

**The benthic ecology and food web dynamics of Te Waihora  
(Lake Ellesmere)**

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by

HANNAH F. WOOD

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## Abstract

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Coastal and shallow lakes are often subjected to eutrophication due to nutrients from catchment farming activities. Lake Ellesmere (Te Waihora) is a hyper-eutrophic lake which has gained recent attention because of concerns over its ecological health and fishery status. This study investigated the benthic ecology of the lake by extensive spatial and temporal sampling. Eight littoral sites were sampled on a single occasion, and 20 benthic sites were sampled once per season for one year. Water chemistry conditions, substrate and invertebrate communities varied significantly around the lake. Salinity, pH, DO and seston were primarily affected by freshwater inputs from inflow streams and salt water intrusion due to the lake opening to the sea. On these occasions, salinity reached 32 ‰ at the lake outlet. The lake invertebrate community was depauperate, comprising of only two species of invertebrate predators restricted to the littoral zone and eight benthic invertebrate taxa, dominated by oligochaetes, amphipods and chironomids. Benthic invertebrate abundances also reflect the dominant local substrate, where oligochaetes and chironomids preferred areas of silt substrate, whereas *Potamopyrgus* preferred harder substrate. Stable isotope and gut analysis determined that the primary food sources within the lake were phytoplankton and algae. Macrophytes provided a minimal contribution to the food web, possibly relating to the change in status from a clear water, macrophyte dominated lake to a turbid, phytoplankton dominated condition since the Wahine Storm in 1968. Isotope analysis also showed that the lake food web was markedly different in its carbon values from food webs of its inflow streams and nearby marine source. However the lake food web did show a marine-derived carbon signature. A mesocosm experiment testing the effect of common lentic predators on the abundance of the lake chironomid *Chironomus zealandicus*, showed that if invertebrate predators were present in the lake they could markedly reduce the abundance of the pest prey species. This study highlights that the frequent re-suspension of bottom sediments, lake level

fluctuation resulting in wetting and drying of littoral zones, and the management of the lake opening to the sea all have an effect on the benthic ecology of Te Waihora.

## Chapter 1

### Introduction

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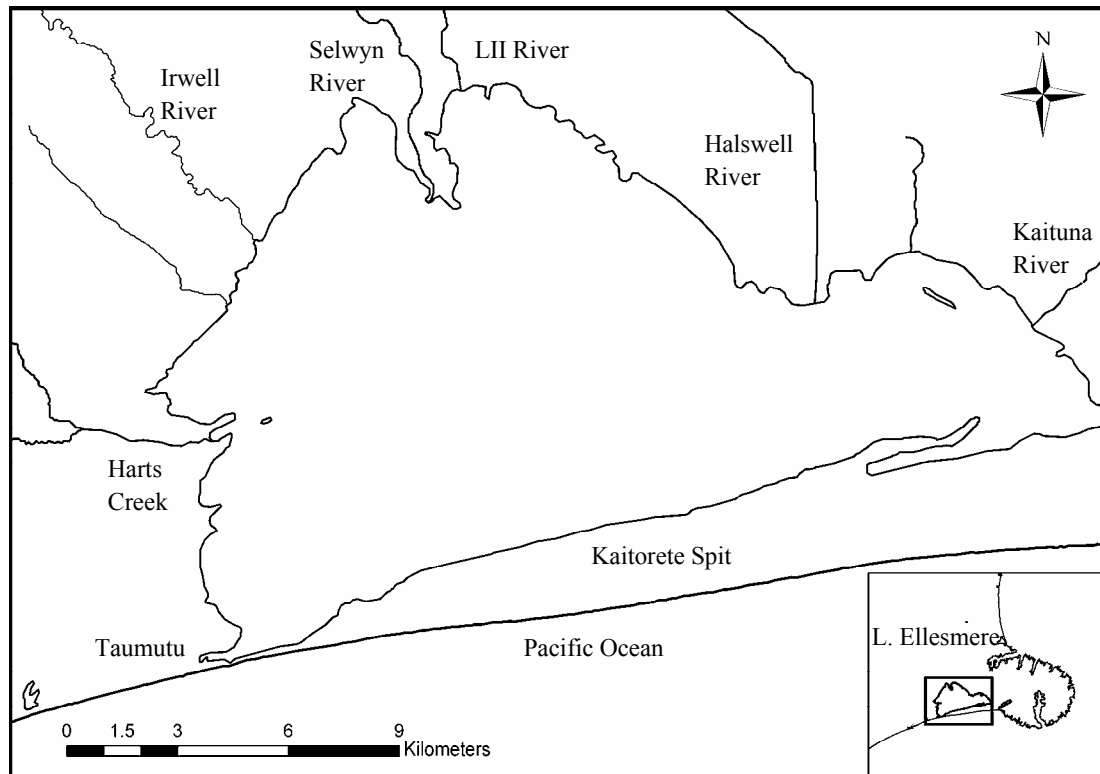
Lake Ellesmere (Te Waihora) is a shallow, coastal lake located on the east coast of the South Island, New Zealand, approximately 40 km south of Christchurch. Historically, the lake has been highly regarded for its cultural (James 1991) and fishery values and extensive bird life (Hughes, McColl & Rawlence, 1974). In recent years, concern has been raised about the health of the lake and fishery (Jellyman & Todd, 1998; Jellyman & Chisnall, 1999). In particular, these concerns are linked to a combination of factors, including marked changes in the lake water quality combined with the human manipulation of the lake opening and lake levels.

#### *Lake formation and evolution*

Te Waihora is approximately 3000 years old (Kirk, 1994; Hemmingsen, 1997). Hemmingsen (1997) proposed that the lake has undergone several transformations beginning as a bay (7,000 years B.P), then forming an estuary (4000 years B.P). This estuary was cut off from the sea and re-formed a lake approximately 3000 years B.P. Te Waihora then underwent two further estuary to lake transformations approximately 1555 years B.P. and 670 years B.P. These estuary-lake states have also been influenced by flood events from the Waimakariri River which has flooded the lake as well as past tsunami events (McFadgen & Goff, 2005). If natural processes are allowed to occur, this sequence of estuary-lake transformation may re-occur (Hemmingsen, 1997).

The catchment area of Te Waihora has undergone substantial land use change from an extensive wetland to farmland since 1850 (Taylor, 1996). The size of the lake has drastically reduced from 30,000 hectares to approximately 20,250 hectares due to agricultural development (Kirk & Lauder, 2000) and to reduce flooding of the surrounding catchment (Hemmingsen, 1997). The bordering farming activity results in high levels of nutrient concentration in the lake, contributing to the lake's current hyper-eutrophic condition (Dawn, 1995), where total nitrogen values in the lake can range from 0.2 - 4.0 mg L<sup>-1</sup> (Kelly & Jellyman, 2007).

Historically, Te Waihora has been recharged by significant freshwater inflows. The major streams and rivers that provide freshwater into Te Waihora comprise of the Selwyn River (Waikirikiri), Irwell River (Waiwhio), LII River, Halswell (Huritini), Harts Creek (Waitatari) and Kaituna River. The Irwell, Halswell and Harts Creek all originate within approximately 19 km of Te Waihora, whereas the Selwyn River flows directly from the foothills and the Kaituna River originates from Banks Peninsula (Hemmingsen, 2001) (Figure 1). The water quality and flow conditions in all of these inflow streams has been highly modified.



**Figure 1.** Study area of Te Waihora showing the main freshwater inflows.

### *Hysteresis*

Moss (1999) describes two general states or conditions which might occur in lakes, either: a clear water and plant dominant state, or a turbid water and phytoplankton dominated state. Each state is stabilized, once it is established, by buffer mechanisms which either promote algal growth or prevent it. Prior to 1968, Te Waihora had high water clarity and extensive emergent macrophyte beds on the west side of the lake extending from Taumutu to the mouth of the Selwyn River. These beds were dominated by *Ruppia megacarpa* and *Potamogeton pectinatus* (Hughes, McColl & Rawlence, 1974). However, after the Wahine storm, fine sediment from the lake bottom became suspended, resulting in poor water clarity and a turbid lake. As a result, this light penetration through the water column was reduced, and the majority of the macrophytes perished (Gerbeaux & Ward, 1991). The macrophytes no longer

stabilized the lake sediment, thus this turbid state has occurred, resulting in a switch to a phytoplankton dominated, turbid state. Since the Wahine storm, the turbid, phytoplankton dominated state has probably been maintained by frequent re-suspension of bottom sediments due to regular wind and wave action which release nutrients into the water column and stimulate phytoplankton growth (Hamilton & Mitchell, 1997).

### *Lake opening*

The lake is separated from the sea by Kaitorete Spit (correctly termed ‘barrier’) (Kirk & Lauder, 2000). This barrier was formed between 7,000 and 6,000 years B.P by a combination of strong northward drift of sediments from the eroding southern Canterbury coast, and sediment loading from the inflow of rivers comprising of silts in suspension, sands, gravels and cobbles (Kirk 1994; Hemmingsen, 1997). Originally, Te Waihora was much deeper (5.0-5.5 m amsl; above mean sea level) and was about twice the area it is today (40,600 ha) (Hemmingsen, 1997). Historically, the lake opened itself naturally upon reaching the height of Kaitorete Barrier (approximately 4 m) (Taylor, 1996; Hemmingsen, 1997). Maori are known to have opened the lake whenever it threatened to flood shoreline settlements, often using horse-drawn scoops. At 4 m, the lake would stretch inland to Taitapu and into Kaituna and Gebbies Valleys (Doc/Ngai Tahu, 2005). Post-European management has not only lowered its level and altered its water level ranges, but also altered the duration and frequency of its connections with the sea (Table 1). The lake is now held at approximately 1 m which is markedly lower than natural levels (Kirk & Lauder, 2000).



**Table 1.** Te Waihora lake opening levels 1901-1959.

Years	Opening Technique	Average opening level
1901-04	Horse-drawn scoops	1.85m amsl (above mean sea level)
1905-1925	Pannett's culvert	1.53m amsl
1926-31	Horse-drawn scoops	1.66m amsl
1932-40	Power scoops	1.54m amsl
1941-1949	Power scoops & dozers	1.35m amsl
1950-1959	Power scoops & dozers	1.19m amsl

Since 1852, the lake opening has been entirely controlled and the pattern in time and duration of openings has been completely altered from its natural state. Typically, the lake is opened by direct excavation, where by a channel is cut through the southern end of Kaitorete Spit near the barrier at Taumutu (Figure 1) allowing both drainage and seawater influx (Hemmingsen, 2001). This occurs when lake water levels have reached a pre-agreed maximum value, which during summer months is 1.05 m and 1.13 m in winter (Hemmingsen, 1997). The shingle bar remains open until southerly storm waves close it. If the lake closes before lake levels are sufficiently reduced, it is manually reopened again (Kirk & Lauder, 2000). The lake has multiple cultural, economic and recreational users, all of whom have differing values and needs, and often conflicting opinions regarding suitable lake levels and opening regimes. For example, commercial eel fishermen are concerned about the productivity of the eel fishery and the timing of openings which are appropriate for adult migration (Jellyman & Chisnall, 1999; Kelly & Jellyman, 2007).

Te Waihora generally experiences relatively predictable weather patterns consisting of southerly wind cycles (storms) followed by coastal sea breezes, northerly and then nor-westerly airflows (DoC/Ngai Tahu, 2005). Average rainfall for the lake area is about 650 mm per year, while average sunshine hours are 2000 per year (DoC/Ngai Tahu, 2005). Mean air temperatures range from 6 °C in July to 16.7 °C in January. (DoC/Ngai Tahu, 2005). Wind

has a significant influence on Te Waihora due to its exposed coastal position on the peninsula and the shallowness of the lake water body. Te Waihora is also frequently subjected to surging or sieching. This is where strong winds can cause water to ‘pile up’ at the downwind end of the lake and simultaneously create a ‘drying’ effect at the other end. This effect is especially strong in Te Waihora in both southerly and north westerly winds due to its shallow basin. One surge event reached a 1.54 m difference in water levels between opposite ends of the lake (Taumutu-west end and Kaituna-east end) (Kirk & Lauder, 2000). As a result, the littoral zone of the lake experiences regular wetting and drying events. This strong wind action also causes fine sediment to be stirred up from the bottom and into the water column, causing high turbidity. The frequency of wind events means the sediment is constantly being re-suspended, making it difficult to settle (Glova & Sagar, 2000). The high volume of suspended solids probably limits light availability available for plant growth and is commonly cited as the factor inhibiting natural plant restoration. However, these wind effects probably mask some of the extreme effects of eutrophication (Dawn, 1995). For example, severe algal blooms as witnessed in nearby Lake Forsyth have not been reported in Te Waihora, and this is probably at least partially due to continual wave action in the lake.

### *Biology and Ecology*

To Ngai Tahu, the local iwi (tribe), Te Waihora is a tribal taonga (treasured) representing a major mahinga kai (customary gathering of food and materials) and an important source of mana (integrity/status). It has national importance as a wildlife habitat and for its ecological values and has been described as the most important wetland habitat of its type in New Zealand (DoC/Ngai Tahu, 2005). Te Waihora is an important location for birdlife. The lake and its associated wetlands support 158 bird species including 133 indigenous (DoC/Ngai Tahu, 2005). The number of birds vary seasonally but up to 98,000 wetland birds have been

estimated to use the lake at any one time, with approximately 80 species recorded as regular inhabitants of Te Waihora (DoC, 2008). Significant mahinga kai species include kakī ānau (black swan), kōtuku (white heron) and kererū (wood pigeon) (DoC/Ngai Tahu, 2005). Recreational game-bird hunting is a popular activity at Te Waihora which includes the Canada goose (*Branta Canadensis*), paradise shelduck (*Tadorna variegata*), mallard duck (*Anas platyrhynchos*) and the New Zealand shoveler (*Anas rhynchotis*). Prior to 1950, the larger Lake Ellesmere was surrounded by extensive and diverse wetlands (Hughes, McColl & Rawlence, 1974). However, almost all of this original wetland has been removed due to intensive farming encroaching on the lake perimeter (Gerbeaux & Ward, 1991). Te Waihora once had extensive macrophyte beds present in the lake including *Ruppia megacarpa* and *Potamogeton pectinatus* (Hughes, McColl & Rawlence, 1974; Taylor, 1996; Doc/Ngai Tahu, 2005) extending from Taumutu to the mouth of the Selwyn River (Hughes, McColl & Rawlence, 1974). These macrophytes almost certainly played an important role in the lake by reducing the amount of wave action that caused lake-shore erosion and re-suspension of sediment into the water column resulting in turbidity. They were also probably an important food source for some bird species contributing to the once large black swan population and also provided fish habitat as in other lakes such as Lake Alexandrina (Talbot & Ward, 1987) and Lake Coleridge (James et al. 1998). There have been reports of periodic disappearance of macrophyte beds since 1904. During the 1920s and again in the 1940s a decline in the macrophyte beds was reported, with reports of a significant recovery in the 1950s, however water clarity remained high (Taylor, 1996). In 1968, most of the beds were destroyed during the Wahine Storm and they have never been able to recover to their former status (Taylor, 1996). Gerbeaux & Ward (1986) studied the cause of poor macrophyte regeneration in Te Waihora, and concluded that the re-establishment of these aquatic plants is possible under favourable lake conditions such as low salinity, high light and water temperature, and calm

conditions. Sites that may demonstrate these conditions include the bay at Taumutu and around the mouths of the Selwyn and Halswell rivers, and Kaituna Lagoon. However, this would come at a substantial cost with unknown short and longer term effects on the lake (Gerbeaux & Ward, 1996).

### *Importance and Uses*

#### Commercial fishing

Commercial fishing is an integral part of the Waihora community and has existed since Pre-european times. Species that are commercially fished are freshwater eel, short-finned (*Anguilla australis*) and long-finned (*A. dieffenbachia*), yellow-eyed mullet (*Aldrichetta forsteri*) and flounder (*Rhombosolea spp.*) (DoC/Ngai Tahu, 2005)

#### Mahinga Kai

The region of Te Waihora has always been a valued food source for Maori, where food supplies were obtained by fishing, hunting and gathering. The lake and surrounding areas were traditionally renowned for an abundance of eel, freshwater mussel, flounder, mullet and other fish species which occasionally entered the lake from the sea, waterfowl, plants and special mud used for dying (Hemmingsen, 1997). For local Maori, this area is one of great mana and is also known as ‘Te Kete Ika O Rakaihautu’ (The Fish Basket of Rakaihautu).

### *Research context*

Specific research has been carried out on various aspects of the lake, including factors affecting water clarity (Gerbeaux & Ward, 1991), the condition of eel stocks and migration (Jellyman, Glova & Todd 1996; Jellyman & Todd, 1998; Graynoth & Jellyman, 2002), food web links (Kelly & Jellyman, 2007), phytoplankton (Lineham 1983), coastal geomorphology (Hemmingsen, 1997) and the effects of plant material on invertebrates (Dawn, 1995). However, despite the proximity of this lake to a major New Zealand city and its cultural, economic and recreational value, surprisingly little work has been done on the ecology of the lake. To my knowledge, no previous large-scale spatial and temporal investigation has been conducted on the benthic ecology of Te Waihora.

In this thesis I have addressed three aspects of the benthic ecology of Te Waihora. Specifically, my objectives were to investigate the following questions:

- 1) Do benthic communities vary spatially and temporally within the lake? If so, how do environmental conditions such as turbidity, salinity and temperature influence benthic invertebrate distribution and abundance across the lake? This is the focus of Chapter 2.
  
