

Intermittent streams in Hawke's Bay:
responses of aquatic invertebrates to variability in annual
rainfall

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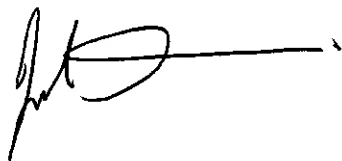
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Reviewed by

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J Quinn

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D Roper

Formatting checked by

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Executive summary

Intermittent streams provide habitat for an abundant and diverse macroinvertebrate community, but are often overlooked in stream management policies. The biological communities of intermittent streams are likely to come under increasing pressure in future due to rising demands for water abstraction and to a warmer and drier climate. This study was commissioned by Hawke's Bay Regional Council to predict the future effects of longer and more intense dry periods from the twin pressures of climate change and increased water abstraction. It did so comparing the taxonomic richness, abundance and composition of the benthic macroinvertebrate community in several central Hawkes Bay intermittent streams among wetter and drier years from 2008 to 2012.

The responses of the macroinvertebrate community to dry period length, intensity and timing were assessed by sampling the community once per year in four forested intermittent streams. The timing of flow cessation, drying of all surface water and resumption of stream flow were also measured over the same period. The responses of forested intermittent streams were compared with pasture intermittent streams and intermittent streams with perennial headwaters, sampled concurrently with the forested intermittent streams. Perennial streams were also sampled to compare the effects of stream drying with those of flow reduction and to determine whether other climatic factors were influencing the communities.

Results showed clear negative correlations between measures of dryness and macroinvertebrate richness, abundance and community composition in forested intermittent streams. The strongest correlations were with the date that flow resumed in autumn, suggesting that as well as the length, the timing of the dry period with respect to invertebrate life histories may be important. Also strongly correlated was the number of weeks with soil moisture deficit >100 mm, a measure that incorporates the intensity of the dry period (in particular, drying of surface stream bed sediments) as well as its length. Mayflies, stoneflies and caddisflies appeared to be the taxa most sensitive to dry period length, intensity or timing, whereas some Diptera and non-insects (e.g., oligochaete worms, snails and microcrustacea) appeared to increase in abundance with a longer dry period.

Invertebrate communities in perennial streams showed some of the same correlations as those in intermittent streams, but to a lesser degree. This suggests that flow reduction may cause similar, but weaker, stresses on aquatic invertebrate communities as compared with stream drying. Water temperature during the flow period, the only other environmental variable likely to influence the communities in this study, had a detectable but minor effect.

Generally, pasture intermittent streams showed a weaker response to dry period length or intensity than forested intermittent streams. This may be because the taxa living in pasture streams are more tolerant of environmental stresses than those in forest, and therefore are better able to tolerate the additional stress of a long dry period.

Intermittent streams with perennial headwaters harboured an invertebrate community very similar to that in perennial streams and distinct from that in intermittent streams without perennial headwaters. This suggests that invertebrate drift from perennial headwaters has a strong influence in shaping the community of such streams. These streams showed a weaker response to dry period length or intensity than streams without perennial headwaters, suggesting that invertebrate drift buffers the invertebrate community from the effects of the

dry period. However, with only two such sites in the study, the differences between sites with and without perennial headwaters were not statistically significant.

The results of this study indicate that macroinvertebrate communities in Hawke's Bay's intermittent headwater streams are likely to become taxonomically poorer and less abundant if global climate change or water abstraction increases the length or intensity of the summer dry period. However, the long-term increases in dry period length and intensity expected with climate change or with long-term water abstraction consents may cause a greater impact on macroinvertebrates than the year-to-year changes in dryness described here. Long-term warming and drying may eliminate source populations of sensitive taxa, thus reduce the potential for recolonisation during wetter years. Planting stream banks with shade trees may mitigate the effects of climate change or water abstraction by reducing other stresses such as the temperature of water and stream bed. However, while they will likely reduce surface water evaporation (by shading the water surface and streambed), trees may also increase evapotranspiration and further increase the length of the dry period so consideration of the balance of these effects will be needed when managing the riparian areas of intermittent streams.

1 Introduction

Intermittent streams are probably very common in Hawke's Bay region. Although no thorough surveys of their abundance have been completed, a brief informal survey in 2008 identified 206 intermittent streams beside roads in central and southern parts of the region (Storey 2008). Intermittent streams in Hawke's Bay include both headwaters (those that dry to their source) and intermittent mid-reaches of medium- and large-sized rivers (those with perennial headwaters). Previous studies (Storey and Quinn 2008, 2011, 2013) have shown that Hawke's Bay intermittent streams support diverse macroinvertebrate communities, though the diversity is typically lower than in perennial streams.

Intermittent streams are very vulnerable to changes in climate in terms of the duration of their dry period and the degree of drying. Global climate change is expected to bring longer, more intense and more frequent drought to eastern parts of NZ, including Hawke's Bay (Mullan et al. 2005). Previous studies of intermittent streams have shown that the length of the dry period has an influence on benthic macroinvertebrate communities (Feminella 1996, Fritz and Dodds 2005, Arscott et al. 2010; Datry 2012). However, New Zealand invertebrates have somewhat different ecology and life histories to those in other countries (Winterbourn et al. 1981, Scarsbrook et al. 2000), and in particular their over-summering strategies may be different to those in other countries (Storey and Quinn 2011). Therefore previous studies are not sufficient for predicting how invertebrate communities in Hawke's Bay may respond to dry period length and/or intensity. Mitigating global climate change is clearly beyond the ability of regional councils, but predicting the likely effects of climate change on natural ecosystems is still important, as the effects of climate change on biological communities may be mitigated through local management actions.

In addition to climate change, intermittent streams may be subject to flow reductions due to water abstraction or impoundment. With increasing human demand for water in Hawke's Bay, consent applications for water abstraction or impoundment are likely to increase in future. Perennial streams are protected from over-abstraction by minimum flow requirements, however there are currently no guidelines for setting limits on abstraction for intermittent streams (where the natural mean annual low flow is zero). The effects on benthic invertebrate communities of extending the dry period of intermittent streams through water abstraction or impoundment are not known.

From previous studies (Storey and Quinn 2008, 2011, 2013; Storey unpubl. data) the following is known regarding invertebrate life histories and over-summering strategies in Hawke's Bay intermittent streams:

1. most taxa seem to complete their aquatic life stages several weeks before drying typically occurs, but a greater number of individuals may be able to complete development in years when drying occurs later
2. most taxa seem able to survive in remnant pools, however
3. when all surface water is gone (i.e., remnant pools have dried), most taxa seem to over-summer in shallow sediments. Some (mostly insects) over-summer as eggs, others (mostly non-insects) as immature stages. In pasture sites, sediment temperatures can cause mortality of over-summering life stages

4. adults of some insect taxa (especially caddisflies) can fly up to 1000 m (and probably more). Therefore some insect taxa probably can recolonise the intermittent sites each year by flying from nearby perennial streams.

1.1 Aspects of drought

Droughts differ from one another in several ways – the intensity, length (at different levels of intensity), timing of onset and finish and whether or not they are interrupted partway through by rainfall events. Each of these aspects of drought may affect a stream invertebrate community in different ways.

Based on what is known of invertebrate over-summering strategies, the following aspects of stream bed drying are predicted to be relevant to the aquatic macroinvertebrate community:

1. Length of time without flow during the previous summer. This is relevant for taxa that require flowing water (cannot live in remnant pools), and whose over-summering stages can survive for only a limited period of time. Such taxa probably are mainly those that survive drought as immature stages (e.g., crustaceans, molluscs and worms), rather than eggs, since eggs are expected to survive relatively long periods without flow.
2. Presence/absence of remnant pools, or length of time with no surface water, during the previous summer. This is relevant for taxa that can live in remnant pools, and whose over-summering stages can survive absence of surface water for only a limited period of time.
3. Length of time with flow during the previous flow period. This is relevant for taxa that need a relatively long period of time with flowing water to complete their life cycle. If the flow period is too short for such taxa to complete their life cycle, recruitment will be limited and the taxa may be rare or absent in the following year. For most invertebrate taxa, a long flow period may allow populations to increase, leading to higher recruitment in the following year.
4. Length of time with surface water present during previous year. This is relevant for taxa that need a certain period of time with surface water (flowing or still) to complete their life cycle. If the period with surface water is too short for such taxa to complete their life cycle, recruitment will be limited and the taxa may be rare or absent in the following year.
5. Timing of the start or end of the dry period, e.g., with respect to temperature or other seasonal cues. This is relevant for taxa whose life cycles are timed with seasonal cues or that are strongly affected by temperature. For example, if flow begins late in the autumn, night-time air temperatures may be too low to allow adult insects (particularly caddisflies) to recolonise intermittent headwaters by flying from nearby perennial streams, resulting in poor recruitment. For other taxa, low water temperatures may result in slower development and lower numbers.
6. Severity of summer drought. This is relevant for taxa that can over-summer in damp streambed sediments but depend on the sediments retaining high moisture levels.

