Factors affecting distribution and abundance of the mayfly *Acanthophlebia cruentata* (Leptophlebiidae) in North Island, New Zealand, streams

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Abstract

We investigated factors affecting distribution and abundance of the leptophlebiid mayfly *Acanthophlebia cruentata* (Hudson) by (1) characterising large-scale environmental features of sites throughout the North Island where *Acanthophlebia* is known to occur, (2) evaluating relationships between land use and abundance of nymphs in a Waikato catchment, and (3) investigating small-scale habitat and hydraulic factors correlated with density in a native forest stream reach sampled monthly over two years. Toprock geology of catchments above known *Acanthophlebia* sites was dominated by argillite, greywacke, and volcanics, and landcover was largely native forest (median = 63% of upstream catchment area). Most records were from low order stream segments (1-3) at moderate elevations (100-300 m a.s.l) and with low to moderate channel slopes (<10%). In the Waikato, *Acanthophlebia* were rarely encountered in streams with entire catchments in pasture, but were relatively common in native forested streams where nymphal densities typically peaked around February-April. Pasture sites with headwater patches of native forest had densities intermediate between sites with catchments entirely in pasture or forest, but abundance was relatively low where native forest comprised <60% of total catchment area. Benthic densities at the intensively sampled native forest site were negatively correlated with maximum mean daily flow in the month prior to sampling and water velocity above sampling quadrats, and positively correlated with streambed cover by gravels and the dry mass of particulate organic matter in samples. This study has highlighted the importance that headwater forest remnants can play in moderating conditions for *Acanthophlebia* in downstream pasture environments, and has characterised the landscape setting where re-establishment of *Acanthophlebia* populations could indicate stream restoration success.

Keywords: Ephemeroptera; land use; native forest; forest remnant; density; habitat; recolonisation; restoration

Introduction

Mayflies are one of the most widespread groups of aquatic invertebrates and are amongst the most sensitive to anthropogenic disturbance (Ward 1992, Hickey 2000, Maxted et al. 2000, Collier 2002). Most New Zealand studies of mayfly ecology have focussed on the cosmopolitan genus *Deleatidium* (e.g., Winterbourn 1974, Towns 1983, Collier & Winterbourn 1990, Scrimgeour 1991, Huryn 1996). Another leptophlebiid mayfly, *Acanthophlebia cruentata* (Hudson) is widespread only in the North Island where it has been reported predominantly in hard-bottomed streams with slow to moderate flow rates and much overhead vegetation (Hitchings 2001, Maxted et al. 2003). *Acanthophlebia* was considered reasonably sensitive to organic pollution impacts by Stark et al. (2001) who recommended a Macroinvertebrate Community Index (MCI) tolerance value of 7 on a scale of 1 (high tolerance) to 10 (low), although the basis for assigning that value is unclear.

A substantial proportion of the annual production of *Acanthophlebia* occurs in the hyporheic zone, and Collier et al. (2004) suggested that restoration of hyporheic function is an important process enabling the recolonisation of this species at sites where it historically occurred. Information on the environmental characteristics of *Acanthophlebia* habitat at a range of spatial scales could also help identify sites where re-establishment of this species would provide a measure of restoration success. In the present study, known locations of *Acanthophlebia* throughout the North Island were compiled from published and unpublished sources to identify large-scale environmental variables characteristic...
of its habitat. Intensive sampling was carried out in one catchment to document changes in *Acanthophlebia* abundance in relation to catchment land use, stream discharge, and micro-habitat conditions. We combine these data from multiple spatial scales to characterise the habitat of *Acanthophlebia* and discuss the implications of these findings for stream restoration.