- 2) What is the structure of the lake food web and what is the primary food source of the lake? Does it change spatially? How does it compare to surrounding food webs from inflow streams and a nearby marine source? Chapter 3 addresses this question.

3) Are there invertebrate predators in the lake? How might invertebrate predators influence chironomid populations from the lake in both clear and turbid water? Chapter 4 describes a brief survey and experiment addressing this question.

The data chapters of this thesis have been written as a series of stand-alone manuscripts. Consequently, there is some repetition of information in some chapter Introductions and Method sections.

## Chapter 2

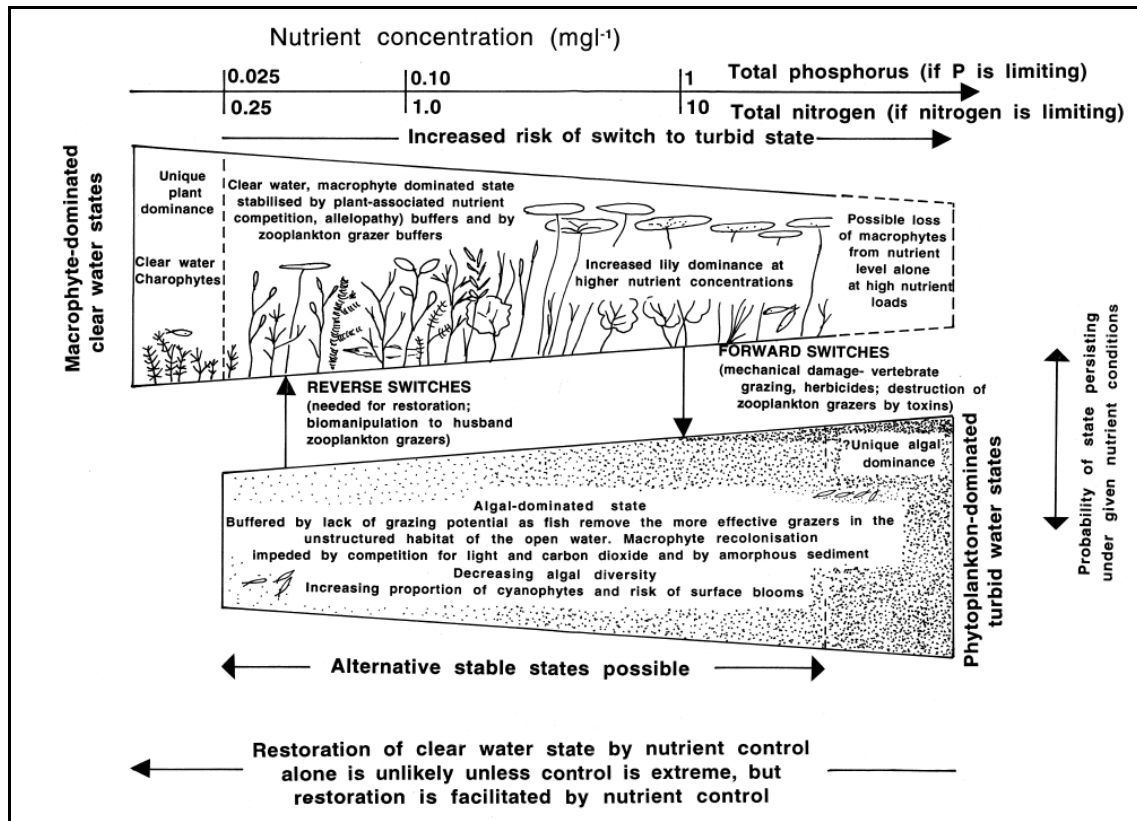
# **Spatio-temporal variation in physico-chemical and aquatic invertebrate communities in Lake Ellesmere (Te Waihora)**

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### **INTRODUCTION**

Lake Ellesmere (Te Waihora) is a large, shallow, turbid coastal lake which has experienced degraded water quality over the past decades (Gerbeaux & Ward, 1991; Kelly & Jellyman, 2007). Historically, the lake covered an area of approximately 30,000 hectares and was surrounded by an extensive wetland and lowland natural forest. Since European settlement in Canterbury the coastal forest has been cleared and the lake has been steadily reduced in area to accommodate urban expansion and increased agriculture. Today, the lake covers approximately 20,250 hectares (Jellyman & Todd, 1996; Jellyman & Chisnall, 1999). Prior to 1968, aquatic macrophytes such as *Ruppia* spp. and *Potamogetan pectinatus* beds were widespread in Te Waihora. These macrophytes helped maintain water clarity by reducing the effect of wind action stirring up bottom sediments and provided important habitat for invertebrates and fish (Glova & Sagar, 2000). In 1968, the Wahine Storm destroyed almost all of these plant beds. In the years preceding the storm, the lake had also been receiving increasing nutrient inputs from its inflow streams and the surrounding catchment (Hughes, McColl & Rawlence, 1974).

Lakes that have high nutrient loading are at a higher risk of undergoing hysteresis. Hysteresis is the process by which a lake switches between two alternative states; a clear water, macrophyte dominated state and a turbid, phytoplankton dominated state (Figure 1). Each of these states can be maintained by a number of differing mechanisms, which either promote



**Figure 1.** Model of two alternative stable states suggested for lake systems; a clear water macrophyte dominated state or, an algal dominated turbid state (Moss, 1999).

algal growth or prevent it. For a lake to switch from one state to another, some perturbation or disturbance needs to occur. A number of factors might support the macrophyte dominated state including allelopathy (growth-inhibiting chemicals released by other plants), nitrogen limitation due to high plant uptake, or heavy grazing of phytoplankton by zooplankters. This condition has been recorded in both New Zealand lakes such as Tomahawk Lagoon in Dunedin (Mitchell, 1989; Scheffer et al. 1993) and Lake Rotorua, Hamilton (Clayton & de Winton, 1994) and overseas in lakes such as Lake Takern, and Lake Krankesjön, Sweden (Scheffer et al. 1993; Hargeby, Blindow & Hansson, 2004). Tomahawk Lagoon (Otago) is a shallow freshwater coastal lake that has shown alternative phases between phytoplankton and macrophyte dominance since 1963 (Mitchell, 1989). Ogilvie & Mitchell (1998) concluded that re-suspension of sediment in three shallow lakes (Tomahawk Lagoon, Hawksbury

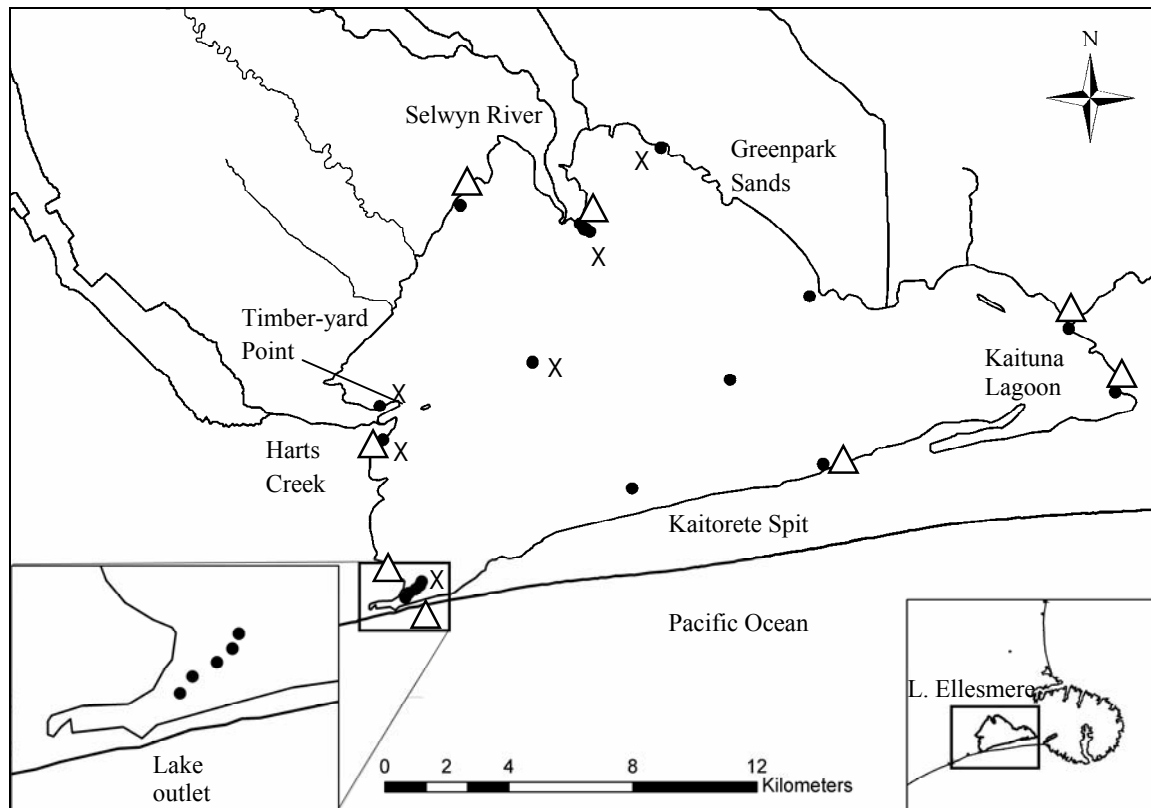


Lagoon and Tuaitoto; Otago) had positive effects on phytoplankton growth, which was associated with relief of nitrogen deficiency in the phytoplankton.

Since the Wahine storm the turbid, phytoplankton dominated state in Te Waihora has probably been maintained by frequent re-suspension of bottom sediments due to regular wind and wave action, which release nutrients into the water column and stimulate phytoplankton growth (Hamilton & Mitchell, 1997). High turbidity in the lake also restricts light penetration through the water column, inhibiting benthic plant growth (Gerbeaux & Ward, 1991). The loss of extensive aquatic macrophyte beds have almost certainly resulted in marked changes in the invertebrate community in Te Waihora (Kelly & Jellyman, 2007). However, few studies have been published on invertebrate communities in the lake either prior to or since 1968 (Yeates, 1965; Dawn, 1995). The lake experiences a number of disturbances, including continued wind-driven sediment re-suspension, large fluctuations in lake levels due to irregular lake opening to the sea, and localised changes in littoral zone wetting and drying caused by wave action and potentially strong salinity gradients. These factors might be expected to strongly influence the diversity and composition of benthic invertebrate communities. In this study I investigated spatial and temporal patterns in benthic communities throughout Te Waihora in order to determine if environmental conditions influenced benthic invertebrate distributions.

### Study Site

Lake Ellesmere (Te Waihora) is a shallow-coastal lake abutting the southern boundary of Banks Peninsula (Figure 2). The lake covers an area of approximately 20,250 hectares making it the largest lake in the alluvial fan of the Canterbury Plains, and the 4<sup>th</sup> largest lake in New Zealand. Historically, the lake reached 4 m in depth where it would breach the coastal barrier (Kaitorete Spit) (Hemmingsen, 1997), whereas its' current maximum depth is approximately 2 m (Kelly & Jellyman, 2007). The lake is opened manually to the Pacific Ocean an average of 3.4 times per year at the south-west corner of the lake at Taumutu. Lake opening occurs to prevent flooding of the surrounding farmland.



**Figure 2.** Distribution of littoral (triangle) and benthic (dots) invertebrate sampling sites around Te Waihora between November 2006 and March 2008. Inset of the lake outlet shows a gradient of five sites. A similar gradient of four sites extends from the Selwyn River mouth into the lake. Dominant substrate (sand/silt) is present at eight sites (X) including three at the lake outlet and one at the Selwyn River mouth.

A total of 28 sites were selected throughout the lake, eight littoral zone sites were sampled on a single occasion in March 2008, and 20 benthic sites were sampled on four occasions (once per season) in November (spring) 2006, March (autumn) 2007, July (winter) 2007 and January (summer) 2008 (Figure 2).

## **METHODS**

### *Water quality and physico-chemical variables*

A range of physico-chemical variables were measured at the 20 benthic sites sampled during each of the four sampling occasions. At each site conductivity, pH, dissolved oxygen, salinity, turbidity and temperature were measured using a Horiba U-10 water quality meter (Horiba Ltd, Japan). Depth was measured at each site and vertical water clarity estimated with a secchi disc. For the first two sampling occasions, a one litre water sample was collected approximately 30 cm below the water surface and total and dissolved nitrogen and phosphorous were measured by Hills Laboratory (Hamilton). Suspended organic and inorganic sediment was estimated by filtering with a Whatman filter (40  $\mu\text{m}$ ) and ashing at 550 °C for four hours. Phytoplankton biomass was estimated by chlorophyll *a* following Standard Methods (19<sup>th</sup> ed. 1995). A sample of the substrate from each site was also collected on a single occasion for sediment composition analysis using a ponar grab sampler (16.5 cm x 15 cm). The substrate was classified according to Analytical Sedimentology (1994).

### *Invertebrate sampling*

Eight littoral zone sampling sites were sampled with a kicknet (250 µm mesh) on a single occasion to determine the presence of any fauna restricted to littoral habitats. Approximately 30 net sweeps were carried out at each site by two collectors, each working independently. At each site all littoral habitats were sampled including emergent and submerged vegetation, wood and bed material. All invertebrates collected were preserved in 70 % ethanol in the field. In the laboratory, invertebrates were identified under a dissection microscope to the lowest taxonomic level possible according to keys by Winterbourn, Gregson & Dolphin (2000).

At the 20 benthic seasonal sampling sites, four replicate ponar grab samples (16.5 cm x 15 cm; 500 µm mesh) were collected. The sample was sieved in the field through a 500 µm mesh and preserved in 90 % ethanol. In the laboratory, invertebrates were identified to the lowest taxonomic level possible according to keys by Chapman & Lewis (1976) and Winterbourn, Gregson & Dolphin (2000) and counted. Oligochaetes and polychaetes were identified to Class. Zooplankton were sampled at each site by three replicate plankton net samples (18 cm diameter x 34.5 cm length). A sample was taken by drawing the net vertically through 1 m of the water column. Samples were preserved in 90 % ethanol in the field. In the laboratory, zooplankton were identified to Genus and counted.

### *Statistics*

Analysis of variance tests were carried out using Sigmastat 3.0. Data was tested for normality and homogeneity and transformed if necessary. Significance was set at  $P < 0.05$ . Multivariate

analysis of assemblage data was conducted by canonical correspondence analysis (CCA) using PC-ORD (McCune & Mefford, 1999).

## RESULTS

### *Spatial patterns*

#### Water chemistry

Water chemistry conditions showed a number of spatial differences depending on location throughout the lake. Both salinity (ANOVA,  $F = 219.36$ ,  $P = 3.3 \times 10^{-13}$ ) and pH (ANOVA,  $F = 3.234$ ,  $P = 0.05$ ) varied significantly (Table 1), with the highest salinity at the lake outlet which was 31.9 ‰, and the lowest at Timber-yard point (2.3 ‰). These changes in salinity indicate differing salt water intrusion around the lake and this probably also affects several other water chemistry parameters. For example, pH ranged from 7.7 – 9.2 with the highest pH values at the lake outlet and the lowest values at Kaituna Lagoon.

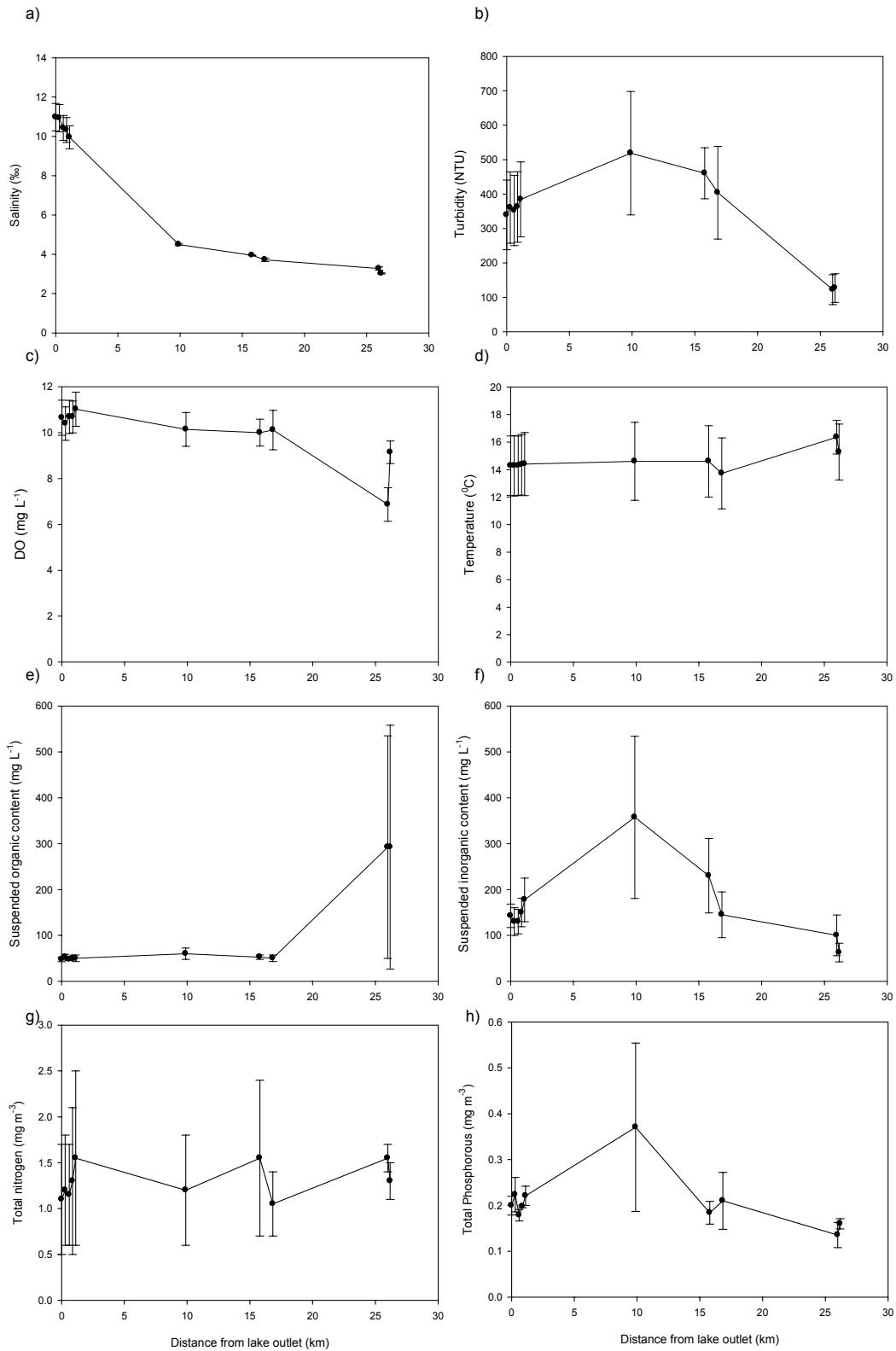
**Table 1.** Water chemistry parameters for 20 sites in four regions across Te Waihora.

