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Effects of emergent structure on the abundance and size distribution of Trichoptera in Bay of Plenty hill-country streams

A thesis

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Abstract

Restoration of streams is not limited to recreating structural habitat complexity, but also requires recolonisation of biota that had been excluded prior to restoration. Aquatic insects are a key component of a streams ecosystem, but often do not recolonise restored sites at expected rates. It is hypothesised that this is due to a lack of suitable habitat for the oviposition of certain groups, particularly the Trichopteran family Hydrobiosidae which is known to use emergent stones to access the stream bed for oviposition.

I investigated associations between Trichoptera groups with different oviposition strategies and emergent structure in the form of boulders in six Bay of Plenty stream sites. I compared abundances and size class distribution of Hydrobiosidae, Conoesucidae and Hydropsychidae at sites with and without emergent boulders. Results from that study suggest that the presence of oviposition structure was not linked to either the abundance or size distribution of Hydrobiosidae within the sites we examined where other factors such as degree of shade, water velocity and substrate size were key determinant of larval abundance. This first suggested that Hydrobiosidae may arrive in sites lacking emergent structure via alternative means.

Two potential pathways for the colonisation of Hydrobiosidae in reaches without emergent structure were subsequently identified and investigated: (i) access via the banks or emergent vegetation for oviposition; and/or (ii) Hydrobiosidae drift from upstream areas with suitable oviposition habitat.

A study on longitudinal patterns of Hydrobiosidae drift showed inconclusive results, with no significant changes in drift densities or larval size with distance downstream of emergent structure.

A study on the lateral distribution of Hydrobiosidae in a reach lacking emergent structure provided evidence that adults were utilising stream banks to access submerged oviposition habitat with higher numbers of smaller Hydrobiosidae found near the stream edges compared to within the channel. Findings from my study suggest that there should not be any constraints on the recolonisation of Hydrobiosidae within a restored reach as long as: (i) there is suitable oviposition habitat <2km upstream of a restored site; (ii) there is a source population of adults capable of reaching oviposition habitat within the targeted stream; (iii) the water quality is suitable for colonisation; and (iv) instream conditions such as shade, substrate size and water velocities are within the preferred ranges.

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Chapter 1: General Introduction

Recent focus on the degraded state of many of New Zealand's waterways has led to an increase in restoration efforts for freshwater ecosystems (Campbell *et al.*, 2010; Peters *et al.*, 2015). Historically restoration efforts have focussed on single species, however this has moved towards a whole ecosystem approach in recent years (Lindenmayer *et al.*, 2007; Palmer *et al.*, 2010). One aim of most stream restoration efforts is increased aquatic biodiversity which offers many benefits to the targeted ecosystem through: (i) enhanced energy uptake by increasing the number of pathways by which energy can be absorbed into a system, leading to improved flow of energy (Paine, 1966; Cardinale, 2011); (ii) greater resilience to potential negative impacts by having a wider range of pathways by which critical ecosystem functions can be achieved (Palmer *et al.*, 1997; Finke & Denno, 2004); and (iii) increased biodiversity at lower trophic levels that can aid in supporting increased diversity among higher trophic levels (Paine, 1966; Menge & Sutherland, 1976; Wallace & Webster, 1996; McIntosh, 2000). To achieve increased biodiversity, most restoration efforts target habitat-based manipulations such as improving pool – riffle systems, reducing sediment loads and riparian re-vegetation aimed at improving habitat heterogeneity (Roni *et al.*, 2002; Bernhardt *et al.*, 2005; Hilderbrand *et al.*, 2005).

Although well-intentioned, many of these restoration efforts have minimal scientific background and have unrealistic expectations (Bernhardt *et al.*, 2005; Lake *et al.*, 2007). Such purely physical approaches are based on the 'Field of dreams' hypothesis, i.e. "if we build it they will come" (Palmer *et al.*,

1997) based on the assumption that increased habitat heterogeneity will increase biodiversity and that the ecology will “self-design” after habitat is restored (Mitsch & Wilson, 1996; Allan & Costello, 2007), an assumption that has been shown to not hold true in many instances (Hiderbrand *et al.*, 2005; Palmer *et al.*, 2010; Sudduth *et al.*, 2011). This approach often fails to take into account the specific requirements of important species and as such, many restoration efforts fail to achieve their desired results or report low biodiversity increases. For example, a review of 78 restoration efforts from around the world that conducted macroinvertebrate monitoring found that only two showed positive increases in diversity (Palmer *et al.*, 2010), while Louhi *et al.* (2011) showed that even after 20 years many restored streams in Finland showed little increase in the density of benthic macroinvertebrates. Similarly, Sundermann *et al.* (2011) reported little improvement in the benthic invertebrate fauna of 24 restoration sites in Germany unless there were source populations within 5km of the restoration site and Stranko *et al.* (2012) found no difference in both macroinvertebrate and overall biodiversity between restored and unrestored urban streams. A meta-analysis of macroinvertebrate responses to stream restoration efforts showed highly variable results occurring, generally with diversity and density showing slight improvements, albeit slowly, determined by surrounding land use conditions (Miller *et al.*, 2010).

Often generalisations are made across aquatic species, but many taxa have been shown to have quite marked species-specific requirements which can change between different life stages (Crosby, 1975; Reich & Downes, 2003a,b;

2004; Lancaster *et al*, 2010a). Therefore a thorough understanding of the life histories and biology of the target species is required to ensure the successful recolonisation of all desired species into a restored stream (Lake *et al.*, 2007; Spänhoff & Arle, 2007). This need is clearly shown by Hoffman & Resh (2003) who showed the varied oviposition behaviours of two Limnephilidae Trichoptera in North America. Although closely related, these two species have quite different oviposition requirements that may be ignored if generalised assumptions are made.

An important component of a stream ecosystem are the benthic macroinvertebrates, the majority of which are insect larvae (Wallace & Webster, 1996; McIntosh, 2000; Winterbourn *et al.*, 2006). Aquatic insects provide the basis of food webs in most waterways, providing for multiple ecosystem functions by: (i) acting as the initial consumers of primary producers such as algae, (ii) breaking down leaf litter, (iii) filtering organic matter from the water column, (iv) acting as primary predators and (v) providing a rich source of food for higher organisms such as fish (Wallace & Webster, 1996).

New Zealand's aquatic insect fauna diversity is considered to be relatively depauperate compared to the rest of the world, with several major groups represented by very few species. However two orders, Diptera and Trichoptera, show considerable diversity (Winterbourn *et al.*, 1981). New Zealand Trichoptera in particular have over 190 known and at least 45 undescribed species belonging to 16 families, and are considered one of our most important taxa in regards to ecological health of running water ecosystems (Cowley, 1978; Ward, 2003). This

wide diversity of Trichoptera covers almost all functional groups. There are shredders that feed on fallen leaf litter such as *Olinga feredayii*, the browsers and scrapers that feed on algae such as *Pycnocentrodes aeris*, the filterers that capture suspended particles of food as they flow past such as *Aoteapsyche colonica* and predatory species that prey on other stream macroinvertebrates such as *Psilochorema bidens* (Cowley, 1978; Winterbourn, 1978; Quinn *et al.*, 2000). Due to this high biological and functional diversity, it is impossible to expect specific requirements of every taxon to be known, although in New Zealand the majority appear remarkably generalist in behaviours (Crosby, 1975; Winterbourn, 1978; Winterbourn *et al.*, 1981).

Within the Trichoptera, one family stands out for its remarkable diversity. The Hydrobiosidae currently have 87 identified species and another 18 awaiting formal description (Ward, 2003). Primarily predatory, they feed on smaller invertebrates among the generally stony substrates they tend to inhabit (Crosby, 1975; Winterbourn, 1978; Reynaga & Martin, 2010). As a low trophic level predator they play a vital role in stream energy dynamics and improve stream ecosystem resilience by moderating the effects of their prey on instream resources (Fink & Denno, 2004), increase larval dispersal rates by triggering invertebrate drift (Wooster & Sih, 1995), and improve faunal diversity by providing top-down pressure and preventing dominant prey species from monopolising resources (Menge & Sutherland, 1976). Therefore if a goal of restoration projects is to obtain a highly diverse aquatic insect community, Hydrobiosidae can be considered a key component, both as part of the diversity

itself, but also in increasing diversity by reducing the likelihood of single species-resource monopolies (Paine, 1966; Menge & Sutherland, 1976; McIntosh, 2000; Finke & Denno, 2004).

One of the critical pieces of knowledge required for stream restoration projects is the method by which biota are expected to recolonise the restored site (Bond & Lake, 2003; Lake *et al.*, 2007; Spänhoff & Arle, 2007). Trichoptera, like most aquatic insects, have a winged adult stage allowing long range dispersal between streams (Collier & Smith, 1997; Landeiro *et al.*, 2012). It is believed that oviposition behaviour may influence the ability of Trichoptera to colonise streams (Storey *et al.*, 2017). Therefore, knowledge of oviposition behaviour and habitat requirements is likely to be key to ensuring the successful recolonisation of restored streams by Trichoptera.

Trichoptera show a wide range of oviposition behaviour. Conoesucidae deposit their eggs on the surface of flowing water, allowing the eggs to drift and sink to the substrate where they hatch (Pendergrast & Cowley, 1966), whereas some Hydropsychidae are able to dive into the water and swim to the substrate to oviposit using specially-modified mesothoracic legs (Deutsch, 1985; Lancaster *et al.*, 2010a). As adult female Hydrobiosidae do not possess leg adaptations allowing them to swim underwater, Hydrobiosidae utilise emergent structure, primarily rocks, within a stream to crawl below the water's surface to access subsurface oviposition sites (Lancaster *et al.*, 2003; Reich & Downes, 2003a; 2004; Lancaster *et al.*, 2010a; Storey *et al.*, 2017). The selection of oviposition sites has been shown to be species specific, and primarily depends on the rock

size and surrounding water velocity (Reich & Downes, 2003a,b; 2004; Lancaster *et al*, 2010a). In experiments where emergent boulders have been added to streams, the addition of structure increased the amount of Hydrobiosidae egg masses found in that stretch by several orders of magnitude, although this was shown to be dependent on: (i) longitudinal position within a stream, i.e. upstream or downstream; and (ii) initial stream condition in regards to the substrate silt burden (Blakely *et al.*, 2006; Roberts, 2012). Therefore as long as in stream conditions can support Hydrobiosidae, the presence or absence of emergent structure may affect their ability to recolonise and persist at a site, in contrast to other taxa such as Conoesucidae and Hydropsychidae which do not require emergent structure.

1.1 Thesis aims

The aim of this thesis was to investigate and elucidate the patterns of Hydrobiosidae distribution in areas with and without instream emergent boulders to identify whether the absence of emergent structure poses a barrier to the successful recolonisation of restored waterways by taxa that rely on emergent structure for oviposition. To do this I studied the Trichoptera larval communities at six sites on four streams within the Waimapu River catchment. Three investigations were conducted to :

- Determine the differences in benthic Trichoptera community structure, diversity and abundance between sites with and without emergent structure.

- Investigate whether Hydrobiosidae in sites lacking emergent structure could be colonising directly via the stream banks.
- Quantify the drift density of Hydrobiosidae both upstream and downstream of a reach containing emergent structure to determine if drift of early instar larvae from upstream areas could be a mode of recolonisation.

These investigations were conducted using both benthic and drift sampling techniques. Larvae collected were identified to the lowest possible taxonomic level and head widths were measured to identify recruitment patterns.

The results of these investigations are synthesised to form recommendations as to the importance of considering emergent structure in future stream restoration efforts aimed at enhancing Trichoptera biodiversity.

1.2 Thesis structure

This thesis is written as stand-alone papers for future submission to scientific journals. In some cases, I have referenced previous chapters to minimise repetition. In Chapter 1, I have given a general background as to the reasons behind this line of study. In Chapter 2, I provide a detailed description of the sites used for these investigations. In Chapter 3, I investigated the differences in Trichoptera community structure, diversity, abundance and larval size between stream sections with and without emergent boulders. In Chapter 4, I investigated both the lateral distribution and size of Hydrobiosidae across a stream section lacking emergent boulders and also the patterns in drift of Hydrobiosidae

downstream from emergent structure in regards to both densities and size.

Finally, in Chapter 5, I summarise the results of the studies conducted, relate it to previous research and frame these conclusions in regards to what they mean for future restoration efforts.

Chapter 2: Study Area

Six sites were selected from four streams within the Waimapu River catchment, Tauranga, Bay of Plenty, New Zealand (Figs 2.1 & 2.2). These sites were selected based on their similar physical and hydrological characteristics as well as comparatively high water quality and similar sources of flow. Additionally, site selection was based on the availability of reaches with and without emergent boulders. All sites were located between 250-300 m a.s.l. (Table 2.1), except the Kirikiri Stream at 131m a.s.l., which was selected due to its physical similarity with the other sites



Figure 2.1: Site location map. Key: 1: Lower Waiohohi, 2: Upper Waiohohi, 3: Lower Waimapu, 4: Upper Waimapu, 5: Kirikiri, 6: Waimapu Trib. (Map modified from www.Topomap.co.nz)

For two streams (the Waiohohi and the Waimapu) emergent and non-emergent sites were on the same streams separated by at least 500m. An additional emergent site was located on the Kirikiri Stream and an additional non-emergent site was selected on a tributary of the Waimapu (henceforth

referred to as 'Waimapu Trib.'). The Waiorohi had an emergent site downstream from the non-emergent site, whereas the Waimapu emergent site was upstream of the non-emergent site. All streams are third order except the Waimapu Trib. site which was second order.



Figure 2.2: Images of study sites used in this study. 1: Upper Waiorohi, 2: Lower Waiorohi, 3: Lower Waimapu, 4: Upper Waimapu, 5: Waimapu Trib. 6: Kirikiri.

Table 2.1: Location of sample sites, coordinates given in NZGD2000 system. Stream order and elevation taken from LINZ.govt.nz. Sites with emergent structure marked with “*”

Site/ Treatment	Coordinates	Elevation (m/a.s.l.)	Adjacent Land-use	Stream Order	Upstream/ Downstream
Lower Waiorohi*	5807083.4, 1877555.1	256	Native bush	3	Downstream
Upper Waiorohi	5805476.6, 1877860.0	300	Recovering bush/Scrub land	3	Upstream
Upper Waimapu*	5809343.9, 1881414.4	261	Farmland	3	Upstream
Lower Waimapu	5809549.2, 1880918.3	259	Farmland	3	Downstream
Kirikiri*	5813850.4, 1879763.2	131	Native bush	3	N/A
Waimapu Trib.	5808831.0, 1880107.0	250	Farmland/P ine forestry	2	N/A

2.1 Sampling dates

Sampling for Chapter 3 was between 5/12/2016 and 15/12/2016. Sampling for the lateral distribution study in Chapter 4 was conducted on 03/04/2017, with an egg mass search conducted on 09/11/2017. Sampling for the drift study in Chapter 4 was conducted on the 29/11/2017, 06/12/2017 and 07/12/2017.

2.2 Geology

All streams were located within the Mamaku Plateau, which is primarily made up of two distinct layers of ignimbrite rock with localised rhyolite deposits (Briggs *et al.*, 1996), one of which is located at the Waimapu stream emergent site. Most streams in this area have eroded through the majority of the softer upper ‘Mamaku’ ignimbrite layer and have bedrock of harder ‘Waimakariri’ ignimbrite. The ignimbrite layers were laid down from two eruptions from the Rotorua caldera between 330,000 and 220, 000 years ago. The weak definition between

the two layers suggests the eruptions happened very close to each other (Briggs *et al.*, 1996). The larger, emergent rocks present in the lower Waiohohi site are primarily composed of this softer ignimbrite rock, whereas the emergent rocks present in the Kirikiri and upper Waimapu sites are primarily rhyolite.

2.3 Climate

The study area is located in one of the Tauranga City water supply catchments. While Tauranga city receives an average of 1200mm of rain per year, the Waimapu catchment area receives between 1600mm and 2000mm depending on elevation (Chappell, 2014). In 2017, a total 2568mm of rain was recorded in the locality of the sampling sites (<http://monitoring.boprc.govt.nz>) This area is classified as “warm and temperate” (<http://en.climate-data.org>) and has a mean summer daily maximum temperature of 21 - 22°C and a mean winter daily minimum temperature of 4 - 5°C. This region is one of the sunniest in New Zealand with an average of 2000 – 2100 hours of sunshine per year (Chappell, 2014). Air temperature loggers were installed at both the Waimapu stream and the Waiohohi stream (Fig 2.3). An anomalous temperature spike was recorded at the Waiohohi Stream in October, 2017 but can be dismissed as it is likely an error with the recording device or its installation.

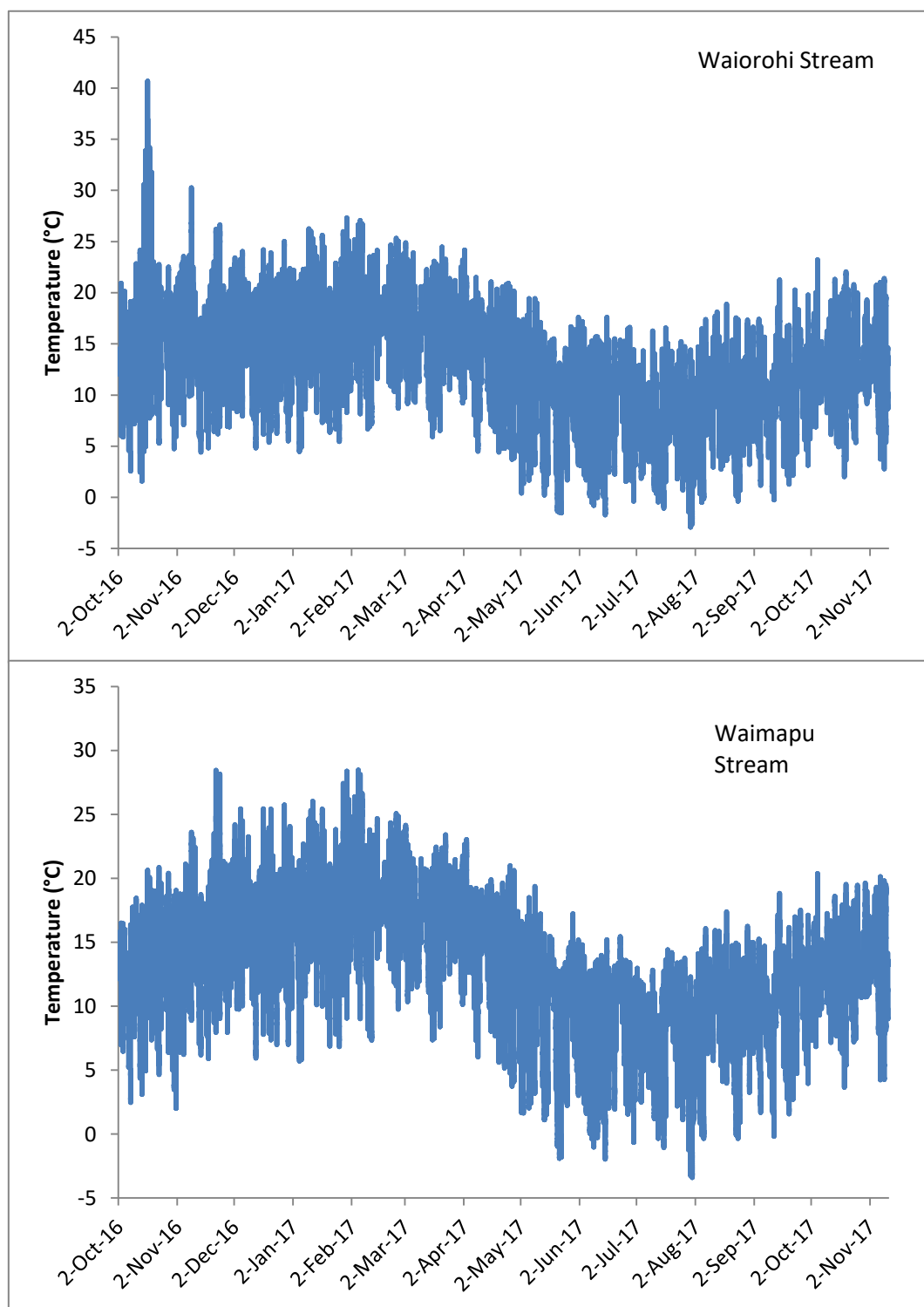


Figure 2.3: Air temperatures recorded at both the Waiorohi and Waimapu Streams between October 2016 and November 2017.