7. Interruption of the summer dry period by a large storm. If followed by a second period of drying, the storm may represent a “false start” to the flow period. Over-summering life stages may be triggered to begin development, but early-development stages may be desiccated when the surface water disappears. This may cause high mortality of invertebrates.

1.2 Aims

The first aim of this study was to determine whether the length of the dry period affects the abundance, taxon richness and community composition of benthic macroinvertebrates in intermittent headwater streams in the following year. I assumed that the only environmental factors affecting the macroinvertebrate communities that may change at the study sites within the monitoring period are climatic variables (temperature, rainfall and evapotranspiration). Therefore, the alternate hypotheses are that benthic macroinvertebrate abundance, richness and community composition are mainly influenced by one of the following factors: 1) intensity of the dry period (i.e., sediment moisture levels and presence/absence of remnant pools); 2) whether the dry period is continuous or interrupted by a summer storm; 3) timing of dry period with respect to life cycles (e.g., dry during the crucial oviposition period during late summer/autumn vs. dry during spring when some taxa may be completing development); 4) length of flow period in the previous year (potential to build up population sizes leading to increased recruitment in the following year); 5) water temperature during the flow phase (warmer water may stimulate faster growth rates and greater abundance); 6) antecedent flow conditions in the few weeks before sampling (e.g., floods that reduce abundance and potentially diversity).

The second aim was to determine whether intermittent streams with perennial headwaters are affected by dry period length as greatly as intermittent headwater streams, in terms of their benthic macroinvertebrate communities. Because they receive invertebrate drift from upstream, intermittent streams with perennial headwaters are expected to be less affected by the length or intensity of the dry period than intermittent headwater streams (those without perennial headwaters).

The third aim was to determine whether the benthic invertebrate community in pasture intermittent streams is affected by dry period length as greatly as that of forested intermittent streams. It was not known whether to expect a greater or lesser response from the community in pasture streams than that in forested streams. The community in pasture streams is considered to be stressed by a number of environmental factors during all flow phases. During the flowing water phase, pasture streams are subject to siltation, elevated daytime temperatures and reduced night-time oxygen levels. During the drying phase, remnant pools in pasture streams fill with aquatic macrophytes and algae, which create large fluctuations in dissolved oxygen. The lack of riparian shade causes midday temperature to reach much higher levels in pasture than in forested pools. Predation and competition may also be much greater in pasture pools, as these are more accessible than forested pools to lentic invertebrates (such as beetles and hemipterans) that colonise from nearby perennial ponds. During the dry phase, dry sediments may reach much higher temperatures and lower moisture levels in pasture than in forested sites, reducing survivorship of over-summering life stages (Storey and Quinn 2013). Therefore, a longer or more intense dry period may have a greater effect on the invertebrate community in pasture intermittent streams than forested ones, as drying represents an added stress in addition to the existing stresses of a pasture

environment. Moreover, a longer or more intense dry period may create more extreme conditions in pasture than in forested intermittent streams as they are more exposed to the elements. Alternatively, the invertebrate community in pasture streams may be more robust than that in forested streams because of the environmental stresses associated with pasture, and therefore may be more resistant or resilient to additional stresses such as stream drying.

2 Methods

2.1 Sites

Thirteen sites were monitored during this study (Fig. 1). The sites included three first-order intermittent streams in native forest (abbreviated as INT_NF1, 2 and 3), three first-order intermittent streams in pasture (INT_P1, 2 and 3), two intermittent streams with perennial headwaters (one second-order IPER_NF1, and one third-order IPER_NF2) and three perennial streams (two second-order PER_NF1 and 3, and one third-order PER_NF2). The sites were all located in central Hawke's Bay, mostly in the Mangaonuku Stream catchment, but two (INT_NF1 and PER_NF1) were located in the Poporangī Stream catchment. All sites were within 18 km of each other.

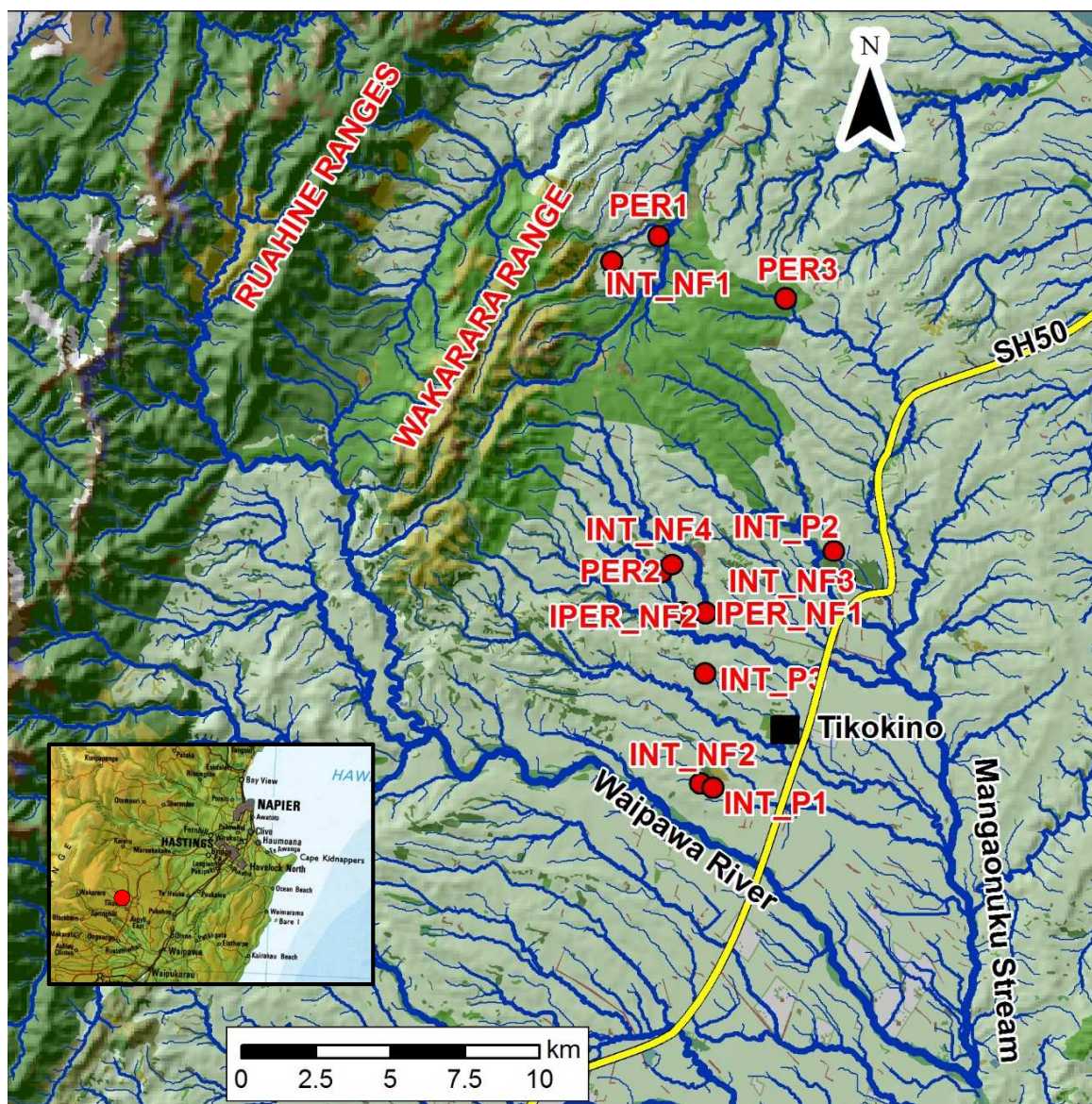


Figure 1: Locations of monitoring sites. Abbreviations are: INT_NF: forested intermittent sites; INT_P: pasture intermittent sites; IPER_NF: forested intermittent sites with perennial headwaters; PER_NF: forested perennial sites.

2.2 Field measurements

The state of flow in the intermittent streams was classified into three phases: flow, no flow (isolated pools remain) and completely dry (absence of all surface water). The start and end of each phase was recorded using two methods. In the first two years of monitoring, modified temperature loggers were placed in the stream bed. The modifications to these loggers allowed them to record the presence or absence of water based on electrical conductivity between two protruding electrodes. At each site, one logger was placed in a riffle to record the presence of flowing water and another was placed in a pool to record the presence of standing surface water. In the final three years of the study, the loggers were replaced by time-lapse cameras mounted above the study sites on overhanging trees or adjacent fence posts. The cameras took 3-4 photos of the site per day, capturing both a riffle and a pool area so that the flow phase could be identified from the image. The cameras and the loggers were equally effective at distinguishing dry vs. wet conditions, so no change in estimates of dry period length are likely due to the change in method.