**Study area**

Data were collated from a range of sites throughout the North Island (see Fig. 1), and more intensively from the Mangaotama catchment (175°5’E, 37°47’S), a tributary of Waipa River located in the eastern uplands of the Waikato Basin near Whatawahata (Fig. 1). Twenty-four sites in the Mangaotama catchment were sampled for aquatic invertebrates from 1992 using a variety of techniques (see Collier *et al.* 2000). In this catchment, fluvial dissection of raised argillite and greywacke blocks has led to the development of steep (>30°) or moderately steep slopes, often with gently-sloping interfluves (De Rose 1998). Soils are predominantly yellow-brown earths, with patches of yellow-brown loams in less steep parts of the catchment where volcanic ash deposits also occur. Average annual rainfall (1952-1992) near Whatawahata is 1614 mm, and mean air temperature is 13.7°C. Portions of the catchment were converted from native podocarp forest some time between 1923 and 1927, and revegetated in clover and pasture grasses for intensive sheep and cattle grazing. Some soil conservation works, principally the planting of poplars and willows, have been undertaken to help stabilise hillslopes and stream channels in pastoral areas. Vegetation alongside native forest sites consists predominantly of nikau palm (*Rhopalostylis sapida*), ferns (*Dicksonia*, *Cyathea* and *Blechnum* spp.), and parataniwha (*Elatostema rugosum*) beneath a mixed forest overstorey that includes tawa (*Beilschmieda tawa*), rimu (*Dacrydium cupressinium*), kanuka (*Kunzea ericoides*), and rewarewa (*Knightia excelsa*).

**Methods**

**National data collation**

Data records of stream locations where *Acanthophlebia* nymphs and adults have been collected were collated from a range of unpublished (mainly regional council and university databases) and published (e.g., Towns 1987, Hitchings 2001, Quinn *et al.* 2004) sources, providing a total of 275 sites from Northland to Wellington (Fig. 1). Most (95%) of the sites were sampled after 1990; 10 were sampled from 1977-88 and four were sampled over 1967-68. Data on catchment attributes, including climate, geology, and land cover upstream of the sampling sites, were obtained from the 1:50,000 map database underlying the River Environment Classification (REC; Snelder & Biggs 2002). All site locations were cross-checked with the REC drainage layer to ensure co-ordinates intersected waterways.

**Fig 1.** Locations of sites used in the large-scale analysis of *Acanthophlebia* distribution, and locations of sites in the Mangaotama catchment (inset). Shaded areas in inset are native forest.
Catchment-scale sampling
Seasonal monitoring. Long-term seasonal sampling was conducted on 21-28 occasions between June 1995 and April 2003 at seven sites (Fig. 1). These comprised two native forest streams (NKL, NW5), three streams with catchments entirely in pasture (PW2, PW3, PW5), and two streams bordered by pasture with upstream headwaters in native forest (PKR, DB4) (see Table 1 for site details). Sampling at NKL was terminated in June 2000; sampling at PKR started in December 1995 and was suspended from September 1997 to June 1998. Ten Surber samples (Surber 1937; 250 µm mesh, 0.04 m² quadrat) were collected on each occasion along a 100 m study reach at each site and these were pooled for subsequent sorting. All Whatawhata invertebrate samples were preserved in 70% iso-propyl alcohol and were then transported back to the laboratory where Acanthophlebia were counted.

Continuum sampling. Comparisons of a series of sites along pasture and forest stream continua were made at ten sites down Mangaotama Stream on 15-25 November 1994, and these data were combined with an additional upstream native forest site (NW1) sampled in November 1992 to provide a total of 11 sites (Table 1; Fig. 1). The pasture stream continuum (i.e., sites with adjacent land use in pasture) comprised PW1, PW2, PW5, M4, M5, and M8 (see Table 1 and Fig. 1). Three sites with upstream catchments entirely in native forest (NW0.5, NW1, and NW5) were also sampled along a stream size continuum. These sites were closely matched to upper pastoral continuum sites (PW1, PW2, PW5) in terms of paired catchment area. Site M3 was located in a patch of native forest, and was included as a comparison for M4 immediately upstream where riparian land use was

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Table 1. Locations and selected physical characteristics of the Mangaotama Stream sampling sites.
Sites referred to are ordered by percent upstream catchment area in native forest. For Study: S, seasonal monitoring; C, continuum study; M, intensive sampling. (ND, no data).