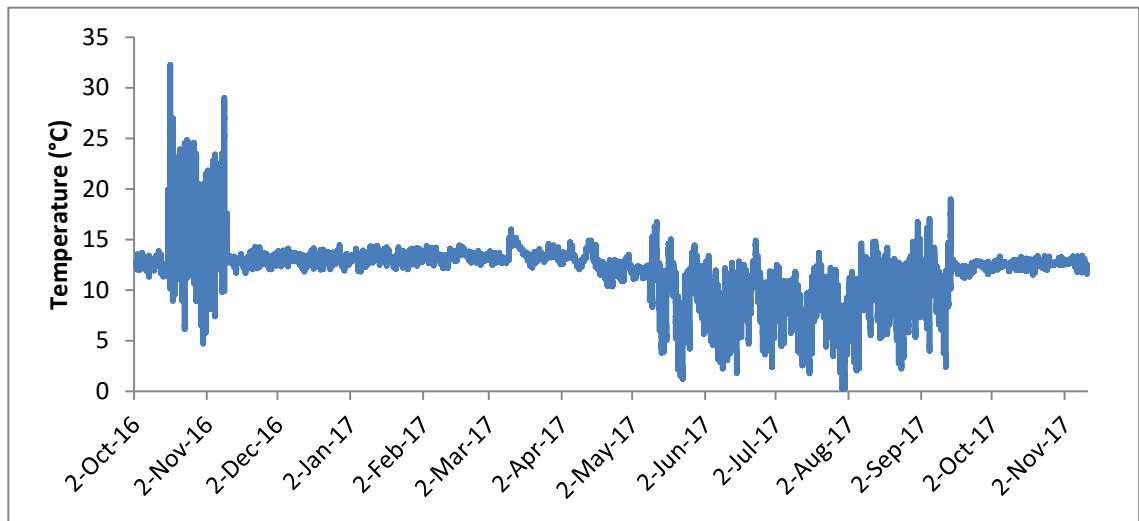


Figure 2.4: Water temperatures recorded in the Waiorohi Stream between October 2016 and November 2017.

2.4 Hydrology

A temperature logger was installed at the Waiorohi stream between October 2016 and November 2017 (Fig. 2.4). Unfortunately it was interfered with by a member of the public soon after installation and was suspended out of the water by debris following a high flow event later in the year; however the remaining data shows an extremely stable water temperature regardless of air temperature variations (Figs. 2.3 & 2.4).

Discharge of the Waimapu River over the 2016-2017 summer averaged ($\pm$ 1 SE) at $1.169 \pm 0.002 \text{ m}^3/\text{s}$, while over the 2017 winter the average was $3.490 \pm 0.021 \text{ m}^3/\text{s}$. Due to the porosity of the soils in this area, flow rates of the Waimapu River are directly, and rapidly, influenced by rainfall. Between the 16th and the 18th of February, 2017 the area was hit by a severe rainfall, as can be seen in the flow rates of the Waimapu stream (Fig.2.5).

Water depth and velocity (both surface and at 60% depth) was measured using a Marsh-McBirney Model 2000 Flo-Mate velocity meter and wading rod at ten equally spaced locations across one transect at each site. As 60% depth velocity is considered to be roughly equivalent to the mean water velocity of a stream, 60% depth water velocity readings will be referred to as 'velocity' in this thesis (Harding, 2009). Discharge (m^3/s) was estimated using the mid-section calculation method defined by ISO 748:2007(CEN, 2007). This was done by calculating the area (m^2) of each sample by multiplying depth of each measured point by $1/10^{\text{th}}$ of the wetted width, then multiplying the resulting area by the 60% depth velocity (m/s). The estimated discharge for each of the measured points was combined to form an estimate of total stream discharge at each site in m^3/s . The Waiorohi stream sites had the highest estimated discharge measured at the time of sampling (5-15/12/2016), and the Waimapu upstream site had the lowest discharge. The relatively large difference between the upper and the lower Waimapu sites is explained by the presence of a small (<1m wide) tributary entering just downstream of the upstream site (Table 2.2).

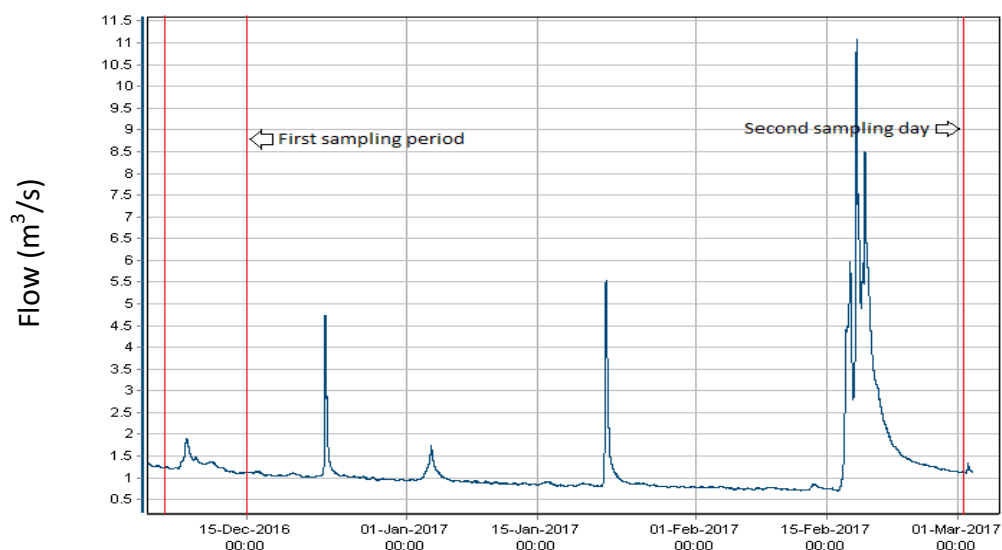


Figure 2.5: Flow rate (m^3/s) of the Waimapu stream during the initial sampling period. Sampling dates indicated by red lines. Recorded at McCarrolls farm, BOPRC live monitoring site. Retrieved from <http://monitoring.boprc.govt.nz>

2.5 Physiochemical attributes

For each site, spot measurements of air temperature, water temperature, dissolved oxygen (DO as % saturation and mg/L), and conductivity (specific and ambient) were made using a YSI Pro 2030 electronic probe at the time of sampling. The Waimapu sites showed increased water temperature compared to other sites, most likely due to the lower shade coverage encountered at this site . All sites had similar DO (mg/L) content but surprisingly the Lower Waiohori had a lower DO (%) reading even though it is located in an area with abundant water aeration due to emergent structure, conductivity at the Lower Waiohori was also much lower than recorded at all of the other sites.

Table 2.2: Physiochemical attributes measured at each site over 5-15/12/2016. Shade cover given as mean (± 1 SE). DO = dissolved oxygen. See table 3.1 for further information

Site/Treatment	Width (m)	Estimated Discharge (m ³ /s)	Water Temp. (°C)	DO (%)	Non-specific Conductivity (µS/cm)	Shade cover (%)
Waiorohi Emergent	6.47	1.91	13.5	97.7	24.4	59.8 $\pm$ 8.9
Waiorohi Non-emergent	4.95	1.74	13	107.2	43.3	36.6 $\pm$ 13.3
Waimapu Emergent	4.37	0.60	16.2	102.7	51.6	9.7 $\pm$ 9.4
Waimapu Non-emergent	4.62	0.98	15.4	103.6	51.5	41.4 $\pm$ 7.4
Kirikiri (Emergent)	4.68	0.78	13	105.5	54.2	98.5 $\pm$ 0.9
Waimapu Trib. (Non-emergent)	5.25	0.78	13.8	108.9	48.8	38.0 $\pm$ 11.0

2.6 Land use

The Waimapu catchment is made up of 50% agricultural land uses, primarily low intensity dairy and drystock farms with some horticulture. The headwaters of the Waimapu stream and its tributaries are in old growth, coastal/podocarp native forest dominated by Rimu (*Dacrydium cupressinum*) and Kahikatea (*Dacrycarpus dacrydioides*), most of which is currently protected (BOPRC, 2012). The Waiorohi stream is the primary water supply catchment for Tauranga City, and as such is primarily surrounded by native bush to protect water quality, as is the case of the downstream site. The upstream site is located in an area that was once a beef cattle farm but was retired and allowed to revert back to native bush to

protect the water supply; it is currently surrounded by thick scrub with a few exotic conifers.

The two Waimapu sampling sites were located within a light dairy/drystock farm and had recently fenced off riparian zones. There was a small riparian zone of native bush on the true left of the upstream site; however this was < 5m wide and on a steep bank. The Kirikiri stream is surrounded by a small, steep-sided valley containing native bush, stretching ~1km upstream from the sampling site while further upstream is a deer farm and exotic forestry. The Waimapu Trib. site is bordered on one side by a lifestyle block that has minimal stock, primarily goats; the banks on this side are partially fenced off and the opposite side has a small exotic forestry plantation.

2.7 Ecology

All sites are known to contain both Rainbow trout(*Oncorhynchus mykiss*) and Brown trout (*Salmo trutta*) and Longfin (*Anguilla dieffenbachii*) and Shortfin (*Anguilla australis*) Eels. No native galaxids or bullies have been recorded in these streams (NIWA, 2017) but anecdotal evidence from local farmers suggests there may be a population of Short-Jaw Kokopu (*Galaxias postvectis*) and/or Koaro (*Galaxias brevipennis*) in the Waimapu and Waimapu Trib. sites. Koura (*Paranephrops planifrons*) were observed in high numbers at all sites.

Macrophytes were present in the non-emergent site on the Waiorohi stream (Figure 2.6) but were absent at all other sites. Species recorded included *Callitriche stagnalis*, *Nasturtium officinale*, *Potamogeton cheesemanii* and *Lemna*

minor. Approximately 23% of the stream bed had submerged macrophytes present, and 7% had emergent species. Additionally various mosses and liverworts were present on most bedrock surfaces covering an estimated 60% of the upper Waiorohi site's stream bed by total area.



Figure 2.6: Example of heavy macrophyte growth present in the non-emergent site of the Waiorohi stream.

Chapter 3: Effect of emergent structure on the distribution, abundance and size range of Trichoptera

3.1 Introduction

Waterways are becoming a key focus of ecological restoration projects around the world, in particular in New Zealand due to the current public awareness of waterway degradation. Habitat heterogeneity is often a primary target of restoration efforts, primarily in the form of restoring more ‘natural’ riffle – pool sequences or introducing large wood to a previously channelized stream (Kail & Hering, 2005; Kail *et al.*, 2007). This approach has been shown to have some merit, such as by increasing nitrogen uptake by the streams ecosystem (Sudduth *et al.*, 2011) and improved habitat assessment scores (Purcel *et al.*, 2002). However, the biological response is often not detectable, indicating some sort of bottleneck that limits recolonisation of ecologically significant taxa.

There are several possible bottlenecks that have been proposed to influence recolonisation of aquatic invertebrates: (i) a lack of source populations limiting the pool of available colonists (Lorenz *et al.*, 2017); (ii) poor initial water quality excluding the establishment of sensitive species (Mackay, 1992; Kail *et al.*, 2012); (iii) lack of suitable instream habitat for target species (Muotka *et al.*, 2002; Palmer *et al.*, 2005); and (iv) a lack of oviposition habitat preventing initial establishment of aquatic insects (Storey *et al.* 2017). To enable a successful

restoration, a species population must be self-sustaining (Palmer *et al.*, 2005), able to both thrive and reproduce successfully within the habitat provided. To achieve this, all stages within a species life cycle must be considered. There is a large body of research on both the aquatic larval and adult dispersal stages (i.e. Waters, 1972; Sagar & Glova, 1992a,b; Smith *et al.*, 2002), however research on the transition point, oviposition, is currently lacking. What information that is currently available shows that many aquatic insect taxa are selective in their oviposition requirements (Lancaster *et al.*, 2003; Reich & Downes, 2003a,b; Storey *et al.*, 2017).

In New Zealand one of the most common and abundant orders of stream insects is the Trichoptera (Winterbourn *et al.*, 1981) which contains most ecological functional groups and is a key component in stream food webs (Burnet, 1969; Mackay & Wiggins, 1979). Amongst the species present in New Zealand, the Hydrobiosidae are particularly well represented comprising 87 described species (Ward, 2003). The oviposition method of Hydrobiosidae is thought to rely on the use of emergent structure within the stream on which they land and then crawl below the water's surface to oviposit on the undersides of the emergent rocks (Reich & Downes, 2004; Storey *et al.*, 2017). This oviposition strategy reflects the lack of swimming hairs on their legs, in contrast to Hydropsychidae which possess these adaptations and are able to swim below the water's surface to access suitable oviposition substrate. Other Trichoptera, such as Conoesucidae, are known to deposit egg masses on the water surface, which then sink to the stream bed (Pendergrast & Cowley, 1966).

Due to the reliance of Hydrobiosidae on emergent structure for oviposition, a lack of emergent structure within a stream may represent a bottleneck that prevents recolonisation of streams following restoration. To test this theory I investigated whether the presence or absence of emergent structure within a stream is related to the composition, abundance and size distribution of the Trichoptera community. I focussed on Hydrobiosidae to test the role of emergent structure, as well as Conosucidae and Hydropsychidae which exhibit contrasting oviposition behaviours not reliant on emergent structure, and which were both abundant in the chosen sampling areas.

Specifically, I tested three hypotheses:

1. There will be a difference in Trichoptera diversity, evenness and community structure between emergent and non-emergent stream reaches. In emergent sites I expected to find: (i) increased diversity due to the increased hydrological heterogeneity caused by emergent structure; (ii) increased Trichoptera community evenness due to the increased diversity of microhabitats available for exploitation; and (iii) higher dominance by Hydrobiosidae due to presence of emergent oviposition structure (Harper *et al.*, 1997; Downes *et al.*, 1998).
2. Difference in taxa abundance will be related to the presence or absence of emergent structures, with (i) Hydrobiosidae more abundant in areas with emergent structure because they rely on these for oviposition; (ii) no differences in abundance of Conoesucidae and Hydropsychidae in relation to the presence of emergent structure because they are not

reliant on them for oviposition. Accordingly, emergent structure presence was expected to explain abundance differences for Hydrobiosidae more than other environmental variables, in contrast to Conoesucidae which were expected to be more influenced by depth and velocity due to the requirement for eggs to settle from the surface, and substrate coarseness for algal growth (Holomuzki & Biggs, 2006). In contrast, Hydropsychidae were expected to be more influenced by velocity as they require flowing water to supply suspended food particles to larvae (Edington, 1968).

3. There will be a significant difference in Hydrobiosidae larval size distribution between emergent and non-emergent sites due to an increased number of smaller individuals near suitable oviposition structure. Accordingly, these differences should not occur in taxa that are not reliant on emergent structure for oviposition (Conoesucidae and Hydropsychidae) whose size distribution was expected to be correlated with environmental variables such as water velocity and substrate size due to: (i) the feeding method of Hydropsychidae which uses a net to capture food and larger individuals are thought to create nets with larger mesh size capable of withstanding stronger water flows (Alstad, 1987); and (ii) potentially substrate size affecting algal growth for Conoesucidae, as food limitation is known to stunt the growth of grazing Trichoptera, potentially leading to a higher proportion of smaller specimens in areas with finer substrates (Holomuzki & Biggs, 2006).

To test these hypotheses I conducted intensive sampling at sites with and without emergent structure during the early summer when oviposition is expected to occur based on adult flight records (Smith *et al.*, 2002)

3.2 Site description

Sampling was conducted at six sites on four different streams in the Waimapu River catchment, Bay of Plenty region, North Island, New Zealand. Two sites were on the upper Waimapu River, one site on an unnamed tributary of the Waimapu Stream and one site on the Kirikiri Stream. Two other sites were located on the Waiorohi Stream (see Figs. 2.1 & 2.2; Tables 2.1 & 2.2 for details of locations and environmental characteristics of all sites). All sites were on 2nd-3rd order streams and at elevations of 130 – 300 m a.s.l.

The “Lower Waimapu” site contains no emergent structure with a gravel/cobble substrate and occasional pockets of sand. The “Upper Waimapu” site is located >600m upstream and cuts through a rhyolite extrusion with abundant emergent structure provided by bedrock with occasional boulders. Both sites are located next to low intensity dairy and dry-stock farms with recently fenced off riparian zones.

The “Upper Waiorohi” site (non-emergent) is surrounded by an old farm that has reverted back to native scrub with the occasional exotic conifer. The substrate at this site is primarily bedrock with gravel/sand trapped in eroded holes and macrophyte and moss growing across the majority of the stream bed. Slower moving sections near the edges have thick aquatic macrophyte growth

dominated by water cress (*Nasturtium officinale*). The “Lower Waiorohi” site is located at the Oropi Gorge road bridge and is surrounded by native bush with numerous soft ignimbrite boulders providing emergent structure.

The other sites were located on: (i) an unnamed tributary of the Waimapu Stream (Waimapu Trib.) where there was no emergent structure and with riparian vegetation consisting of scrub with the occasional large exotic tree, and adjacent pine forestry; and (ii) the Kirikiri Stream, a tributary of the lower Waimapu River, where there were abundant emergent boulders. The Kirikiri Stream sampling site is located at a lower elevation than the other five sites (170m a.s.l. compared to 250-300 m a.s.l.) and is surrounded by native bush, but upstream passes through several dry-stock farms and exotic forestry.

3.3 Methods

3.3.1 Field sampling

Sampling was conducted between 5/12/2016 and 15/12/2016 on reaches 50 m in length. Each 50m reach was divided up equally into 10 transects spaced 5m apart. For each transect the shade was measured in the centre of the channel using a spherical densiometer. Four shade cover measurements were taken facing true left, upstream, downstream and true right. Spherical densiometer readings were taken by counting the number of shaded squares out of a grid of 96 squares; the resulting figures were converted to % shade cover by multiplying the count of shaded squares by 1.04 (Harding *et al.*, 2009).

A random number generator was used to select macroinvertebrate sampling points as a distance (in increments of 10%) from the true right bank across each transect. At each sampling point a visual assessment was undertaken of the substrate prior to invertebrate collection. Substrate was classified using a modified Wentworth scale with the size classes across the b-dimension : >4 m = Bedrock, 256-4000 mm = Boulder, 64-256 mm = Cobble, 8-64 mm = Coarse Gravel, 2-8 mm = Fine gravel and <2 mm = Sand/silt. Substrate composition was then converted into a substrate size index using the method described by Jowett & Richardson (1990) calculated with the equation:

$$\begin{aligned} \text{Substrate size index} = & (0.08 * \% \text{bedrock}) + (0.07 * \% \text{boulder}) + \\ & (0.06 * \% \text{cobble}) + (0.05 * \% \text{coarse gravel}) + (0.04 * \% \text{fine gravel}) + \\ & (0.03 * \% \text{sand/silt}). \end{aligned}$$

At each benthic sampling point, water depth and velocity were measured using a Marsh-McBirney Model 2000 Flo-Mate velocity meter and wading rod. Water velocity readings were taken from 60% depth to approximate the mean water column velocity (Harding *et al.*, 2009).

3.3.2 Benthic invertebrate collection and processing

Benthic macroinvertebrate samples were collected using a 0.1m² Surber sampler with 250 µm mesh net. All rocks encountered within each sample were lifted and scrubbed with a stiff nylon brush to remove invertebrates. The remaining substrate was agitated using the handle of the brush to a maximum depth of 5cm. Samples were preserved in 70% ethanol for later processing.

In the laboratory, Trichoptera were separated from debris on white trays under strong lighting. When it was assumed all had been removed, the sample was given a final scan with a 10x magnifying glass to ensure no smaller specimens were missed. Sorted samples were preserved in 70% ethanol for later identification at 10 – 80x magnification under a Nikon SMZ1000 microscope fitted with an eyepiece micrometer divided into 10µm gradations to enable measurement of larval size. Both head and pronotum maximum widths were recorded for all Hydrobiosidae while only maximum head widths were recorded for all other Trichoptera taxa. Measurements were converted to mm by adjusting for magnification. Identifications were based on the keys of Cowley (1978), Smith & Ward (2005) and Winterbourn *et al.* (2006).

3.3.3 Statistical analysis

Only the Waimapu and Waiorohi Stream were considered for between site comparisons as they had paired emergent and non-emergent sites. The Waimapu Trib. and Kirikiri Stream sites were not considered appropriate for paired comparison, but were included in overall comparisons of emergent and non-emergent status.

Statistical analysis was conducted using Statistica 13 (Dell Inc.). Each data set was tested for normality using the Shapiro-Wilk test and the Levene's test was used for homoscedasticity. Where appropriate, data were transformed using $\ln(x+1)$ to improve normality and homoscedasticity for parametric tests.

Non metric multidimensional scaling (nMDS) ordination plots were used to visualise the dissimilarities between sites for species abundance data, and

vector overlays were used to identify species associations and environmental variable relationships. A PERMANOVA analysis, with a post-hoc pair-wise comparison was used to detect differences in species abundance between sites and between emergent/non-emergent statuses.

The Marascuilo procedure was applied to identify significant differences in percentage contributions of families between treatments (Marascuilo & McSweeney, 1967). This procedure compares the significance of differences between k proportions or percentages by producing a critical value using the equation:

$$r_{ij} = \sqrt{\chi^2_{1-\alpha, k-1}} \sqrt{\frac{p_i(1-p_i)}{n_i} + \frac{p_j(1-p_j)}{n_j}} .$$

where: $\chi^2_{1-\alpha, k-1}$ = critical value for a set α level as determined from a chi-squared critical value chart, r_{ij} = critical value, p = percentage contribution of families i and j , k = number of families and n = number of individuals within each family.

This critical value is compared to the difference in proportion ($P_{i1}-P_{i2}$) and if the difference is lower than the critical value then the difference is significant to below the α level. The critical values were calculated for three significance levels, α = 0.05, 0.01 and 0.001.

The Shannon diversity index (Shannon, 1948) was used to describe the diversity and evenness of species at each site.

A nested ANOVA was used to identify differences in taxa abundance with emergent/non-emergent status as the primary factor, and site as secondary.

T-tests were conducted for comparisons of mean diversity, abundance, head width and environmental variables between paired emergent and non-emergent sites.

Pearson product moment correlations were used to identify relationships between taxa abundances and environmental variables.

Two sample Kolmogorov-Smirnoff tests were used to test for differences in size distribution of dominant genera between emergent and non-emergent sites.