Because the loggers were susceptible to burial or loss in floods, and the cameras occasionally lost power or disappeared from the site, no site had a complete measurement record for the entire 5 year monitoring period. INT_NF3 had the most complete record, and at this site measured data were supplemented by occasional observations by the landowner.

A climate station at Gwavas provided a complete rainfall record for the period. Data on soil moisture deficit were obtained from the NIWA climate station Waipawa EWS (agent number 31620, network number D96962, lat -39.9515, long 176.61706, alt 130 m a.s.l.).

At most sites, stream water temperature (stream bed temperature during dry periods), and air temperature on the stream bank were recorded using Onset Tidbit and Pendant temperature loggers. However, various factors (e.g., burial or loss during floods, small differences in temperature readings between loggers that were used in different years, etc.) made it difficult to obtain a consistent record of water temperature across all years at any monitoring site. Since the main aim of recording temperature was to compare average temperatures between years, it was decided to use the air temperature record from a climate station in nearby Waipawa. It is reasonable to assume that during winter, changes in air temperature over the monitoring period were closely correlated with changes in water temperature, since other factors influencing water temperature, such as shading, did not change at the monitoring sites.

Dissolved oxygen, temperature, pH and conductivity were measured with field meters once per year when benthic invertebrates were sampled.

2.3 Benthic macro-invertebrates

Benthic macro-invertebrates were sampled once per year between mid-September and late October, allowing a minimum of four months for the invertebrates to recolonise the intermittent sites after flow returned. According to Storey and Quinn (2008) this should be sufficient time for the benthic aquatic community to fully establish. Macro-invertebrates were sampled using four replicate Surber samples collected each year from the same 20 m reach at each site. The Surber was placed in riffles such that the amount of cobbles, pebbles, gravels and organic matter (leaves and small wood) as a percentage of the Surber area remained roughly constant from one year to the next. Samples were preserved on site in

70% isopropyl alcohol, and were identified under 10x magnification using the key of Winterbourn et al. (2006).

2.4 Measures of dryness

The dryness of each year in the study was calculated using four different numerical measures:

1. The number of weeks without flow during the summer prior to invertebrate sampling.
2. The number of weeks between 1 January and the start of flow (i.e., how late in the year flow began).
3. The number of weeks with soil moisture deficit >100 mm.
4. The number of weeks with water flow during the year prior to invertebrate sampling.

In addition to these numerical measures, the occurrence of storms during the dry period and the presence of remnant pools throughout the dry period were recorded as present or absent in each year.

Four of the six measures of dryness relate specifically to intermittent streams as they measure presence/absence of stream flow or surface water. Although perennial streams, by definition, do not experience total loss of flow, these measures are expected to correlate with the degree of flow reduction in perennial streams, and are used as such in the absence of flow data for perennial streams. Therefore, when I refer to “dryness” of different years, I mean the duration or intensity of stream drying in the case of intermittent streams, and the duration or intensity of flow reduction in the case of perennial streams.

Because the most complete data record of flow phases was for INT_NF3, this site was used to calculate the dryness measures that were applied to all the analyses, i.e., to derive the correlations for all sites.

2.5 Statistical analyses

Invertebrate data were summarised for univariate analyses using three richness metrics (total taxonomic richness, EPT* richness and Diptera richness), two abundance metrics (total abundance, EPT* abundance) and one composition metric (%EPT* abundance). “EPT” refers to the insect orders Ephemeroptera (mayflies), Plecoptera (stoneflies) and Trichoptera (caddisflies). The asterisk indicates that species in the caddisfly family Hydroptilidae were not included in these metrics. Hydroptilidae have different habitat requirements and feeding mode to other caddisflies, and are commonly excluded from EPT metrics. Each of these invertebrate metrics was correlated with the four measures of dryness, using Pearson’s correlation coefficient. For testing the significance of correlations, richness metrics were square-root transformed, abundance metrics were $\log_{10}(x+1)$ -transformed and the % abundance metric was arcsine-transformed to meet assumptions of data distribution.

The perennial sites acted as controls to compare the effects of stream drying with those of flow reduction, and to distinguish effects of stream drying from those of other climatic factors. Therefore, the final test to demonstrate that invertebrate richness and abundance in the INT sites were responding to the duration (or intensity) of stream drying was to test whether the

richness and abundance metrics responded to (i.e., were correlated with) the dryness measures more strongly in the intermittent sites than in the perennial sites.

Differences in the strength of correlations between INT_NF and PER_NF sites were tested in two ways. The first was by a simple Analysis of Variance (ANOVA) for significant differences between correlation coefficients. The second was by analysis of covariance (ANCOVA), with flow type (intermittent vs. perennial) as the categorical factor and dryness measures as the continuous factor.

Patterns in the macroinvertebrate community composition were also examined using multivariate methods. Non-metric multidimensional scaling (MDS) was used to display differences among flow types and (within each flow type) between years. Correlations between MDS axis 1 and dryness measures at each individual site were tested for significance using a randomisation technique. This involved replacing the values for the various dryness measures in each year with random numbers and calculating the coefficient of correlation between MDS axis 1 and the "random factor." This was repeated 20 times, then the correlation coefficient for each dryness measure was compared with the distribution of correlation coefficients for the 20 random factors using a Z test (Zar 1984). The null hypothesis for this test was that the correlation coefficient between MDS axis 1 and the dryness measure came from the population of correlation coefficients between MDS axis 1 and random factors. Rejecting the null hypothesis means that the correlation between MDS axis 1 and the dryness measure could not be explained by chance alone.

3 Results

3.1 Measures of dryness

The period 2008 to 2012 included both very wet and very dry years. For example, in the 12 month period before September 2009 there were 31 weeks without flow, including 11-13 weeks without any surface water, at INT_NF3. In contrast, during the 12 months before September 2012 there were no days without flow at this site. The timing of drying and rewetting for this site, which had the most complete record of direct observations, is shown in Table 1. Table 2 gives statistics describing the duration, intensity and timing of wet and dry periods for this site.

As these tables show, the length, intensity and timing of drought are not necessarily correlated with each other from year to year. For example, in 2010 there were 17 weeks without flow, but surface water remained throughout the dry period, whereas in 2011 there were only 11 weeks without flow but for three of these there was no surface water. Nevertheless, the various dryness measures showed strong concordance: 2012 was the wettest year, 2009 the driest and 2010 the second driest year by all measures. Only 2008 and 2011 were ranked differently by the different measures, e.g., 2009>2010>2008>2011>2012 for “number of weeks after 1 Jan when flow began” and “number of weeks with soil moisture deficit >100 mm”, compared with 2009>2010>2011>2008>2012 for “number of weeks without flow”.

The dryness measure “number of weeks with flow in the previous year” was very similar among the years 2008-2011 (ranging from 27-33 weeks), but was extremely high in 2012 (79 weeks) because no drying occurred during summer 2011-12. This means that correlations of biological metrics with this dryness measure were strongly driven by this one extreme value, thus the correlations must be treated with some caution. The other dryness measures had a more even spread of values and did not suffer this problem.

Table 3 shows the timing of drying and rewetting for all intermittent sites during the 12 month period before September 2011. This was the only year when a continuous record was obtained for all intermittent sites. There were marked differences among sites in relation to the timing of flow cessation and disappearance of surface water, indicating that some sites are more sensitive to drying than others. One site (INT_NF4) did not dry at all during this period. However, the timing of flow resumption (on 28 January and again on 29 April) was more consistent among sites, probably because on both occasions it was triggered by a large rainfall event that affected all sites. Such large events do not occur in all years, but are commonly the cause for flow resuming in these streams.

Table 1: State of flow at site INT_NF_2 during the five-year monitoring period. Columns are labelled by invertebrate sampling year, and show the state of flow during the 12 months prior to invertebrate sampling. Thus, the first 14 rows refer to dates in the previous calendar year. Regular font indicates actual observations/measurements. Italic font indicates where state of flow was inferred from data before/after the corresponding date.