Variable		Area				ANOVA	
		Lake outlet (n=5)	Harts Creek (n=4)	Selwyn River (n=5)	Kaituna Lagoon (n=6)	F Stat	P-value
Salinity ‰	Mean	10.5	3.4	3.3	3.9	219.37	0.000
	SE	0.19	0.21	0.04	0.32		
	Range	10.33-10.98	2.95-3.9	3.25-3.43	3.28-5.15		
pH	SE	0.01	0.04	0.04	0.10	3.23	0.05
	Range	8.56-8.61	8.46-8.63	8.56-8.61	7.92-8.56		
DO mg L <sup>-1</sup>	Mean	10.7	10.4	10.3	9.2	3.22	0.051
	SE	0.10	0.18	0.39	0.51		
	Range	10.4-10.69	10-10.83	10.47-10.79	6.87-10.14		
Temperature °C	Mean	14.3	14.9	14.5	15.5	1.10	0.377
	SE	0.03	0.45	0.50	0.73		
	Range	14.28-14.35	13.65-15.78	13.95-14.15	13.73-18.75		
Turbidity NTU	Mean	359	351	462	301	2.11	0.139
	SE	7.40	17.52	28.27	61.93		
	Range	339.25-362.5	310.75-395.25	547.75-414.75	122.25-519		
Susp. Org mg L <sup>-1</sup>	Mean	49.5	46.9	46.00	132.9	2.13	0.137
	SE	0.94	4.72	2.18	50.49		
	Range	47.5-52.5	40-60	42.5-50	50-292.5		
Susp. Inorg mg L <sup>-1</sup>	Mean	146.0	131.9	153.00	169.2	0.26	0.851
	SE	8.75	10.67	23.74	44.10		
	Range	130-150	105-152.5	110-145	100-357.5		
Total N mg m <sup>-3</sup>	Mean	1.26	1.59	1.37	1.35	0.80	0.514
	SE	0.08	0.30	0.12	0.08		
	Range	1.1-1.3	1.1-2.45	0.9-1.55	1.05-1.55		
Total P mg m <sup>-3</sup>	Mean	0.20	0.21	0.22	0.20	0.08	0.969
	SE	0.01	0.02	0.05	0.04		
	Range	0.18-0.22	0.17-0.25	0.10-0.21	0.12-0.37		

Spot temperature ranged from 6 °C – 26.6 °C with the highest temperatures at Kaituna Lagoon. These temperature values probably affect dissolved oxygen and so DO was lowest at Kaituna Lagoon (mean = 5.1 mg L<sup>-1</sup>) and highest at the lake outlet (mean = 12.8 mg L<sup>-1</sup>). Several parameters were probably also influenced by freshwater inflows. For example, turbidity values were highest at the Selwyn River mouth (999 NTU) and lowest at Kaituna Lagoon (30 NTU). While suspended organic matter (seston) showed an opposite pattern

ranging from 40 - 292.5 mg L<sup>-1</sup> with the highest values at Kaituna Lagoon (1090 mg L<sup>-1</sup>) and the lowest values at the Selwyn River mouth (0 mg L<sup>-1</sup>). By contrast, suspended inorganic matter was lowest at Kaituna Lagoon (20 mg L<sup>-1</sup>) and highest at Kaitorete Spit (860 mg L<sup>-1</sup>). Nutrient loads were also associated with inflow streams. Total nitrogen values ranged from 0.2 – 3.3 mg m<sup>-3</sup> and were highest at Timber-yard point and lowest at the Selwyn River mouth. While total phosphorous values ranged from 0.004 – 0.554 mg m<sup>-3</sup>, where the highest values were at Kaitorete Spit.

Water chemistry conditions changed across the lake from the south west corner of the lake at the outlet to the sea, to the south east corner of the lake at Kaituna Lagoon. A strong salinity gradient was present across the lake ranging from 3.0 – 10.9 ‰ (Figure 3a). The highest salinity value was at the lake outlet decreasing to the lowest value at a point furthest from the sea at Kaituna Lagoon (26 km from the outlet). During winter when the lake was open to the sea, salinity reached 31.9 ‰ at the lake outlet. There was an overall decrease in pH, DO, turbidity and suspended inorganic content from the outlet to the east end of the lake (Figure 3). Conversely, suspended organic content and temperature increased across this west to east gradient. Total nitrogen and total phosphorous however, did not display any consistent pattern laterally across the lake.



**Figure 3.** Spatial patterns of water chemistry from the lake outlet to Kaituna Lagoon. Salinity (a), turbidity (b) DO (c), temperature (d), suspended organic content (e) suspended inorganic content (f), total nitrogen (g) and total phosphorous (h). Values are mean  $\pm$  SE (n=4).



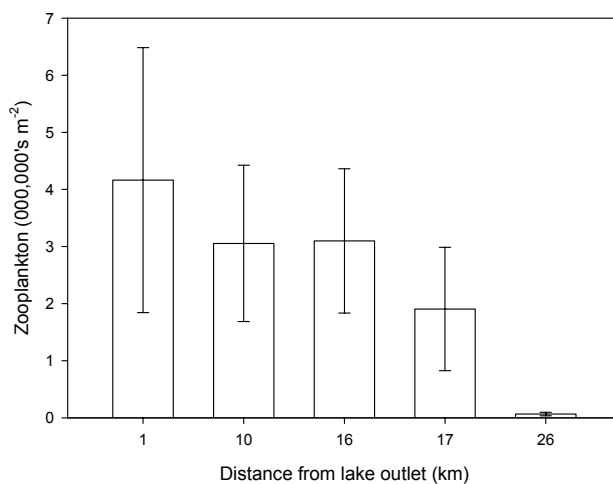
## *Spatial patterns*

### Littoral zone

A total of eight taxa were collected from littoral zone sites around the lake. These were dominated by taxa found in the benthos such as the amphipod *Paracorophium excavatum*, the snail *Potamopyrgus antipodarum*, the mysid *Tenagomysis chiltoni* and the midge *Chironomus zealandicus*. However, at the Selwyn River mouth and in the Kaituna Lagoon, two macroinvertebrate predator species were collected; the damselfly *Xanthocnemis zealandica*, and the backswimmer *Anisops wakefieldi*, as well as the water boatman *Sigara* species, all which had not been collected in any benthic or pelagic samples.

### Benthic and pelagic zone

The zooplankton was dominated by *Gladioferens pectinatus*, and decreased with distance from the lake outlet (4.2 million individuals  $m^{-2}$ ) to Kaituna Lagoon (65,000 individuals  $m^{-2}$ ) (Figure 4).



**Figure 4.** Zooplankton densities at sites ranging from the lake outlet to Kaituna Lagoon (mean  $\pm$  SE;  $n=3$ ).

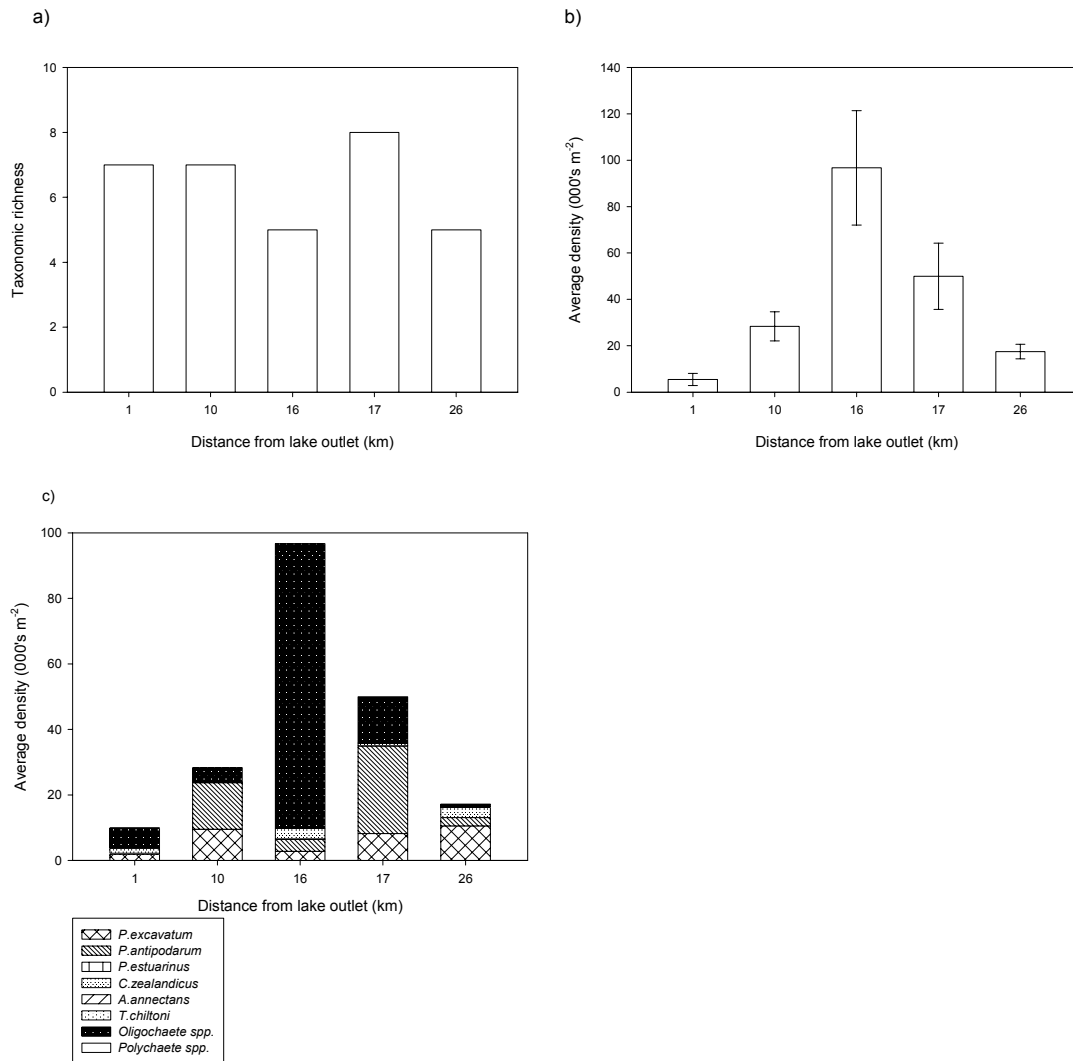
The total number of benthic invertebrate taxa collected was eight (Table 2). Overall, benthic invertebrate taxonomic richness varied from the lake outlet to Kaituna Lagoon, where the maximum number of taxa (8) are found at the east end of Kaitorete Spit, and the minimum number of taxa (5) are found at the middle of the lake and at Kaituna Lagoon (Figure 5a). Oligochaete species, *Paracorophium excavatum*, *Potamopyrgus antipodarum* and *Chironomus zealandicus* were present in relatively high numbers at almost all of the sites. While *Austridotea annectens*, *Tenagomysis chiltoni*, *Potamopyrgus estuarinus* and polychaete species were present at several sites but in low numbers. Oligochaetes dominated 60 % of benthic sites, while the amphipod *Paracorophium excavatum* was dominant at 25 % of sites, and *Potamopyrgus antipodarum* dominated 15 % of sites.

**Table 2.** Invertebrate species found during benthic seasonal sampling from November 2006 to January 2008.

	Family	Species
Amphipoda	Corophidae	<i>Paracorophium excavatum</i>
Mollusca	Hydrobiidae	<i>Potamopyrgus antipodarum</i>
	Hydrobiidae	<i>Potamopyrgus estuarinus</i>
Diptera	Chironomidae	<i>Chironomus zealandicus</i>
Isopoda	Idoteidae	<i>Austridotea annectens</i>
Crustacea	Mysidae	<i>Tenagomysis chiltoni</i>
Oligochaeta	Tubificid	<i>Limnodrilus species</i>
Polychaeta		<i>Polychaete species</i>

Average invertebrate density was lowest at the lake outlet (5,500 m<sup>-2</sup>), increasing to a maximum of 97,700 m<sup>-2</sup> at the lake centre, and decreasing to 17,500 m<sup>-2</sup> at Kaituna Lagoon (Figure 5b).

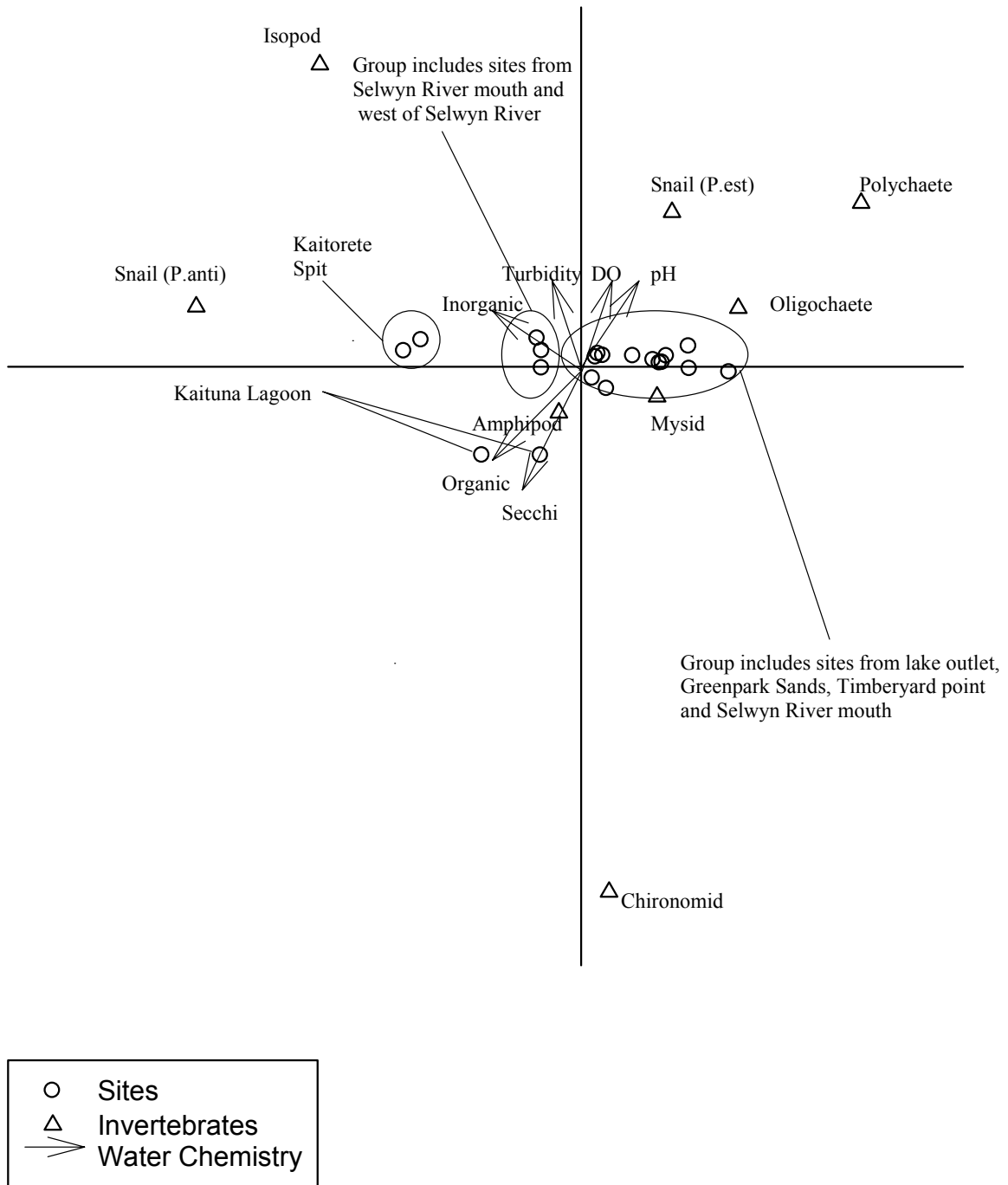
Furthermore, benthic invertebrate composition also varied with distance from the lake outlet (Figure 5c). Oligochaetes dominated the composition in the centre of the lake, whereas *Potamopyrgus antipodarum* dominated sites along the Kaitorete Spit. Low densities of amphipods, snails, chironomids, oligochaetes and polychaetes occurred at the lake outlet and sites furthestest away from the outlet at Kaituna Lagoon (Fig 5c).