To adjust for multiple comparisons the Holm-Bonferroni method was used to adjust p values for correlation analyses and Kolmogorov-Smirnoff tests, marked as adjusted p in results section.

3.4 Results

3.4.1 Habitat characteristics

Emergent sites were on average slightly wider and deeper, and had more shade cover than non-emergent sites which had coarser substrates and faster water velocities (Table 3.1). The Waiorohi had a greater discharge than the other sites and the upper Waimapu site had the smallest discharge. The Kirikiri and Waimapu Trib. sites showed almost identical discharge rates ($0.78\text{m}^3/\text{s}$). There was a difference in discharge rates between the Waimapu Stream sites with the upper section having a much lower discharge rate than the lower section. This

was likely due to increased groundwater inputs as there were a number of small springs between the two sections and a small, <1m wide, tributary below the emergent site..

A t-test comparison of environmental variables in the Waiorohi stream showed a significant difference in substrate size index scores, with the non-emergent site containing coarser substrate, specifically large patches of bedrock (Table 3.2). In the Waimapu Stream there was a significant difference in substrate size and shade coverage with the emergent site having coarser substrate and less shade. Overall, there were significant differences in water velocity and shade, with emergent sites having slower flows and greater shade.

Table 3.1: Mean ($\pm$ 1 SE) Physical characteristics of sites and combined emergent/non emergent status. Emergent sites marked with “*” .

Site	Depth (m)	Water Velocity (m/s)	Substrate Size Index	Shade Cover (%)
Lower Waiorohi*	0.34 $\pm$ 0.09	0.40 $\pm$ 0.08	5.65 $\pm$ 0.44	71.29 $\pm$ 8.91
Upper Waiorohi	0.24 $\pm$ 0.03	0.60 $\pm$ 0.10	7.10 $\pm$ 0.10	39.44 $\pm$ 13.27
Lower Waimapu	0.30 $\pm$ 0.04	0.18 $\pm$ 0.03	5.18 $\pm$ 0.11	31.36 $\pm$ 9.41
Upper Waimapu*	0.21 $\pm$ 0.02	0.18 $\pm$ 0.05	6.05 $\pm$ 0.28	12.19 $\pm$ 7.35
Kirikiri*	0.21 $\pm$ 0.07	0.20 $\pm$ 0.04	6.18 $\pm$ 0.31	97.99 $\pm$ 0.90
Waimapu Trib.	0.20 $\pm$ 0.06	0.43 $\pm$ 0.10	6.57 $\pm$ 0.44	33.02 $\pm$ 10.97
Emergent*	0.32 $\pm$ 0.04	0.26 $\pm$ 0.04	5.72 $\pm$ 0.20	60.49 $\pm$ 7.61
Non-Emergent	0.25 $\pm$ 0.03	0.40 $\pm$ 0.06	6.23 $\pm$ 0.25	34.61 $\pm$ 6.52

Table 3.2: Results of t-test comparisons between emergent and non-emergent sites/status (data Ln (x+1) transformed to approximate assumption of normality). Significant differences shown in bold.

Variable	t-value	df	p
Waiorohi			
Water Velocity	1.67	18	0.11
Depth	2.48	18	0.02
Substrate Size Index	4.13	18	0.00
Shade Coverage	2.14	18	0.03
Waimapu			
Water Velocity	0.17	18	0.87
Depth	1.63	18	0.12
Substrate Size Index	3.83	18	0.00
Shade Coverage	3.06	18	0.01
All Sites			
Water Velocity	2.28	29	0.02
Depth	0.18	29	0.43
Substrate Size Index	1.57	29	0.06
Shade Coverage	4.29	29	<0.001

3.4.2 Trichoptera Fauna

A total of 2492 Trichoptera were collected from 60 samples, 1919 from non-emergent sites and 573 from emergent sites (Table 3.3). Altogether, 27

Trichoptera taxa were identified from 9 families. Of these, 1174 *Pycnocentroides* spp. were identified making it the most common genus overall. This taxon was present at all sites and in 80% of samples. *Pycnocentroides* was identified to

genus level only due to the difficulty in distinguishing species differences in small larvae (Winterbourn *et al.*, 2006). The second most common genus was *Pycnocentria* spp. with 393 specimens identified, primarily in samples from the Upper Waiorohi, mainly consisting of *P. evecta*, although some *P. gunni* and *P. sylvestris* were also present in low numbers making definitive identification uncertain. The most common Hydrobiosidae genus was *Psilochorema* spp. with 89 specimens identified from two species, *P. donaldsoni* and *P. mimicum*. *Psilochorema* were found in 52% of samples and were present at all sites except the Lower Waiorohi. However, larvae have been previously observed in this stream outside of the sampling reach. The only Hydropsychidae identified was *Aoteapsyche colonica*, which was present at all sites and in 62% of all samples. *Zeiolessica cheira* accounted for 121 individuals but was found in only 20% of the samples with 103 out of the 121 individuals were collected from the Upper Waiorohi. Statistical differences in Trichoptera abundance and diversity between emergent and non-emergent sites are presented below.

Table 3.3: Abundance totals for each site and emergent/non-emergent status for dominant taxa. Emergent sites marked with “*”.

Site	Hydrobiosidae	<i>Psilochorema</i>	Conoesucidae	<i>Pycnocentrodes</i>	<i>Aoteapsyche</i>	Total Trichoptera	# of Taxa
Lower Waiorohi *	5	0	137	91	48	241	17
Upper Waiorohi	58	24	615	264	74	907	21
Lower Waimapu	48	28	48	17	14	116	19
Upper Waimapu*	28	20	157	104	115	305	19
Kirikiri*	8	3	15	1	2	27	14
Waimapu Trib.	32	7	780	697	78	896	20
Combined Emergent	41	23	309	196	165	573	23
Combined Non-emergent	138	59	1443	978	166	1919	24

Shannon diversity index and evenness scores (Table 3.4) showed very little difference between sites and emergent status. The Waimapu Trib. site showed a lower diversity and markedly lower evenness due to the extreme abundance (697 per m²) of *Pycnocentroides* encountered at this site.

T-tests conducted between Shannon diversity for sites within the same stream and for emergent versus non-emergent sites showed no significant differences between paired sites on the same stream or treatments (Fig. 3.1 & Tables 3.5 & 3.6).

Table 3.4: Shannon diversity index and even-ness scores of all sites and emergent/non-emergent status.

Site/Treatment	Shannon diversity	Evenness
Emergent Sites		
Lower Waiorohi	1.80	0.68
Upper Waimapu	1.61	0.65
Kirikiri	1.50	0.77
Non-Emergent Sites		
Upper Waiorohi	1.71	0.58
Lower Waimapu	2.04	0.82
Waimapu Trib.	0.95	0.34
Emergent/Non-emergent status		
Emergent	1.96	0.64
Non-emergent	1.74	0.55

Table 3.5: Results of t-test of Shannon-Weiner diversity index scores between emergent and non-emergent sites. Data transformed with $\ln(x+1)$ to improve normality.

Comparison	t-value	df	p
All sites	0.57	42	0.57
Waiorohi Stream	0.66	31	0.40
Waimapu River	0.85	22	0.51

Community structure

Conoesucidae was the most abundant family with a total of 1752 specimens collected making up 70% of all Trichoptera encountered, followed by Hydropsychidae at 13%. Larval Conoesucidae were dominant at all sites except the Lower Waimapu, where equal percentages of Hydrobiosidae were encountered. At the Waimapu Trib. site, Conoesucidae relative abundance were extremely high, contributing over 87% of all Trichoptera encountered at this site. Hydrobiosidae and Hydropsychidae were more dominant in the Lower Waimapu when compared to the Upper Waimapu. Helicophidae and Leptoceridae were the fourth and fifth most abundant overall, making up 5% and 3% of the total Trichoptera count, respectively.

Philopotamidae larvae were noticeably abundant in the Lower Waiorohi (11% of all Trichoptera encountered at this site) compared to all other sites. This site contributed 26 out of the 32 Philopotamidae encountered across all sites but due to the low numbers at other sites this difference was not statistically significant.

Using the Maraculo procedure to test for significant differences between percent contributions to community composition (Fig. 3.1 & Table 3.6), non-emergent site communities showed a significantly higher percentage of Conoesucidae compared to emergent sites.

Hydropsychidae larvae were significantly more abundant in emergent sites compared to non-emergent sites, largely reflecting the differences in the Waimapu Stream (Fig. 3.1 & Table 3.6). However, the percentage contribution of Hydrobiosidae found in emergent and non-emergent sites were almost identical (7.16% and 7.19% respectively).

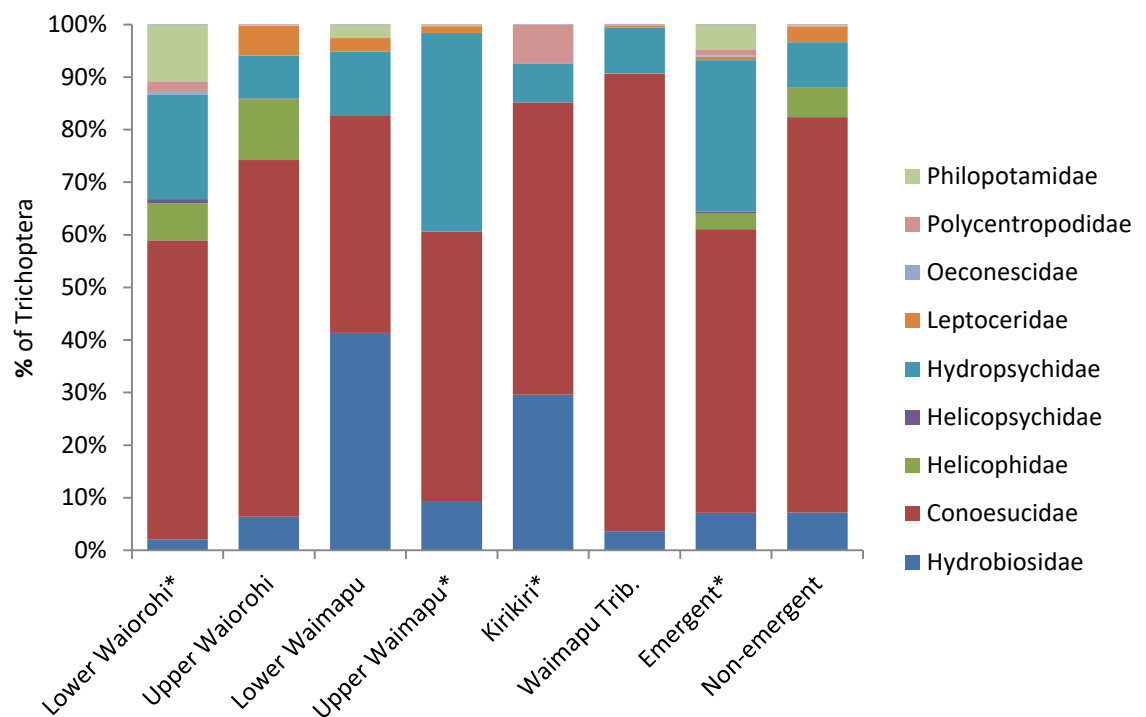


Figure 3.1: Community composition based on percentage abundance of Trichoptera families for sites and emergent/non-emergent status. Emergent sites denoted with “*”.

Table 3.6: Summary of significant results from a Marascuilo procedure analysing differences in family percentage contributions between sites and emergent/non-emergent status.

Family	Emergent	Proportion	Non-emergent	Proportion	Significance
Leptoceridae	Lower Waiorohi	0%	Upper Waiorohi	5.7%	<0.001
Hydrobiosidae	Upper Waimapu	9.2%	Lower Waimapu	41.4%	<0.001
Hydropsychidae	Upper Waimapu	37.7%	Lower Waimapu	12.1%	<0.01
Conoesucidae	All	53.9%	All	75.2%	<0.001
Hydropsychidae	All	28.8%	All	8.7%	<0.001

Ordination analysis of species abundance

Taxa abundances plotted in two dimensional ordination space using nMDS had a stress level of <0.2 indicating an adequate fit of the data allowing interpretations of patterns among samples (Sturrock & Rocha, 2000). The nMDS plots showed relatively strong grouping of samples from the Upper Waiorohi and Waimapu Trib. sites towards the top and left of the ordination, respectively, but a weaker grouping of samples from both Waimapu sites and the Lower Waiorohi (Figs. 3.2A&B).

The Lower Waimapu site had two samples that showed rather large deviations from the other eight, with one sample (far right) containing only a single *Hydrobiosella mixta* while the other (bottom left) contained only two Trichoptera, one *Aoteapsyche colonica* and one *Hydrobiosis copis*. Samples from the Kirikiri Stream were omitted from these plots due to the low number of

Trichoptera present (n = 27) and the large proportion of samples with no Trichoptera (50%).

The Upper Waiorohi site community showed an association with *Pycnocentria* spp., *Zelolessica cheira*, *Hudsonema amabile* and *Hydrobiosis styracine*, whereas the Waimapu Trib. site was more closely associated with *Aoteapsyche colonica*, *Pycnocentrodes* spp., *Neurochorema armstrongi* and *Baereoptera roria* (Fig. 3.2A). Both of these sites were associated with higher water velocities and substrate size index scores, whereas the Lower Waiorohi and some parts of the Upper Waimapu were associated with deeper, slower-flowing water (Fig 3.2B).

PERMANOVA analysis conducted on community level abundances of all taxa showed a significant difference between emergent and non-emergent sites, as well as a significant difference among sites (Tables 3.7 & 3.8). The Upper Waiorohi and the Waimapu Trib. sites showed the strongest difference despite both being faster flowing non-emergent sites with a large proportion of bedrock substrate. The Lower Waimapu and the Waimapu Trib. sites also showed a large difference despite both being non-emergent sites located relatively close to each other and connected to the same river.

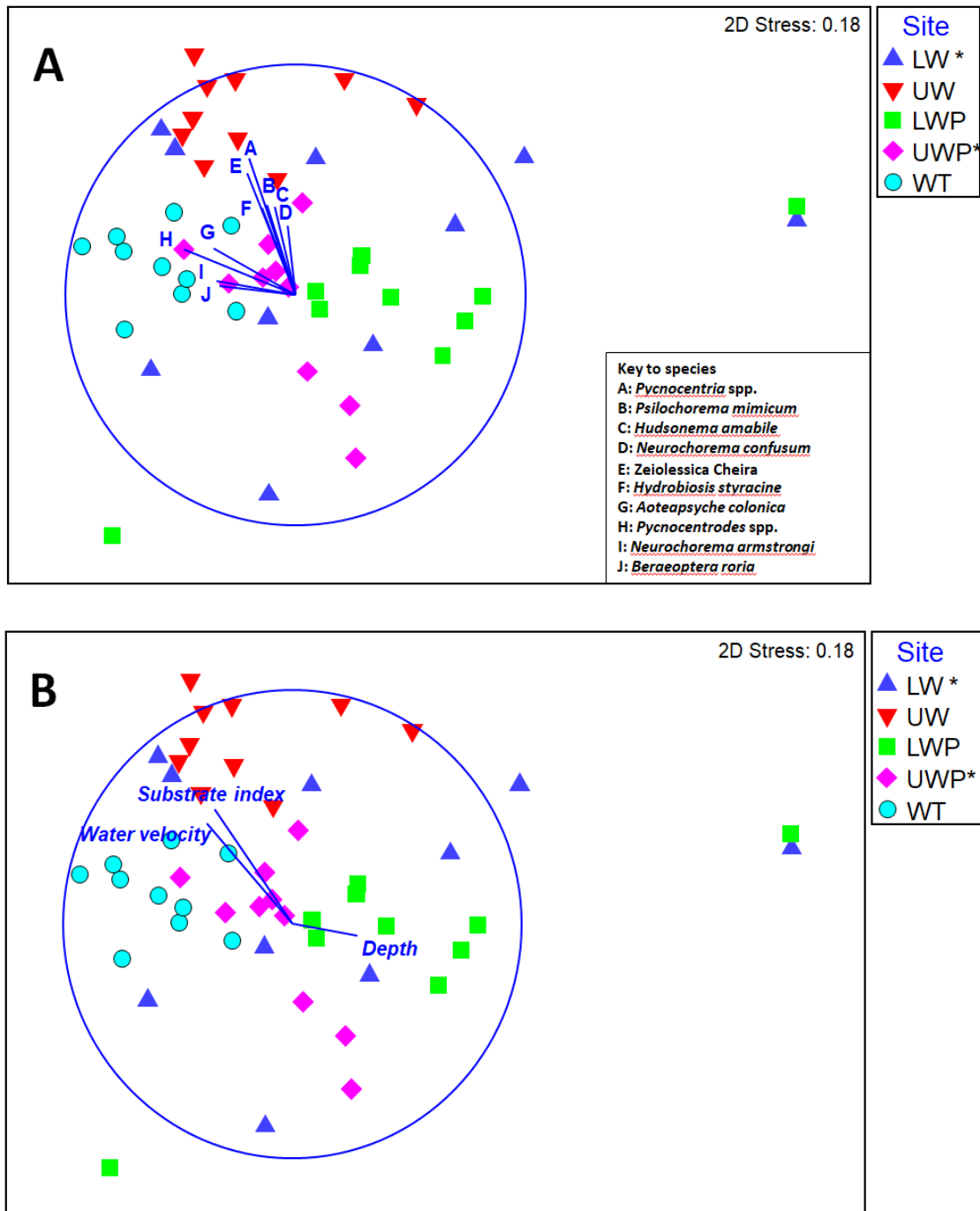


Figure 3.2: Non-metric multi-dimensional scaling plots of $\ln(x+1)$ species abundance by site using Bray Curtis similarities. Overlays are shown depicting A: species-based associations with $r > 0.3$ B: environmental variable associations with $r > 0.2$. Sites: LW = Lower Waiohori, UW = Upper Waiohori, LWP = Lower Waimapu, UWP = Upper Waimapu, WT = Waimapu Tributary. Sites with a "*" indicate emergent sites. Kirikiri Stream omitted from analysis due to low number of Trichoptera.

Table 3.7: PERMANOVA analysis results of species abundance counts between emergent/non-emergent status and by site.

Factor	df	SS	MS	Pseudo-F	P (permutation)
Emergent (Y/N)	1	6333.4	6333.4	3.726	0.002
Site	4	49356	12339	7.259	0.001
Residual	50	84990	1699.8		
Total	55	1.05E+05			

Table 3.8: Pairwise comparison between sites of species abundance counts. Emergent sites indicated with a “*”.

Site 1	Site 2	t value	P (Permutation)
Lower Waiorohi*	Upper Waimapu*	1.7705	0.002
Lower Waiorohi*	Kirikiri*	2.2279	0.001
Upper Waiorohi	Lower Waimapu	2.9858	0.001
Upper Waiorohi	Waimapu Trib.	3.4394	0.001
Lower Waimapu	Waimapu Trib.	3.0153	0.001
Upper Waimapu*	Kirikiri*	3.0790	0.001

3.4.3 Taxa densities

A nested ANOVA comparison of species abundances using emergent/non-emergent status as the main factor, and between sites within emergent status, showed there to be significant differences in total Trichoptera abundances across all taxa except *A. colonica* (Table 3.9), both between emergent and non-emergent status overall and between sites within each status. As shown earlier in Table 3.3, emergent sites had lower abundances across all taxa and in total number of Trichoptera collected.

T-test comparisons of $\ln(x+1)$ transformed abundance data between paired emergent/non-emergent sites on the same streams showed several significant differences (Table 3.10).

In all taxa non-emergent sites showed significantly higher densities than emergent sites except for Hydropsychidae which were slightly more abundant in emergent sites, but not significantly so.

Between the Lower and Upper Waiohoro sites, Hydrobiosidae, Conoesucidae and all Trichoptera showed significant differences. The Lower Waiohoro showed lower densities of all taxa, although *Psilochorema* was unable to be tested as none were collected there.

Between the Lower and Upper Waimapu, only *Pycnocentroides* showed significantly higher abundance in the emergent site compared to the non-emergent site.

Table 3.9: Results of a nested ANOVA test of species abundances using emergent/non-emergent status as main categorical factor, and site as nested factor. Data transformed using $\ln(x+1)$ to approximate assumption of normality. Significant effects ($P < 0.05$) shown in bold.

	SS	df	MS	F	p
All Trichoptera					
Emergent status	30.569	1	30.569	38.874	<0.001
Site x Emergent status	51.697	4	12.924	16.436	<0.001
Hydrobiosidae					
Emergent status	9.949	1	9.949	23.443	<0.001
Site x Emergent status	5.491	4	1.373	3.235	0.019
<i>Psilochorema</i>					
Emergent status	2.659	1	2.659	9.039	0.004
Site x Emergent status	8.627	4	2.157	7.330	<0.001
Conoesucidae					
Emergent status	33.512	1	33.512	41.220	<0.001
Site x Emergent status	58.987	4	14.747	18.139	<0.001
<i>Pycnocentrodes</i>					
Emergent status	24.141	1	24.141	37.304	<0.001
Site x Emergent status	78.890	4	19.723	30.476	<0.001
<i>Aoteapsyche</i>					
Emergent status	1.192	1	1.192	1.101	0.299
Site x Emergent status	20.607	4	5.152	4.755	0.002

Table 3.10: T-test results species abundances between paired emergent and non-emergent sites. Data transformed using $\ln(x+1)$ to improve normality, p-values adjusted for multiple comparisons using the Holm-Bonferroni method. N/A = not applicable. n.s = not significant.