Week beginning		2008	2009	2010	2011	2012
1-Oct		<i>flow</i>	flow	flow	flow	flow
8-Oct		<i>flow</i>	flow	flow	flow	flow
15-Oct		<i>flow</i>	flow	flow	flow	flow
22-Oct		<i>flow</i>	flow	<i>flow</i>	flow	flow
29-Oct		<i>flow</i>	flow	<i>flow</i>	flow	flow
5-Nov		<i>flow</i>	flow	<i>flow</i>	flow	flow
12-Nov		<i>flow</i>	flow	<i>flow</i>	flow	flow
19-Nov		<i>flow</i>	flow	<i>flow</i>	flow	flow
26-Nov		<i>flow</i>	no flow	<i>flow</i>	flow	flow
3-Dec		<i>flow</i>	no flow	<i>flow</i>	flow	flow
10-Dec		<i>flow</i>	no flow	<i>flow</i>	no flow	flow
17-Dec		<i>flow</i>	no flow	<i>flow</i>	no flow	flow
24-Dec		<i>flow</i>	no flow	<i>flow</i>	no flow	flow
31-Dec		<i>flow</i>	no flow	<i>flow</i>	no flow	flow
7-Jan		<i>flow</i>	no flow	no flow	dry	flow
14-Jan		flow	no flow	no flow	dry	flow
21-Jan		flow	no flow	no flow	dry	flow
28-Jan		flow	no flow	flow	flow	flow
4-Feb		flow	no flow	flow	flow	flow
11-Feb		flow	no flow	flow	flow	flow
18-Feb		no flow	no flow	no flow	no flow	flow
25-Feb		no flow	no flow	no flow	no flow	flow
3-Mar		no flow	no flow	no flow	no flow	flow
10-Mar		no flow	no flow	no flow	flow	flow
17-Mar		no flow	no flow	no flow	no flow	flow
24-Mar		no flow	no flow	no flow	flow	flow
31-Mar		no flow	no flow	no flow	flow	flow
7-Apr		no flow	no flow	no flow	flow	flow
14-Apr		no flow	dry	no flow	flow	flow
21-Apr		no flow	dry	no flow	flow	flow
28-Apr		no flow	dry	no flow	flow	flow
5-May		no flow	dry	no flow	flow	flow
12-May		flow	dry	no flow	flow	flow
19-May		flow	dry	no flow	flow	flow
26-May		flow	dry	flow	flow	flow
2-Jun		flow	dry	flow	flow	flow
9-Jun		flow	dry	flow	flow	flow
16-Jun		flow	dry	flow	flow	flow
23-Jun		flow	dry	flow	flow	flow
30-Jun	flow	flow	flow	flow	flow	flow
7-Jul	flow	flow	flow	flow	flow	flow
14-Jul	flow	flow	flow	flow	flow	flow
21-Jul	flow	flow	flow	flow	flow	flow
28-Jul	flow	flow	flow	flow	flow	flow
4-Aug	flow	flow	flow	flow	flow	flow
11-Aug	flow	flow	flow	flow	flow	flow
18-Aug	flow	flow	flow	flow	flow	flow
25-Aug	flow	flow	flow	flow	flow	flow
1-Sep	flow	flow	flow	flow	flow	flow
8-Sep	flow	flow	flow	flow	flow	flow
15-Sep	flow	flow	flow	flow	flow	flow
22-Sep	flow	flow	flow	flow	flow	flow

Table 2: Duration, intensity and timing of dry period at site INT_NF_3 during the five-year monitoring period. Column headings refer to the 12 month period before the September invertebrate sampling (e.g., 2008 refers to October 2007 to September 2008). Row headings in bold refer to metrics that are used in data analyses. Asterisk means best estimate.

	2008	2009	2010	2011	2012
Date when flow stopped	18-Feb	26-Nov	7-Jan	10-Dec	none
No. of weeks after 1 Jan when flow stopped	7	-6	2	-4	N/A
Date when all surface water gone	none	btw 1 Apr & 12 May	none	7-Jan	none
Date when flow started	12-May	30-Jun	26-May	24-Mar	N/A
No. of weeks after 1 Jan when flow started	19	26	21	12	0
No. of weeks without flow	12	31	20	15	0
Remnant pools	Yes	No	Yes	No	N/A
No. of weeks without any surface water	0	12*	0	3	0
No. of weeks with flow in previous year	33	28	27	28	79
No. of weeks with soil moisture deficit >100 mm	19	24	22	9	0
Storm during dry period?	No	No	Yes	Yes	N/A

Table 3: State of flow at intermittent sites during the 12 months prior to the September 2011 invertebrate sampling.

	INT_NF_1	INT_NF_2	INT_NF_3	INT_NF_4	INT_P_1	INT_P_2	INT_P_3	IPER_1	IPER_2
1-Oct	flow	flow	flow	flow	flow	flow	flow	flow	flow
8-Oct	flow	flow	flow	flow	flow	flow	flow	flow	flow
15-Oct	flow	flow	flow	flow	flow	flow	flow	flow	flow
22-Oct	flow	flow	flow	flow	flow	flow	flow	flow	flow
29-Oct	flow	flow	flow	flow	flow	flow	no flow	flow	flow
5-Nov	flow	flow	flow	flow	flow	flow	no flow	flow	flow
12-Nov	flow	flow	flow	flow	flow	flow	no flow	flow	flow
19-Nov	flow	flow	flow	flow	flow	flow	no flow	flow	flow
26-Nov	flow	flow	flow	flow	flow	flow	no flow	flow	flow
3-Dec	flow	flow	flow	flow	flow	flow	no flow	flow	flow
10-Dec	flow	no flow	no flow	flow	flow	flow	no flow	flow	flow
17-Dec	flow	no flow	no flow	flow	no flow	flow	no flow	flow	flow
24-Dec	flow	no flow	no flow	flow	no flow	flow	no flow	flow	flow
31-Dec	no flow	no flow	no flow	flow	no flow	flow	no flow	flow	flow
7-Jan	no flow	no flow	dry	flow	no flow	flow	no flow	no flow	flow
14-Jan	no flow	dry	dry	flow	no flow	no flow	no flow	dry	flow
21-Jan	flow	dry	dry	flow	dry	dry	no flow	dry	no flow
28-Jan	flow	flow	flow	flow	flow	flow	flow	flow	flow
4-Feb	flow	flow	flow	flow	flow	flow	flow	flow	flow
11-Feb	flow	flow	flow	flow	flow	flow	flow	flow	flow
18-Feb	flow	flow	no flow	flow	flow	flow	flow	flow	flow
25-Feb	flow	flow	no flow	flow	flow	flow	flow	flow	flow
4-Mar	flow	flow	no flow	flow	flow	flow	flow	flow	flow
11-Mar	flow	flow	flow	flow	flow	flow	flow	flow	flow
18-Mar	no flow	no flow	no flow	flow	no flow	flow	flow	flow	flow
25-Mar	no flow	no flow	flow	flow	no flow	flow	flow	flow	flow
1-Apr	no flow	no flow	flow	flow	no flow	flow	flow	flow	flow
8-Apr	no flow	no flow	flow	flow	no flow	flow	flow	flow	flow
15-Apr	no flow	no flow	flow	flow	no flow	flow	flow	flow	flow
22-Apr	no flow	no flow	flow	flow	no flow	flow	flow	flow	flow
29-Apr	flow	flow	flow	flow	flow	flow	flow	flow	flow
6-May	flow	flow	flow	flow	flow	flow	flow	flow	flow
13-May	flow	flow	flow	flow	flow	flow	flow	flow	flow
20-May	flow	flow	flow	flow	flow	flow	flow	flow	flow
27-May	flow	flow	flow	flow	flow	flow	flow	flow	flow
3-Jun	flow	flow	flow	flow	flow	flow	flow	flow	flow
10-Jun	flow	flow	flow	flow	flow	flow	flow	flow	flow
17-Jun	flow	flow	flow	flow	flow	flow	flow	flow	flow
24-Jun	flow	flow	flow	flow	flow	flow	flow	flow	flow
1-Jul	flow	flow	flow	flow	flow	flow	flow	flow	flow
8-Jul	flow	flow	flow	flow	flow	flow	flow	flow	flow
15-Jul	flow	flow	flow	flow	flow	flow	flow	flow	flow
22-Jul	flow	flow	flow	flow	flow	flow	flow	flow	flow
29-Jul	flow	flow	flow	flow	flow	flow	flow	flow	flow
5-Aug	flow	flow	flow	flow	flow	flow	flow	flow	flow
12-Aug	flow	flow	flow	flow	flow	flow	flow	flow	flow
19-Aug	flow	flow	flow	flow	flow	flow	flow	flow	flow
26-Aug	flow	flow	flow	flow	flow	flow	flow	flow	flow
2-Sep	flow	flow	flow	flow	flow	flow	flow	flow	flow
9-Sep	flow	flow	flow	flow	flow	flow	flow	flow	flow
16-Sep	flow	flow	flow	flow	flow	flow	flow	flow	flow
1-Oct	flow	flow	flow	flow	flow	flow	flow	flow	flow

Table 4: Duration, intensity and timing of dry period at intermittent sites during the 12 months before September 2011.