<table>
<thead>
<tr>
<th>Site</th>
<th>Map. ref.</th>
<th>Study</th>
<th>% of catchment in native forest</th>
<th>Riparian land use</th>
<th>Catchment area (ha)</th>
<th>Elev. (m a.s.l.)</th>
<th>Slope (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>PW1</td>
<td>913758</td>
<td>S,C</td>
<td>0</td>
<td>Pasture</td>
<td>6</td>
<td>220</td>
<td>19.4</td>
</tr>
<tr>
<td>PW2</td>
<td>923764</td>
<td>S,C</td>
<td>0</td>
<td>Pasture</td>
<td>95</td>
<td>90</td>
<td>3.2</td>
</tr>
<tr>
<td>PW3</td>
<td>924763</td>
<td>S</td>
<td>0</td>
<td>Pasture</td>
<td>49</td>
<td>100</td>
<td>3.5</td>
</tr>
<tr>
<td>PW5</td>
<td>928777</td>
<td>S,C</td>
<td>0</td>
<td>Pasture/willow</td>
<td>259</td>
<td>60</td>
<td>1.8</td>
</tr>
<tr>
<td>M8</td>
<td>963805</td>
<td>C</td>
<td>54</td>
<td>Pasture</td>
<td>2118</td>
<td>15</td>
<td>0.08</td>
</tr>
<tr>
<td>M5</td>
<td>953796</td>
<td>C</td>
<td>55</td>
<td>Pasture</td>
<td>1927</td>
<td>25</td>
<td>0.15</td>
</tr>
<tr>
<td>M1</td>
<td>630785</td>
<td>C</td>
<td>59</td>
<td>Native</td>
<td>915</td>
<td>80</td>
<td>1.6</td>
</tr>
<tr>
<td>M4</td>
<td>942789</td>
<td>C</td>
<td>62</td>
<td>Pasture</td>
<td>1595</td>
<td>35</td>
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<td>65</td>
<td>Native</td>
<td>1543</td>
<td>40</td>
<td>0.36</td>
</tr>
<tr>
<td>DB4</td>
<td>924776</td>
<td>S</td>
<td>73</td>
<td>Pasture/willow</td>
<td>266</td>
<td>80</td>
<td>ND</td>
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<td>PKR</td>
<td>921772</td>
<td>S</td>
<td>75</td>
<td>Pasture</td>
<td>130</td>
<td>100</td>
<td>0.77</td>
</tr>
<tr>
<td>NW0.5</td>
<td>910782</td>
<td>C</td>
<td>100</td>
<td>Native</td>
<td>23</td>
<td>180</td>
<td>8.8</td>
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<tr>
<td>NKL</td>
<td>919775</td>
<td>S</td>
<td>100</td>
<td>Native</td>
<td>53</td>
<td>120</td>
<td>3.9</td>
</tr>
<tr>
<td>NW1</td>
<td>917785</td>
<td>C</td>
<td>100</td>
<td>Native</td>
<td>98</td>
<td>100</td>
<td>1.9</td>
</tr>
<tr>
<td>NW5</td>
<td>926785</td>
<td>S,C,M</td>
<td>100</td>
<td>Native</td>
<td>300</td>
<td>70</td>
<td>1.0</td>
</tr>
</tbody>
</table>
pasture.

Surber sampling \((n = 8-10)\) was carried out at each site as described above, and concurrent measurements were made of wetted width, channel width, and percent macrophyte cover at 10 cross-sections \((n = 20\) at NW1). Water depths were measured at five points across each cross-section \((10, 30, 50, 70,\) and \(90\%\) of wetted width). Suspendable organic and inorganic sediment samples were collected at randomly selected points \((n = 3-7)\) at all sites except for M5 and M8, by stirring sediments to depths of \(4.1-6.1\) cm and collecting water samples for later drying and ashing, as described by Quinn et al. (1997). The diameters of all wood pieces lying submerged or out of the channel were measured across ten \(1\) m long swathes in each reach to provide a measure of wood volume per \(m^2\) of channel or wetted area.

**Reach-scale sampling**

Intensive sampling at site NW5 on Whakakai Stream, a native forest tributary of Mangaotama Stream located in the Hakarimata Ranges (Fig. 1), was carried out monthly between September 2000 and August 2002. Physico-chemical characteristics of this and other nearby native forest streams are summarised by Quinn et al. (1997) and Quinn and Stroud (2002). The sampling reach was 100 m long and encompassed a range of habitat types including riffles, runs, and pools. Substratum ranged from bedrock outcrops to sand and fine gravel in depositional zones. The reach had a mean width of \(3.2\) m (Boulton et al. 1997), was \(70\) m a.s.l., and drained a \(3.0\) km\(^2\) catchment. Discharge was recorded every 15 minutes at a weir just downstream of the sampling reach.