Emergent	Mean±SD	Non-emergent	Mean±SD	t-value	df	Adjusted p
All Trichoptera						
Lower Waiohori	2.66±1.16	Upper Waiohori	4.25±0.80	-3.58	18	<0.01
Upper Waimapu	3.04±0.98	Lower Waimapu	2.30±0.83	-1.82	18	0.26
Hydrobiosidae						
Lower Waiohori	0.32±0.43	Upper Waiohori	1.67±0.80	-4.72	18	<0.01
Upper Waimapu	1.23±0.53	Lower Waimapu	1.45±0.93	0.63	18	n.s
<i>Psilochorema</i>						
Lower Waiohori	N/A	Upper Waiohori	1.02±0.69	-4.64	N/A	N/A
Upper Waimapu	1.01±0.48	Lower Waimapu	1.08±0.81	0.23	18	n.s
Conoesucidae						
Lower Waiohori	2.01±1.27	Upper Waiohori	3.80±0.86	-3.67	18	<0.01
Upper Waimapu	2.40±0.94	Lower Waimapu	1.53±0.84	-2.19	18	0.17
<i>Pycnocentroides</i>						
Lower Waiohori	1.70±1.20	Upper Waiohori	2.81±1.08	-2.18	18	0.08
Upper Waimapu	2.19±0.73	Lower Waimapu	0.84±0.59	-4.53	18	<0.01
<i>Aoteapsyche</i>						
Lower Waiohori	1.03±1.17	Upper Waiohori	1.38±1.27	-3.58	18	0.53
Upper Waimapu	1.84±1.34	Lower Waimapu	0.70±0.64	-2.42	18	0.13

Correlations with environmental variables

Hydrobiosidae density showed significant correlations with all environmental variables across all sites, the strongest correlation being with shade cover (Table 3.11). This relationship was stronger at emergent sites than at non-emergent sites where no measured environmental variables showed significant correlations with Hydrobiosidae density. The dominant Hydrobiosidae genus, *Psilochorema*, showed similar results with a significant correlation with shade coverage across all sites and at emergent sites but not at non-emergent sites.

Conoesucidae abundance across all sites showed significant correlation with water velocity, substrate size index scores and shade coverage but not with depth. At emergent sites the only significant correlation was with shade coverage whereas at non-emergent sites only velocity was significantly correlated. The dominant Conoesucidae genus, *Pycnocentroides*, made up a large proportion of the Conoesucidae abundance counts (67% of all Conoesucidae) and therefore showed almost identical relationships, but in most cases the correlations were stronger. However, at emergent sites the correlations were all weaker while in non-emergent sites there was an additional significant correlation with substrate index scores.

Aoteapsyche showed a significant correlation with water velocity across all sites. This relationship was evident in non-emergent sites but not at emergent sites where shade coverage was the only significant correlation identified.

Table 3.11: Pearson product moment correlation results of taxa abundance across four environmental variables. Data were Ln(x+1) transformed improve normality. p-values were adjusted for multiple comparisons using the Holm-Bonferroni method. "n.s". indicates p values >1.0 due to adjustment. Significant relationships (P<0.05) shown in bold.

Taxa	Statistics	Velocity	Depth	Substrate Size Index	Shade Cover
All Sites					
Hydrobiosidae	r	0.26	-0.31	0.32	-0.52
	Adjusted p	0.04	0.03	0.04	<0.001
<i>Psilochorema</i>	r	-0.07	-0.23	0.18	-0.52
	Adjusted p	0.60	0.25	0.33	<0.001
Conoesucidae	r	0.44	-0.17	0.43	-0.36
	Adjusted p	<0.001	0.19	<0.01	0.01
<i>Pycnocentroides</i>	r	0.46	-0.18	0.46	-0.40
	Adjusted p	<0.001	0.16	<0.001	<0.01
<i>Aoteapsyche</i>	r	0.46	-0.26	0.31	-0.21
	Adjusted p	<0.001	0.09	0.05	0.10
Emergent Sites					
Hydrobiosidae	r	-0.13	-0.29	0.40	-0.62
	Adjusted p	0.50	0.23	0.08	<0.001
<i>Psilochorema</i>	r	-0.30	-0.33	0.24	-0.70
	Adjusted p	0.22	0.23	0.21	<0.001
Conoesucidae	r	0.20	-0.09	0.33	-0.54
	Adjusted p	0.64	0.56	0.23	<0.01
<i>Pycnocentroides</i>	r	0.17	-0.03	0.24	-0.47
	Adjusted p	0.73	0.87	0.63	0.04
<i>Aoteapsyche</i>	r	0.32	-0.15	0.40	-0.50
	Adjusted p	0.17	0.42	0.09	0.02
Non-emergent sites					
Hydrobiosidae	r	0.32	-0.27	0.17	-0.37
	Adjusted p	0.24	0.31	0.38	0.16
<i>Psilochorema</i>	r	-0.10	-0.06	0.06	-0.33
	Adjusted p	n.s	0.75	n.s	0.30
Conoesucidae	r	0.47	-0.17	0.43	-0.09
	Adjusted p	0.04	0.75	0.05	0.64
<i>Pycnocentroides</i>	r	0.54	-0.25	0.59	-0.23
	Adjusted p	<0.01	0.37	<0.01	0.22
<i>Aoteapsyche</i>	r	0.56	-0.40	0.19	0.26
	Adjusted p	<0.01	0.09	0.32	0.32

3.4.4 Larval sizes

Head widths were strongly correlated to pronotum widths for Hydrobiosidae ($r=0.96$, $p<0.001$) and *Psilochorema* ($r=0.94$, $p<0.001$) so only results from head width comparisons are presented. Two sample Kolmogorov-Smirnoff tests showed significant differences in *Pycnocentroides* head sizes with larvae at emergent sites on average larger than those at non-emergent sites (Table 3.12). No differences in size distributions were detected for *Aoteapsyche* and *Psilochorema* in relation to the presence or absence of emergent structure at combined emergent/non-emergent sites. However, both *Pycnocentroides* and *Aoteapsyche* head size distributions were significantly different at the Waiorohi but not in the Waimapu sites. *Pycnocentroides* spp. in the Waiorohi Stream were on average larger in the emergent site than the non-emergent site whereas it was the opposite with *Aoteapsyche* which were on average larger in the non-emergent site compared to the emergent site. These differences were reversed in the Waimapu Stream where, on average, *Pycnocentroides* were smaller and *Aoteapsyche* were larger in the emergent site.

Pycnocentroides in emergent sites showed an extra spike in head sizes around the 0.7-1mm head width range suggesting the possible presence of a second cohort that was not present in non-emergent sites. *Aoteapsyche* within the Waiorohi Stream showed a similar pattern at both sites, however the largest cohort (between 1.65 and 2.4mm head width) was much more pronounced in non-emergent sites (Fig. 3.3). Analysis was not possible for *Psilochorema* in the Waiorohi Stream as none were collected in the emergent site.

Table 3.12: Differences in mean (± 1 SE) larval head widths and two-sample Kolmogorov - Smirnov test results comparing the distribution of head sizes in emergent and non-emergent sites. N/A signifies no *Psilochorema* collected in the lower Waiorohi site. Significant effects ($p < 0.05$) shown in bold.

Genus	Emergent (mm)	Non-emergent (mm)	Max. +ve diff.	Max. -ve diff.	Emergent n	Non-emergent n	p
Combined Sites							
<i>Psilochorema</i>	0.60 $\pm$ 0.04	0.68 $\pm$ 0.03	0.19	-0.03	58	23	>0.10
<i>Pycnocentroides</i>	0.64 $\pm$ 0.02	0.49 $\pm$ 0.01	0.32	0	196	981	<0.001
<i>Aoteapsyche</i>	1.06 $\pm$ 0.03	1.08 $\pm$ 0.04	0.1	-0.08	165	166	>0.10
Waiorohi Stream							
<i>Psilochorema</i>	N/A						
<i>Pycnocentroides</i>	0.67 $\pm$ 0.02	0.49 $\pm$ 0.01	0.62	-0.01	91	264	<0.001
<i>Aoteapsyche</i>	1.10 $\pm$ 0.07	1.27 $\pm$ 0.07	0.2	-0.37	48	74	<0.001
Waimapu River							
<i>Psilochorema</i>	0.60 $\pm$ 0.04	0.70 $\pm$ 0.04	0.38	-0.024	20	27	<0.10
<i>Pycnocentroides</i>	0.61 $\pm$ 0.02	0.65 $\pm$ 0.05	0.19	-0.08	104	17	>0.10
<i>Aoteapsyche</i>	1.06 $\pm$ 0.04	0.97 $\pm$ 0.09	0.12	-0.24	115	14	>0.10

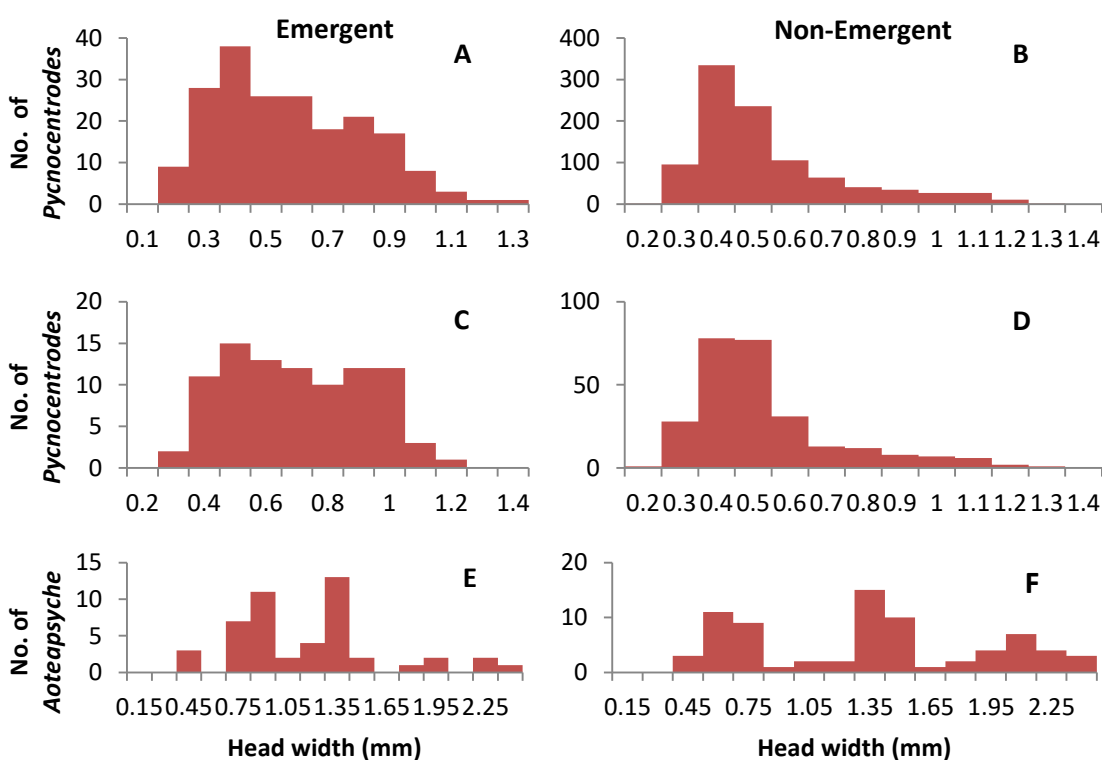


Figure 3.3: Histograms of head size distributions for three taxa by emergent/non-emergent status. A & B: *Pycnocentroides* across all sites. C & D: *Pycnocentroides* within the Waiorohi Stream, E & F: *Aoteapsyche* within the Waiorohi Stream.

Correlations of taxa head widths with environmental variables

Psilochorema head widths showed no significant correlations with any environmental variable across all sites or at non-emergent sites, but showed a strong significant correlation with water velocity at emergent sites ($r = 0.72$, $P < 0.001$, $n = 23$). *Pycnocentrodes* head widths showed no correlation with environmental variables across all sites combined, but at emergent sites was significantly, although weakly, positively correlated with depth ($r = 0.19$, $P = 0.02$, $n = 196$) and substrate index ($r = 0.17$, $P = 0.02$, $n = 196$), whereas at non-emergent sites this genus showed significant but weak correlations with water velocity ($r = 0.11$, $P = 0.01$, $n = 978$), depth ($r = -0.09$, $P = 0.02$, $n = 978$) and shade coverage ($r = 0.07$, $P = 0.04$, $n = 978$). *Aoteapsyche* head widths showed a significant but weak correlation with substrate index scores across all sites ($r = 0.14$, $P = 0.05$, $n = 331$). There were no significant correlations at emergent sites, however at non-emergent sites *Aoteapsyche* showed a weak but significant correlation between head width and shade coverage ($r = 0.21$, $P = 0.03$, $n = 166$).

3.5 Discussion

The aim of this study was to identify the effects of emergent structure on the Trichoptera community within four hill-country streams in the Bay of Plenty. It was expected that taxa with differing oviposition behaviours would respond differently to the presence of emergent structure within a stretch of river. Initially it was predicted that diversity and evenness would be greater in sites with emergent structure, primarily due to increased habitat heterogeneity, reflecting responses of the taxonomically dominant Trichopteran group in New

Zealand streams, the Hydrobiosidae, which are thought to require emergent structure for oviposition (Reich & Downes, 2004; Storey *et al.*, 2017). Accordingly, I predicted that Hydrobiosidae would be more abundant at emergent sites compared to non-emergent sites and make up a larger proportion of the Trichoptera community with more smaller individuals at sites with emergent structure. I also predicted that these differences would not be apparent in other taxa such as Hydropsychidae and Conoesucidae as they do not required emergent structure for oviposition (Cowley, 1978; Deutsch, 1985; Lancaster *et al.*, 2010a). Rather their distributions would be predicted by environmental variables more closely related to feeding methods (Eddington 1968; Alstad, 1987; Holomuzki & Biggs, 2006).

3.5.1 Comparison of study areas / study limitations

There were a few significant differences between sites that may have had an impact on comparisons based on the presence or absence of emergent structure (Table 3.2). Firstly, there was much greater shade coverage in emergent sites that may have had a significant effect on the abundances and species composition (Quinn *et al.*, 1997a,b). There were also higher water velocities in non-emergent sites, which similarly may influence species composition, and potentially size distributions (Eddington, 1968; Cowley, 1978; Alstad, 1987; Shearer *et al.*, 2015).

Additionally, the substrate size index used for analysis partly reflects the habitat stability, with larger substrates more resistant to high flows, but substrate effects on invertebrate fauna are often linked to habitat heterogeneity

provided by interstitial spaces and hydraulic variability (Jowett & Richardson, 1990; Quinn & Hickey, 1990b; Jähnig & Lorenz, 2008). As such this index over-values bedrock substrate which generally has decreased microhabitat complexity with reduced interstitial spaces and lower hydraulic variability, suggesting that bedrock-dominated sites which were assigned higher substrate size index scores do not necessarily provide increased habitat heterogeneity.

Finally, the Kirikiri Stream was chosen due to its apparently pristine condition situated in an old forest valley. Unfortunately samples from this stream provided very few macroinvertebrates, especially Trichoptera (n=27) which rendered this stream unsuitable for many analyses and lowered the overall power of this study. It is unknown why there was such low invertebrate populations collected at this site considering previous sampling had produced relatively high numbers (Cooper, unpubl. data). This difference suggests a recent stressor event (Wright *et al.*, 1994). Additionally, the Kirikiri Stream was not directly linked to the Waimapu Trib. site due to the limited availability of paired sites with desired physical characteristics, and therefore pair-wise comparisons between the Kirikiri Stream and the Waimapu Trib. site were not conducted.

3.5.2 Community structure and taxa densities

Diversity and community structure in relation to emergent structure

The first stage of this study was to identify differences in community structure and diversity between sites with and without emergent structure.

It was expected that trichopteran diversity would increase at emergent sites due to the increased habitat heterogeneity, and subsequent increased diversity of microhabitats available for colonisation. Counter to what was predicted, there was no significant difference in taxa diversity and evenness between emergent and non-emergent sites (Table 3.5), and there was more variability in diversity and evenness between the non-emergent sites than the emergent sites. This may be related to the substrate types at each site, whereby emergent sites were relatively similar to each other and the non-emergent sites showed greater variation in substrate size. The Upper Waiorohi substrate consisted of large amounts of bed rock with thick macrophyte growth, the Waimapu Trib. site consisted of large sections of bare bedrock with sections of cobble in between, and the Lower Waimapu site was primarily cobble dominated and had higher diversity and evenness similar to the higher macroinvertebrate diversity found in cobble substrates in other studies (Harrison *et al.*, 2004; Jähnig & Lorenz, 2008). As noted above, the low structural diversity of bare bedrock is likely to translate into a low diversity macroinvertebrate community, similar to the responses of aquatic invertebrates to habitat complexity in macrophytes shown by Taniguchi & Tokeshi (2004). Alternatively, it may be that the taxa reliant on emergent structure made up too small a percentage of the population

to have a significant effect on community diversity and evenness (Barrantes & Sandoval, 2009)

It was predicted that Hydrobiosidae would make up a greater percentage of the Trichoptera community within sites that contained suitable oviposition sites in the form of emergent boulders. Contrary to this prediction, there was no significant difference in percentage contribution by Hydrobiosidae between emergent and non-emergent sites; in fact the percentage contribution was almost identical. However in the Waimapu Stream there was a significant difference in the opposite direction to what was predicted (Table 3.6). These results suggest that factors other than the presence of emergent structure or related environmental variables may have shaped the diversity, evenness and composition of the Trichoptera community within the streams sampled.

Conoesucidae made up a significantly greater percentage of the Trichoptera community in non-emergent sites, whereas Hydropsychidae made up a significantly greater percentage in emergent sites. If the presence of oviposition sites was not a factor limiting distribution, it makes sense that *Pycnocentroides* larvae dominated in non-emergent sites, as they had significantly lower shade coverage which would improve periphyton growth and therefore food abundance for these algal grazers (Towns, 1981; Quinn *et al.*, 1997a; Holomuzki & Biggs, 2006). This conclusion was supported in the Waimapu Stream, where the emergent site showed significantly less shade cover and significantly higher *Pycnocentroides* densities than the corresponding non-emergent site. Similarly, as Hydropsychidae are generally filter feeders, they

would be expected to dominate in areas with turbulent flows that increase the possibility of particulate organic matter being caught in their nets (Lancaster & Downes, 2010; Nikora, 2010). Again this was clearly shown in the Waimapu Stream where Hydropsychidae made up a significantly larger proportion of the Trichoptera community.

Each site was shown to have distinctive community structures irrespective of the presence of emergent structure, as shown by the nMDS ordination plots (Fig. 3.2A). The Upper Waiohori was associated with *Pycnocentria* and *Z. cheira*, which are known to favour streams with the mosses and liverworts that were plentiful in this site (Winterbourn *et al.* 2006). The Waimapu Trib. site, which lacked the macrophyte growth of the Upper Waiohori, was associated with *Pycnocentroides* and *B. roria*. Non-emergent sites tended to show closer grouping than emergent sites overall, indicating greater variation in community composition based on taxa abundances among emergent sites, potentially reflecting greater micro-habitat heterogeneity caused by more structurally diverse substrates (Beisel *et al.*, 2000; Lancaster & Downes, 2010).

The PERMANOVA analysis showed a significant difference in overall taxa abundances between sites with and without emergent structure (Table 3.7). Additionally there were significant differences between sites within each treatment (Table 3.8), indicating that the Trichoptera communities are influenced by at least one key variable that differed between the sites. One possible source for this difference may be the influence of shade which was significantly higher in emergent sites in all cases, as noted earlier. Quinn *et al.*

(1997a) showed that macroinvertebrate abundances dramatically dropped in heavily-shaded areas, and Towns (1981) clearly demonstrated the community composition changes depending on shade cover. This is also supported by the distribution of the community of the Upper Waimapu site, which had the lowest shade levels of all the emergent sites, and was closer to those of the non-emergent sites in the nMDS ordination plot (Fig. 3.2A & B).

Taxa density responses to emergent structure

The second aim of this study was to identify differences in taxa densities between emergent and non-emergent sites. It was predicted that Hydrobiosidae would be more abundant in areas with suitable oviposition structure, whereas densities of Conoesucidae and Hydropsychidae, which do not rely on emergent structure for oviposition, would be affected more by the suitability of habitat for food acquisition.

As predicted, Conoesucidae did not appear to be greatly influenced by the presence of emergent structure and had significantly higher densities in more open non-emergent sites. In emergent sites densities were negatively correlated with shade coverage (Table 3.11) underscoring the importance of this variable, while in non-emergent sites densities were positively correlated with water velocities. Previous works have shown cased caddis are able to resist relatively high water flows (Waringer, 1989 ; 1993) therefore allowing them to dominate in these habitats. Less shaded non-emergent sites presumably had higher autochthonous energy supplies, enabling hydrological variables to assume

a greater role in defining the abundance of Conoesucidae species which have an ability to withstand higher water velocities than most other cased caddisfly species (Cowley, 1978; Duncan & Brusven, 1985; Winterbourn *et al.*, 2006; Li & Dudgeon, 2008; Hagen *et al.*, 2010).