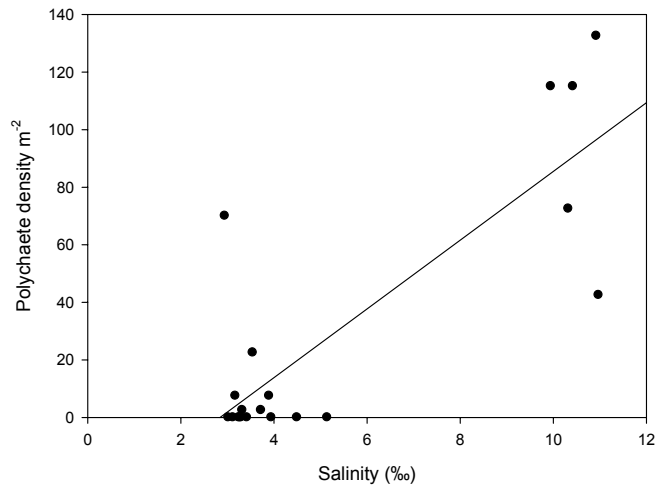
**Figure 5.** a) Taxonomic richness, b) average benthic invertebrate density across a spatial gradient and c) benthic invertebrate composition (average density) over a spatial gradient (lake outlet to Kaituna Lagoon).

An ordination of environmental variables indicated that the most important factors driving site differentiation were turbidity, DO, pH, secchi depth, suspended organic matter and suspended inorganic matter (Figure 6). Suspended organic matter and secchi depth are probably closely related and appear to drive communities at Kaituna Lagoon, where organic matter and secchi depth were generally low. These sites are also characterised by high densities of *C. zealandicus*. Turbidity and suspended inorganic matter are also probably closely related and appear to drive communities along the Kaitorete Spit, where the snail *P. antipodarum* and the isopod *A. annectens* occurred commonly. At these sites, turbidity and inorganic matter were generally high. Whereas DO and pH appear to drive a number of sites including sites at the lake outlet, the centre of the lake, the Selwyn River mouth and Greenpark Sands. At these sites, the snail *P. estuarinus*, polychaetes and oligochaetes were important members of the community. Finally, the mysid *T. chiltoni* occurred in higher numbers at the lake outlet and at Timber Yard point. Several other distributional relationships were apparent, for example, the density of polychaete worms showed a positive correlation with salinity ( $r^2 = 0.6793$ ,  $p < 0.0001$ ) (Figure 7).

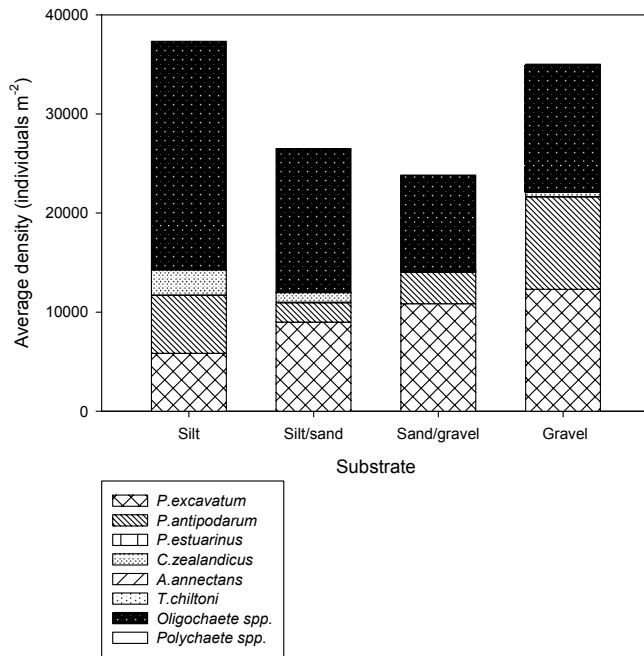
Despite many sites being dominated by sand/silt substrate (Figure 2), benthic invertebrate composition did vary with dominant substrate type in an area (Figure 8). For example, *C. zealandicus* and oligochaetes had higher densities at Kaitorete Spit, the lakecentre, Greenpark sands and Kaituna Lagoon where silt was the dominant substrate, whereas sand/gravel substrate had reduced densities of these species. *P. antipodarum* had a higher density in gravel substrates at the lake outlet, eastern Kaitorete Spit and the north-west corner of the lake (Fig 8).



**Figure 6.** CCA of all benthic invertebrates sampled at 20 sites from November 2006 to January 2008.



**Figure 7.** Salinity and Polychaete spp. density from benthic sites over four sampling occasions.

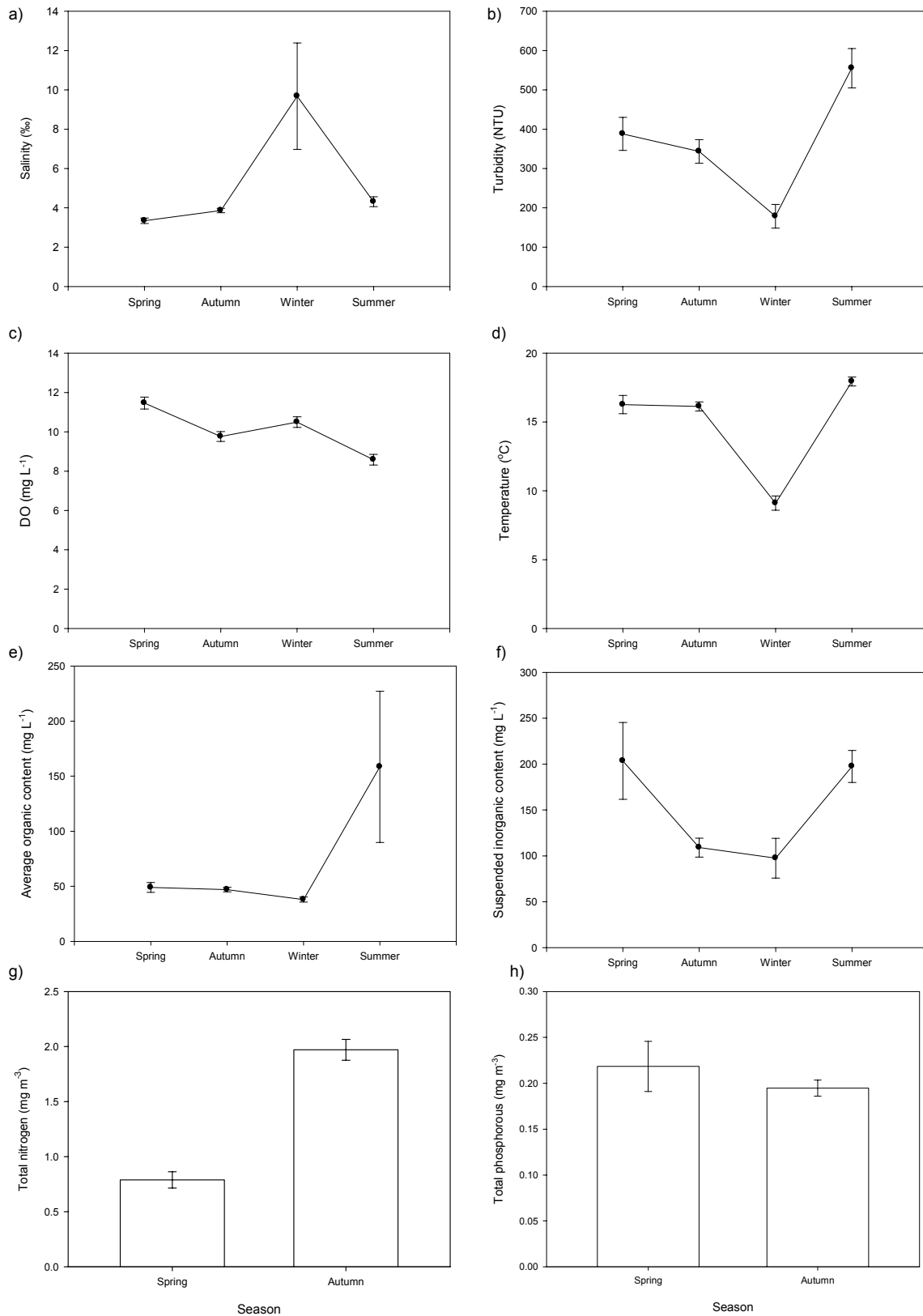


**Figure 8.** Benthic invertebrate composition (average density) in each common substrate type found in Te Waihora.

## *Seasonal patterns*

### Water chemistry

Water chemistry conditions changed markedly in winter, which also coincided with the time the lake was open to the sea. Salinity was significantly higher during winter (F stat = 4.77, P = 0.004), and reached 31.9 ‰ at the lake outlet, whereas the Selwyn River still remained relatively low during winter at 2.6 ‰ (Figure 9a). Similarly, pH was significantly lower in winter (F stat = 18.1, P =  $5.7 \times 10^{-9}$ ) as was temperature (F stat = 66.3, P =  $3.6 \times 10^{-21}$ ) turbidity (F stat = 15.8, P =  $4.6 \times 10^{-8}$ ), suspended organic content (F stat = 2.8, P = 0.048) and suspended inorganic content (F stat = 4.8, P = 0.004) (Figure 9). These water chemistry variables were all higher during summer and spring, while DO levels fluctuated between 5.1 mg L<sup>-1</sup> and 12.8 mg L<sup>-1</sup>, and were highest in spring and lowest in summer (F stat = 19.5, P =  $1.7 \times 10^{-9}$ ) (Figure 9). Total nitrogen also fluctuated significantly between seasons being higher in autumn and lowest in summer (F stat = 95.9, P =  $6.13 \times 10^{-12}$ ), however phosphorous concentrations did not vary seasonally (Figure 9).



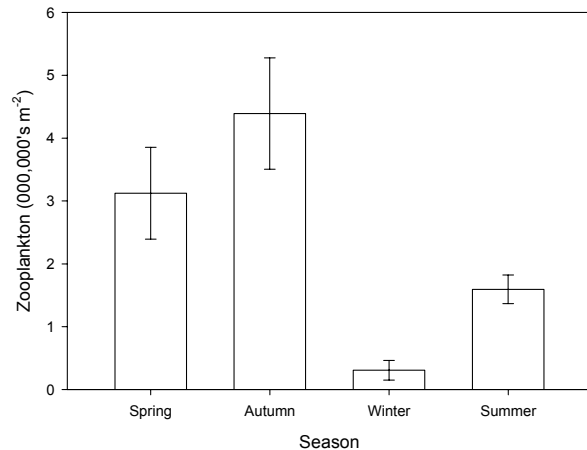
**Figure 9.** Seasonal patterns of Salinity (a), turbidity (b), DO (c), temperature (d), suspended organic content (e), suspended inorganic content (f), total nitrogen (g) and total phosphorous (h). Values are mean  $\pm$  SE (n=4).



### Seasonal patterns

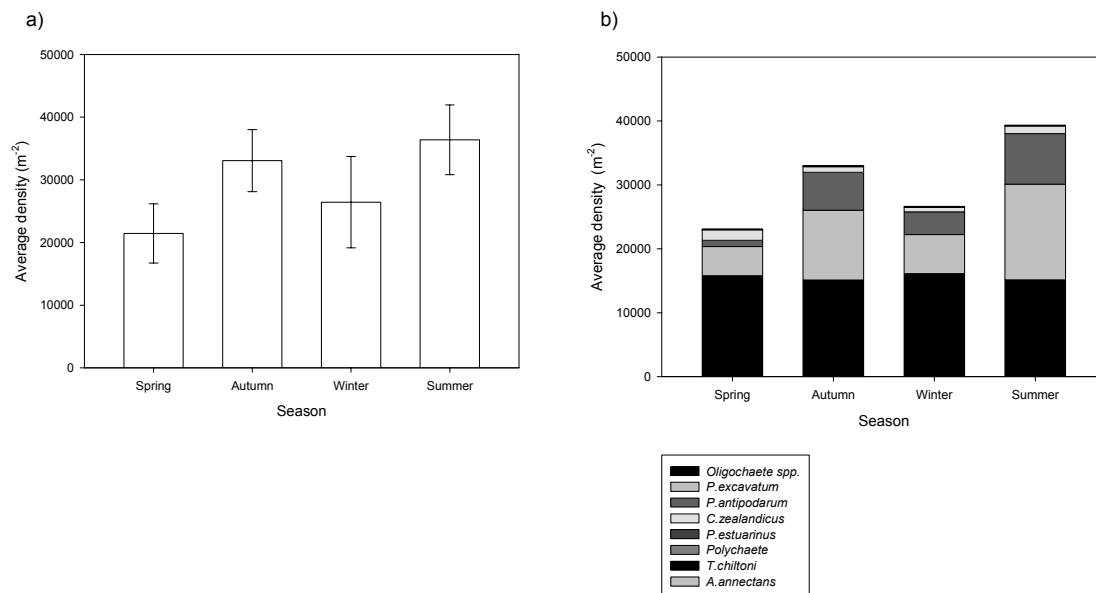
#### Benthic invertebrates and zooplankton

Zooplankton numbers were lowest in winter at 310,000 individuals  $\text{m}^{-2}$  and highest in autumn at 4,400,000 individuals  $\text{m}^{-2}$  (Figure 10).



**Figure 10.** Mean zooplankton densities over four sampling occasions. Values are mean  $\pm$  SE (n=4).

All benthic invertebrate species were found throughout the lake during all sampling occasions, so no temporal patterns in species richness were present. The highest benthic invertebrate density was found in summer with 36,000 individuals  $\text{m}^{-2}$ , and the lowest density in spring with 21,000 individuals  $\text{m}^{-2}$  (Figure 11a). However, benthic invertebrate composition did change between seasons (Figure 11b), the amphipod *P. excavatum* provided a greater proportion of the community during autumn and summer, whereas the snail *P. antipodarum* comprises of a significantly lower proportion of the community in spring.



**Figure 11.** a) Mean benthic invertebrate density and b) benthic invertebrate composition over four sampling occasions ( $\pm$  SE,  $n=4$ ).

## DISCUSSION

Despite the apparent uniformity of water conditions Te Waihora experiences, spatial differences in water chemistry and bed conditions occur across the lake. In particular, several water chemistry conditions changed markedly with distance from the lake outlet. This west to east gradient spans approximately 26 km from the south-west corner of the lake at Taumutu to the east corner at Kaituna Lagoon, and these changing conditions subtly influence the composition of pelagic and benthic communities spatially throughout the lake. The magnitude and presence of this gradient was almost certainly influenced by the timing of lake openings by the Regional Council.

The most variable environmental factor was salinity, which was highest at the lake outlet and decreased towards Kaituna Lagoon. In fact, most water chemistry variables showed either a

positive (suspended organic content, temperature) or negative (salinity, pH, DO, turbidity) gradient with distance from the lake outlet.

Kaituna Lagoon has permanent shallow water even during low lake levels and provides sheltered waters for wildlife during storms. The area also contains small islands, mudflats, raupō and rushes (DoC/Ngai Tahu, 2005). Also, this gradient may be present because Kaituna Lagoon is potentially more sheltered and much farther from the sea, creating a different environment than the lake outlet area. Salinity gradients have been recorded in other lakes (Schallenberg, Hall & Burns, 2003; Schallenberg & Burns, 2003; Schallenberg & Waite, 2003; Kipriyanova et al. 2007). Schallenberg and Burns (2003) found that Lake Waihola, New Zealand displayed salinity and nutrient (total nitrogen and phosphorous) gradients, which also significantly negatively correlated with zooplankton abundances, whereas Schallenberg & Waite (2003) recorded changes in macrophyte distribution in Lake Waihola with salinity gradients.

I expected to see a similar gradient in water chemistry and invertebrate composition in the sites extending from the Selwyn River mouth to the lake outlet. However, both water chemistry values and invertebrate composition did not show a consistent pattern around this inflow. The reason I did not see any gradient in water chemistry or invertebrate composition may be because the influence inflow water from the Selwyn River may not be significant enough or as significant as the opening to the sea.

The benthic invertebrate species of Te Waihora in my study comprised of eight taxa. This species richness is lower than reported values in a number of New Zealand lakes. Timms (1982) surveyed 20 South Island lakes and that the average number of benthic macroinvertebrate species recorded was 12.4, ranging from 1 to 26 taxa. However, in the littoral zone of Lake Coleridge, James et al. (1998) recorded 47 invertebrate taxa, which was high compared with many New Zealand lakes. Although the Waitaki lakes have an average of 54 taxa, Waikaremoana has 26 taxa, and the lakes of the Upper Clutha valley have 26 species (James et al. 1998).

As for coastal lakes, Schallenberg & Waite (2003) recorded 12 taxa from Lake Waihora, a shallow coastal lake in the Otago district. The snail *Potamopyrgus* and midge larvae dominated the community, with the remainder of the community comprising of caddisfly larvae, amphipods, shrimp, water boatmen and dragonfly larvae. Waituna Lagoon (Southland) is another shallow coastal lake that has clear water and tall aquatic plants, with salinity values ranging from 0.9 - 5.1 ‰ (Thompson & Ryder, 2003). The benthic invertebrates of Waituna Lagoon were sampled by Riddell, Watson & Davis (1988), who concluded that invertebrates in Waituna Lagoon were uncommon, with the snail *Potamopyrgus antipodarum* and the amphipod *Paracalliope fluviatilis* as dominant members of the community. Other invertebrates recorded included various platyhelminth flatworm species, isopods, caddisflies and oligochaetes. It is believed that a prolonged opening of the lagoon during 1997-2000 had a profound effect on the benthic invertebrate community (Thompson & Ryder, 2003).