Nymphs were collected using a Surber sampler \((0.1\ m^2, 250\ \mu m\) mesh). On each occasion, five benthic samples were collected to a depth of c. \(10\) cm from randomly selected \(x-y\) coordinates along the study reach. *Acanthophlebia* were counted on site following elutriation and sieving, and nymphs were then preserved in \(70\%\) iso-propyl alcohol. Depth (to the nearest cm), velocity (at mid-water using a Montedoro-Whitney model PVM2A meter), and substratum compaction, embeddedness, and size distribution were recorded within each \(0.1\ m^2\) benthic sampling quadrat. Compaction was estimated on a categorical scale \((1 - 4)\) following Pfankuch (1975): \(1\) = assorted sizes tightly packed &/or overlapping; \(2\) = moderately packed with some overlap; \(3\) = mostly a loose assortment with little overlap; \(4\) = no packing/loose assortment easily moved. Embeddedness was assessed on a \(1-5\) scale after Platts et al. (1983) according to percentage of gravel-boulder particles covered by fine sediment: \(1\) = \(<5\%\) gravel-boulder particles covered by fine sediment; \(2\) = \(5-24\%\); \(3\) = \(25-49\%\); \(4\) = \(50-75\%\); \(5\) = \(>75\%\). Substratum size distribution was determined by estimating relative abundance of substrata within \(6\) size classes based on \(b\)-axis dimensions: boulder \((>256\ mm)\), large cobble \((128-256\ mm)\), small cobble \((64-127\ mm)\), pebble \((16-63\ mm)\), gravel \((2-15\ mm)\) and sand/silt \((<2\ mm)\). The resulting particle size distributions were converted into a substratum size index (SSI) after Jowett & Richardson (1990). Particulate organic matter (POM; \(>250\ \mu m\)) collected from Surber samples was dried at \(60°C\) to a constant weight, and weighed to the nearest \(0.1\) g.

**Statistical methods**

Relationships between environmental factors and densities of *Acanthophlebia* were explored using Pearson correlations with Bonferroni-adjusted probabilities. Data were log transformed where appropriate to improve normality, which was confirmed by examining normal probability plots (Systat® v. 9.0). Spearman rank correlations were used for categorical data (substratum embeddedness and compaction). To examine relationships between *Acanthophlebia* density and percent of catchment upstream of the sampling sites in native forest, continuum data were combined with mean densities from seasonal monitoring over September 1995 to March 1996 and normalised by the density at NW5 in each dataset. Relationships between nymphal density and percent native forest upstream (seasonal monitoring and continuum sampling) or preceding flow regime (reach-scale data) were examined using regression analysis following log transformation of data where appropriate.
Results

Large-scale factors

Catchment toprock geology of collated *Acanthophlebia* locations was dominated by argillite, greywacke, and volcanics including ash and hardened rock such as ignimbrite (Fig. 2A). Peat, mudstone/siltstone, windblown sand and loess, and alluvium comprised minor proportions of catchment geology. Native forest cover of catchments above *Acanthophlebia* locations averaged 55% (median = 63%), with scrub, pasture and planted forest comprising 12-15% on average (Fig. 2B). Urban and horticultural landcover were rarely encountered in catchments where *Acanthophlebia* were found. Most records came from low order (1-3) stream segments at elevations between 100 and 300 m a.s.l., and with channel slopes <10% (Fig. 3).

Catchment-scale factors

*Acanthophlebia* nymphs were rarely encountered (7% of samples) in pasture streams draining Mangaotama catchment between 1995 and 2003, and when found at pasture sites densities were low (<8 m$^{-2}$) (Fig. 4). In contrast, benthic densities were higher at the two native forest sites, particularly at NW5 where they reached 228 m$^{-2}$, and peaked around March-April in most years. The two pasture sites with upstream headwaters in native forest (PKR, DB4) generally supported densities that were intermediate between sites with upstream catchments entirely in pasture or native forest (Fig. 4).