Aoteapsyche densities responded to emergent structure as predicted, with no significant differences between emergent and non-emergent sites (Table 3.11). However this response appeared to be site-specific suggesting other factors influence their abundance. As expected, water velocity appeared to be the primary factor explaining their distribution as has previously been shown to be the case with most net-spinning caddis which rely on the water flow to bring food particles to them (Edington, 1968; Williams & Hynes, 1973; Alstad, 1987). Additionally, in non-emergent sites, there was a significant negative correlation with shade coverage (Table 3.11) consistent with the findings of Quinn *et al.* (1996) who suggested reduced periphyton growth in shaded sites improved near bed hydraulic flows, therefore likely increasing food capture by net-spinning caddis (Edington, 1968; Williams & Hynes, 1973; Alstad, 1987).

My predictions of the response to emergent structure for Hydrobiosidae were not supported by the data in this study. Rather, Hydrobiosidae were found in significantly greater densities in non-emergent sites compared to emergent sites (Table 3.10). As it is believed that Hydrobiosidae are reliant on emergent structure for oviposition (Reich & Downes, 2004; Storey *et al.*, 2017) this was surprising and suggests that they were entering non-emergent reaches by other means such as: (i) drift from suitable oviposition habitat into areas with none as

suggested by a genetic survey of a similar species *Plectrocnemia conspersa* known to use emergent structure for oviposition (Wilcock *et al.*, 2005); or (ii) from the stream edges suggesting the reliance on emergent structure has been over emphasised in terms of its role as oviposition habitat. This type of behavioural plasticity has been observed in other insect orders such as Odonata (Uéda, 1979) and Lepidoptera (Wiklund, 1981).

Shade coverage was the strongest predictor of Hydrobiosidae abundance, consistent with Quinn *et al.* (1997b) who found much higher abundances of Hydrobiosidae in unshaded, pasture sites. This may be due to the increased presence of preferred prey in the form of Chironomidae larvae (Winterbourn, 1978), which also show a strong positive association with well-lit reaches due to increased algal food supply (Townes, 1981; Quinn *et al.*, 1997a).

When diversity and densities of Trichoptera were examined together, it became apparent that factors other than the presence of emergent structure regulate the distribution of Trichoptera in the spring-fed, upland streams investigated in this study. Many studies have previously investigated other factors that influence Trichoptera distribution, with the primary variables being: depth, velocity, substrate and shade cover (Jowett & Richardson, 1990; Quinn *et al.*, 1997; Downes *et al.*, 1998). This study confirms the importance of these habitat variables and suggests they may be more important than the presence of oviposition sites in determining the structure and abundances of larval trichopteran communities.

3.5.3 Size distribution responses to emergent structure

The third aim of this study was to identify differences in larval size distributions between emergent and non-emergent treatments. It was predicted that emergent sites would have more smaller individuals than non-emergent sites as they hatch and disperse from oviposited egg masses. It was also expected that taxa not reliant on emergent structure for oviposition would not show this size difference.

Contrary to what was predicted, both *Pycnocentroides* and *Aoteapsyche* size distributions showed significant differences between emergent and non-emergent sites, with *Pycnocentroides* larvae being generally larger in emergent sections, and *Aoteapsyche* larvae being generally larger in non-emergent sections, except in the Waimapu Stream (Table 3.12 & Fig. 3.3). These size distribution patterns correspond with those found by Stark (1981), who attributed this to a single cohort with larger specimens persisting from the previous year. The differences in *Pycnocentroides* head widths between sites may be explained by microhabitat complexity due to macrophyte and moss growth in the Upper Waiohori site providing greater habitat opportunities for smaller individuals, whereas in the emergent site habitat complexity was formed by larger objects, i.e. boulders, which provide larger habitat niches that would benefit larger individuals as they are less restricted by space and can out compete smaller individuals (Osborne & Herricks, 1987; Taniguchi & Tokeshi, 2004; McAbendroth *et al.*, 2005). *Aoteapsyche* showed a different distribution within the Waiohori stream, with an increase in larger individuals in the non-

emergent section (Fig. 3.1, Table 3.10), likely due to the increase in food availability due to macrophyte and algal growth as observed elsewhere (Glasgow, 1936; Crosby, 1975; Cowley, 1978; Harding, 1997).

Both *Pycnocentrodes* and *Aoteapsyche* head widths showed relationships with several environmental variables. All of the correlations for *Pycnocentrodes* could be attributed to food resource availability, with: (i) larger specimens withstanding higher velocities, and therefore able to capitalise on areas with less competition (Waters, 1972; Otto, 1976; Osbourne & Herricks, 1987); (ii) Larger larvae colonising substrates with greater algal growth (Holomuzki & Biggs, 2006); and (iii) higher periphyton growth in areas with less surface turbulence, such as the laminar flow over bedrock substrates observed in both the Upper Waiorohi and Waimapu Trib. sites (Singer *et al.*, 2006; Bessemer *et al.*, 2007). The correlation with shade coverage could be explained by larger specimens out competing smaller individuals for limited food resources (McAuliffe, 1983). However, as these correlations are so weak ($r < 0.19$), it is likely that they are artefacts of the large sample sizes for this taxa and are unlikely to be ecologically significant (Greenwald *et al.*, 1996).

Aoteapsyche showed a significant positive correlation between head width and substrate size index scores, in line with a well-documented relationship between *Aoteapsyche* abundance and substrate size, often attributed to the increased stability of larger substrates providing enhanced long term habitat (Jowett *et al.*, 1990; Winterbourn & Harding, 1993; Quinn & Hickey, 1990a; 1990b). There was also a significant positive correlation detected with

shade cover at non-emergent sites, opposite to that detected between abundance and shade cover overall, which could also be explained by competition for limited food resources, due to reduced productivity in shaded areas, benefitting larger individuals which may out-compete the smaller individuals with smaller and less efficient nets (Blackburn *et al.*, 1993; White *et al.*, 2007).

Psilochorema was not distributed as expected in terms of larval size with no significant difference between emergent and non-emergent sites detected. This may be partly due to the low numbers collected (Table 3.3) limiting the power of statistical tests. However, combined with the significantly higher abundances found in non-emergent sites it seems unlikely that the hypothesis is supported and that factors other than oviposition site availability influenced the size distribution Hydrobiosidae. A strong positive correlation found between *Psilochorema* head width and water velocity at emergent sites suggests that hydraulic factors may be key influences on the distribution of Hydrobiosidae. It has been previously demonstrated that smaller individuals show higher drift propensity than larger specimens, which are able to grip using their larger, stronger anal claw (Sagar & Glova, 1992; Collier *et al.*, 1995). This suggests that smaller individuals may be removed by faster flows and drift out of the emergent sections, allowing larger specimens to dominate in areas of higher flow.

3.6 Conclusion

This study suggests that environmental variables, especially substrate types, water velocity and shade cover, have a larger influence than emergent structure on Trichoptera community composition and diversity, as well as the abundance and size structure of Hydrobiosidae populations

Conoesucidae tended to show a preference for sites lacking emergent structure, with higher flow rates and less shade. This is likely to be due to increased food availability and improved ability to withstand higher flow rates compared to other taxa. In contrast, *Aoteapsyche* showed a preference for sites with emergent structure and higher water velocities, suggesting that food supply, and possibly intra-specific competition, are key determinant of distribution for these taxa.

Hydrobiosidae also appeared to prefer sites with less shade cover similar to findings by Quinn *et al.* (1997a), and the dominant genus, *Psilochorema*, also showed a strong correlation between head size and water velocity.

Collectively, these findings indicate that physical habitat selection, rather than oviposition site selection, may be a key determinate of the in stream distribution of Hydrobiosidae. In the Waiorohi stream, where the emergent site was situated downstream of the non-emergent site, there were significantly higher densities of Hydrobiosidae in the non-emergent site, however there is no known emergent structure upstream of this site for at least 2km. Similarly, in the Waimapu stream, the non-emergent site showed significantly higher densities of Hydrobiosidae, which made up a significantly larger percentage of the

Trichoptera community. In this stream, where the differences were more pronounced, the non-emergent site was situated approximately 600m downstream of the emergent site, and >300m from the nearest small patch of emergent structure. These patterns suggest that Hydrobiosidae are arriving at non-emergent sites via another pathway. Two possibilities are: (i) adult females may be entering the stream via the banks and ovipositing on suitable submerged substrates or (ii) larvae may be drifting into non-emergent reaches from upstream emergent reaches, which would explain the increased densities encountered in the Waimapu stream where the emergent site was upstream of the non-emergent site. I examine the potential roles of these alternative pathways in Chapter 4.

Chapter 4: Lateral distribution and longitudinal drift of larval Hydrobiosidae in Waimapu Stream.

4.1 Introduction

Hydrobiosidae are thought to lay their eggs on the undersides of stones in stream channels by crawling down the sides of emergent structure (Reich & Downes, 2003a). Due to this specialised oviposition behaviour and their inability to swim, this family of Trichoptera has been shown to exhibit species specific selectivity for oviposition sites (Lancaster *et al.*, 2003) . Adults have been shown to increase oviposition rates with the addition of emergent rock structure (Blakely *et al.*, 2006; Roberts, 2012) and to select abnormal oviposition sites in the absence of natural emergent substrates, for example by laying eggs on wooden stakes driven into a stream bed (B. Smith, NIWA, pers. comm.).

Hydrobiosidae are also recorded in areas that do not appear to contain suitable local emergent structure for oviposition (R. Storey, NIWA, unpubl. data). In Chapter 3, I found that within the Bay of Plenty hill-country streams I examined, the presence or absence of emergent boulders, considered to be

preferred oviposition structures for Hydrobiosidae (Reich & Downes, 2003a; 2004; Storey *et al.*, 2017), did not explain either the abundance or size distribution of larvae which were more influenced by other environmental variables, most notably: (i) shade cover; (ii) substrate type; and (iii) water velocity. This finding suggests that another pathway may potentially be in play that influences oviposition and subsequent size distribution within streams. Two possible explanations may account for the absence of a response to emergent structure, either: (i) Hydrobiosidae are entering the water laterally via the stream banks to access suitable sub-surface oviposition sites; and/or (ii) Hydrobiosidae are arriving via drift from suitable oviposition sites upstream. This study aims to test both of these potential explanations to determine the effect they have on the abundance and size distribution of Hydrobiosidae.

A large, bed-moving, flood event on the between the 16th and 18th of February 2017 (Fig. 2.5) provided the opportunity to test whether ovipositing adult Hydrobiosidae access streams from the edges leading to differences in abundance and size frequency with distance across the channel. It was expected that the large flood would have washed the majority of the benthic community out of the intended sampling reach, enabling recolonisation by Hydrobiosidae through oviposition to be monitored. Adult Hydrobiosidae have been shown to have extended flight periods (Smith *et al.*, 2002), and were expected to have persisted through the storm in terrestrial refugia. Sampling was conducted six weeks after the flood event to allow sufficient time for new oviposition and hatching to occur (B. Smith, NIWA, pers. comm.)

The alternative pathway of longitudinal drift from upstream oviposition sites is supported by a genetic study on *Plectrocnemia conspersa* (Polycentropodidae) (Wilcock *et al.*, 2005) which exhibits similar oviposition behaviour to Hydrobiosidae. This study suggested that high drift rates in early instar *Plectrocnemia* allowed rapid, long-range dispersal, increasing genetic diversity in this species which potentially colonised areas without emergent structure. Reich & Downes (2004) showed that early instar Hydrobiosidae larvae were present in greater abundances in areas without emergent structure and with higher water velocities. Additionally they showed that in areas with emergent structure, early instar larvae were present in lower numbers in areas with higher water velocities suggesting high rates of drift in this early life-stage. Two studies on the life stages of *Rhyacophila* spp. collected in drift nets showed an increased propensity to drift in the second instar and fifth instars (Elliot, 1968; Fjellheim, 1980). As *Rhyacophila* spp. are closely related to Hydrobiosidae, both taxonomically and in trophic position, their findings suggest that drift may be important in determining the distribution of Hydrobiosidae within a stream.

The investigations in this chapter were carried out in Waimapu stream which provided a comparatively large Hydrobiosidae community (see Chapter 3) and suitable combinations of reaches with and without emergent structure to test recolonisation from laterally accessed oviposition sites, and the role of longitudinal drift from patches of emergent structure. I tested the following hypotheses in relation to these two pathways:

Lateral distribution

To determine the role of oviposition on the post-flood lateral distribution of Hydrobiosidae I tested two hypotheses: (i) Hydrobiosidae abundance across transects will be higher nearer the stream edges than in the channel centre due to oviposition by females entering from the sides of the stream; and (ii) due to recruitment from egg masses laid near stream edges, head widths of the dominant Hydrobiosidae taxa will be, on average, smaller nearer the edges of the stream than in the channel centre. If these hypotheses were supported, differences in larval abundance and size would be related more to lateral position within the stream than to environmental variables such as water velocity, depth or substrate composition.

Longitudinal drift

To determine the role of drift on the distribution of Hydrobiosidae I tested four hypotheses: (i) drift densities of Hydrobiosidae will be higher below sections of emergent structure compared to sections lacking suitable oviposition structure; (ii) there will be higher densities of early instar Hydrobiosidae larvae in the drift below patches of emergent structure compared to sections lacking suitable oviposition structure, due to higher numbers of smaller individuals near oviposition habitat; (iii) numbers of Hydrobiosidae within the drift will decrease with distance from emergent structure as larvae settle out of the water column and enter the benthos; and (iv) average size of Hydrobiosidae within the drift will increase with distance from emergent structure as fewer smaller instar larvae enter the drift from oviposition sites.

4.2 Methods

4.2.1 Site description

The site for both studies was the Upper Waimapu Stream (N5809553.5, E1880895.3) at an altitude of 260m a.s.l. The Waimapu originates from springs on the slopes of Otanewainuku, a protected forest reserve. The section of the Waimapu Stream used for this study is third order and surrounded by low intensity farmland with recent riparian fencing and planting of native trees. There are several sections where the riparian vegetation consists of exotic trees, primarily poplar (*Populus nigra*). Steeper banks support native bush, consisting primarily of tree ferns and manuka (*Leptospermum scoparium*). The substrate is a mix of cobble/gravel in riffle sections with sand/silt in deeper pool sections. Two emergent sections exist where the rhyolite bedrock is exposed, creating a mix of boulder substrate and protruding bedrock. The upper emergent section is approximately 120m long and the lower emergent section is only 10m long (Fig. 4.1) (see Chapter 2 for more details).

4.2.2 Lateral distribution sampling

Sampling took place on the 03/04/2017, approximately 6 weeks after an intense rainfall event between the 16/02/2017 and 18/02/2017 (195mm over three days), when the stream's flow rate increased by over 10 fold (Fig.2.5). The six week waiting period was assumed to provide sufficient time for new oviposition, hatching and initial dispersal of early instar larvae into the disturbed area (Jackson & Sweeny, 1995; Kefford *et al.*, 2004).

Sample collection and processing

Six transects with relatively even flow rates and depths across the stream were selected over a 180m long reach with no emergent structure within 100m upstream. At each transect five samples were collected at 10%, 30%, 50%, 70% and 90% across the stream channel from the true right bank..

Each sample was collected by using a 0.1 m² Surber sampler fitted with a 250µm mesh net. All rocks within the sample quadrat were lifted and brushed with a stiff nylon brush, and the substrate agitated with the brush handle to a depth of around 5cm. Samples were preserved in isopropyl alcohol for later sorting and identification.

Within each sample quadrat, substrate was visually assessed using a modified Wentworth scale (Wentworth, 1922), and converted into a substrate size index score as per the method used by Jowett & Richardson (1990) using the equation:

$$\begin{aligned} \text{Substrate size index} = & 0.08 * \% \text{bedrock} + 0.07 * \\ & \% \text{boulder} + 0.06 * \% \text{cobble} + 0.05 * \\ & \% \text{coarsegravel} + 0.04 * \% \text{finegravel} + 0.03 * \\ & \% \text{sand} \end{aligned}$$

Depth and water velocity were measured using a Flomate Model 2000 Marsh – McBirney doppler velocity meter with a wading rod.

Macroinvertebrate samples were initially processed on a white tray under bright lighting to separate out the majority of the invertebrates from sand and

detritus. After all visible invertebrates were removed, the sample was scanned again under a 10x magnifying glass to ensure smaller specimens were collected. At this stage Hydrobiosidae were separated from the other invertebrates for species level identification based on the key of Smith & Ward (2005).

Sorted samples were preserved in isopropyl alcohol for identification of Hydrobiosidae which was conducted at 10 – 80x magnification under a Nikon SMZ1000 microscope fitted with an eyepiece micrometer divided into 10µm gradations to enable measurement of larval size. Both head and pronotum maximum widths were recorded for all Hydrobiosidae. Measurements were converted to mm by adjusting for magnification.

Statistical analysis

Psilochorema was the dominant genus, making up 63% of the Hydrobiosidae collected. Therefore analyses were conducted on this genus and for all Hydrobiosidae combined. As head width and pronotum width showed an extremely strong correlation ($r=0.97$, $P<0.001$) only head width was used for statistical analysis. Due to the wide variability in head sizes between taxa, larval instars were also identified and grouped into “early”, “middle” and “late” pseudo-instars based on prosternal plate development (McFarlane, 1951). Pseudo-instars were given a ranked value depending on developmental stage where early = 1, middle = 2 and late = 3, allowing for analysis of both absolute size and developmental stage.

Data was analysed by both: (i) percent across the stream from true right bank, i.e. 10%, 30%, 50%, 70% & 90%; and (ii) by distance to nearest bank, i.e.

10% and 90% across stream combined into “near bank” grouping, and 30% and 70% across stream samples combined into “channel edge” grouping, and 50% samples as “channel centre” grouping.

All data sets were tested for normality using a Shapiro-Wilk test and for homoscedasticity using a Levene’s test in Statistica 13 (Dell Inc.). The three environmental variables recorded, water velocity, depth and substrate size index all adhered to normality and homoscedasticity assumptions. Taxa density and head width data failed to approximate normality regardless of transformation so non-parametric testing was required for analysis of those data.

Accordingly, a one-way ANOVA test was used to identify differences in environmental variables across the stream channel, and by distance to nearest bank, while Kruskal-Wallis tests were used to test for differences in larval densities and mean head widths using percent distance from true right bank and associated across-channel groupings as factors. Where significant differences were identified in Kruskal-Wallis tests, a Dunn’s test of multiple comparisons of mean ranks was used as a post-hoc analysis to determine the location of differences identified.

Spearman rank order correlations were used to identify correlations between head widths and measured environmental variables.

4.2.3 Longitudinal drift distribution study

Drift sampling was conducted on three dates, the 29/11/2017, 06/12/17 and 7/12/17. This was approximately four weeks after Hydrobiosidae were recorded

flying in larger numbers from light trapping (Cooper, unpubl. data). This four week period was selected to allow enough time for at least one round of oviposition to have occurred and the eggs to have hatched (Jackson & Sweeny, 1995; Kefford *et al.*, 2004)

The 610m stretch was divided into three sections (Fig. 4.1): (i) an 'Upper' section consisted of three nets located 90.5, 40 and 3m upstream of the main emergent structure reach; (ii) the 'Below-1' section consisted of four nets located 12.5, 110.5, 206 and 293m downstream of the 120m-long main emergent structure section, and 15m upstream of the 10m-long secondary emergent structure section; and (iii) the 'Below-2' section consisted of five nets located 70.5, 131, 197.5, 252.5 and 311m below the secondary emergent boulder section.

Sample collection and processing

The drift nets used in this study were based on the design described by Field-Dodgson (1985). Each one consisted of a single device constructed out of PVC down-piping fittings with a mouth area of 0.0058m². Attached to each sampler was a 1 m long net with 250 µm mesh. A total of 12 drift nets were installed in the river; 10 nets were secured using wooden stakes driven into the stream bed or, due to bed-rock at two sampling locations (nets 1 and 8), using monofilament line attached to stakes driven into the banks with a weight set to the appropriate depth to hold the nets in position.



Figure 4.1: Satellite view of sampling area with emergent structure patches shown (circled areas) and net locations (dots). Stream flows from right to left. Lateral distribution study section extends downstream from lower emergent structure patch

Nets were deployed starting from the upstream sampling point (Net 1) and finishing at the downstream sampling point (Net 12) and retrieved from the bottom net to the top net to minimise disturbance related drift. Times of deployment and retrieval for each of the 12 nets were recorded. Nets were deployed between 10.25 and 16.55 h depending on date set with an average total deployment taking 3 hours 17 minutes. Nets were retrieved the following day between 9.51 and 14.59 h depending on date with an average deployment time of 23 hours 16 minutes (± 4 hours) for each net.

Depth and water velocity were measured using a Flomate Model 2000 Marsh – McBirney doppler velocity meter with a wading rod. Nets were set at

60% of the water depth and water velocity at the mouth of the net was recorded both at deployment and retrieval.

Upon retrieval, all nets were emptied into containers, a visual inspection of each net was conducted to ensure all invertebrates were collected and the nets were given a rinse with 70% ethanol to dislodge any smaller invertebrates that were missed. Samples were preserved in 70% ethanol for later processing on a white tray under strong lighting. All Hydrobiosidae larvae were separated out by eye, once each sample was considered complete a further inspection under a magnifying glass was undertaken to ensure no smaller larvae were missed. Separated larvae were preserved in 70% ethanol for identification and measurement.

All Hydrobiosidae larvae were identified under a Nikon SMZ1000 microscope at 40-80x magnification based on the key of Smith & Ward (2005). Maximum head widths were measured using an eye-piece micrometer divided into 10µm gradations and converted to mm by adjusting for magnification.