Subtle changes in the benthic community also occurred with changes in substrate around the lake. For example, gravel substrates supported the snail *Potamopyrgus antipodarum* which

seemed to require stable substrate (Dawn, 1995). Oligochaetes were frequently associated with fine grained sediment (Weatherhead and James, 2001) high organic material and higher temperatures. However, other lake studies have reported that sediment characteristics are not reflected in the benthic species richness and composition (Timms, 1982). During this study of seven Canterbury high country lakes, Timms (1982) found that other environmental variables showed significant relationships with invertebrate abundance. For example, certain oligochaete species in Lake Pearson, Grassmere, Letitia and Marymere seemed to respond to larger amounts of particulate detritus or organic matter.

The results of my study suggest that some seasonal variation also exists in Te Waihora. The most variable physico-chemical factor I observed was salinity where it reached 31.9 ‰, compared to 35 ‰ seawater, at the lake outlet during the lake opening in winter. Conversely, zooplankton numbers were at their lowest during winter, compared to autumn. Salinity affects an aquatic organisms' ability to osmoregulate (Schallenberg, Hall & Burns, 2003). Schallenberg, Hall & Burns (2003) found that the diversity and abundance of zooplankton in Lake Waihora was markedly reduced after regular saline intrusions. Furthermore, they found that zooplankton abundance declined exponentially with increasing salinity, and salinities of just 1.5 ‰ resulted in mortality of all zooplankton species in less than 11 days. With salinities reaching up to 31.9 ‰ at some sites during the lake opening in Te Waihora and with an average of 2.7 ‰ over the whole lake during this time, it is likely that salinity is an important factor driving the low abundances of zooplankton during winter.

I also observed seasonal variation in invertebrate density, with the highest average density of invertebrates in summer, which is consistent with the findings of Dawn (1995) in Te

Waihora. This higher density during summer may be related to the chironomid emergence events that occur in both spring and summer in Te Waihora (Ngai Tahu/DoC, 2005). Forsyth (1976) concluded chironomid larvae numbers were highest prior to emergence in five North Island lakes, where numbers were highest in winter prior to emergence in spring.

Yeates (1965) undertook one of the few studies of invertebrate communities prior to the Wahine Storm of 1968. Interestingly, he found that *Potamopyrgus antipodarum*, the amphipod *Paracalliope fluviatilis* and tubificid worms dominated the fauna of Te Waihora. However, in a more recent study after the switch from a macrophyte dominated lake to a phytoplankton dominated lake, Kelly and Jellyman (2007) found *Chironomus zealandicus* to be the dominant invertebrate species. I found that Oligochaete species dominated 60 % of the benthic sites, while the amphipod *Paracorophium excavatum* and the snail *P. antipodarum* dominated 25 % and 5 % of sites respectively. Kelly and Jellyman (2007) found the total invertebrate density to be threefold higher than reported by Yeates (1965) however, biomass was 36 % lower due to a change in composition from *Potamopyrgus antipodarum* to smaller sediment dwelling species such as *Chironomus zealandicus* and oligochaetes. This change of composition from the snail *P. antipodarum* to chironomids and oligochaetes may reflect the loss of macrophytes and therefore habitat for *Potamopyrgus*. In addition, dominant substrate in Te Waihora now comprises a soft sand/silt mix, which is an ideal habitat for chironomids and oligochaetes (Weatherhead & James, 2001).

Oligochaete species and amphipods were the dominant invertebrates in the lake, with the remainder of species present at most sites but in low numbers. Chironomids and oligochaetes made up the majority of the fauna in a survey of benthic macroinvertebrates in seven New

Zealand lakes in the North Island (Forsyth, 1978), comprising of over 90 % by numbers of the macrofauna in three of the lakes. Weatherhead and James (2001) showed that chironomids and oligochaetes were significantly correlated with substrate size, where they were generally found in finer mud/silt and sand. My findings are consistent with this study, in that these softer bodied invertebrates (chironomids and oligochaetes) preferred softer sediments including silt/sand substrates opposed to coarser particles such as gravel.

Weatherhead and James (2001) also found that other factors as well as substrate type were correlated with invertebrate distribution in lakes. In a survey of nine New Zealand lakes, they concluded that substrate, macrophyte biomass and detritus were the most important factors directly controlling macroinvertebrate distribution and abundance in lakes. They also mention that factors such as depth, exposure to wave action, secchi depth and recent lake level history were of lesser importance, but could have a considerable indirect effect on macroinvertebrate distribution and abundance, and substrate characteristics.

There are several reasons why invertebrate species richness in Te Waihora may be low. Firstly, fluctuating lake levels may affect invertebrates directly and indirectly. The lake level is frequently in a state of flux both due to artificial lake openings and wind-blown dewatering. Macroinvertebrates which cannot migrate or withstand periods of desiccation or freezing might be lost from this system, while the large areas of the lakes littoral zone are now ephemeral. Exposed littoral zone can potentially lead to loss of habitat for invertebrates. These shore areas are usually composed of large particles such as cobbles which provide refuge from predators, and stable surfaces for egg laying and periphytic algal growth.

Hunt and Jones (1971) found that fluctuating water level in the manually opened lake (now a reservoir) Lyn Tegid in North Wales had long term effects on the littoral fauna. They found large reductions in numbers of invertebrates, with a total of 12 species completely disappearing from the littoral zone as a result of its conversion to a reservoir.

Many studies conclude that the snail, *Potamopyrgus antipodarum*, is usually the dominant or subdominant invertebrate in both the littoral and profundal fauna of most New Zealand lakes (Talbot and Ward, 1987). Furthermore, *P. antipodarum* is often closely related to macrophyte biomass (Yeates, 1965; Weatherhead and James, 2001). However, they do not consume the macrophyte themselves, but rather graze on the epiphytic algae growing on the macrophyte surface. It is this characteristic that allows macrophytes to be capable of supporting large numbers of grazers, while providing a refuge from both turbulence and predation (Weatherhead and James, 2001). *P. antipodarum* were widespread in Te Waihora, however they were no longer the dominant invertebrate as Yeates found in 1965. It is likely that the main contributing factor for this change in dominance was due to the loss of macrophytes during the Wahine Storm (1968) (Hughes, McColl & Rawlence, 1974; Taylor, 1996). Macrophytes are often correlated with invertebrate abundance and diversity, and provide habitat for both macroinvertebrates and epiphytic algae, which forms the basis of the littoral food web (Biggs & Malthus, 1982).

Since the loss of macrophytes, it is possible that gravel fills the niche of the pre-existing macrophytes because algae, which are fed on by *P. antipodarum*, are able to grow on the larger/coarser substrate. The lake is now dominated by oligochaetes and *C. zealandicus*, which are associated with softer silt sediment. One possible explanation for their dominance



of the invertebrate composition could be that macrophytes are no longer stabilising the sediment, promoting the re-suspension of silt substrates and the growth of phytoplankton, thus a stable turbid state. The presence of macrophytes and habitat stability both have a major effect on the distribution of macroinvertebrates (James et al. 1998). The reasons macrophytes are limited in Te Waihora are most likely due to salinity, sediment re-suspension, unstable substrate, light limitation through the water column and wave action disturbance.

Finally, sudden changes in salinity in the lake caused by the regular opening to the sea may have strong effects on invertebrates. Species richness and composition are shown to be highly correlated with salinity in several overseas lakes (Williams, Boulton and Taaffe, 1990; Green et al. 2005; Kipriyanova et al. 2007).

In conclusion, the water chemistry and benthic diversity and community within Te Waihora experiences both spatial and temporal changes. These changes are primarily the result of changes in salinity and lake level associated with the manual lake opening as well as spatial variation in the lake bed substrate, which may be a legacy of historic bed altering events and current land use.

## Chapter 3

### **The composition and linkages of Lake Ellesmere's benthic food web**

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#### **INTRODUCTION**

Most New Zealand coastal lakes are being subjected to increasing human pressures which have had marked effects on the structure and composition of lake communities (Mitchell, 1975; Schallenberg & Burns, 2003). Despite these marked impacts, few studies have investigated the response of lake food webs to these pressures. Coastal lakes are often strongly influenced by marine inputs and can span the range of salinities from hyper-saline to completely fresh water (Kjerfve, 1994). Salinity can have a marked effect on aquatic macrophytes (Spalding & Hester, 2007) causing reduced growth and eventual death. Pelagic and benthic invertebrates are also affected by salinity gradients (Schallenberg, Hall & Burns, 2003). For example, Schallenberg, Hall & Burns (2003) found that the survival of zooplankton in the coastal Lake Waihora was markedly reduced at high salinity levels.

Lake Ellesmere (Te Waihora) is a large, brackish, turbid, coastal lagoon in the South Island of New Zealand that is manually opened to the sea approximately 3.4 times per year (Gerbeaux & Ward, 1991). This artificial opening occurs to prevent flooding of surrounding farmland. Seawater usually encroaches into the lake during the latter stages of this procedure, resulting in the lake reaching a salinity of up to 32 ‰ (see Chapter 2). Since pre-European colonisation, the opening procedure has changed periodically in conjunction with a reduction in lake size from 30,000 hectares to 20,250 hectares (Jellyman & Chisnall, 1999). The depth at which the lake is opened has been lowered, the openings have become more frequent, and the technique has varied from horse-drawn scoops to the present use of power scoops and

bulldozers. Kirk and Lauder (2000) suggested that the distribution of plants and animals in and associated with Te Waihora and other manually opened lakes has adjusted to the modified hydrological regime and seasonal timing of lake opening procedures.

Subsequently, much of the marginal swampland of Te Waihora has been drained and converted to farmland (Glova & Sagar, 2000). Furthermore, intensive farming in its catchment has also resulted in high nitrogen levels ( $0.2 - 4.0 \text{ mg L}^{-1}$ ) (Kelly & Jellyman, 2007). Te Waihora also experiences frequent southerly and westerly winds which result in significant wave action, which alternatively inundates and dries the littoral zone depending on wind direction. Increasing nutrient input coupled with frequent wind-induced sediment re-suspension and other environmental pressures have contributed to poor water clarity in the lake. However, this has not always been the case. Prior to 1968 the lake was described as a clear, macrophyte dominated system (see Chapter 2). In 1968, the Wahine storm severely damaged and caused the subsequent loss of aquatic macrophyte beds such as *Ruppia megacarpa* and *Potamogeton pectinatus* which had dominated significant areas of the lake (Kelly & Jellyman, 2007). This switch between the two states of clear, macrophyte dominated and turbid, phytoplankton dominated, or 'hysteresis' (Moss, 1999) can be maintained by a number of differing mechanisms, which either promote algal growth or prevent it. The invertebrate composition of the lake has also altered in response to this change of state, with the dominant snail *Potamopyrgus antipodarum* being displaced by the midge *Chironomus zealandicus* and oligochaetes (Yeates, 1965; Kelly and Jellyman, 2007).

The effect of this switch on the whole lake food web is poorly known. Nevertheless, food for carnivorous fish appears to be abundant and includes mysids (*Tenagomysis* spp.) snails

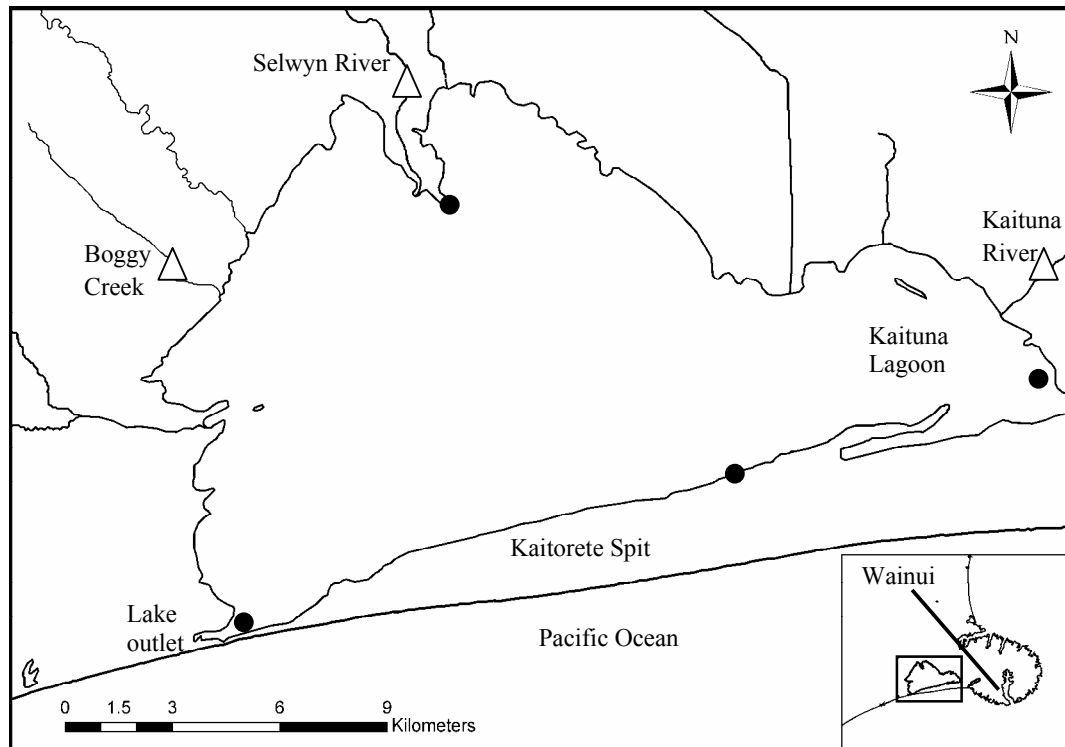
(*Potamopyrgus* spp.), chironomids, amphipods and ostracods (Glova & Sagar, 2000). Recently there has been concern over the slow growth rates of juvenile shortfin eels (*Anguilla australis*) and low abundances of several year classes (Graynoth & Jellyman, 2002). Slow growth rates may be the result of complex interactions between food availability and quality and competition with other predator species (Jellyman & Todd, 1998). Whereas, recruitment failures are probably linked to the timing and magnitude of the lake opening (Kelly & Jellyman, 2007).

Te Waihora has several significant inflow streams, several of which have historically been recognised for their trout migrations. We might expect that food resources and likely migration of species between the lake and its inflow streams might result in overlaps in lake-stream food webs. Thus, in this study I used stable isotope analysis to determine the primary food sources driving the food web of Te Waihora, and investigated spatial variation in the food web and its linkage to inflow streams and marine food webs.

## **METHODS**

### *Study sites*

Sites were sampled from three ecosystems (Figure 1.); a) Te Waihora (four sites: Kaituna Lagoon, Selwyn River mouth, Kaitorete Spit and lake outlet at Taumutu), b) three inflow streams (Kaituna River, Selwyn River at Coes Ford and Boggy Creek), and c) one marine site (Wainui Beach in Akaroa Harbour).



**Figure 1.** Sites sampled in Te Waihora (dots), three inflow stream sites (Kaituna River, Selwyn River at Coes Ford and Boggy Creek; triangles) and the marine site (Wainui), sampled in May 2007.

### *Field sampling*

I attempted to collect basal food resources and organisms representative of each trophic level for stable isotope analysis (C and N). Samples from the lake comprised of living plant material (littoral and benthic), filamentous algae, plankton, lake bottom sediment, dead leaves/detritus, seston, benthic invertebrates and fish. All lake samples were collected within 5 m of the shore at a depth of approximately 40 cm. Plankton was filtered from a one litre water grab sample, while seston was collected using a sweep net (250  $\mu\text{m}$  mesh) pulled over the water surface. Living plant material, leaves and detritus were collected by hand from the lake littoral zone. Sediment was collected from a substrate grab sample and filamentous algal clumps were removed from emergent vegetation. In the littoral zone, benthic invertebrates were collected by kick sampling with a 250  $\mu\text{m}$  mesh sweep net. Smelt (*Stokellia anisodon*),

common bullies (*Gobiomorphus cotidianus*) and mysid shrimp (*Tenagomysis chiltoni*) were collected from the benthos and water column using drag nets (3 mm mesh size).

Samples from the inflow streams were collected in the same manner as lake samples, except the fish were obtained by electro-fishing. A stream section was spot shocked approximately 5 - 10 times until the desired fish species were obtained and captured in a kicknet (250 µm mesh). Marine samples were collected at low tide on the water mark. Molluscs and algae were collected by picking individuals from the under-surfaces of rocks or with the use of a small scalpel. At the marine site, parrot fish (*Pseudolabrus* spp.), brittle star (*Ophiomyxa brevirima*) and paddle crab (*Ovalipes catharus*) were caught in a wire frame crab pot (500 mm x 300 mm x 300 mm) in Akaroa Harbour near Wainui. Samples from all three ecosystems were placed on ice in the field and transported to the laboratory for processing.

#### *Laboratory analysis*

Organisms were identified to the lowest taxonomic level possible prior to analysis. The snails (*Potamopyrgus antipodarum*, *Physella acuta* and *Turbo smaragdus*), the brittle star (*Ophiomyxa brevirima*), paddle crab (*Ovalipes catharus*), black mussel (*Xenostrobus pulex*), limpets (*Cellana ornata*) and cased caddisflies (*Pycnocentroides* spp.) were removed from their outer shells. Samples of muscle tissue were cut from fish, and the central body of crabs and legs of brittle stars. Plant material and seaweed were washed to remove foreign material.