	INT_NF1	INT_NF2	INT_NF3	INT_NF4	INT_P1	INT_P2	INT_P3	IPER_NF1	IPER_NF2
Date when flow stopped	31-Dec-10	10-Dec-10	10-Dec-10	none	17-Dec-10	14-Jan-11	29-Oct-10	7-Jan-11	21-Jan-11
No. of weeks after 1 Jan when flow stopped	0	-3	-3	N/A	-2	2	-9	1	3
Date when all surface water gone	none	14-Jan-11	7-Jan-11	none	21-Jan-11	21-Jan-11	none	14-Jan-11	none'
Date when flow started	21 jan 2011, 29 apr 2011	28 jan, 29 apr 2011	28 jan, 25 mar 2011	N/A	28 jan, 29 apr 2011	28-Jan-11	28-Jan-11	28-Jan-11	28-Jan-11
No. of weeks after 1 Jan when flow started	3, 17	4, 17	4, 12	N/A	4,17	4	4	4	4
No. of weeks without flow	9	11	8	0	11	1	13	1	1
Remnant pools	Yes	No	No	Yes	No	No	Yes	No	Yes
No. of weeks without any surface water	0	2	3	0	1	1	0	2	0

3.2 Invertebrate richness and abundance: correlations with dryness measures

Evidence that the duration and/or intensity of stream drying affected invertebrate richness and abundance was a strong (and statistically significant) correlation between the various dryness measures and the richness/abundance metrics in intermittent streams but a weak or non-significant correlation between them in perennial streams. The strength and significance of these correlations for the different stream types are shown in Figs. 2 and 3.

Total taxon richness was more strongly correlated with the four dryness measures among the INT_NF and INT_P sites than among the IPER_NF and PER_NF sites. Among the stream types, only the INT_NF sites showed statistically significant correlations. These results indicate that stream drying affected total taxon richness more than flow reduction or other climatic variables. Total richness at the INT_P sites was less strongly correlated with dryness measures than at INT_NF sites (and correlations were not statistically significant), but was more strongly correlated than at IPER and PER sites. At the IPER sites, correlations between total richness and dryness measures were weak and not significant.

EPT* richness was more strongly correlated with dryness measures than was total taxon richness (Fig. 3). Significant correlations occurred not only at INT_NF and INT_P but also at PER_NF sites, showing that flow reduction or another climatic variable also affected EPT*

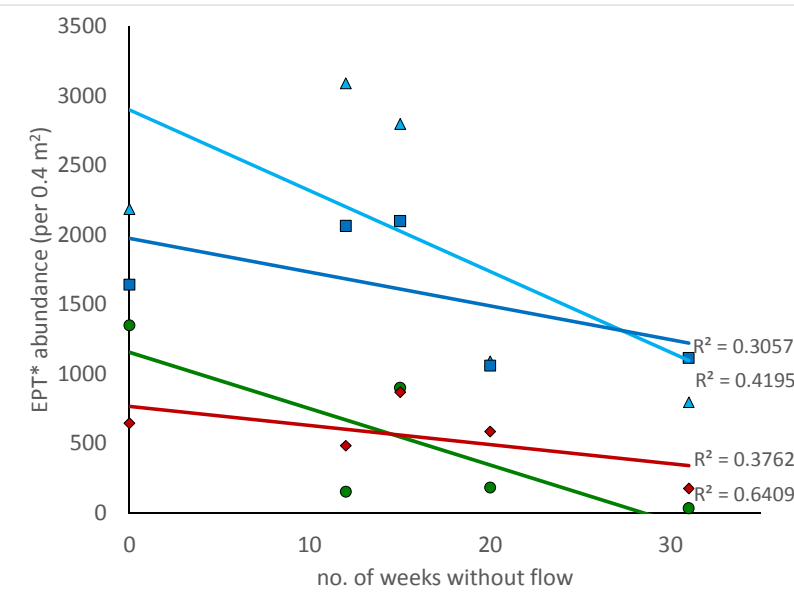
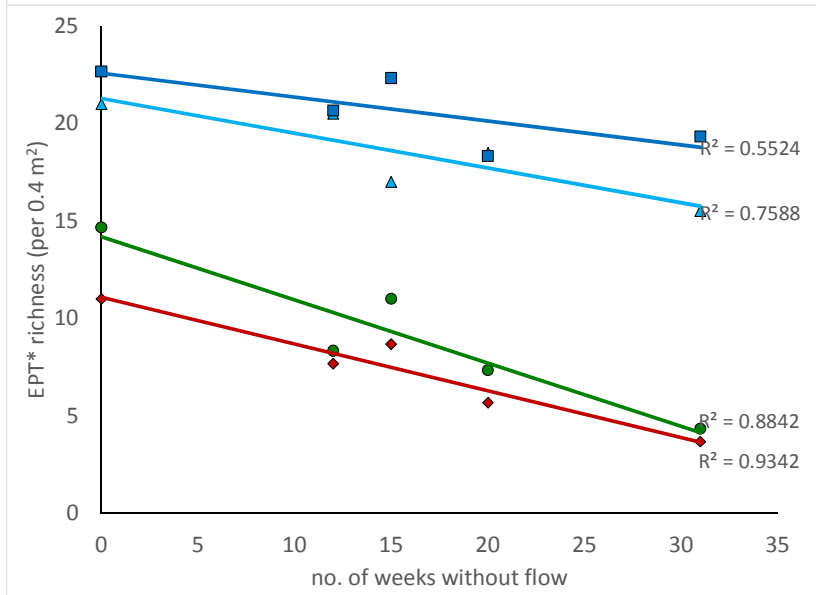
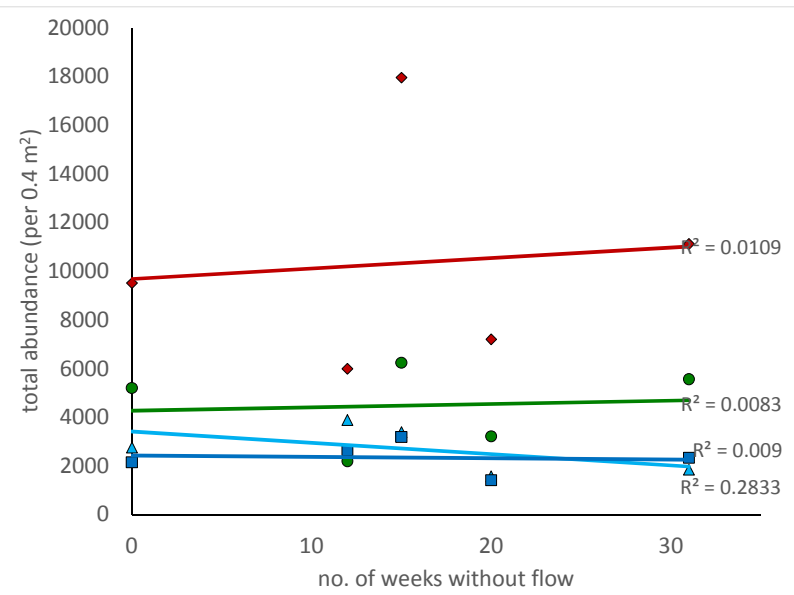
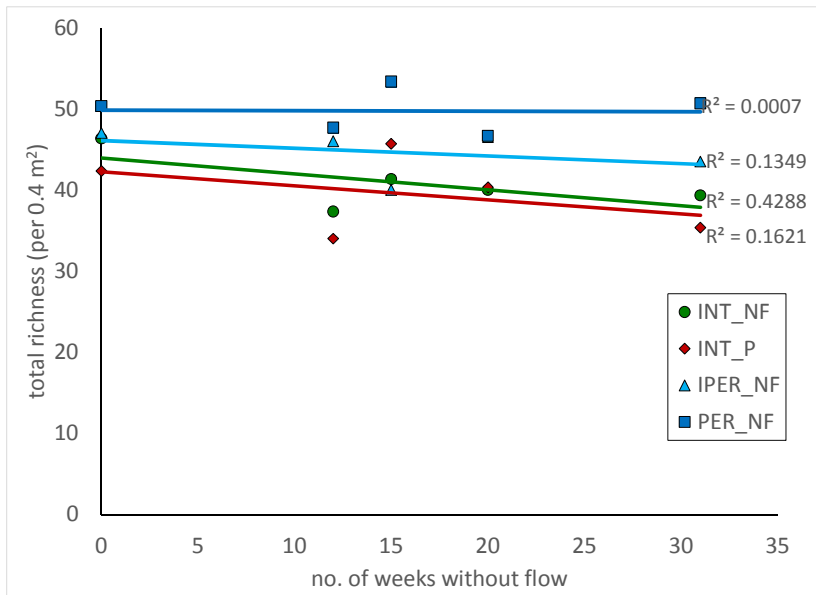
taxa. However, the correlations among the intermittent sites (INT_NF and INT_P) were stronger than those among perennial sites, indicating that EPT taxa in intermittent streams were more sensitive to dryness than were those in perennial streams. Correlations were about as strong among INT_P sites as among INT_NF sites. Correlations among the IPER sites were weaker than those at INT_NF and INT_P sites, and were non-significant.