Statistical analysis

Volume of water through each net was calculated by multiplying water velocity (m/s) by deployment time (in seconds) multiplied by the mouth area of the net (0.0058 m^2) giving a volume in m^3 . Drift densities were calculated as individuals per 100m^3 to allow comparison with other New Zealand studies (i.e. Sagar & Glova, 1992a,b; Collier & Wakelin, 1992).

Hydrobiosidae drift densities and head width data was tested for normality using Shapiro-Wilk test and for homoscedasticity using Levene's test in Statistica 13.1.1 (TIBCO Software Inc.). Taxa density data met both assumptions, however head width data did not conform to normality regardless of transformation, and therefore non-parametric tests were used to analyse these data.

As statistical assumptions were adhered to for the drift densities data-set, a repeated measures ANOVA was used to identify differences in taxa drift densities between section (Upper, Below-1 and Below-2) with date of sampling as the repeated measure. Pearson's product moment correlations were used to investigate relationships between taxa densities and distance downstream from emergent structure (i.e. excluding Upper section) for all dates combined and for each sampling date separately.

As parametric statistical assumptions were not met for head width data, comparisons of larval head widths between sections and between days were conducted using Kruskal-Wallis tests. Spearman rank correlation was used to identify relationships between larval head sizes and distance downstream of emergent structure (i.e. excluding Upper section).

4.3 Results

4.3.1 Lateral distribution study

Transect characteristics

Transects were specifically selected for relative evenness of flow rates and depth within each transect to minimise effects of habitat variability on the results. All sampling sites were between 0.24m and 0.40m deep and had moderately swift, laminar flows over primarily cobble substrates (Table 4.1). There were no significant differences detected between environmental variables by percent distance across the stream or by distance to bank (Table 4.2).

Table 4.1: Summary of measured environmental variables at all transects in Waimapu Stream. Figures (except width) given as mean ($\pm$ 1 SE).

Transect	Wetted	Depth(m)	Water	Substrate Size
Number	Width (m)		Velocity (m/s)	Index
1	8.1	0.40 $\pm$ 0.03	0.22 $\pm$ 0.03	5.04 $\pm$ 0.48
2	5.6	0.36 $\pm$ 0.03	0.43 $\pm$ 0.07	5.26 $\pm$ 0.23
3	5.7	0.30 $\pm$ 0.01	0.46 $\pm$ 0.05	5.76 $\pm$ 0.13
4	6.0	0.25 $\pm$ 0.04	0.54 $\pm$ 0.04	5.65 $\pm$ 0.08
5	4.2	0.24 $\pm$ 0.04	0.81 $\pm$ 0.02	6.73 $\pm$ 0.32
6	4.3	0.31 $\pm$ 0.03	0.59 $\pm$ 0.11	5.63 $\pm$ 0.18

Table 4.2: ANOVA results for measured environmental variables by percentage distance across Waimapu Stream.

Environmental variable	Grouping	n	df	F	p
Depth	% across stream	30	4	0.08	0.99
	Distance from bank	30	2	0.01	0.99
Velocity	% across stream	30	4	0.70	0.59
	Distance from bank	30	2	0.66	0.53
Substrate size index	% across stream	30	4	0.12	0.98
	Distance from bank	30	2	0.24	0.79

Density and position across stream

Total numbers of Hydrobiosidae collected in samples were relatively low and were primarily middle instar individuals (Table 4.3). In addition to *Psilochorema* spp., 26 *Hydrobiosis* spp., 10 *Neurochorema* spp. and three *Costachorema* sp. were identified. No significant differences in taxa densities were identified between sampling positions (Table 4.4 & Fig. 4.2).

Table 4.3: Summary statistics of Hydrobiosidae and *Psilochorema* collected in the Waimapu Stream. Figures given as mean $\pm$ 1SE

Taxa	Total	Density	Head width	Pseudo-instar
	number	(#/m²)	(mm)	rank
Hydrobiosidae	106	35.33 $\pm$ 3.58	0.59 $\pm$ 0.002	2.06 $\pm$ 0.007
<i>Psilochorema</i>	67	23.33 $\pm$ 2.43	0.53 $\pm$ 0.024	2.07 $\pm$ 0.091

Table 4.4: Results of a Kruskal - Wallis test on taxa densities by both percent distance across Waimapu Stream, and distance to nearest bank.

Taxa	Taxa & Grouping	n	df	H-stat	p
Hydrobiosidae	% across stream	30	4	1.17	0.88
	Distance from bank	30	2	0.52	0.77
<i>Psilochorema</i>	% across stream	30	4	2.13	0.25
	Distance from bank	30	2	0.84	0.70

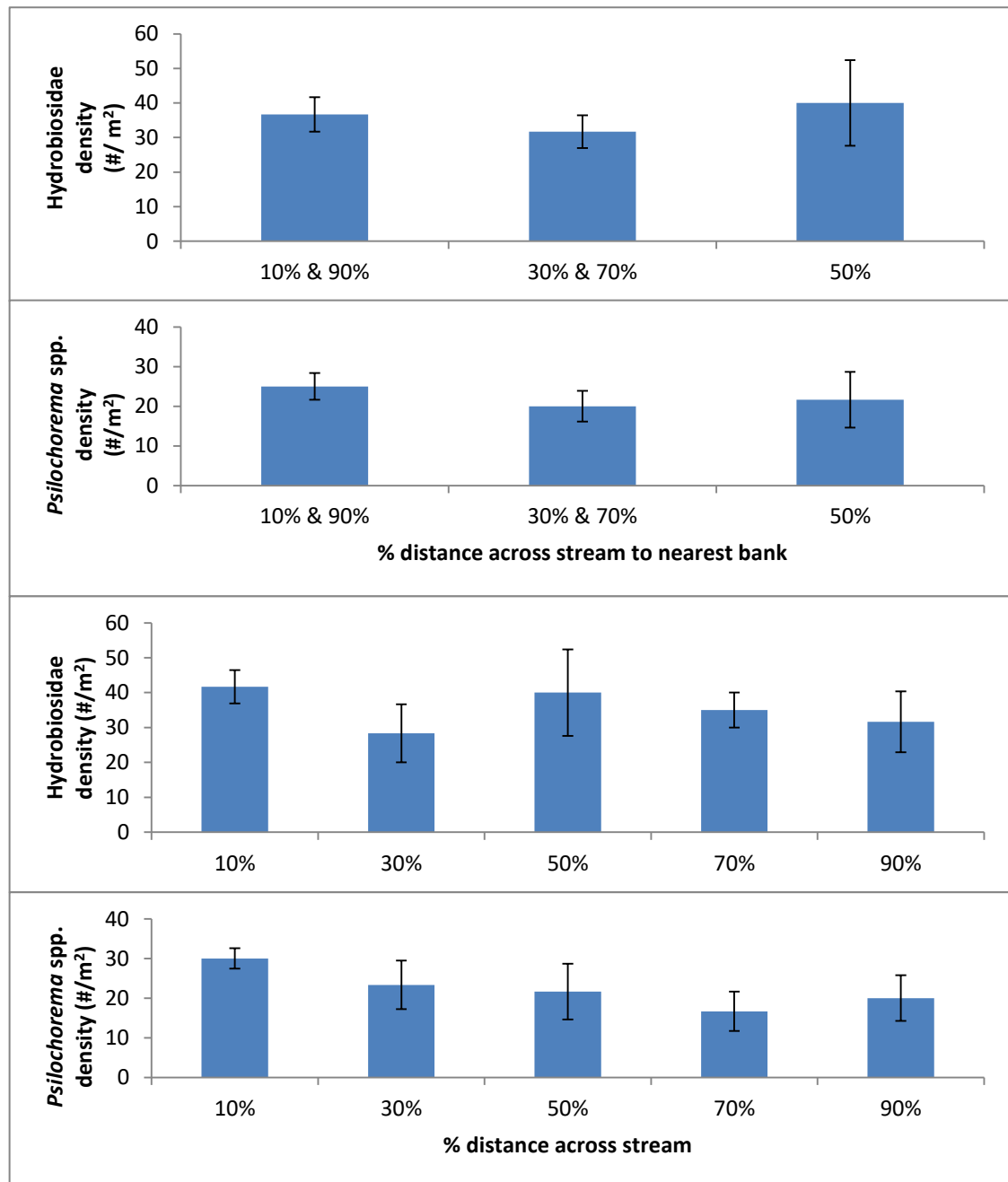


Figure 4.2: Distribution of mean (± 1 SE) Hydrobiosidae and Psilochorema densities across Waimapu stream by both distance from nearest bank and percent distance across stream

Head width and position across stream

There was a significant difference in head widths for all Hydrobiosidae and *Psilochorema* when analysed by percent across stream, However when *Psilochorema* was analysed by distance from the nearest bank, there was no significant difference (Table 4.5). When the developmental stage was compared, all tests showed significant differences with those coming from near the stream banks being, on average, smaller than those closer to the centre of the channel (Fig. 4.3).

Table 4.5: Results of a Kruskal - Wallis test on larval head width and pseudo-instar rank by percent across Waimapu Stream when considered separately and grouped

Taxa	Grouping	n	df	H	p
Head widths					
Hydrobiosidae	% across stream	106	4	12.69	0.013*
	Distance from bank	106	2	7.57	0.023*
<i>Psilochorema</i>	% across stream	67	4	10.50	0.033*
	Distance from bank	67	2	5.92	0.052
Pseudo instar ranking					
Hydrobiosidae	% across stream	106	4	16.96	0.002**
	Distance from bank	106	2	8.10	0.017*
<i>Psilochorema</i>	% across stream	67	4	11.15	0.025*
	Distance from bank	67	2	7.26	0.027*

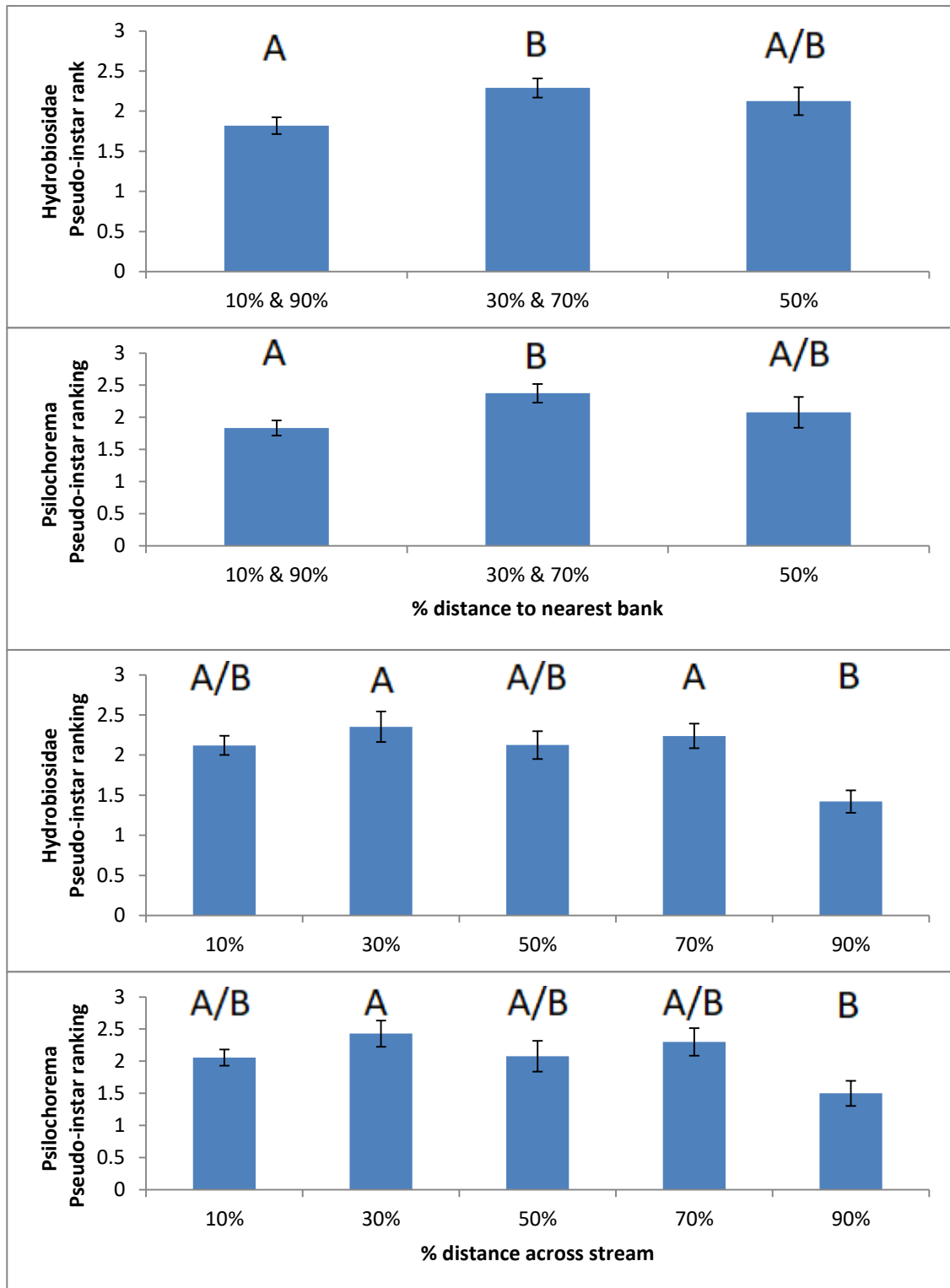


Figure 4.3: Size distribution of Hydrobiosidae and Psilochorema by both % distance from nearest bank and % distance across stream based on mean (± 1 SE) pseudo-instar ranking. Letters above columns indicate significantly different groupings.

Size distributions

Head width distributions clearly show a preponderance of smaller individuals near the edges of the stream for both Hydrobiosidae, and the dominant genus, *Psilochorema* (Fig. 4.4). Nearer the centre of the channel, size distributions peaked nearer the middle instar sizes, with *Psilochorema* showing a peak in the later instars in the 30%/70% across stream width group.

No correlations were identified between larval size and measured environmental variables for both Hydrobiosidae and *Psilochorema* using Spearman's rank order correlation.

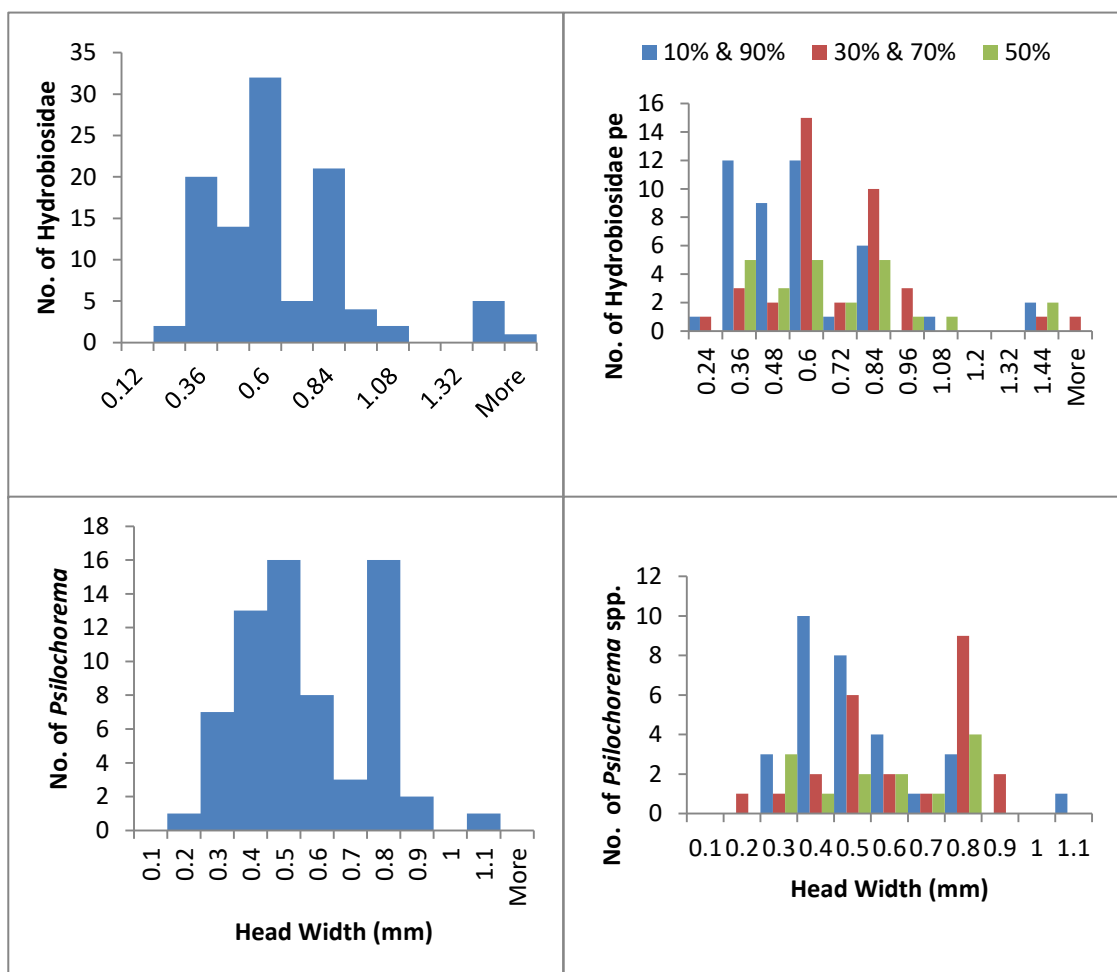


Figure 4.4: Size distribution of Hydrobiosidae (top) and *Psilochorema* (bottom) across all sites and by distance to nearest bank.

4.3.2 Longitudinal drift distribution study

Water depth and velocity measured at drift net deployment locations are summarised in Table 4.6. The stream was generally deeper and slower flowing in the upper sections, progressively getting shallower and faster flowing downstream.

Taxa density

A total of 23 Trichoptera taxa were identified from 468 individuals collected (Table 4.7). Of these 187 were *Oxyethira albiceps*, however the majority of these (63%) were collected from just two nets that were located downstream from large pool sections. The second most common taxa belonged to the Hydrobiosidae making up 186 individuals, of which 125 were *Hydrobiosis* spp. The only other abundant species was *Aoteapsyche colonica* of which 64 individuals were collected. The results that follow pertain only to Hydrobiosidae which was the focus of the hypotheses tested.

The Upper section produced the lowest drift densities of Hydrobiosidae and the Below-2 section produced the highest densities. However there was no significant difference between sections or between sampling days for either Hydrobiosidae and *Hydrobiosis* spp. densities (Table 4.8; Figs. 4.5 & 4.6).

Table 4.6: Summary of section characteristics (mean $\pm$ 1 SE). Distance range signifies distance from the upper major emergent structure section in the Waimapu stream.