Lake water samples were filtered using a vacuum pump to obtain suspended phytoplankton. The phytoplankton was then carefully scraped off the filter paper with a scalpel. All samples

were placed in aluminium trays, put in a drying oven at 40 °C for 2 - 3 days, and then ground with a mortar and pestle to pass through a 200 µm mesh sieve. The required amounts (20 – 50 mg dry weight) were weighed, sealed in labelled, capped Eppendorf tubes, and sent to the stable isotope unit at the Waikato University for analysis of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Stable isotope analysis was undertaken by continuous-flow mass spectrometry (Europa Scientific 20/20 isotope analyser) at the Waikato Stable Isotope Unit (University of Waikato). Carbon ( $^{13}\text{C}$ :  $^{12}\text{C}$ ) and nitrogen ( $^{15}\text{N}$ :  $^{14}\text{N}$ ) isotope ratios are expressed in  $\delta$  (‰) notation, defined as parts per thousand (‰) deviation from the respective international standards for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Analytical precision was  $\pm 1$  ‰ ( $\delta^{15}\text{N}$ ).

International standards are based on isotope ratios calculated as per ml (‰) deviation from atmospheric N ( $^{14}\text{N}$ ) and the international limestone standard Vienna Pee Dee Belemnite (VPDB) ( $\delta^{13}\text{C}$ ):

$$\delta \text{ (‰)} = 1000 \times \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}}$$

Where  $R_{\text{sample}}$  is the ratio of the heavy to the light isotope and  $R_{\text{standard}}$  is the corresponding ratio for the standard (Winterbourn, 2007).

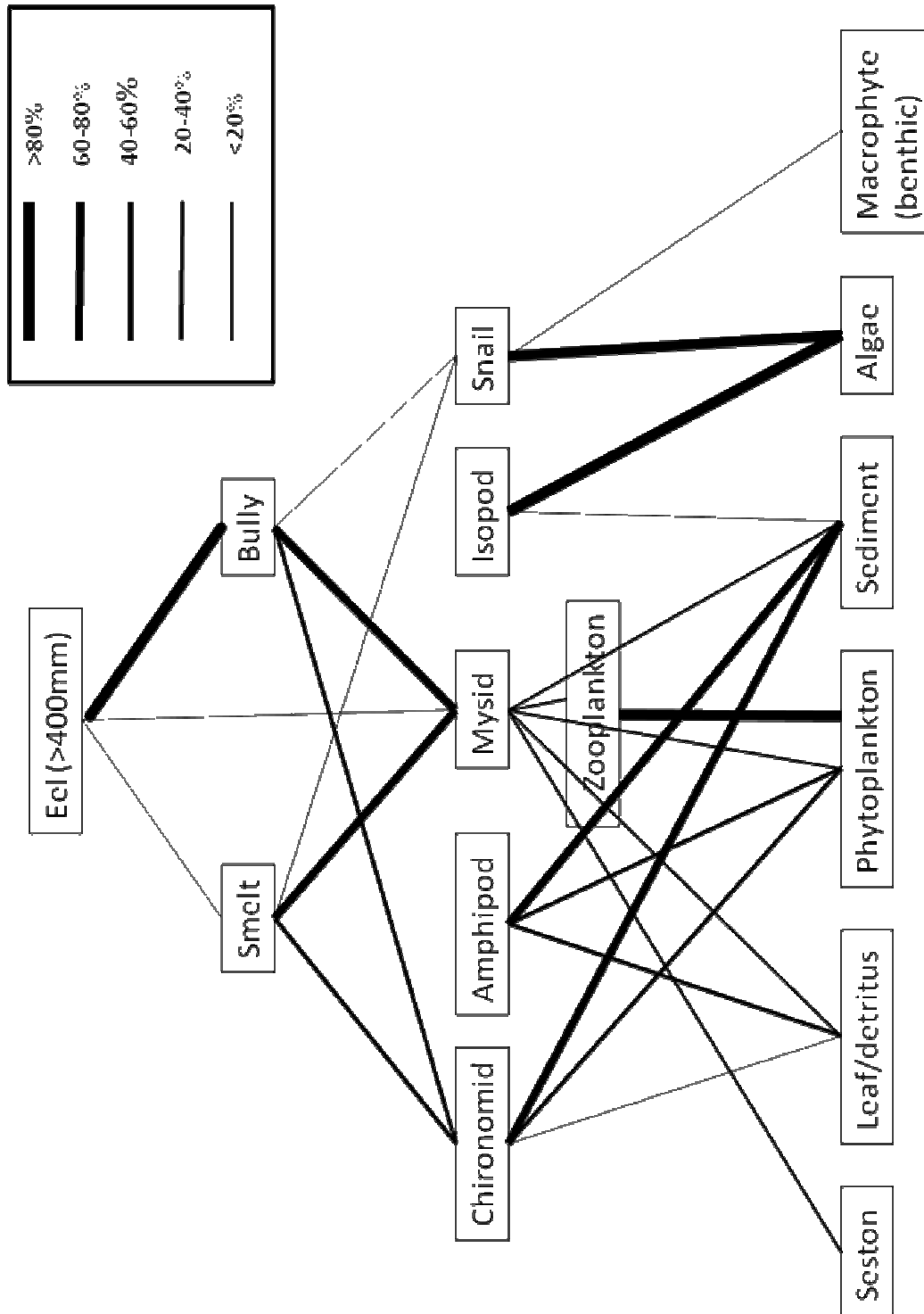
I also analysed gut contents from two fish species (smelt and common bullies) and five invertebrate species (chironomids, amphipods, mysids, snails and isopods) from Te Waihora. Foreguts were dissected under a microscope, mounted on slides in lactophenol and dried at 40 °C for 2 - 3 days. Guts were then viewed under a compound microscope at 40x magnification and presence of food items were recorded, including animal, diatoms, filamentous green algae, phytoplankton and organic and inorganic matter.

## RESULTS

### *Stomach analyses*

Chironomid (*Chironomus zealandicus*) and amphipod (*Paracorophium excavatum*) diet was dominated by inorganic matter/sediment (60 %), with some phytoplankton/algal cells (35 %) and organic detrital matter (5 %) (Figure 2). Diatoms (20 %) and filamentous algae (80 %) dominated the diet of *Potamopyrgus antipodarum* while algae (80 %) also dominated the diet of the isopod (*Austridotea annectens*), with the remainder comprising of inorganic matter/sediment (20 %). The diet of mysids was made up of a range of items including zooplankton (20 %), phytoplankton (20 %), seston (20 %), detrital material (20 %) and amorphous inorganic matter/sediment (20 %). Mysids (*Tenagomysis chiltoni*) (60 %) and chironomids (*Chironomus zealandicus*) (30 %) dominated the diet of bullies with some *Potamopyrgus* matter (10 %), whereas smelt guts contained mainly mysids (60 %) and large oligochaetes (15 %) with some chironomid (15 %) and *Potamopyrgus* matter (10 %) (Figure 2).





**Figure 2.** Food web diagram of all components sampled in Te Waihora with weighted links according to percentages of food items found in foregut analysis (addition of eel data from Kelly & Jellyman, 2007).

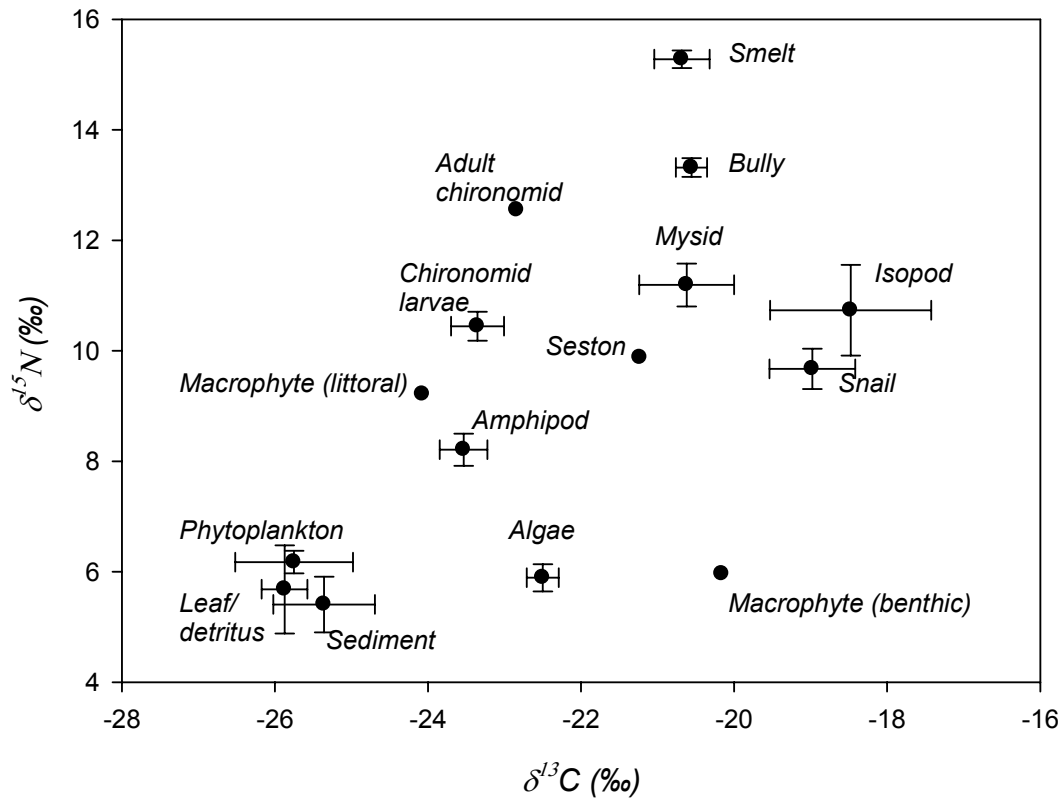
### *Isotope analyses*

Carbon and nitrogen stable isotope values were analysed for 15 components of the food web at four sites in Te Waihora (Figure 3). Primary producers in Te Waihora were comprised mainly of benthic macrophytes, epiphytic algae and phytoplankton. Some benthic algae probably occur on gravel substrate but this was very difficult to sample. Benthic macrophytes collected from Kaituna Lagoon had a  $\delta^{13}\text{C}$  value of - 20.2 ‰ and a  $\delta^{15}\text{N}$  value of 6.0 ‰ which differed markedly from littoral macrophytes from the lake margin ( $\delta^{13}\text{C}$  = - 24.1 ‰,  $\delta^{15}\text{N}$  = 9.21 ‰). By contrast, algae (filamentous/epiphytic) had a  $\delta^{13}\text{C}$  value of - 22.5 ‰, indicating an enrichment of  $\delta^{13}\text{C}$  over phytoplankton, which had an even lower  $\delta^{13}\text{C}$  value of - 25.8 ‰ compared to that of benthic macrophytes.

The sediment dwellers *Chironomus zealandicus* ( $\delta^{13}\text{C}$  = - 23.4 ‰,  $\delta^{15}\text{N}$  = 10.4 ‰) and *Paracorophium excavatum* ( $\delta^{13}\text{C}$  = - 23.5 ‰,  $\delta^{15}\text{N}$  = 8.2 ‰) had relatively  $^{13}\text{C}$  depleted values indicating a dependence on detritus, organic sediment and phytoplankton that may have settled out of the water column. In contrast, *Austridotea annectens* ( $\delta^{13}\text{C}$  = - 18.5 ‰,  $\delta^{15}\text{N}$  = 10.7 ‰) and *Potamopyrgus antipodarum* ( $\delta^{13}\text{C}$  = - 19.0 ‰,  $\delta^{15}\text{N}$  = 9.7 ‰) had strongly enriched  $^{13}\text{C}$  values, suggesting strong dependence on algae and benthic macrophytes as food. Mysids ( $\delta^{13}\text{C}$  = - 20.6 ‰,  $\delta^{15}\text{N}$  = 11.2 ‰) probably had a diet consisting of a combination of benthic macrophytes, seston, algae and most likely phytoplankton.

Common bullies ( $\delta^{15}\text{N}$  = 13.3 ‰) had a diet consisting of chironomids, mysids and snails. Of the organisms collected, smelt was the top predator ( $\delta^{15}\text{N}$  = 15.3 ‰) which seemed to share a

similar diet to that of common bullies, feeding on mysids and probably chironomids and snails (Figure 3).



**Figure 3.** Carbon and nitrogen stable isotope values (mean + -SE) of biota collected at four sites from Te Waihora (Kaitorete Spit, Selwyn river mouth, Kaituna Lagoon and the lake outlet at Taumutu).

There is some variation in the isotopic values of organisms from the four different regions of the lake. For example, *Austriodotea annectens* exhibited  $\delta^{13}\text{C}$  ratios ranging from - 20.05 to - 16.5 ‰ with the most enriched  $^{13}\text{C}$  values being closer to the sea, i.e. the lake outlet and Kaitorete Spit, and the most depleted  $^{13}\text{C}$  values near the freshwater inflow at the Selwyn River mouth (Table 1). Other potentially less mobile species showed a similar trend. *Potamopyrgus* from Kaitorete Spit and the lake outlet had  $\delta^{13}\text{C}$  values of - 17.5 ‰ and - 18.9

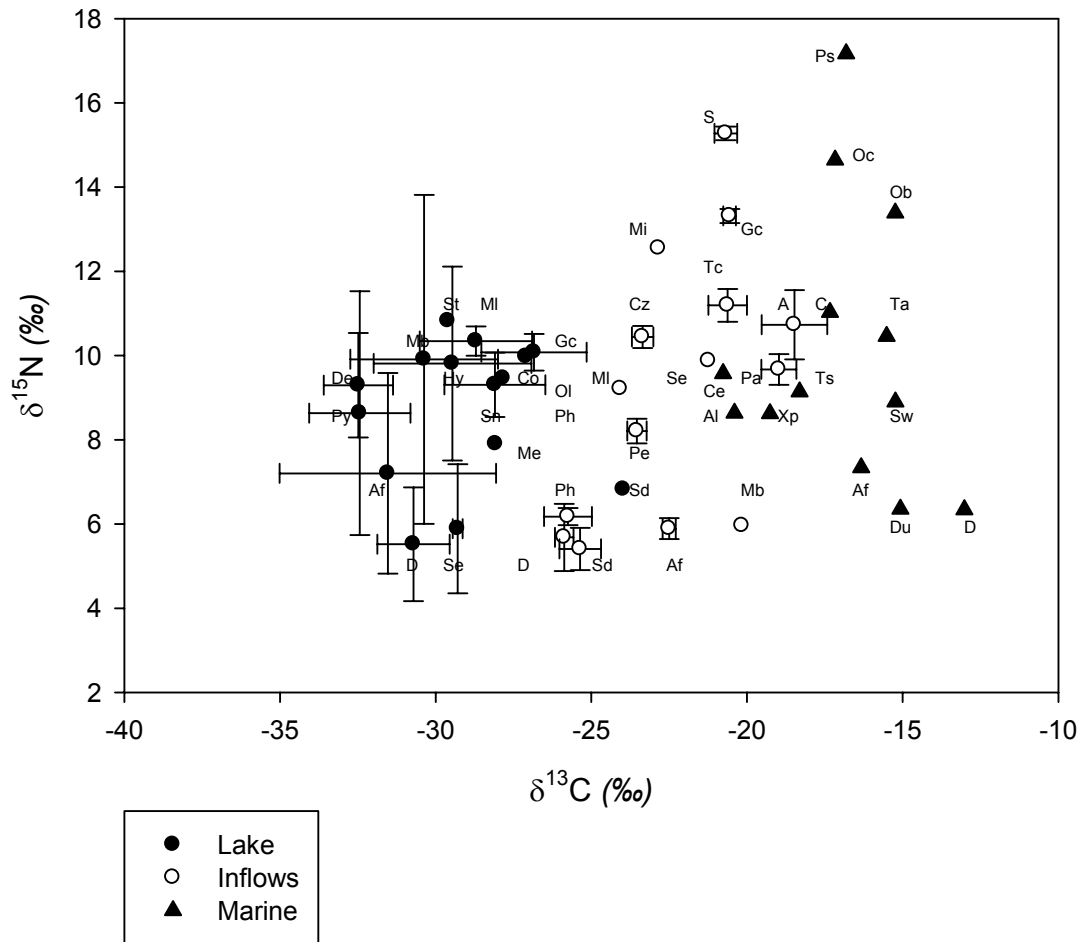
‰ respectively, while *Potamopyrgus* collected from Kaituna and Selwyn River mouth had values of - 19.4 ‰ and - 20.1 ‰ (Table 1).

**Table 1.**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotopic values for each food web group at each ecosystem; lake (Te Waihora), streams and marine sampled in May 2007.

