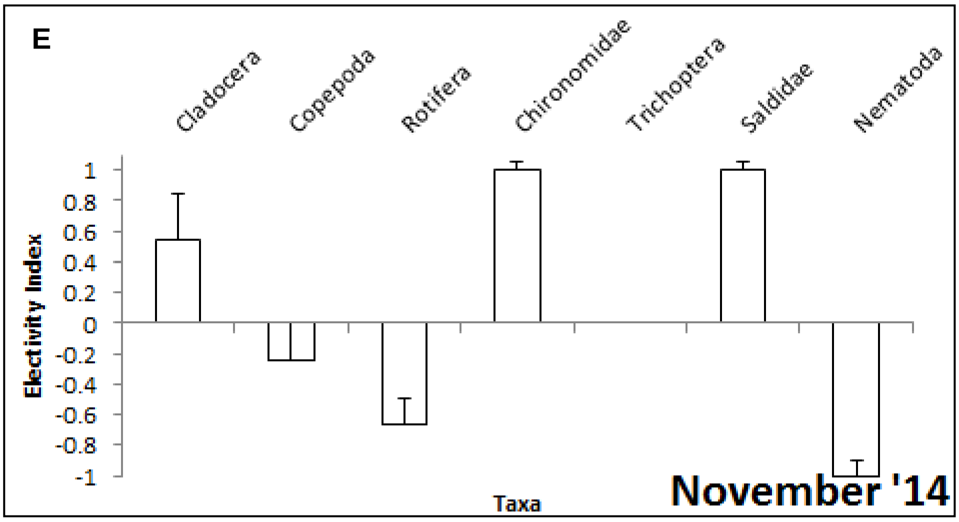
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
Taxa
October '14


E
Cladocera
Copepoda
Rotifera
Chironomidae
Trichoptera
Saldidae
Nematoda
Electivity Index
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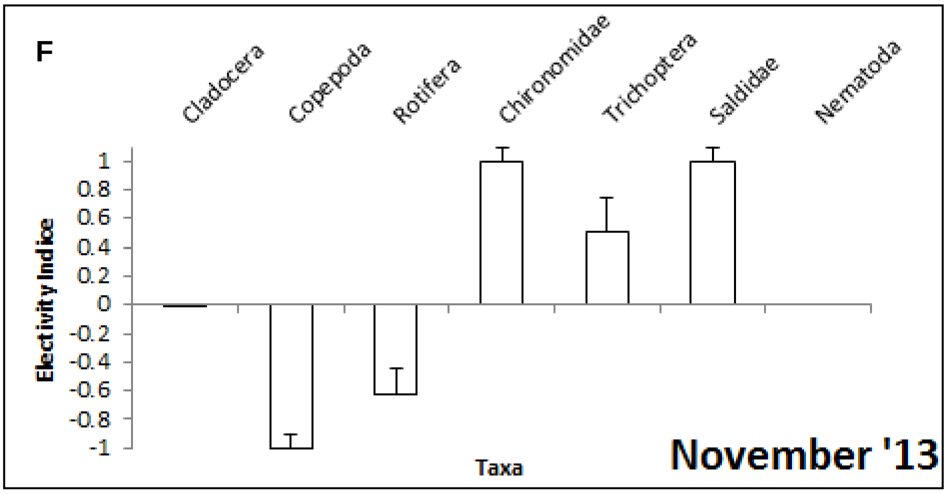
-1
Taxa
November '14


F
Cladocera
Copepoda
Rotifera
Chironomidae
Trichoptera
Saldidae
Nematoda
Electivity Indice
1
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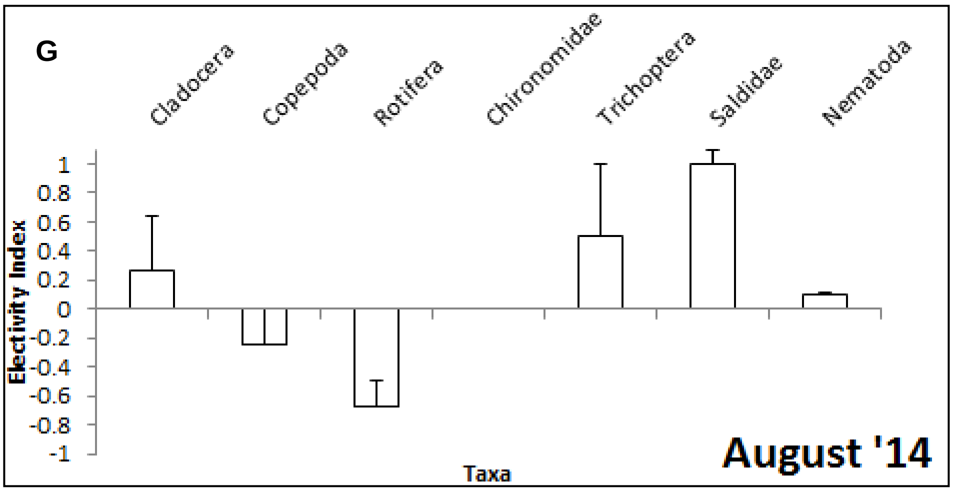
Taxa
November '13