Richness of Dipteran taxa (data not shown) showed only weak and insignificant correlations among all stream types and all dryness measures. At most INT_NF sites the correlations were positive, suggesting that Dipteran richness may actually increase with increasing dryness, but this correlation remains unconfirmed as it was relatively weak ($r=0.3$) and insignificant.

Total invertebrate abundance was not strongly correlated with any of the dryness measures. Correlations with “number of weeks with soil moisture deficit >100 mm” were slightly stronger (up to $r=-0.5$) than with other measures of dryness, and INT_NF sites had slightly stronger correlations than other stream types. However, none of the correlations were statistically significant.

In contrast, EPT* abundance was strongly and significantly correlated with dryness measures among INT_NF streams. At PER sites, correlations were weak and non-significant, indicating that EPT* abundance was much more sensitive to stream drying than to flow reduction or other climatic factors. Notably, EPT* abundance at INT_P sites was not strongly correlated with dryness measures. At IPER sites, EPT* abundance was significantly correlated with the number of weeks without flow. Correlations with other dryness measures were weaker and non-significant at IPER sites, and in all cases were weaker than at INT_NF sites.

Percent EPT* abundance was strongly (and significantly) correlated with dryness measures at INT_NF sites, and almost as strongly at IPER_NF and PER_NF sites. This suggests that flow reduction may be as important as stream drying, or that another climatic factor may have been responsible for the correlations at all sites. However, among the correlations at PER_NF sites, only the correlation with “number of weeks without flow” was significant.



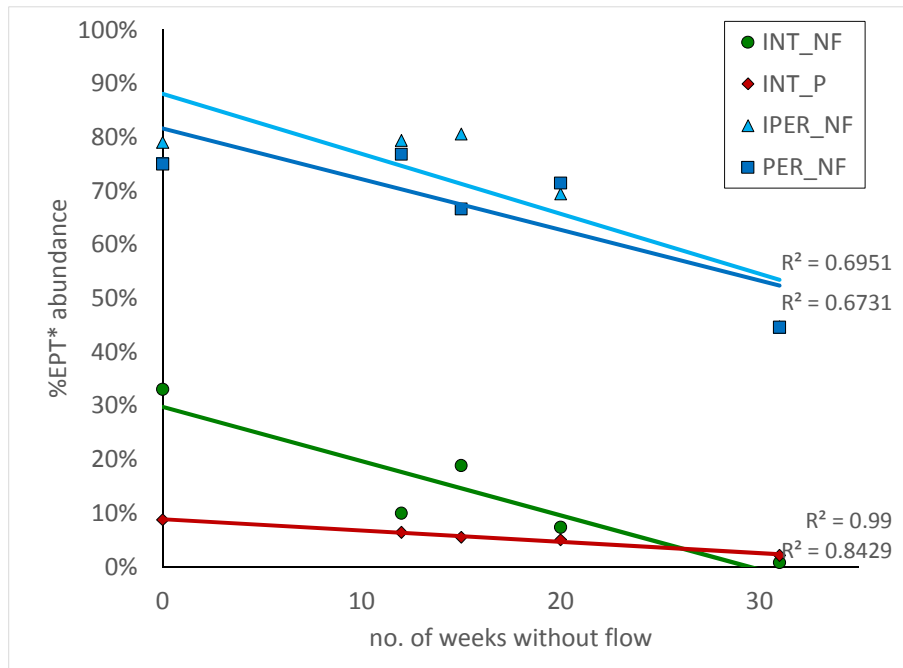
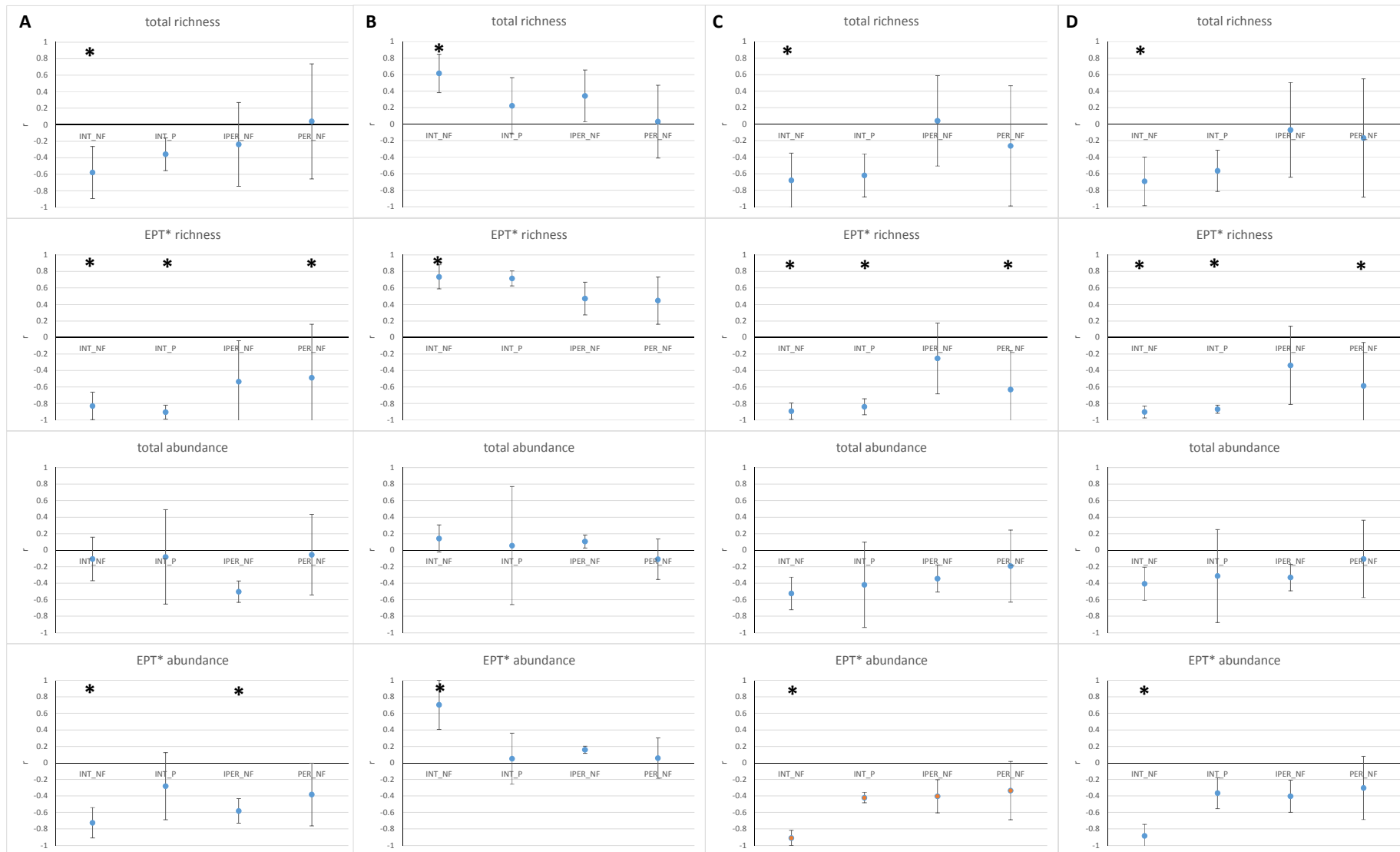


Figure 2: Correlations between macroinvertebrate metrics and duration of the no-flow period during monitoring (2008-2012).