Section	Water Velocity (m/s)	Depth (m)	Distance Range (m)
Upper	0.06 $\pm$ 0.01	0.53 $\pm$ 0.03	-90.5 to -3
Below-1	0.21 $\pm$ 0.01	0.38 $\pm$ 0.02	12.5 to 293
Below-2	0.37 $\pm$ 0.03	0.29 $\pm$ 0.01	363.5 to 604

Table 4.7: Summary of Trichoptera caught in drift nets in the Waimapu Stream by section related to emergent structure. Upper = above main emergent structure, Below-1 = below upper emergent structure, Below-2 = below secondary emergent structure. Density (number per 100m³) and larval head width figures are given as mean $\pm$ 1 SE

Section	Total No. of Trichoptera	No. of Trichoptera Taxa	Hydrobiosidae	Hydrobiosidae Density	Hydrobiosidae Head Width (mm)
Upper	55	5	8	2.15 $\pm$ 1.16	1.00 $\pm$ 0.21
Below-1	110	12	49	3.58 $\pm$ 0.67	0.87 $\pm$ 0.05
Below-2	303	17	129	5.15 $\pm$ 0.98	0.98 $\pm$ 0.03
Total	468	23	186	3.87 $\pm$ 0.56	0.95 $\pm$ 0.03

Table 4.8: Repeated measures ANOVA results of Hydrobiosidae drift densities by section (Above, Below-1 and Below-2) with day as the repeated measure in Waimapu Stream

Dependant Variable	Between Effect	df	F	p
Hydrobiosidae density	Day	2	0.08	0.92
	Section	2	1.63	0.24
	Day/Section	4	0.59	0.67
Hydrobiosis spp. density	Day	2	0.52	0.60
	Section	2	1.39	0.30
	Day/Section	4	1.05	0.41

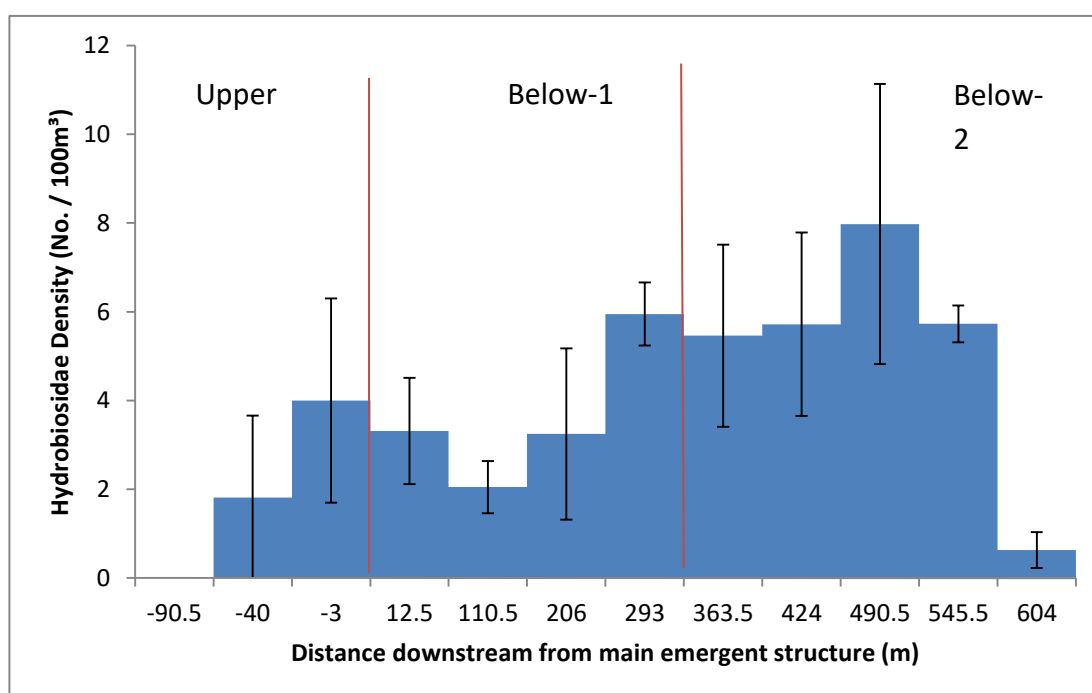


Figure 4.5: Mean (± 1 SE) drift density of Hydrobiosidae in the Waimapu Stream by distance upstream (negative numbers) or downstream from main emergent structure section. Upper, Below-1 and Below-2 sections separated by red lines

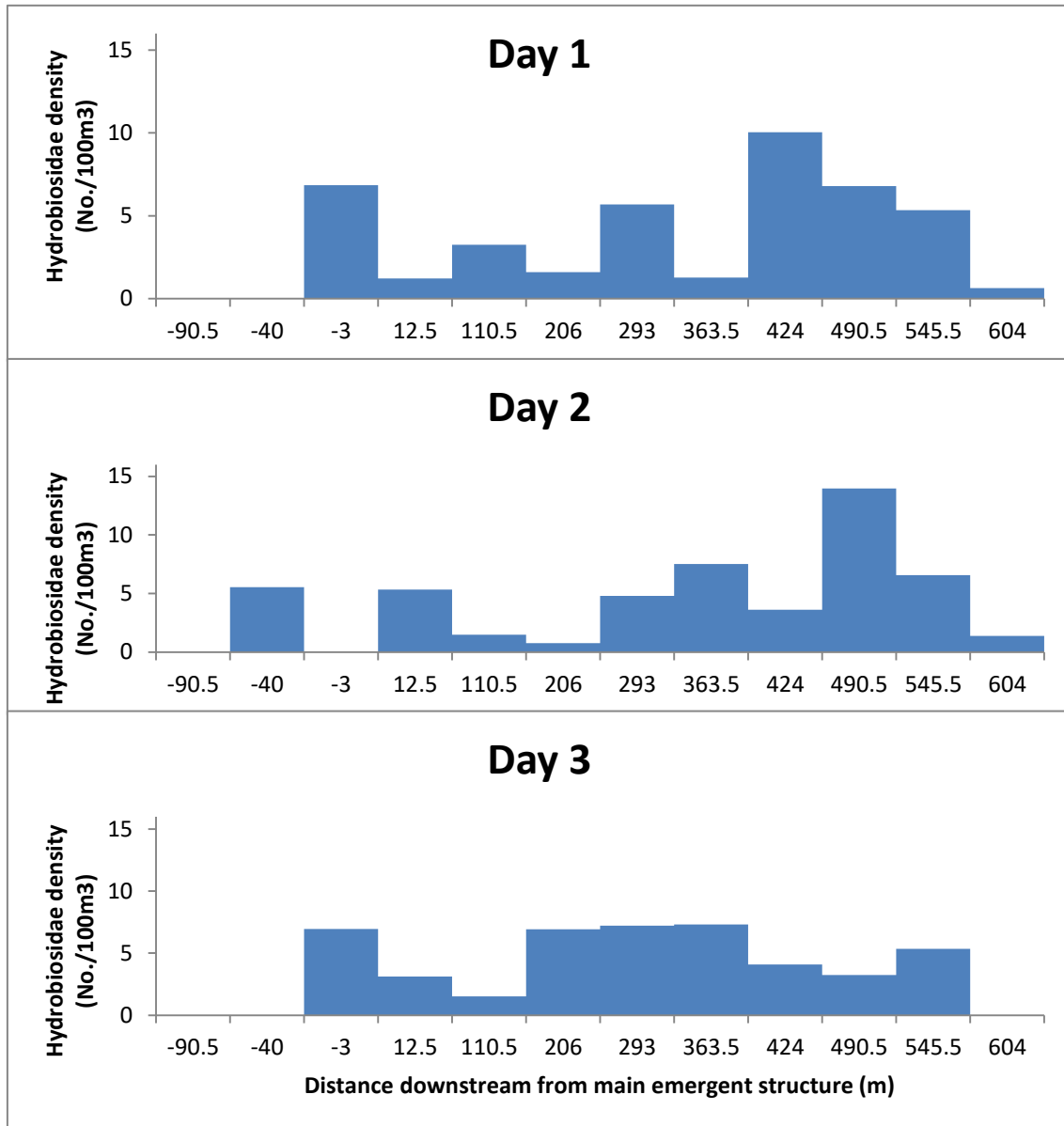


Figure 4.6: Drift density of Hydrobiosidae by distance downstream of main emergent structure section (m) for each sampling day. Emergent structure located between -3m and 12.5m, and between 293m and 363.5m

There was no relationship detected between Hydrobiosidae and *Hydrobosis* drift density and distance from emergent structure in the upper and middle sections. However, in the lower section, below the smaller secondary emergent structure site, there was a significant negative correlation between *Hydrobosis* spp. drift densities and distance downstream ($r=-0.54$, $p=0.04$, $n=15$).

Larval size and distance downstream

There were no significant differences in larval sizes in the drift between either section or date collected (Table 4.9), nor were any significant correlations observed. Generally, larval size was relatively even across all sites sampled (Figs 4.7 & 4.8).

Table 4.9: Results of a Kruskal - Wallis test of both drifting Hydrobiosidae and *Hydrobiosis* larval head widths between stream sections in relation to emergent structure (Upper, Below-1 & Below-2) as well as day sampled.

Taxa	Grouping	n	df	H-value	p
Hydrobiosidae	Section	186	2	3.22	0.20
	Day	186	2	3.45	0.18
<i>Hydrobiosis</i> spp.	Section	125	2	1.79	0.41
	Day	125	2	5.20	0.07

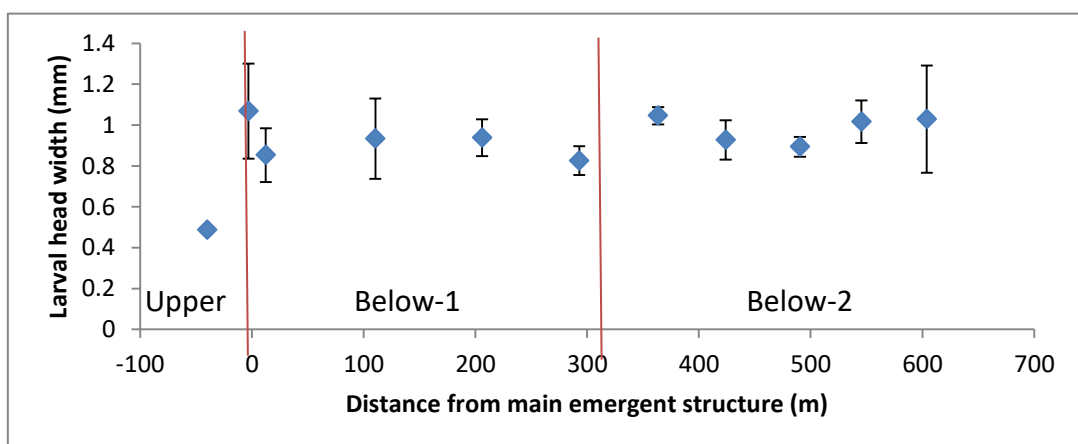


Figure 4.7: Mean (± 1 SE) head widths of drifting Hydrobiosidae by distance downstream from major emergent structure section in Waimapu Stream. Red lines indicate locations where emergent structure is present.

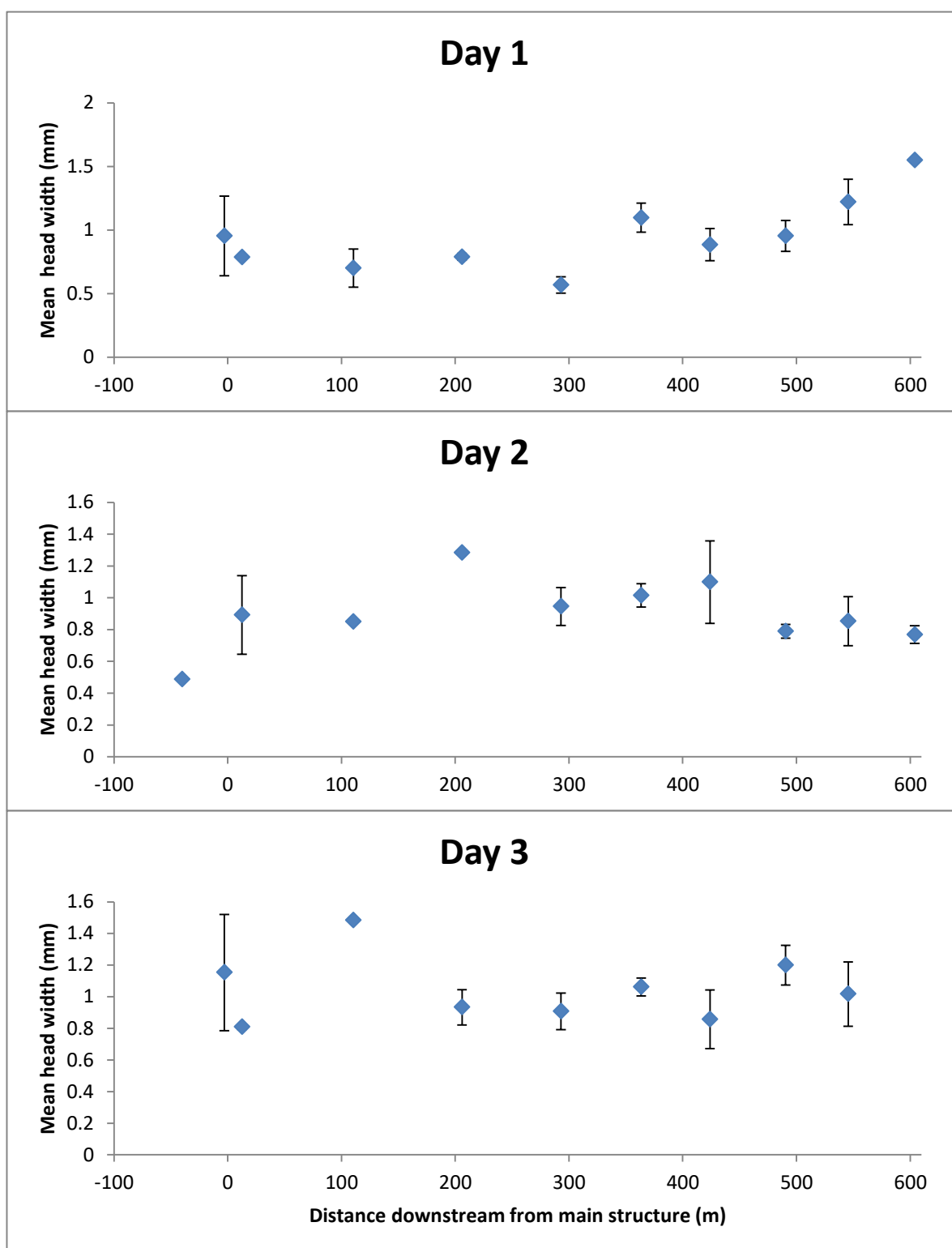


Figure 4.8: Mean (± 1 SE) head widths of drifting Hydrobiosidae by distance downstream of major emergent structure sections in Waimapu Stream by day sampled. Emergent structure located at 0m and between 200m and 300m.

4.4 Discussion

The aim of these studies was to identify whether lateral movement or longitudinal drift explained the distribution of Hydrobiosidae larvae in sites with and without suitable oviposition habitat. Previous work (see Chapter 3) indicated that the presence or absence of suitable oviposition structure did not directly influence Hydrobiosidae larval distribution in these Bay of Plenty streams. Conversely, my earlier analysis showed that Hydrobiosidae were present in greater numbers in areas without emergent structure where environmental variables such as shade cover, water velocity and substrate type were determinants of larval abundance and size. This finding indicated that factors other than emergent structure were influencing the distribution of small Hydrobiosidae larvae and suggested that other pathways were possibly involved in oviposition. Two possible explanations were investigated for this apparent discrepancy: (i) Hydrobiosidae adults were utilising the stream banks to access submersed oviposition habitat near stream edges; and/or (ii) Hydrobiosidae larvae were arriving at sites lacking emergent structure via drift from upstream sites with suitable oviposition habitat.

If Hydrobiosidae were utilising the stream banks as hypothesised, then I expected to find greater numbers of smaller larvae nearer the stream banks and larger ones near the centre of the channel following a large flood that was expected to have reset colonisation by Hydrobiosidae. If drift was a major determinant of early instar Hydrobiosidae distribution, then I expected to find high densities of drifting larvae directly downstream of emergent structure, with

densities declining further downstream. Additionally I expected to find, on average, smaller Hydrobiosidae larvae directly downstream of emergent structure with average size increasing with distance downstream due to lower numbers of early instar Hydrobiosidae entering the drift directly downstream from emergent structure.

4.4.1 Lateral distribution study

Densities

Comparisons between differing positions across the stream showed that there was no significant difference in density between the edges of the stream and the centre of the channel for all Hydrobiosidae. A previous study on Hydrobiosidae based in Victoria, Australia, has shown that they are normally more abundant near the centre of the stream than at the edges (Dean & Cartwright, 1987). The data collected in my study showed a small, non-significant difference in the distribution of Hydrobiosidae that was similar to the results of Dean & Cartwright (1987), however *Psilochorema* showed the opposite with higher densities recorded nearer the streams edges. Based on this study, and the findings of Dean & Cartwright (1987) it appears that the density distribution of Hydrobiosidae when compared to the position within the stream may be taxon specific.

Size distribution

In support of the lateral oviposition hypothesis, the results of this study show that there is a preponderance of smaller Hydrobiosidae nearer the stream edges

when compared to the centre of the stream. This was apparent for all Hydrobiosidae and *Psilochorema*. Several potential reasons may be used to explain this result. A previous disturbance event could have created a similar result with smaller individuals avoiding the disturbance by using the lateral fringes and bank side vegetation as refugia. However prior to this experiment no disturbance events are known to have occurred for at least six weeks, indicating that this explanation is unlikely as it would be expected that the smaller individuals would have both grown significantly and are likely to have migrated out of these zones during this time period (Jackson & Sweeny, 1995; Kefford *et al.*, 2004). Rather, if stream edge recruitment was occurring as proposed, there would be a regular input of smaller individuals leaving a higher population of small individuals near the stream edges.

Environmental variables were considered as potential causes of this disparity. However, there was no correlation between any of these variables and Hydrobiosidae head width. There were no significant differences between lateral position within the stream and any environmental variable therefore making it unlikely that habitat variation provided an explanation for the observed distribution of the different size classes across the stream channel.

One alternative causative effect may be that early instars may show an omnivorous diet and therefore congregate near the stream banks where there is increased allochthonous input and instream detritus is more likely to build up (Gurtz *et al.*, 1988). This behaviour is currently unknown for the majority of the species identified in this study but has been previously suggested for *H.*

parumbripennis (Crosby, 1975), although it has been clearly shown to not occur in other Hydrobiosidae such as the South American and Australian species *Atopsyche yunguensis*, *A. spinosa*, *Ulmerochorema* spp., *Ethochorema* spp. and *Apsilochorema obliquum* (Chessman, 1986; Reynaga & Martin, 2010). Even if a few species showed early instar omnivory, it is highly unlikely that all species would and therefore it is unlikely that this would affect results significantly.

The only remaining explanations therefore would be that either: (i) a hydrological constraint, undetectable using the data gathered in this experiment, i.e. shear stress, is controlling the distribution of early instar Hydrobiosidae as reported by Collier et al. (1995) in the Tongaririo River; or (ii) that early instar Hydrobiosidae are recruiting directly into the edge zones and over time migrate into other parts of the stream. To confirm this, egg masses must be present near the stream edges in areas where no emergent oviposition structure is accessible. This was supported by a cursory search of the sampling site on 09/11/2017 which resulted in the discovery of *Psilochorema* egg masses on two submerged rocks near the stream bank with no emergent structure nearby (Fig. 4.9). Unfortunately a planned systematic search and quantification of oviposition rates was unable to be completed due to high flow events and time constraints.



Figure 4.9: *Psilochorema* egg masses found on submerged stones and location where they were discovered (indicated by red circles) in a section of the Waimapu Stream lacking emergent structure.

4.4.2 Longitudinal drift study

Drift density

The drift density of Hydrobiosidae recorded in this study was relatively low compared to other studies; however densities were still within expected ranges. Sagar & Glova (1992a,b) reported Hydrobiosidae drift densities ranging from 1.8 to 88.2 individuals per 100m³, and between 1.5 and 5.2 per 100m³ for *Hydrobosis frater* and *H. parumbripennis* compared to the 3.87±0.56 per 100m³ recorded here. The proportion of Hydrobiosidae in the drift far exceeds that found in previous benthic samples (see Chapter 3 & 4), likely due to taxadependant drift entrainment and settling rates (Brittain & Eikland, 1988). As Hydrobiosidae are extremely active due to their predatory nature (Winterbourn, 1978) it is expected that they will enter the water column more often than sedentary species, especially during the night when their activity peaks (Sagar & Glova, 1992a).

It was expected that the Hydrobiosidae drift densities would decrease with distance from emergent oviposition habitat, but this was not clearly observed in my study. The significant decrease in the lowest section by distance was primarily driven by the last net, which showed unexpectedly low drift densities and may be considered an outlier. It is likely that the low numbers caught in this bottom net are due to high sedimentation rates caused by the nearby gravel road. A site visit during a rainfall event provided evidence of regular large sedimentation events occurring at this site (Fig. 4.10). Fine sediment is well-known to have an adverse effect on benthic aquatic insects,

which is attributed to the reduction of interstitial habitat, blocking of primary production and increasing drift of benthic fauna out of the affected reach (Ryan, 1991). Additionally, sedimentation from roads, as what occurs at this site, is known to carry a wide range of potentially toxic contaminants which can build up in the substrate and hamper the recovery of benthic fauna (Trombulak & Frissel, 2000).



Figure 4.10: Sediment flowing into the Waimapu stream from a gravel road upstream of the last drift net. The upstream drift net visible in left image (bottom). Right image shows mixing of stream water and sediment runoff from road.

The lack of a decline in Hydrobiosidae drift was surprising considering most invertebrates show extremely short drift distances of ~2m (Elliot, 1971; Brittain & Eikland, 1988) and it was expected that 300m would provide sufficient distance to identify changes. This finding suggests that either: (i) the distance sampled was too short to detect the expected changes in drift densities; (ii) settling rates were much higher than expected and drifting larvae from emergent

structure had already settled out before reaching the nets; or (iii) that drift entrainment rates are relatively constant regardless of distance from oviposition habitat.

Larval sizes

The size of Hydrobiosidae larvae collected across all sites was relatively constant, consisting primarily of middle-to-late instar larvae. Contrary to what was predicted, larvae collected immediately downstream of emergent structure were no smaller than those further downstream. A related species from the northern hemisphere, *Rhyacophila nubiola*, has been shown have increased drift propensity in the second instar, likely due to increased intraspecific competition (Fjellheim, 1980). Similarly, Elliot (1968) found increased drift of instars 2 and 5 of *Rhyacophila* spp. in an English stream. However, early instar Hydrobiosidae were poorly represented in the samples collected for my thesis. Indeed, very few early instar larvae were collected overall (n=11), possibly due to unforeseen variances in the vertical distribution of Hydrobiosidae in the drift. Other taxa have been shown to have variable vertical drift distributions, with poor swimming taxa drifting closer to the bottom (Matter & Hopwood, 1980; Shearer *et al.*, 2002). Therefore it is possible that the position of the nets at 60% of the stream depth may have missed larvae drifting lower or higher in the water column.

4.5 Summary

The data presented here show larger numbers of small Hydrobiosidae near the stream banks and larger Hydrobiosidae near the channel centre, although there

appeared to be no difference in abundances related to lateral position within the stream. The data also suggested that larger Hydrobiosidae are more likely to be found in the invertebrate drift, but there was no clear evidence of higher drift densities of smaller larvae below emergent boulders.

Although some Hydrobiosidae are arriving into reaches with no emergent structure via drift, these are more likely to be later instar larvae. Drift, although obviously important in the downstream migration of Hydrobiosidae as evidenced by the high numbers found in the drift samples, does not appear to have a significant influence on the distribution of different life-stages within the stream.