Densities of *Acanthophlebia* at the continuum sites ranged from 0 at several of the lower reach sites to 108 m$^{-2}$ at the largest native forest site (Table 2). Highest correlations between densities and environmental factors were for water depth and concentration of suspendable inorganic sediments ($r = -0.54$ and $-0.41$, respectively, $n = 11$), but
Bonferroni-adjusted probabilities were not significant. Percent catchment in native forest accounted for 46% of the variation in normalised Acanthophlebia density. There was considerable variation in density at native forest sites (range of values = 0 to 263 per m$^2$ of streambed) where abundance appeared to increase with increasing stream size. This contrasted with pasture sites where abundance was highest at the most upstream site (see Table 2). Relative density of Acanthophlebia was consistently low (average $\leq$ 20% of NW5 densities) where upstream native forest cover was below 60% of total catchment area (Fig. 5A).

Reach-scale factors
Mean benthic densities of Acanthophlebia at NW5 varied from 2 to 470 m$^{-2}$ over the two years of sampling (September 2000 to August 2002) (Fig. 6A). Numbers peaked in February of the first year and in October of year 2, and declined sharply following large floods. The effects of floods on benthic densities were reflected by the significant negative relationship with maximum mean daily flow in the month prior to sampling (Fig. 6B). Few nymphs were collected in Surber samples from NW5 at depths $>0.4$ m and water velocities $>0.4$ m s$^{-1}$ (Figs. 7A & B), and densities were negatively correlated with velocity in mid-water above the sampling quadrat ($r = -0.49, P <0.001, n = 130$). Densities were also positively related to the percentage of quadrat substrata comprising gravels ($r_s = 0.28, P <0.05$), and this relationship was reflected in most nymphs occurring at substratum size index values of 4-5 (Fig. 7E). No statistically significant relationships were detected with substratum compaction or embeddedness using rank correlations, although nymphal densities were clearly highest where there was little sediment deposition (i.e., low embeddedness scores; Fig. 7C) and the substratum was uncompacted (Fig. 7D). Finally, nymphal abundance was significantly and positively correlated with the dry mass of POM in the Surber quadrat ($r = 0.34, P <0.001$), although there was considerable scatter in the data (Fig. 7C).

### Table 2. Mean Acanthophlebia abundance and physical habitat characteristics.
Data are for 11 sites along pasture and native forest continua in the Mangaotama catchment ordered by percent upstream catchment area in native forest. (ND, no data).

<table>
<thead>
<tr>
<th>Site</th>
<th>Acanthophlebia (no. m$^{-2}$)</th>
<th>Wetted width (m)</th>
<th>Channel width (m)</th>
<th>Depth (m)</th>
<th>% macrophyte cover</th>
<th>Channel wood (cm$^3$ m$^{-2}$)</th>
<th>Instream wood (cm$^3$ m$^{-2}$)</th>
<th>Inorganic sediment (g m$^{-2}$)</th>
<th>Organic sediment (g m$^{-2}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>PW1</td>
<td>6.0</td>
<td>0.44</td>
<td>0.47</td>
<td>0.04</td>
<td>28.0</td>
<td>5034.1</td>
<td>0</td>
<td>270.3</td>
<td>25.8</td>
</tr>
<tr>
<td>PW2</td>
<td>2.5</td>
<td>1.02</td>
<td>1.09</td>
<td>0.14</td>
<td>0</td>
<td>295.3</td>
<td>348.6</td>
<td>653.3</td>
<td>54.5</td>
</tr>
<tr>
<td>PW5</td>
<td>0</td>
<td>2.26</td>
<td>2.26</td>
<td>0.27</td>
<td>0</td>
<td>5.5</td>
<td>579.2</td>
<td>1113.6</td>
<td>64.9</td>
</tr>
<tr>
<td>M8</td>
<td>0</td>
<td>4.98</td>
<td>5.86</td>
<td>0.26</td>
<td>0</td>
<td>54.5</td>
<td>916.2</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>M5</td>
<td>0</td>
<td>3.53</td>
<td>3.64</td>
<td>0.45</td>
<td>0</td>
<td>402.8</td>
<td>2004.2</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>M1</td>
<td>7.5</td>
<td>5.3</td>
<td>5.8</td>
<td>0.25</td>
<td>0</td>
<td>64.8</td>
<td>45.3</td>
<td>1310.7</td>
<td>83.0</td>
</tr>
<tr>
<td>M4</td>
<td>20</td>
<td>4.89</td>
<td>4.89</td>
<td>1.24</td>
<td>38.3</td>
<td>56.1</td>
<td>1208.3</td>
<td>1284.3</td>
<td>211.6</td>
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<tr>
<td>M3</td>
<td>0</td>
<td>5.19</td>
<td>7.22</td>
<td>0.27</td>
<td>0</td>
<td>171.7</td>
<td>1481.3</td>
<td>583.7</td>
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</tr>
<tr>
<td>NW0.5</td>
<td>5</td>
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<td>69119.9</td>
<td>2214.6</td>
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<td>1164.6</td>
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<td>63.0</td>
<td>2256.8</td>
<td>553.4</td>
<td>360</td>
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</table>