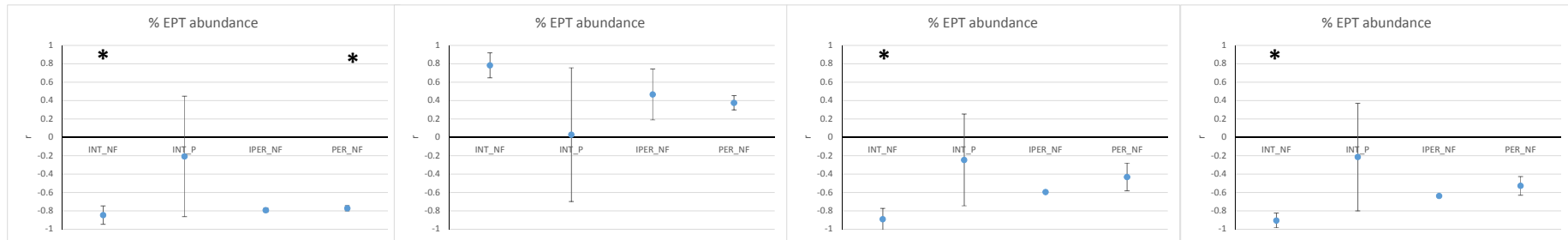


Figure 3: Correlations between macroinvertebrate metrics and the four measures of dryness. (A: number of weeks without flow; B: number of weeks with flow during the previous year; C: number of weeks after 1 January when flow began; D: number of weeks when soil moisture deficit was >100 mm) in each of the flow types (INT_NF: forested intermittent streams (n=4); INT_P: pasture intermittent streams (n=3); IPER_NF forested intermittent streams with perennial headwaters (n=2); and PER_NF: forested perennial streams(n=3)). Strength of correlations are shown in the vertical axis as Pearson correlation coefficient (r). Correlations that were statistically significant after transforming the invertebrate metrics are indicated by asterisks. Error bars are 1 standard deviation.

3.2.1 Significance of differences in correlations

The perennial sites acted as controls to compare the effects of stream drying with those of flow reduction, and to distinguish the effects of stream drying from those of other climatic factors.

In most cases, the correlations between the dryness measures and the invertebrate richness/abundance metrics at INT_NF sites were not significantly stronger than those at PER_NF sites, when tested by ANOVA (Table 5) or ANCOVA (data not shown). The only exceptions were correlations between EPT* abundance and “number of weeks with soil moisture deficit >100 mm”, and between EPT* abundance and “number of weeks since 1 Jan when flow returned.”

The lack of a significant difference in most of the correlation coefficients between INT_NF and PER_NF sites may mean that invertebrate abundance and richness are affected as much by flow reduction as by stream drying. Or it may mean that the correlations between richness/abundance metrics and dryness measures in the INT sites could be due to another climatic factor that affected the PER sites as well as the INT sites. Alternatively, the lack of significant difference in most of the correlation coefficients may be due to a lack of power in the statistical analyses. With only 5 years of data and only 3-4 sites in each flow type, the number of data points may be too few to find the differences I was looking for.

Table 5: Statistics from Analysis of Variance comparing correlation coefficients among stream types. (INT_NF (n=4), INT_P (n=3) and PER (n=3)). Degrees of freedom = 2,7 for all analyses. Significant differences (p<0.05) are shown by asterisk and bold type.

	Number of weeks without flow		Number of weeks with flow in previous year		Number of weeks after 1 Jan that flow returned		Number of weeks with soil moisture deficit >100 mm	
	F	p	F	p	F	p	F	p
total richness	1.69	0.25	2.75	0.13	1.20	0.36	0.74	0.51
EPT richness	0.99	0.42	1.89	0.22	1.05	0.40	0.78	0.49
total abundance	0.14	0.87	0.32	0.74	0.41	0.68	0.56	0.60
EPT* abundance	2.34	0.17	9.49*	0.010	11.04*	0.007	7.58*	0.018
%EPT* abundance	3.08	0.11	3.07	0.11	4.68	0.051	4.00	0.070

3.3 Effect of summer storms

Summer storms were not associated with reduced invertebrate abundance or richness as hypothesised (Fig. 4). Instead, richness and abundance appeared to be slightly higher in years with summer storms, though the difference between years with and without summer storms was not statistically significant and was not much greater at intermittent sites than at perennial sites.

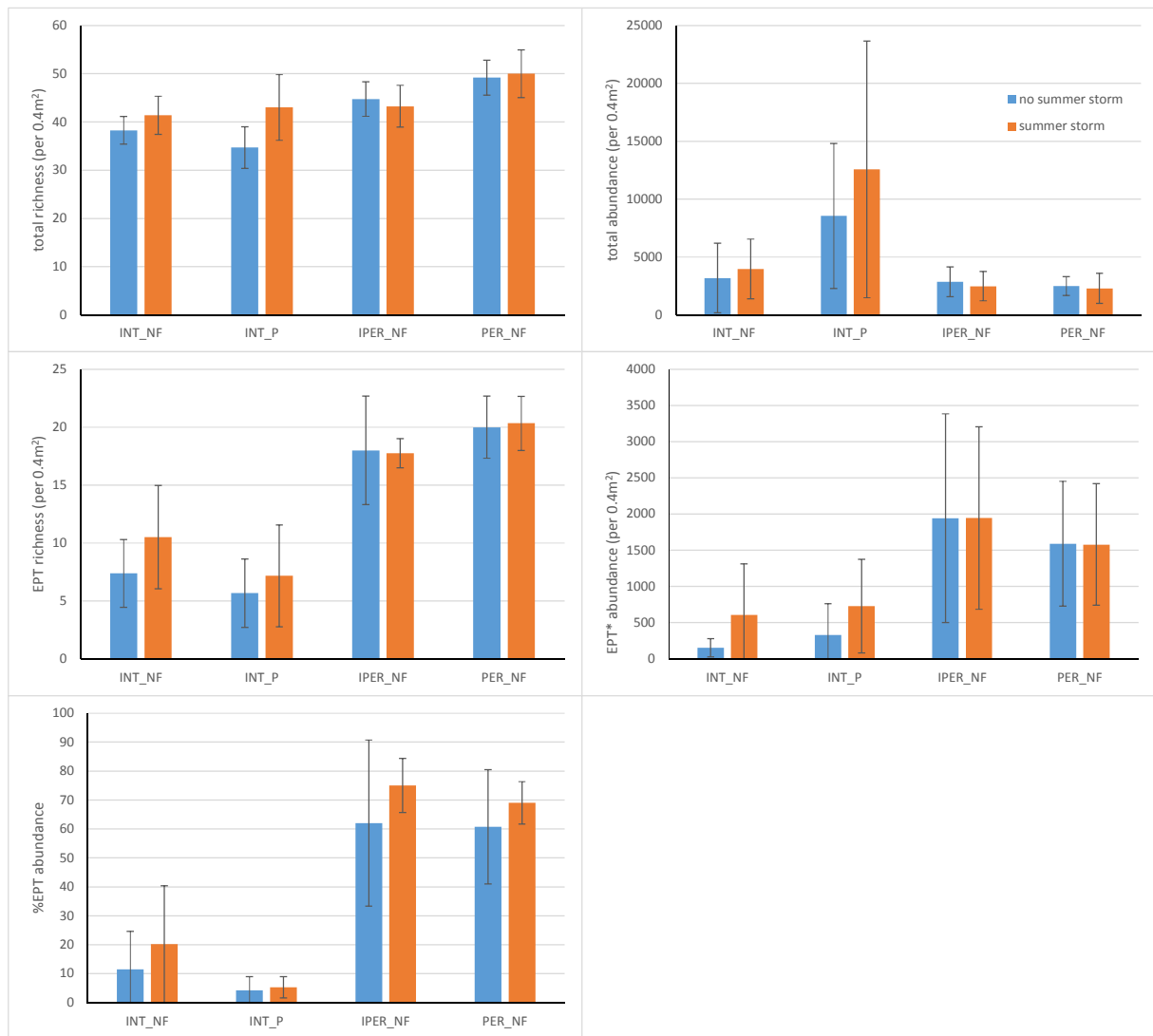


Figure 4: Effect of storms during the summer dry period on macroinvertebrate richness and abundance in intermittent and perennial streams. Error bars are ± 1 standard deviation.

3.4 Effect of remnant pools

During moderately dry years, isolated pools remained at intermittent sites. Since a number of taxa can survive in isolated pools despite their poor water quality, it was thought that years with pools remaining may show greater richness or abundance than years when pools dried completely. Total invertebrate richness and abundance were not found to be greater in years with pools remaining (Table 6). EPT* richness and abundance were higher in years with remnant pools, but because the data were highly variable, the effect of remnant pools on these metrics was not significant.

Table 6: Richness and abundance metrics. (± 1 std deviation) for years with and without pools remaining throughout the dry season (data from sites INT_NF1 and INT_NF2 only).

metric	remnant pools absent	remnant pools present
Total richness (per 0.4m ²)	39 (± 2.4)	40.4 (± 4.8)
EPT* Richness (per 0.4m ²)	6.2 (± 3.3)	9.6 (± 3.4)
Diptera Richness (per 0.4m ²)	14.4 (± 2.1)	13 (± 1.4)
Total abundance (per 0.4m ²)	6513 (± 2865)	4248 (± 2138)
EPT* abundance (per 0.4m ²)	165 (± 196)	428.8 (± 388)
%EPT* abundance	2.9 (± 3.7)	10 (± 9)

3.5 Temperature

Winter mean temperature is one of the environmental variables most likely to cause year-to-year changes in the invertebrate community in both intermittent and perennial streams.