G
Cladocera
Copepoda
Rotifera
Chironomidae
Trichoptera
Saldidae
Nematoda
Electivity Index
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0.8
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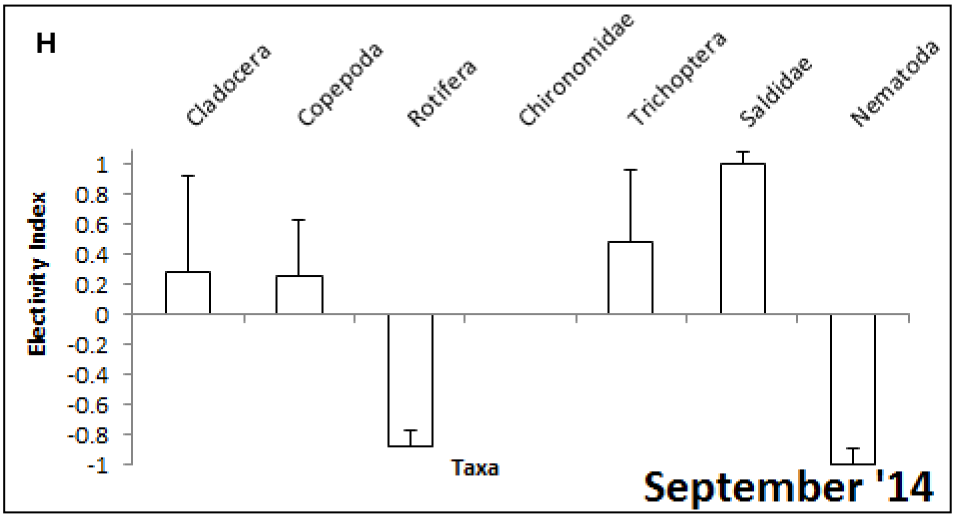
-0.2
-0.4
-0.6
-0.8
-1
Taxa
August '14


H
Cladocera
Copepoda
Rotifera
Chironomidae
Trichoptera
Saldidae
Nematoda
Electivity Index
1
0.8
0.6
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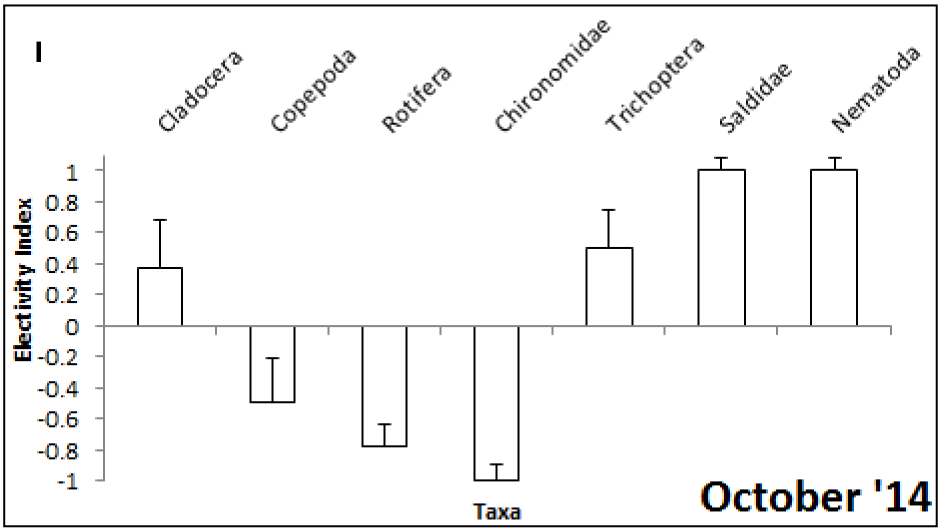
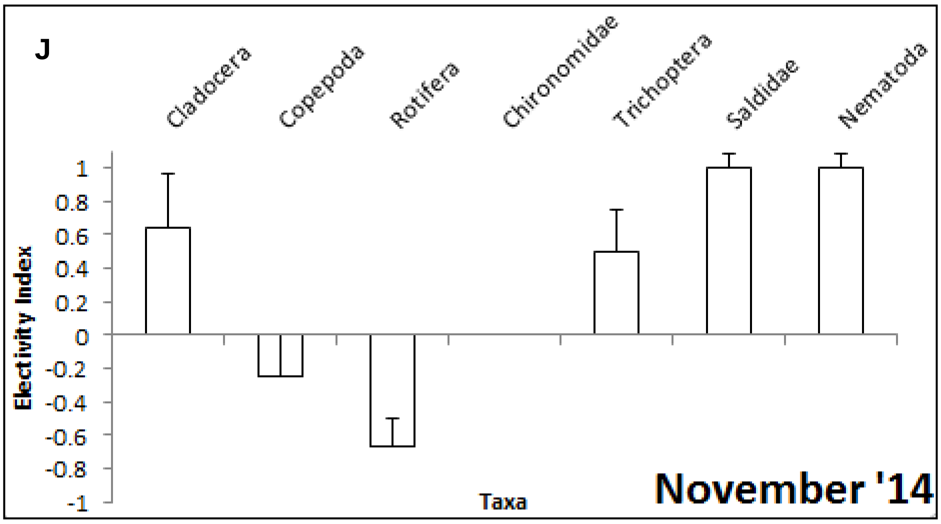
-0.2
-0.4
-0.6
-0.8
-1
Taxa
September '14


I
Cladocera
Copepoda
Rotifera
Chironomidae
Trichoptera
Saldidae
Nematoda
Electivity Index
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
Taxa
October '14


J
Cladocera
Copepoda
Rotifera
Chironomidae
Trichoptera
Saldidae
Nematoda
Electivity Index
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
Taxa
November '14