	Food web group	Abbreviation	Site	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Lake	Smelt ( <i>Stokellia anisodon</i> )	S	Kaitorete	-20.78	15.39
			Kaituna	-21.59	15.58
			Outlet	-20.52	14.83
			Selwyn	-19.84	15.31
	Bully ( <i>Gobiomorphus cotidianus</i> )	Gc	Kaitorete	-20.76	13.52
			Kaituna	-20.85	13.05
			Outlet	-20.66	13.68
			Selwyn	-19.96	13.01
	Mysid ( <i>Tenagomysis chiltoni</i> )	Tc	Kaitorete	-19.24	10.49
			Kaituna	-22.07	10.58
			Outlet	-21.13	12.05
			Selwyn	-20.04	11.64
	Larval chironomid ( <i>Chironomus zealandicus</i> )	Cz	Kaitorete	-22.82	10.72
			Kaituna	-23.34	9.71
			Outlet	-22.92	10.45
			Selwyn	-24.33	10.88
	Adult chironomid/midge ( <i>Chironomus zealandicus</i> )	Mi	Kaitorete	-22.84	12.55
			Pe	-22.69	8.03
	Amphipod ( <i>Paracorophium excavatum</i> )	Pe	Kaituna	-23.45	7.46
			Outlet	-24.05	8.65
			Selwyn	-23.95	8.69
			A	-23.95	8.69
	Isopod ( <i>Austridotea annectens</i> )	A	Kaitorete	-16.48	9.24
			Outlet	-18.90	12.07
Selwyn			-20.05	10.89	
Snail ( <i>Potamopyrgus antipodarum</i> )	Pa	Kaitorete	-17.48	8.93	
		Kaituna	-19.44	9.47	
		Outlet	-18.88	9.61	
		Selwyn	-20.11	10.68	
Macrophyte (benthic)	Mb	Kaituna	-20.16	5.96	
Macrophyte (littoral)	MI	Kaitorete	-24.07	9.21	
Phytoplankton	Ph	Kaitorete	-23.81	5.94	
		Kaituna	-27.51	6.14	
		Outlet	-26.17	5.86	
		Selwyn	-25.51	6.76	
		Se	-25.51	6.76	
Seston	Se	Kaitorete	-21.23	9.87	
Algae-filamentous	Af	Kaitorete	-22.29	6.14	
		Outlet	-22.71	5.64	

	Detritus/dead leaves	D	Kaitorete	-25.49	6.95
			Kaituna	-26.71	3.45
			Outlet	-25.89	6.69
			Selwyn	-25.40	5.64
	Sediment	Sd	Kaituna	-26.66	5.36
			Outlet	-24.94	6.30
			Selwyn	-24.47	4.56
Stream	Bully ( <i>Gobiomorphus cotidianus</i> )	Gc	Coes	-28.53	9.64
			Kaituna	-25.15	10.51
	Trout ( <i>Salmo trutta</i> )	Str	Coes	-30.51	9.99
			Kaituna	-26.90	10.69
	Snail ( <i>Potamopyrgus antipodarum</i> <i>/Physella acuta</i> )	Sn	Coes	-30.94	8.41
			Boggy	-28.02	10.83
			Kaituna	-25.33	8.68
	Macrophyte (benthic)	Mb	Kaituna	-28.00	6.00
	Macrophyte (littoral)	MI	Boggy	-32.74	13.82
			Boggy	-29.60	10.82
	Seston	Se	Coes	-29.59	7.06
			Boggy	-29.24	7.76
			Kaituna	-29.05	2.84
	Algae-filamentous	Af	Coes	-35.01	4.82
			Boggy	-28.06	9.58
	Detrital/dead leaves Leaves	D	Boggy	-29.99	8.04
			Coes	-29.16	3.42
			Kaituna	-32.98	5.10
	Sediment	Sd	Boggy	-23.97	6.82
	<i>Hydrobiosid</i> spp.	Hy	Kaituna	-25.54	7.99
			Coes	-33.95	8.42
			Boggy	-28.88	13.03
	<i>Deleatidium</i> spp.	De	Coes	-34.65	7.47
			Boggy	-30.95	11.67
			Kaituna	-31.85	8.74
	<i>Pycnocentroides</i> spp.	Py	Coes	-34.06	5.74
			Boggy	-30.81	11.53
	<i>Coloburiscus</i>	Co	Kaituna	-27.83	9.46
	<i>Megaloptera</i> spp.	Me	Kaituna	-28.07	7.90
	Oligochaetes	Wo	Boggy	-27.10	9.97
Marine	Algae-filamentous	Af	Wainui	-16.33	7.34
	Algae-lettuce	Al	Wainui	-20.40	8.64
	Detritus-spiral seaweed	D	Wainui	-13.02	6.34
	Limpet ( <i>Cellana ornata</i> )	Ce	Wainui	-20.77	9.58
	Sandhopper ( <i>Talorchestia</i> spp.)	Ta	Wainui	-15.52	10.46
	Catseye ( <i>Turbo smaragdus</i> )	Ts	Wainui	-18.31	9.14
	Black mussel ( <i>Xenostrobus pulex</i> )	Xp	Wainui	-19.26	8.62
	Crab-small (Crustacea)	C	Wainui	-17.34	11.03
	Paddle crab ( <i>Ovalipes catharus</i> )	Oc	Wainui	-17.17	14.65
	Brittle star ( <i>Ophiomyxa brevirima</i> )	Ob	Wainui	-16.82	17.17
	Parrot fish ( <i>Pseudolabrus</i> spp.)	Ps	Wainui	-15.24	13.39
	Bull kelp ( <i>Durvillea</i> spp.)	Du	Wainui	-15.07	6.35
	Seaweed-spiral	Sw	Wainui	-15.23	8.90

The  $\delta^{13}\text{C}$  values of all components of the food web in Te Waihora were distinctively different from those taken from the freshwater inflow streams and from marine sources (Figure 4). For example, mean  $\delta^{13}\text{C}$  values of all samples from the three ecosystems were - 29.5 ‰ (streams), - 22.3 ‰ (lake) and - 18.3 ‰ (marine). Thus, organisms within Te Waihora showed intermediate  $\delta^{13}\text{C}$  values indicating both freshwater and marine influences in their carbon values. As indicated previously within the lake, a gradient of freshwater to marine influence was also apparent (Table 1). However in general, the organisms from Te Waihora had a more marine-influenced carbon value than a freshwater one (Figure 4).



**Figure 4.** Carbon and Nitrogen stable isotopes values (mean+ -SE) of biota collected from four sites in Te Waihora, three inflow streams (Kaituna River, Boggy Creek and Selwyn River at Coes Ford), and one marine site (Wainui Beach, Akaroa Harbour).

## DISCUSSION

My results indicate that the food web in Te Waihora is based on two primary producer groups: Phytoplankton, and algae and macrophytes. Although terrestrial leaves and detritus may also form part of this basal food resource, their  $\delta^{13}\text{C}$  values could not be distinguished from those of phytoplankton. The importance of phytoplankton as a primary food resource is

not surprising. Kelly and Jellyman (2007) concluded that the food web of Te Waihora was driven predominantly by phytoplankton and epipellic (living in or on sediment) algae. The importance of phytoplankton in lake food web ecosystems is well known (Peterson & Howarth, 1987; Sullivan & Moncreiff, 1990; Keough, Sierszen and Hagley, 1996). Although several studies of lake and estuarine systems have found that epiphytic microscopic algae is often a major source of organic carbon underpinning much of the production (Fry & Sherr, 1984; James et al, 2000).

The 1968 Wahine storm is believed to have triggered a switch in alternative stable states from a macrophyte dominated lake to a phytoplankton dominated condition (Kelly & Jellyman, 2007). We might therefore expect that the primary food source for higher trophic levels has changed from macrophytes to phytoplankton. However, numerous studies have showed that macrophytes are rarely eaten directly by invertebrates and therefore do not generally contribute to the food web as a significant source of carbon (Keough, Sierszen and Hagley, 1996; James et al. 2000). Therefore, although the dominant biomass of primary producers has changed in Te Waihora from macrophytes to phytoplankton, it is possible that phytoplankton and epipellic algae have always been the primary producer contributing the majority of carbon to the food web.

Although the three ecosystems sampled for isotope analysis are geographically connected, it is evident that many components of the food web of Te Waihora are separated from the inflow streams and nearby marine systems. This result is somewhat surprising in that fish species such as smelt and bullies might be expected to move freely between the lake and



inflow streams. However, my data indicate that neither bullies nor brown trout (the likely top predator in streams) feed on food resources from the lake.

The disconnection of Te Waihora from the surrounding inflow streams was not expected and may have occurred in part from the reduced flows of lowland streams in the catchment caused by irrigation demands for neighbouring farmland (Datry, Larned & Scarsbrook, 2007). The Selwyn River is the major freshwater inflow to Te Waihora which flows from the Canterbury foothills. The Selwyn River experiences seasonal drying during spring/early summer, with ephemeral, intermittent and perennial reaches. Datry, Larned & Scarsbrook (2007) found that benthic invertebrate diversity and density increase directly with flow permanence. The decreasing flow of the Selwyn River may have contributed to the weakening of the stream-lake food web connection. Furthermore, lake openings to the sea have become more frequent and longer in duration than previous years (Hemmingsen, 1997), which may have contributed to the lakes increasing marine-influence. Lake salinity is determined by the frequency and duration of these openings, and is a critical factor not only in the distribution, growth and community composition of aquatic plant species, but also in determining the range of habitats for biological communities in Te Waihora (Williams, Boulton & Taaffe, 1990; Ngai Tahu/DoC, 2005; Kipriyanova et al. 2007). In Lake Chany, Russia, Kipriyanova et al. (2007) found that as salinity increased from 0.8 to 6.4 g L<sup>-1</sup> the species richness of aquatic vascular plants decreased from 16 to 12 species, phytoplankton decreased from 98 to 52 species, and zooplankton decreased from 61 to 16 species.

In conclusion, increasing duration and frequency of lake openings coupled with decreasing flows of lowland streams into Te Waihora have most likely contributed to the lake's  $\delta^{13}\text{C}$ -enriched value and disconnection from surrounding food webs.

## Chapter 4

# Comparing predation rates on *Chironomus zealandicus* by four common lentic invertebrate predators

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### INTRODUCTION

Numerous studies have shown that many of our coastal lakes are subjected to increasing human impacts (Jellyman, 1996; Johnson & Partridge, 1998; Schallenberg & Burns, 2003). Schallenberg & Burns (2003) noted that low-lying coastal lakes such as Lake Waihola, in Otago are often sites of intensive urban and agricultural land use, which result in the addition of high concentrations of nutrients, sediments and other pollutants. These land use pressures have had marked effects on the hydrology, water quality and biotic communities in these lakes.

In general, New Zealand lakes have relatively low species richness compared to many lakes overseas. Forsyth (1978) concluded that many groups typical of the benthos in northern hemisphere lakes are absent or poorly represented in New Zealand, and that species richness in the groups that are present here is low. For example, Timms (1982) surveyed 20 South Island lakes and noted that the average number of species recorded was 12.4, while the same author also looked at a further seven lakes in the Canterbury High country finding an average of 20.4 species per lake. In contrast, a study of Lake Winnipeg in Canada recorded a total of 26 gastropod species alone (Pip, 2006). While in Lake Gregory, Australia, 174 invertebrate species were recorded (Halse, Shiel & Williams, 2004).

Despite such low species richness, New Zealand lakes typically still support diverse, functioning food-webs including a range of producers, consumers and invertebrate predators (Rowe & Graynoth, 2002). In particular, invertebrate predators are usually relatively common in our lakes (Crumpton, 1977; Biggs & Malthus, 1982; Talbot & Ward, 1987). In Lake Wanaka, the damselfly larvae (*Xanthocnemis zealandica*), dragonfly larvae (*Procordulia grayii*) and predatory caddisfly larvae (*Hydrobiosis parumbripennis*) were abundant in the littoral vegetation zone (Biggs & Malthus, 1982). While both *Xanthocnemis zealandica* and *Procordulia grayii* have been recorded in Lake Mahinapua (Crumpton, 1977), and Talbot & Ward (1987) recorded both *X. zealandica* and *P. grayii* as well as a Coleopteran species; *Antiporus strigosulus*, and two predatory platyhelminthes species; *Cura pinguis* and *Glossiphonia multistriata* in Lake Alexandrina. Timms (1982) also found the invertebrate predators *P. grayii*, *X. zealandica* and *C. pinguis* during a study of the benthic communities of 20 lakes in the South Island. Biggs & Malthus (1982) also recorded *P. grayii* and *X. zealandica* in several lakes of the upper Clutha Valley, while Timms (1982) conducted an invertebrate survey of seven Canterbury High country lakes, in which *X. Zealandica*, *P. grayii*, *A. strigosulus*, *C. pinguis* and *G. multistriata* were recorded.

However, Schallenberg and Waite (2004) noted that invertebrate predators have not been widely reported in our coastal lakes. In the shallow, coastal Lake Waihora, dragonfly larvae were collected but in low numbers. In Te Waihora (Lake Ellesmere), a shallow, turbid coastal lake located 40km south of Christchurch, invertebrate predators are very rare and in low abundances (Yeates, 1965; Dawn, 1995; Taylor, 1996). Long term intensive agricultural land use in the catchment has led to high nitrogen and phosphorous concentrations in the lake, which have resulted in it becoming highly eutrophic. After the Wahine storm in 1968, the lake switched from a macrophyte dominated clear lake, to a phytoplankton dominated, turbid

lake (Kelly & Jellyman, 2007). This process, known as ‘hysteresis’ (Moss, 1999), is usually triggered by some significant perturbation (See Chapter 2). This switch in states has occurred in several other New Zealand lakes (Scheffer et al. 1993; Clayton & de Winton, 1994). For example, the Tomahawk Lagoon in Dunedin has switched states on multiple occasions, where phytoplankton and aquatic vegetation have predominated in turn for periods of 1-5 years since 1963 (Scheffer et al. 1993). Similarly, two shallow lakes in the south of Sweden; Lake Takern and Lake Krankesjön, have alternated between periods of clear, abundant vegetation and turbid, sparse vegetation over the past 40 - 50 years (Scheffer et al. 1993). This switch between states (from clear to turbid) and macrophyte removal almost certainly resulted in a marked change in invertebrate communities. Kelly and Jellyman (2007) surveyed the benthic invertebrate communities in Te Waihora and found a higher proportion of smaller sediment dwelling species such as *Chironomus zealandicus* and oligochaetes. Since the switch, these taxa accounted for 82 % of the mean total invertebrate biomass (Kelly & Jellyman, 2007). In comparison, prior to the occurrence of the 1968 storm and the subsequent switch in states, Yeates (1965) noted that *Potamopyrgus antipodarum* comprised over 90 % of the mean total biomass and *C. Zealandicus* and oligochaetes together made up only 2% of the overall biomass. However, both Yeates (1965) and Kelly and Jellyman (2007) did not record any invertebrate predators in their studies of Te Waihora.

Other studies on the benthic communities in Te Waihora after the 1968 storm report limited predator species, but in very low numbers (Crumpton, 1977; Dawn, 1995). *Xanthocnemis zealandica* was reported in low numbers in Te Waihora during Crumpton’s study (1977) and also in Dawn’s littoral zone investigation (1995). Because limited studies were carried out prior to the 1968 storm, it is difficult to make robust comparisons between the food webs in each of the alternative stable states, and to determine the degree of change in the benthic

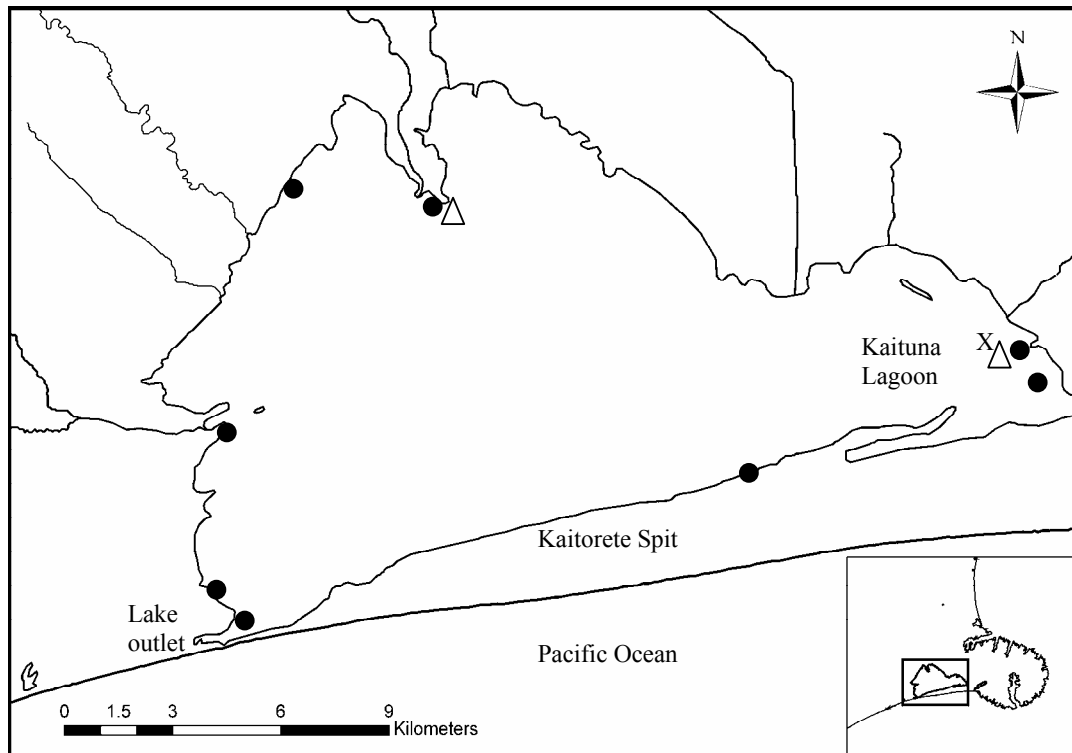
ecology of Te Waihora. Vegetation zones are frequently associated with abundant invertebrate populations and can be areas of high invertebrate productivity and biodiversity (James et al. 1998). Consequently, it is possible that the loss of aquatic macrophytes and the switch to a turbid, phytoplankton dominated lake has resulted in a loss of diversity, thus invertebrate predators in the lake (Scheffer, 1998; Hann, 2005).

The aim of this study was to determine the presence and spatial coverage of benthic invertebrate predators in Te Waihora and to test the likely impact of the loss of invertebrate predators on a dominant invertebrate prey, the chironomid *Chironomus zealandicus*. *Chironomus zealandicus* is very abundant throughout the lake and is considered a significant pest by local residents as emerging adults coat buildings and vehicles, and are attracted to lights at night.