The greater numbers of smaller larvae found near the stream banks, and the subsequent discovery of Hydrobiosidae egg masses in a section where emergent rocks were not present provides strong evidence that Hydrobiosidae are utilising the stream banks to access submerged oviposition structure in the absence of emergent habitat. I have shown that colonisation from the edges of the stream is likely to be having an effect on the distribution of Hydrobiosidae, and provided evidence that behavioural plasticity in Hydrobiosidae oviposition may be much more common than previously thought.

Chapter 5: General discussion

Trichoptera is one of New Zealand's most diverse aquatic insect orders (Winterbourn *et al.*, 1981), and as such is key to monitoring stream health and restoration efforts (Wright-Stow & Winterbourn, 2003). Within Trichoptera, Hydrobiosidae is the most diverse family (Ward, 2003), therefore warrants special consideration, but there is little knowledge of what influences their distribution within streams. This thesis aims to investigate whether oviposition behaviour of Hydrobiosidae and other Trichoptera influences their distribution within a stream with a focus on: (i) the direct effects of emergent oviposition habitat on the abundance and size distribution of Trichoptera; (ii) the abundance and size distribution of Hydrobiosidae laterally across a stream in the absence of emergent oviposition habitat; and (iii) the densities and size distribution of Hydrobiosidae in the drift in relation to emergent oviposition habitat.

5.1 Environmental context and study design

To investigate the aspects outlined above, three studies were conducted in streams of the Waimapu catchment, Bay of Plenty, New Zealand. As described in Chapter 2, these streams were chosen due to their close proximity to each other, similar physical and hydrological characteristics, and the presence of reaches both with and without emergent boulders as oviposition habitat for Hydrobiosidae. The four streams chosen for this study are spring fed hill-country streams with relatively high water quality and show similar characteristics with other streams in this area.

A total of 28 Trichoptera species were collected during the course of this study, and each site showed distinctly different communities. Conoesucidae dominated across all sites, making up between 41% and 87% of the Trichoptera community, especially in sites with no emergent structure. In contrast, the second most common family was Hydropsychidae, which made up higher proportions of the Trichoptera community in sites with emergent structure. Hydrobiosidae made up a relatively small proportion of the Trichoptera community across all sites, but was still the third most common family. The non-emergent reach in the Waimapu stream showed the highest representation by Hydrobiosidae at 41% of Trichoptera numbers and as such was chosen as the study site for the two investigations detailed in Chapter 4.

Trichoptera show a wide range of oviposition behaviours. For example, Conoesucidae lay eggs on the surface of flowing water where they sink to the stream bed (Pendergrast & Cowley, 1966). Hydropsychidae generally dive through the water's surface and swim using specially modified legs to access substrate to oviposit (Deutsch, 1985; Lancaster *et al.*, 2010a). In contrast, Hydrobiosidae lack the modified legs of Hydropsychidae and utilise emergent boulders to crawl beneath the water's surface to sub-surface oviposition sites (Lancaster *et al.*, 2003; Reich & Downes, 2003a; 2004; Lancaster *et al.*, 2010a; Storey *et al.*, 2017). Due to these contrasting oviposition behaviours, and the community structure in the streams sampled, these three taxa were chosen for analysis and comparison of the effects of emergent structure on Trichoptera distribution in Chapter 3.

Several potential issues with the investigations conducted were identified during the course of this study. These have been discussed in detail in their respective chapters, and key points are summarised here: As shown in Chapter 3, the Kirikiri Stream site produced far fewer macroinvertebrates than expected, leading to an inability to include this site in some analyses. Also, due to the characteristics of streams within the sampling area, only two sites provided suitable sampling areas with both emergent structure and non-emergent structure on the same stream and the remaining two sites were located on different streams - the Kirikiri Stream (emergent) and an unnamed tributary of the Waimapu Stream(non-emergent). This design led to only two streams suitable for paired analyses. In Chapter 4, drift sampling nets set at 60% depth to account for assumed mean water velocities (Harding *et al.*, 2009) may have missed invertebrates drifting nearer the stream bed, while the distance sampled may have been too short to detect significant changes in drift density. Compounding this, drifting early instar Hydrobiosidae may have settled more quickly than expected, preventing them from being captured in the first drift nets down-stream from emergent structure

The substrate index of Jowett & Richardson (1990) used for analysis reflected substrate stability, rather than size or habitat heterogeneity as previously thought (Jowett *et al.*, 1991) due to the weighting placed on bedrock which was relatively common in the areas sampled in this thesis. However, it is assumed due to the localised occurrence of bedrock substrates, that this factor has had only a minor effect on the conclusions of this thesis. In fact it identified a

strong relationship between *Pycnocentrodes* and bedrock in areas of high flow (see Chapter 3).

5.2 Role of emergent structure.

In Chapter 3, I investigated the abundance and size distribution of Trichoptera in reaches both with and without emergent structure considered suitable for the oviposition of Hydrobiosidae based on previous observations of Lancaster *et al.* (2010a, b) and Storey *et al.* (2017). Overall, I found that there was no direct relationship between Trichoptera community composition, or the abundance and size distribution of Hydrobiosidae in relation to the presence of emergent structure.

Several other studies, both in New Zealand and overseas, have clearly shown that Hydrobiosidae show selective oviposition behaviour, normally selecting emergent boulders within a stream channel (Reich & Downes, 2003a; Blakely *et al.*, 2006; Lancaster *et al.*, 2010a; Storey *et al.*, 2017). Different species select their oviposition sites dependant on different physical cues (Reich & Downes, 2003a) and it has been hypothesised that this would have an effect on the distribution of their larvae (Storey *et al.*, 2017). The evidence presented in Chapter 3 suggests that other environmental factors are more influential on the abundance and size distribution of Hydrobiosidae larvae than the presence/absence of emergent structure both between sites and on a local scale. This is similar to the findings of Reich & Downes (2004) in an upland South Australian stream where oviposition site selection of three species of Hydrobiosidae was directly related to the habitat selection of larvae, even in

areas lacking oviposition structure. In that study, Reich & Downes showed that larval Hydrobiosidae abundances were strongly related to the same water velocities that oviposition rates were related to; however Hydropsychidae did not show this relationship. This finding suggests that high rates of early instar Hydrobiosidae larval dispersal by drift, downstream from emergent structure, may be a key factor in determining size distribution within a stream.

A study by Lancaster *et al.* (2010a) investigated the oviposition site selectivity of three Trichoptera species in two Scottish high country streams. The three species investigated were *Polycentropus flavomaculatus* (Polycentropodidae), *Hydropsyche siltalai* (Hydropsychidae) and *Rhyacophila dorsalis* (Rhyacophilidae). Both *P. flavomaculatus* and *R. dorsalis* selected oviposition sites that were related to larval habitat preferences in regards to faster flowing riffle habitat, whereas *H. siltalai* oviposited more often in pools, while larval abundances were normally higher in riffle habitats (Muotka, 1990). It has been shown that some Hydropsychidae inhabit slower moving pool sections during their early life stages, migrating into faster flowing sections later in life (Osbourne & Herricks, 1987), which may explain the findings of Lancaster *et al.* (2010a) who concluded that oviposition site selectivity may be directly related to the instream distributions of larval Trichoptera.

The conclusion described above contrasts with those presented in Chapter 3 for dominant taxa in these Bay of Plenty streams where larval distributions were more related to environmental factors than the assumed location of emergent rocks expected to be used for oviposition. Thus,

Hydrobiosidae abundances appeared to be related more to lower shade cover, increased water velocity and larger substrate size, and due to these factors densities were much higher in sites lacking emergent structure.

In Chapter 3, I compared the differences in larval abundance and size distribution between sites with and without emergent boulders and compared it between three taxa, Hydrobiosidae which require emergent structure for oviposition as well as Conoesucidae and Hydropsychidae which oviposit by other methods. Size class distribution of the dominant Hydrobiosidae genus, *Psilochorema*, showed a strong positive relationship with water velocity. Conoesucidae larval abundances increased in habitats with higher water velocities, larger substrates and decreased shade coverage while size distributions showed no conclusive relationships. Hydropsychidae abundances were greater in areas with higher water velocities, whereas size distribution was weakly related to substrate size, with larger individuals on larger substrates. Previous work has found similar relationships. For example, Wilcock *et al.* (2005) used genetics to show high larval survivorship and dispersal by site selective Trichoptera, and Bovill *et al.* (2013) showed that site selectivity was related to optimising the hatching ability of egg masses of two species of Hydrobiosidae. These findings suggest that the oviposition site selectivity behaviours of stream insects are likely to ensure greater hatching rates and therefore larval survival.

5.3 Alternative colonisation pathways

The findings and observations from this first study (Chapter 3) raised the prospect of two alternative pathways by which small Hydrobiosidae may be

entering reaches lacking emergent structure following oviposition: (i) oviposition following entry from the stream edges; or (ii) drift downstream from upstream emergent structures.

If Hydrobiosidae are entering the stream via the banks to oviposit, I expected to find greater numbers of smaller instar larvae nearer the stream bank. While there were no observed differences in total abundance across Waimapu Stream, there were a significantly higher proportion of smaller individuals found near the stream banks supporting the proposition that adult Hydrobiosidae may be entering from the edges of the stream to oviposit. Very little work appears to have previously been done on the lateral distribution of aquatic insects across streams. Indeed only one previous study was identified that provided data comparable to this study. Dean & Cartwright (1987) provided comparisons of Trichoptera abundance between midstream and the edge of a stream, but unfortunately larval size was not compared. Contrary to what was found in Waimapu Stream, they found lower abundances of Trichoptera, including Hydrobiosidae, near the edge of the stream compared to the channel centre where as I found no differences between these areas. This may be due to differences in other environmental factors affecting the distribution of Hydrobiosidae, as shown in Chapter 3, or it may be due to species-specific or regional differences as their study was conducted in Victoria, Australia.

If Hydrobiosidae adults oviposited near the edges of streams, as suggested by the larval size distribution in my study, then egg masses should be evident along the stream edge. Due to inclement weather conditions, a

systematic search for egg masses was not possible during the timeframe of this thesis, however a casual pilot search conducted within the sampling reach turned up two rocks with Hydrobiosidae egg masses, near the stream bank, in an area with no obvious emergent structure, further supporting this hypothesis. Many insects will chose alternative oviposition sites when presented with differing conditions in which their preferred oviposition site is unavailable, such as host plant/animal availability (Wiklund, 1981; Xu *et al.*, 2012). It is possible that adult Hydrobiosidae may exhibit similar behavioural plasticity. Although the rate of oviposition near stream banks was not quantified in this thesis, overall oviposition rates from the stream banks in reaches lacking structure are expected to be much lower than oviposition rates in areas with suitable emergent structure as only two oviposition sites were found in the pilot investigation whereas previous studies of oviposition rates showed comparatively large numbers of egg masses on emergent structure (Lancaster *et al.*, 2003; Blakely *et al.*, 2006; Lancaster *et al.*, 2010b) suggesting that even though an alternative pathway may exist, the main pathway is likely to provide the majority of colonisation within a stream.

Also in Chapter 4, I examined the densities and size distribution of Hydrobiosidae in the drift in relation to distance downstream from emergent structure in Waimapu Stream, expecting to find both higher drift densities, and higher numbers of small instar Hydrobiosidae in the drift directly downstream from emergent structure. Even though Hydrobiosidae drift densities were relatively low compared to other studies (Sagar & Glova, 1992a,b),

Hydrobiosidae made up a large proportion of the trichopteran drift in my study, as also found by McLay (1968) who attributed this to the active predatory behaviour of Hydrobiosidae larvae. There was little evidence that drift densities decreased with distance from emergent structure; however there did appear to be a slight, but non-significant, increase in drift density below a secondary patch of emergent structure. Size class analysis of Hydrobiosidae within the drift showed no difference in the size of Hydrobiosidae drifting below emergent structure. The high rate of drift of late instar larvae found in my study is similar to that of the related northern hemisphere family, Rhyacophilidae reported by Elliot (1968) and Fjellheim (1980), although in my study early instar larvae were almost completely absent in the drift.

This study provided evidence for only one of the alternative pathways proposed, the evidence given for the other pathway was inconclusive. The hypothesis that Hydrobiosidae were utilising the stream banks to access submerged oviposition structure was supported by the evidence that higher numbers of early instar Hydrobiosidae are present near the edges of the Waimapu Stream compared to the centre of the channel. The subsequent discovery of egg masses near the stream banks in an area lacking emergent structure provided strong evidence that this plasticity in oviposition behaviour is occurring.

5.3 Implications on restoration projects

Waterways are considered to be one of the habitats most threatened by human activity globally (Vörösmarty *et al.*, 2010). New Zealand in particular has many serious issues in regards to waterway degradation and aquatic ecosystem health (Weeks *et al.*, 2014). In recent years public awareness of the issues facing New Zealand waterways has increased dramatically, and water quality is now considered to be one of New Zealand's leading political issues. Such concern has led to an increase in waterway restoration efforts around the world (Campbell *et al.*, 2010; Peters *et al.*, 2015), often by improving the physical in-stream habitat through the use of wood/rock structure additions, de-sedimentation and riparian planting (Roni *et al.*, 2002; Bernhardt *et al.*, 2005; Hilderbrand *et al.*, 2005; Roni *et al.*, 2006). Although well-intentioned, and based on relatively solid principles, these projects often lack adequate monitoring after restoration has been completed. Several reviews of restoration efforts around the world have shown that in-stream fauna responses to restoration efforts, especially those of aquatic insects, have been slower than expected (Miller *et al.*, 2010; Palmer *et al.*, 2010; Louhi *et al.*, 2011; Sundermann *et al.*, 2011; Stranko *et al.*, 2012). The causes of this slow response are often unclear, although several potential reasons have been mooted. One such potential cause is a lack of suitable oviposition habitat acting as a bottleneck that limits the recolonisation of aquatic insects with specific oviposition requirements (Lancaster *et al.*, 2010b; Storey *et al.*, 2017).

Hydrobiosidae are believed to rely on emergent rocks to provide oviposition habitat (Lancaster *et al.*, 2003; Reich *et al.*, 2003a; 2004; Lancaster *et*

al., 2010a; Storey *et al.*, 2017). The addition of boulders to streams, in an attempt to improve habitat heterogeneity, is a common method employed in stream restoration efforts (Bernhardt *et al.*, 2005). However, it is currently unknown if this will have a beneficial effect on the recolonisation of Hydrobiosidae into restored streams. Previous studies have clearly shown that the addition of emergent boulders significantly increases oviposition rates of Hydrobiosidae (Blakely *et al.*, 2006; Roberts, 2012). However once the eggs have been laid, little is known about the fate of the hatched larvae. This thesis focussed on the responses of one of New Zealand's most diverse aquatic insect families, Hydrobiosidae, to the presence of suitable oviposition structure and compared it to that of Conoesucidae and Hydropsychidae.

The results obtained from my thesis suggest that the distribution of larval Trichoptera within a stream is more likely to be influenced on various environmental variables than by oviposition site selection of adults. Of all the environmental variables measured, shade cover showed the strongest relationship with Trichoptera distribution, followed by water velocity and substrate type with higher abundances in areas of lower shade coverage, higher water flow and larger substrates. My results suggest that restoring shade and hydraulic habitat will have a greater influence on Trichoptera than introducing emergent substrates for oviposition, at least in streams where they are already established. One site in particular, the upper Waiorohi Stream, had a relatively high population of Hydrobiosidae larvae even though there are no known emergent boulders within 2 km upstream. One potential interpretation of this

observation is that, if suitable emergent structure is located within 2 km upstream of the targeted site, then drift or colonisation from stream edges will allow Hydrobiosidae to colonise the area.

Therefore, based on my study, I tentatively conclude that there should not be any constraints on the recolonisation of Hydrobiosidae within a restored reach as long as: (i) there is suitable oviposition habitat < 2 km upstream of a restored site; (ii) there is a source population of adults capable of reaching oviposition habitat within the targeted stream; (iii) the water quality is suitable for colonisation; and (iv) instream conditions such as shade, substrate size and water velocities are within the preferred ranges.

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Appendices

Appendix 1: Trichoptera species lists

Chapter 3

Table 6.1: Species identified in benthic sampling of six sites in the Waimapu Catchment, Bay of Plenty, New Zealand.

Family	Genus	Species
Conoesucidae	Pycnocentria	evecta
	Pycnocentria	sylvestris
	Pycnocentria	gunni
	Olinga	feredayi
	Beraeoptera	roria
	Pycnocentrodes	aureolus
	Pycnocentrodes	aeris
	Confluens	hamiltoni
Hydropsychidae	Aoteapsyche	colonica
Helicophidae	Zeiolessica	cheira
	Alloecentrella	magnicornis
Philopotamidae	Hydrobiosella	mixta
Polycentropodidae	Polyplectropus	aurifusca
Helicopsychidae	Helicopsyche	albiscens
Oeconesidae	Oeconesus	maori
Leptoceridae	Hudsonema	amabile
	Triplectides	obsoletus
Hydrobiosidae	Hydrobiosis	styracine
	Hydrobiosis	copis
	Hydrobiosis	gollanis
	Hydrobiosis	soror
	Hydrobiosis	umbripennis
	Psilochorema	donaldsoni
	Psilochorema	mimicum
	Costachorema	xanthopterum
	Neurochorema	confusum
	Neurochorema	armstrongi

Chapter 4: Lateral distribution

Table 6.2: Species identified in Lateral distribution benthic samples from Waimapu Stream, Bay of Plenty, New Zealand.

Family	Genus	Species
Conoesucidae	Pycnocentrodes	aureolus
	Pycnocentria	evecata
	Pycnocentria	gunni
Hydropsychidae	Aoteapsyche	colonica
Philopotamidae	Hydrobiosella	mixta
Polycentropodidae	Polypsectopus	aurifusca
Hydrobiosidae	Hydrobiosis	silvicola
	Hydrobiosis	copis
	Hydrobiosis	gollanis
	Hydrobiosis	soror
	Hydrobiosis	umbripennis
	Psilochorema	donaldsoni
	Psilochorema	mimicum

Chapter 4: Drift distribution

Table 6.3: Species identified in longitudinal drift sampling

Family	Genus	Species
Calocidae	Pycnocentrella	eruensis
Conoesucidae	Pycnocentria	sp.
	Olinga	feredayi
	Confluens	hamiltoni
	Pycnocentrodes	sp.
Hydropsychidae	Aoteapsyche	colonica
Leptoceridae	Triplectides	obsoletus
	Hudsonema	amabile
Polycentropodidae	Polypsectopus	sp.
Hydroptilidae	Oxyethira	albiceps
Hydrobiosidae	Costachorema	xanthopterum
	Costachorema	sp.
	Neurochorema	confusum
	Neurochorema	armstrongi
	Neurochorema	sp.
	Psilochorema	mimicum
	Psilochorema	donaldsoni
	Psilochorema	sp.
	Hydrobiosis	centralis
	Hydrobiosis	parumbripennis
	Hydrobiosis	soror
	Hydrobiosis	copis
	Hydrobiosis	styracine
	Hydrobiosis	sp.

Appendix 2: Taxa Abundances

Chapter 3:

Table 6.4: Abundances of Trichoptera taxa recorded from benthic samples at six sites in the Waimapu Catchment, Bay of Plenty, New Zealand. Emergent sites marked with “**”

	Lower Waiorohi*	Upper Waiorohi	Lower Waimapu	Upper Waimapu*	Kirikiri*	Waimapu Trib.	Emergent*	Non- emergent	Total
Hydrobiosis styracine	2	10					2	10	12
Hydrobiosis copis	1		5			9	1	14	15
Hydrobiosis gollanis	2	1	1				2	2	4
Hydrobiosis soror		4	3		4		4	7	11
Hydrobiosis umbripennis		1		2		1	2	2	4
Psilochorema donaldsoni		11	28	20		7	20	46	66
Psilochorema mimicum		13	0	0	3		3	13	16
Costachorema xanthopterum		3	4	5	1	3	6	10	16
Neurochorema confusum		14	7			2		23	23
Neurochorema armstrongi		1		1		10	1	11	12
Beraeoptera roria	1			4		41	5	41	46
Confluens hamiltoni	2			21		29	23	29	52
Olinga feredayi	6	7	29	24	14	7	44	43	87
Pycnocentria spp.	37	344	2	4		6	41	352	393
Pycnocentroides aureolus	91	264	17	104	1	697	196	978	1174
Aoteapsyche colonica	48	74	14	115	2	78	165	166	331
Oeconesus maori	1						1		1
Hydrobiosella mixta	26	2	3	1			27	5	32

Helicopsyche albiscens	2	1				2	1	3
Zelolessica cheira	17	103			1	17	104	121
Alloeocentrella magnicornis		2					2	2
Hudsonema amabile		51			1		52	52
Triplectides obsoletus		1	3	4	2	4	6	10
Polyplectropus aurifusca	5				2	2	7	9
All Trichoptera	241	907	116	305	27	896	573	2492

Chapter 4:

Table 6.5: Abundances of Hydrobiosidae recorded in lateral distribution study in Waimapu Stream, Bay of Plenty, New Zealand.

Transect	Hydrobiosis centralis	Hydrobiosis soror	Hydrobiosis parumbripennis	Hydrobiosi s spp.	Psilochorema donaldsoni	Psilochorema mimicum	Neurochorema spp.	Chostachorema spp.	Total
1	0	1	0	0	9	0	2	0	12
2	1	1	0	1	11	0	3	0	17
3	0	1	3	3	14	2	2	2	27
4	0	2	0	3	10	0	0	1	16
5	0	1	4	3	8	2	0	0	18
6	0	2	0	1	10	1	2	0	16
Total	1	8	7	11	62	5	9	3	106