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Fig 4. Densities of *Acanthophlebia* nymphs found over 6-8 years at two native forest sites (black symbols), three pasture sites (open symbols), and two sites bordered by pasture but with native forest headwaters (grey symbols). Note that sampling of NKL was terminated in June 2000.

Fig 5. Relationship between relative density of *Acanthophlebia* (as a percentage of NW5 density for equivalent datasets) and percentage of upstream catchment area in native forest for sites along Mangaotama Stream.

Fig 6. Mean (± 1SE) benthic density of *Acanthophlebia* collected at monthly intervals (A), and relationship between mean density and the maximum mean daily flow for the month prior to sampling (B) over two years at NW5.
Fig 7. Scatterplots of relationships between benthic densities of *Acanthophlebia* and six habitat factors measured in randomly selected quadrats (0.1 m²) sampled monthly (n = 5-10 per date) over two years at NW5.
Discussion

A consistent theme in the large-scale and catchment-scale analyses was the significance of native forest cover upstream of the sampling site in determining the occurrence and relative abundance of nymphs. Indeed, the median percentage (63%) of catchment forest cover characteristic of *Acanthophlebia* locations was remarkably similar to the threshold of 60% cover above which nymphal abundance increased markedly in Mangaotama Stream tributaries. Although these patterns reflect benthic densities, Scarsbrook and Halliday (2002) similarly reported that *Acanthophlebia* was common in the hyporheos of pine and native forest sites, and at a pasture site in the Mangaotama catchment with 65% of upstream catchment area in native forest, but was absent from the hyporheos of a nearby site where the entire upstream catchment was in pasture.

Only 14% of the known North Island *Acanthophlebia* locations had >40% of upstream catchment area in pasture, and where nymphs did occur in pasture streams in the Mangaotama catchment they were most abundant in incised headwater segments close to forested streams in adjacent catchments. This finding suggests that intercatchment dispersal from forested source areas and subsequent oviposition may help maintain *Acanthophlebia* populations in the pasture headwaters of Mangaotama Stream. Although preliminary laboratory trials indicate that *Acanthophlebia* nymphs can tolerate high water temperatures (mean longevity at 25°C = 16 days; K. Collier unpubl. data), we currently have no data on water temperatures required for successful egg hatching which may limit colonisation of open streams in predominantly pastoral catchments.

A substantial proportion of the secondary production of *Acanthophlebia* populations in native forest streams can occur in the hyporheic zone, and it has been suggested that restoration of hyporheic function should be an important part of stream rehabilitation objectives (Collier et al. 2004). Given the apparent tolerance of nymphs to moderately high water temperatures and the likelihood that cumulative sedimentation impacts in pastoral catchments increase in a downstream direction, the apparent halo effect of native forested headwaters below forest/pasture boundaries is more likely to be related to hyporheic function. This suggestion is in line with the conclusions of Boulton et al. (1997) and Scarsbrook and Halliday (2002) that intact hyporheic function, especially surface-hyporheic water exchange, is important for *Acanthophlebia*. A positive effect of forested headwaters on sensitive invertebrate taxa in downstream pastoral settings was also reported on Banks Peninsula by Harding (2003). However, it may take several hundred metres of shaded habitat before invertebrate communities in native forest remnants with pasture headwaters resemble those in forested headwater streams (Storey & Cowely 1997, Scarsbrook & Halliday 1999). Even then sediment levels were high suggesting hyporheic function had not recovered.