## **METHODS**

### *Study sites*

A field survey was conducted in May 2008 of eight littoral zones distributed around the lake (Figure 1). Sites were selected to include littoral zone vegetation which comprised predominantly of submergent species such as native musk (*Mimulus repens*), freshwater species such as raupō (*Typha orientalis*) and halophytes such as glasswort (*Sarcocornia quinqueflora*) (DoC/Ngai Tahu, 2005).



**Figure 1.** Eight littoral zone sites (circle) surveyed in May 2008 and location of where invertebrate predators were located: *Xanthocnemis zealandica* (triangle), *Anisops wakefieldi* (X).

### *Field survey*

A survey of the littoral zone at eight sites around the lake was carried out with a kicknet (250  $\mu\text{m}$  mesh) to determine the presence and spatial distribution of any invertebrate predators inhabiting the lake. Approximately 30 net sweeps were carried out at each site by two collectors, each working independently. At each site all littoral habitats were sampled including emergent and submerged vegetation, wood and bed material. All predators collected were preserved in 70 % ethanol in the field and returned to the laboratory for identification. Invertebrates were identified using Winterbourn, Gregson & Dolphin (2000).

*Mesocosm experiment*

The paucity of invertebrate predators in Te Waihora may have a marked effect on benthic invertebrate communities. In order to determine the level of predation release we conducted a mesocosm experiment using four common New Zealand lake invertebrate predators: a dragonfly (*Procordulia grayii*), a damselfly (*Xanthocnemis zealandia*), a backswimmer (*Anisops wakefieldi*) and a diving beetle (Dytiscidae) and measured their predation on the non-biting midge (*Chironomus zealandicus*), which is abundant in Te Waihora. I also investigated the predator efficiency in both clear and turbid water.

Live chironomid larvae were collected from soft sediment at Timber Yard point on the southwestern end of Te Waihora, using a sweep-net. They were placed in lake water and transported to the University of Canterbury campus. Sufficient water was collected from Te Waihora to provide 11 litres of water per mesocosm. Soft mud sediment from the lake bed was also collected and sieved (500  $\mu\text{m}$ ) to remove organic matter. A total of 32 plastic tanks were set up in a sheltered outdoor area at the University of Canterbury campus. These comprised of eight replicate mesocosms for each predator; four for each treatment of clear and turbid water. Replicate mesocosms of treatments were randomly arranged to reduce the possibility of external environmental conditions affecting some treatments and not others. Approximately 750 ml of fine sand was added to the bottom of each tank and 11 litres of water added to provide chironomids with natural mud habitat to form burrows. Approximately 50 ml of pre-sieved mud was then added to each tank. The chironomids were kept in the laboratory overnight in aerated water until the sand and mud in the tanks had settled. Subsequently, 10 chironomids were added to each tank the following day and were left to settle for approximately 10 hr before invertebrate predators were added. Mesh covers

were then placed over the mesocosms to prevent prey and predators escaping and to reduce possible bird predation. Four invertebrate predator species were collected from a pond near Te Waihora, in Motukarara; dragonfly larvae (*P. grayii*), damselfly larvae (*X. zealandia*), adult diving beetle (Dytiscidae), and the backswimmer (*A. wakefieldi*). These were collected by sweeping through pond vegetation with a kicknet (250 µm mesh). In the backswimmer and damselfly treatments, two predators were added per tank, whereas in the dragonfly and beetle treatments, one predator was added per tank.

The experiment was run for 7 days. On Day 3 and 5 the turbid treatments were stirred by hand for 10 seconds to re-suspend substrate and maintain turbidity. On these days (3 and 5) spot temperature and dissolved oxygen levels were measured in six randomly selected tanks using a YSI 550 water chemistry meter. At the end of Day 7 the experiment was concluded, predators removed and noted if still alive and the sand/mud was sieved (500 µm mesh) and surviving chironomids counted.

### *Statistics*

Two-way Analysis of Variance and multiple comparison procedures (Holm-Sidak method) were carried out for the tank experiment results in Sigmastat 3.0.



## RESULTS

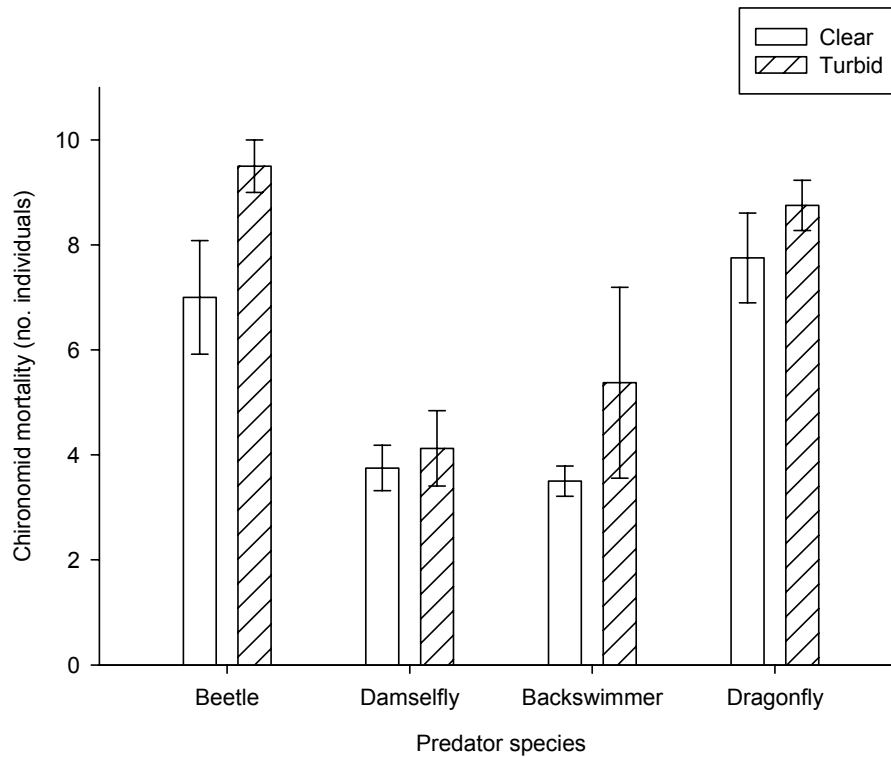
### *Field Survey*

Despite extensive collecting only two invertebrate predator species were found during the field survey, these were the backswimmer (*A. wakefieldi*) and the damselfly larvae (*X. zealandia*). At the Kaituna Lagoon at the east end of the lake, backswimmers and damselflies were relatively abundant. This was the only site that had abundant emergent littoral vegetation. The only other site where predators were found was at the mouth of the Selwyn River where a single, small *Xanthocnemis* was collected.

### *Mesocosm experiment*

During the experiment, temperatures ranged from 18 °C to 19.2 °C in the tanks, while dissolved oxygen levels were high ranging from 8.7 mg L<sup>-1</sup> to 9.5 mg L<sup>-1</sup>. There was no significant difference in temperature (ANOVA, F stat = 0.299, P = 0.597) and dissolved oxygen (ANOVA, F stat = 0.65, P = 0.439) between tanks during the experiment.

The mortality of chironomids differed significantly between predator species (ANOVA, F stat = 13.71, P < 0.001). The adult diving beetle (Dytiscidae) and dragonfly larvae (*P. grayii*) consumed significantly more chironomids on average than damselfly larvae (*X. zealandia*) and backswimmers (*A. wakefieldi*) (Figure 2). Turbidity had a significant effect on predation rates (ANOVA, F stat = 5.111, P = 0.033). However, there was no significant interaction between predator species and turbidity level (ANOVA, F stat = 0.544, P = 0.657). Surprisingly, chironomid mortality was highest for all predator species in the turbid water (Figure 2).



**Figure 2.** Mean ( $\pm$ SE) mortality of chironomids for four predator species in a 7 - day mesocosm experiment ( $n = 4$ ). Clear = settled lake water, turbid = turbid lake water.

## DISCUSSION

During my field survey of the littoral zone of Te Waihora, only two species of invertebrate predators; *Xanthocnemis zealandia* and *Anisops wakefieldi*, were collected. These two species were only found at two sites; the Selwyn River mouth and Kaituna Lagoon. The presence of the small damselfly at the Selwyn River mouth was almost certainly associated with permanent flow from the Selwyn River, whereas Kaituna Lagoon area had many sheltered pools and emergent littoral vegetation. Despite common wetting and drying of the lake margin, this area had numerous semi-isolated ponds which probably retained water during drying periods. Similarly, the Selwyn River mouth area has permanent water and damselflies probably persist in the lower river mouth region. At Kaituna Lagoon, we did not observe any fish, particularly common bullies, which were common at the other seven sites that were

sampled. The lack of fish found at this site may facilitate the presence of invertebrate predators, since invertebrate predators have been found to use vegetation to avoid predatory fish (Lombardo, 1997).

The virtual absence of invertebrate predators from Te Waihora is somewhat surprising, as invertebrate predators have been recorded in the lake historically. Best (1965) found damselfly larvae in the vegetation zone of Te Waihora, suggesting that invertebrate predators may have been present in higher numbers prior to the switch from a clear, macrophyte dominated lake to a turbid, phytoplankton dominated lake than they are at present. Because this study was conducted prior to the 1968 Wahine storm and the switch in states, it is possible that this disturbance event contributed to the decline in invertebrate predators in Te Waihora. However, invertebrate data from Te Waihora prior to 1968 is scarce, so it is difficult to make conclusions as to whether the present low invertebrate numbers is due to macrophyte decline, changes in turbidity, nutrient enrichment, fluctuations in the lake level resulting in wetting and drying of the littoral zones, increased fish predation or some combination of these factors.

In the mesocosm experiment, the diving beetle and the dragonfly consumed more chironomids than the damselfly and backswimmer. This result is not surprising, because dragonfly and beetle larvae are active, visual predators. The damselfly *Xanthocnemis* is usually a 'sit and wait' predator, often associated with vegetation and so its lower predation rates in this experiment may be a result of its typical foraging strategy. Similarly, the backswimmer *Anisops* probably feeds primarily on prey in the water column, so the midge

larvae's construction of dwellings in the sediment probably made this prey less available to the backswimmer.

This mesocosm experiment shows that if invertebrate predators were present in Te Waihora they could have a significant effect on chironomid numbers. From this experiment, we might extrapolate that if Dytiscid beetles were present in Te Waihora, one beetle could consume as many as 9.5 chironomids on average during one week. Thus, if there were 20 beetles per  $\text{m}^2$ , this could markedly change the average chironomid density of  $1119 \text{ m}^{-2}$  (Chapter 2).

All four predator species consumed more chironomids in turbid conditions than clear water. This result however, seems counterintuitive. Since all predator species rely on mainly visual cues to feed, we would expect predation rates to be higher in clear water rather than turbid. One possible explanation for this high predation rate in turbid water may relate to the predator avoidance by the prey. The high turbidity may have resulted in encounters by the predators being more successful than in clear water.

Van de Meutter, Stoks and Meester (2005) also offer another possible explanation why more chironomids were consumed in turbid water. After sampling six shallow lakes (three clear, three turbid), they found different assemblages and predator-prey interactions across both stable states, where larvae prey were more active in turbid than in clear water. Their results agree with Abrahams and Kattenfeld (1997) who hypothesise that in turbid systems, anti-predator behaviour of the prey will become ineffective and will occur less frequently. As a result, the nature of predator-prey interactions is expected to shift from both direct and indirect in clear water to dominantly direct in turbid water. Thus, the impact of predation may increase in turbid environments.

These results do not provide an explanation as to why invertebrate predators are not found in Te Waihora. There are several other potential reasons why the presence of backswimmers, damselflies and other invertebrate predators are in very low numbers or completely absent in Te Waihora. One of the possible explanations for this low diversity of invertebrates is the fact that macrophyte beds and littoral vegetation has decreased since the 1968 Wahine Storm. It is now predominantly a phytoplankton dominated lake, whereas prior to the Wahine storm the lake had substantial beds of aquatic plants and clear water. Benthic invertebrates are frequently more abundant in macrophyte beds than in non-vegetated patches in lakes (Beckett, Aartila & Miller, 1992). Beckett, Aartila & Miller (1992) found mean benthic invertebrate densities in sediments of macrophyte beds to be up to 13 times those of nearby non-vegetated areas within the littoral zone. The diversity of macroinvertebrates was greatest in macrophyte beds (James et al. 1998). James et al (1998) suggested that the presence of macrophytes and habitat stability both have a major effect on the distribution of macroinvertebrates. Conversely, open areas that lack plants have greater disturbance effects and increased fish predator efficiencies (Beckett, Aartila & Miller, 1992).

Another possible reason for the lack of invertebrate predators in Te Waihora may be the frequent lake level fluctuations and intense wave action that occurs in the lake. The littoral zone of the lake often becomes dry even on a daily basis, causing an unfavourable habitat for invertebrates that require vegetation to hide from predatory fish (Diehl, 1992). Invertebrate predators such as dragonfly and damselfly larvae prefer slow-moving or standing (lentic) water (Kadoya, Suda & Washitani, 2004). Therefore, any moderate wave action may be unsuitable for these types of predators. However, other wind-affected lakes such as Lake Grassmere and Sarah have records of the invertebrate predators *P. grayii*, *X. zealandica*, *C. pinguis* and *G. multistriata* (Timms, 1983). Finally, unsuitable water chemistry conditions

such as high salinity, dissolved oxygen levels or high nitrogen levels may create unfavourable conditions for invertebrate predators.

Regardless of the causes of invertebrate predator absence from Te Waihora, the result of this study indicate that the presence of invertebrate predators could have significant effects on *Chironomus zealandicus* populations. *C. zealandicus* is seen by local residents as a major pest as swarms of emerging adults enter homes, are attracted to lights, and coat vehicles and buildings. The absence of natural populations of invertebrate predators may mean that this release from predation pressure has enabled particularly high densities of chironomids to occur in Te Waihora.

## Chapter 5

### Discussion

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Lake Ellesmere (Te Waihora) has been the focus of considerable public interest over the last decade. In a 2005 newspaper article it was suggested that the lake is dead (Christchurch Press, 2005). This perception of the lake has been partially driven by a decline in the commercial and recreational fish, declines in trout numbers in inflow streams, eutrophication and poor water clarity. In this study, I investigated water chemistry conditions and the structure of Te Waihora's benthic communities in order to determine the general ecological health of the lake.

Overall, water chemistry conditions, substrate and invertebrate communities varied significantly around the lake, both spatially and seasonally. Water chemistry conditions, particularly salinity, pH, DO and suspended organic content displayed the most variation. Differing conditions seemed to be mainly associated with freshwater inflows and the salt water intrusion associated with the opening to the sea. Invertebrate communities were depauperate, with only eight taxa in the benthic zone. The low diversity was probably a product of the turbid, eutrophic condition of the lake combined with highly fluctuating lake levels and irregular saline intrusion. Interestingly, small-scale differences in the distribution of invertebrate taxa seemed to reflect the dominant substrate, such that oligochaetes and chironomids preferred areas of the lake with soft silt substrate, and areas with harder substrate supported *Potamopyrgus*.

Periods of saline intrusion also had marked effects on some individual groups. For example, polychaete densities increased in saline conditions while zooplankton numbers were

negatively affected by salinity. I was not able to address the effect of these irregular saline intrusions on other components of the food web, but it seems likely that changes in zooplankton densities will have consequences for phytoplankton biomass and on organisms which feed on zooplankton such as mysid shrimps and bullies.

In order to better understand the effects of turbidity, eutrophication and phytoplankton dominance I investigated the benthic food web using gut analysis and stable isotopes. Not surprisingly, phytoplankton and algae appeared to be the primary food source in the lake. Although macrophytes are still present in very low densities in the littoral zone, they are no longer a dominant source of carbon in the benthic food web, since the Wahine storm in 1968 destroyed the majority of these macrophyte beds (Hughes, McColl & Rawlence, 1974; Taylor, 1996). The loss of these plants almost certainly resulted in the loss of habitat and ephiphytic algae as a food source for the once dominant *Potamopyrgus* (Yeates, 1965). My study showed that today, the invertebrate communities are dominated by oligochaetes, indicating an increase in importance of softer substrate habitat as opposed to a more stable substrate stabilised by macrophytes.

The lack of pre-1968 data means that it is difficult to confidently determine the effect any change from a clear, macrophyte dominated lake to a turbid, enriched, phytoplankton condition had on the lake food web. However, my study shows that it is now distinctively different in its carbon values from the food web of the inflow streams and marine source, showing a carbon-enriched (marine-influenced) food web. This suggests a strong saline influence from the lake outlet to the sea, a disconnection of the lake from its inflow streams and minimal exchange of carbon resources, invertebrates and fish between these ecosystems.



One interesting characteristic of the invertebrate food web is the lack of invertebrate predators compared to previous years and other New Zealand lakes (Timms, 1982; Biggs & Malthus, 1982; Talbot & Ward, 1987). Several possible reasons may exist for this, including a lack of macrophyte habitat which might mediate fish predation, lake level fluctuations in the littoral zone and high loss of habitat due to regular wind driven turbidity and suspended sediment. My mesocosm experiment aimed to assess the possible effect that typical lentic invertebrate predators might have on a key prey species in the lake. It showed that if invertebrate predators were present in the lake they could have a large impact on *C. zealandicus* populations, reducing the impact that emerging adult swarms have on local residents. Interestingly, these predators were more effective in turbid conditions than clear water conditions, which suggests that turbidity in Te Waihora is probably not a major factor influencing their absence.

This study outlines that Te Waihora is a unique ecosystem with a distinct food web, and that it is not a dead lake. But my findings show that the frequency and duration of the lake opening, lake level fluctuations resulting in wetting and drying of littoral zones, and frequent re-suspension of bottom sediments all impact on the benthic ecology of Te Waihora.

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