In addition to sites draining catchments with predominantly native forest, *Acanthophlebia* nymphs also occurred mainly in small streams with low-intermediate channel slopes at moderate elevations, and in catchments characterised largely by hardened toprock. Relatively few known *Acanthophlebia* locations occurred in catchments that were dominated by unconsolidated or easily erodible toprock, and few locations had low elevations (<100 m a.s.l.) or high channel slope (>10%). Although we were not able to make direct comparisons with habitat availability, these data collectively indicate that *Acanthophlebia* typically occurs today in hill-country streams draining catchments predominantly in forest and with hard-rock geologies.

Temporal patterns in benthic density, as indicated by nine years of seasonal monitoring at a range of sites and two years of monthly sampling at a native forested site, demonstrated that peaks often occurred around February to April. This period coincides with the time of peak emergence (Norrie 1969, Collier et al. 2004), and high benthic densities may be caused by nymphs moving from hyporheic habitats, where large numbers can occur (Scarsbrook & Halliday 2002, Collier et al. 2004), to the benthos prior to emergence. The periodicity and intensity of floods also clearly had a significant impact on temporal abundance patterns. Bed mobilisation occurred at the native forest site (NW5) when peak daily flows exceeded 3000 litres s⁻¹. During our two year sampling period, flows of this magnitude occurred on average every 4 months and, in one year, just prior to peak emergence.
resulting in low numbers of adults (Collier et al. 2004). Nevertheless, *Acanthophlebia* adults were present over eight months, and the ecological flexibility provided by this extended emergence period probably confers some population-level insurance against the catastrophic effects of floods, as suggested by Winterbourn et al. (1981) for New Zealand aquatic insects colonising streams with highly variable and unpredictable flow regimes. Variations in baseflow hydraulic conditions, notably water depth and velocity, appeared to contribute to the patchy abundance of *Acanthophlebia* nymphs in the heterogenous stream reach at NW5, and also potentially along the stream continuum where few nymphs were found at deeper downstream sites. Most nymphs were collected at low to moderate depths and velocities, and at sites dominated by non-embedded and uncompacted gravel substrata, typical of conditions occurring at the downstream ends of pools. These areas were noted by Collier et al. (2004) to be hot-spots of *Acanthophlebia* production which was attributed to high hyporheic function in water recharge zones. Nymphal densities also tended to be higher in areas with higher POM accumulation, and this finding may be partly related to benthic *Acanthophlebia* apparently deriving a substantial proportion of their nutrition from fine particulate matter (possibly including bacteria) and fungi, presumably associated with or derived from coarse organic matter (Collier et al. 2004). Quinn et al. (2004) reported that *Acanthophlebia* nymphs were sensitive to logging practices in Coromandel streams, and found a large proportion of the variation in their abundance was explained by channel stability, periphyton biomass and spot measurements of dissolved oxygen and water temperature. This synthesis of data from multiple spatial scales has highlighted factors related to *Acanthophlebia* distribution and abundance that can be addressed during stream rehabilitation planning. Firstly, protection or replanting of headwater areas in forest is likely to secure existing habitat or create habitat suitable over the long-term for *Acanthophlebia*, particularly if hyporheic function can be restored. Restoration of hyporheic function may require several bed-moving flows to flush out stored interstitial silt in replanted headwater areas. These headwater areas can be expected to provide a downstream halo effect, such that there is a high probability of *Acanthophlebia* nymphs successfully utilising instream habitat down to where upstream forest cover is more than around 60% of catchment area. In addition, intact headwater forest fragments can provide important refugia for rare or locally endemic aquatic insects (Harding 2003). Secondly, activities aimed at restoring habitat for *Acanthophlebia*, potentially a useful indicator of restoration success at sites where it historically occurred, are more likely to be successful in low order streams at intermediate elevations and with low to moderate channel slopes. Finally, the success of such activities will depend in part on the proximity of the restored site to population source areas from which they can disperse, either through nymphal drift or adult flight. To quantify the effect of dispersal constraints on restoration outcomes, more information is required on factors affecting the movement of aquatic insects through the landscape.

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