3.5.1 Temperature patterns during the monitoring period

Daily maximum air temperatures, averaged by month, for the five monitoring years are shown in Fig. 5. Average winter (May to September) temperatures are summarised in Table 7.

The rank order of winter temperatures was 2011>2008>2010>2012>2009. Winter average temperature was not strongly correlated with any of the dryness measures (Table 8).

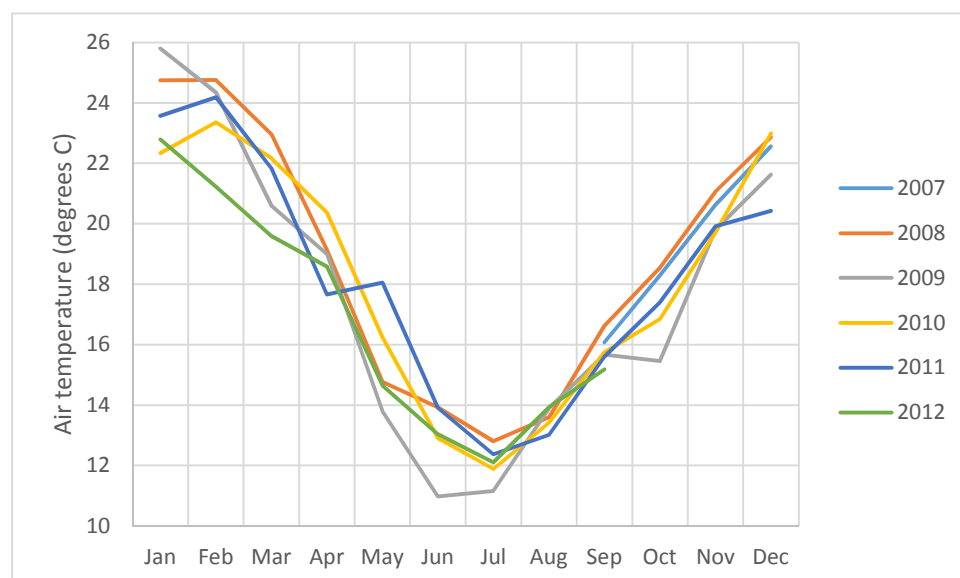


Figure 5: Monthly air temperature (average of daily maxima) at Waipawa EWS during the monitoring period.

Table 7: Average of daily temperature maxima during winter (May to September) prior to each macroinvertebrate sampling occasion. Temperatures are in °C.

Year	Winter average temperature (°C)
2008	14.3
2009	13.1
2010	14.0
2011	14.6
2012	13.8

Table 8: Correlations between winter air temperature. (May to September) and the four dryness measures over the monitoring period (2008-2012). r = Pearson correlation coefficient; p = probability of statistical significance.

Dryness measure	Winter average temperature (°C)	
	r	p
No. of weeks with flow in previous year	-0.15	0.81
No. of weeks without flow	-0.45	0.44
Weeks after 1 Jan when flow started	-0.29	0.64
No. of weeks with soil deficit >100 mm	-0.29	0.64

3.5.2 Correlations with macroinvertebrate metrics

Overall, macroinvertebrate richness and abundance increased with increasing winter temperature (Table 9). At the PER and IPER sites, total abundance and EPT* abundance were more strongly correlated with winter temperature than with any of the dryness measures. But at the INT_NF sites, the same correlations were much weaker. This suggests that winter temperature is an important control of total and EPT* abundance but at INT_NF sites other factors (e.g., summer stream drying) overwhelm the effect of winter temperature.

Table 9: Correlations between invertebrate metrics and winter. (May-September) air temperature. Values are Pearson correlation coefficients. Statistically significant correlations ($p < 0.05$) are shown with bold type and asterisk.

Invertebrate metric	Stream type	Winter average temperature (°C)
total richness	INT_NF	0.11
	INT_P	0.41
	IPER_NF	-0.22
	PER_NF	-0.01
EPT* Richness	INT_NF	0.35
	INT_P	0.45
	IPER_NF	0.08
	PER_NF	0.2
Diptera Richness	INT_NF	-0.48*
	INT_P	0.45
	IPER_NF	-0.06
	PER_NF	-0.04
Total abundance	INT_NF	0.13
	INT_P	0.19
	IPER_NF	0.64
	PER_NF	0.3
EPT* abundance	INT_NF	0.25
	INT_P	0.48
	IPER_NF	0.69*
	PER_NF	0.55
%EPT* abundance	INT_NF	0.29
	INT_P	0.33
	IPER_NF	0.59*
	PER_NF	0.66*

3.6 Flow conditions prior to sampling

The other environmental variable most likely to cause year-to-year changes in the macroinvertebrate community is the flow history prior to sampling. High flow events up to 6 weeks before sampling may reduce the richness and/or abundance of the macroinvertebrate fauna. Fig. 6 shows that in 2010, streams in the study area experienced significant rainfall in the 3-4 weeks prior to sampling that could have resulted in disturbance to the benthic macroinvertebrate community. In other years, much less rainfall occurred in the few weeks prior to sampling.

Macroinvertebrate richness and abundance values were relatively low in 2010 compared to other years, but were significantly greater than those in 2009. Conversely, the gradients in macroinvertebrate richness and abundance between 2009 and other years are not reflected in the size and number of heavy rainfall events. Therefore there appears to be no strong correlation between high flow disturbance and macroinvertebrate richness or abundance.

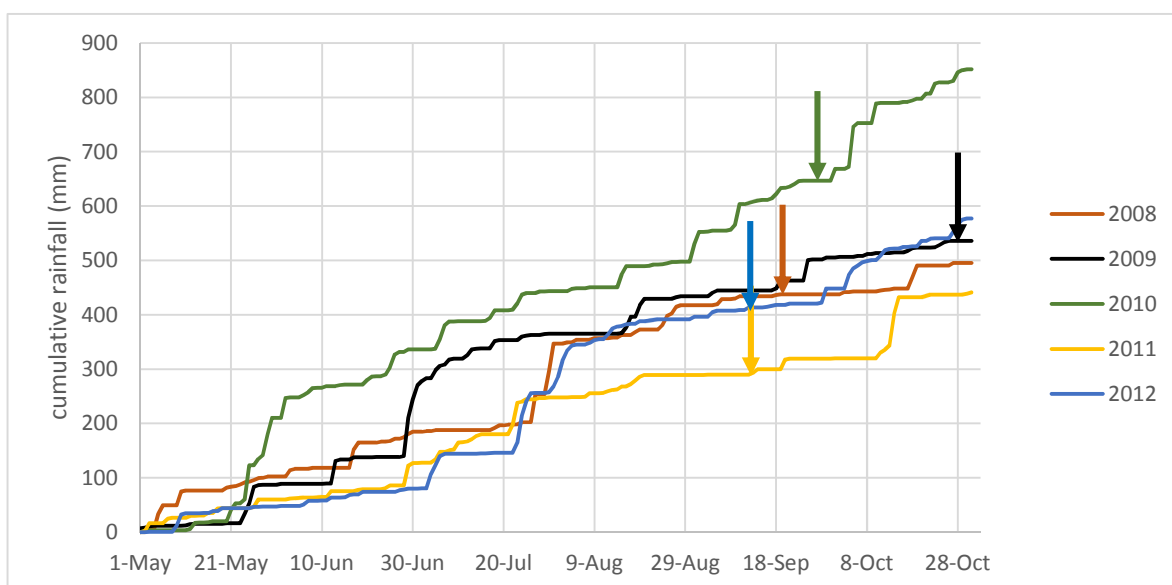


Figure 6: Cumulative rainfall from 1 May to 31 October in each of the monitoring years at Gwavas climate station (near INT_NF3). Steep rises indicate periods of heavy rainfall. Arrows indicate the date of benthic macroinvertebrate sampling.

3.7 Intermittent headwaters vs. intermittent mid-reaches

Differences in the values of invertebrate metrics between the wettest and driest years are shown in Figure 7. The difference in total taxon richness and EPT* richness at IPER sites was midway between that of INT and PER sites. However, with only two IPER sites in the study, this comparison was not statistically significant due to high variability within each stream type. EPT* abundance and %EPT* abundance were similar among IPER, INT and PER sites. Total abundance was less during dry years than wet years at IPER sites but greater at INT and PER sites.

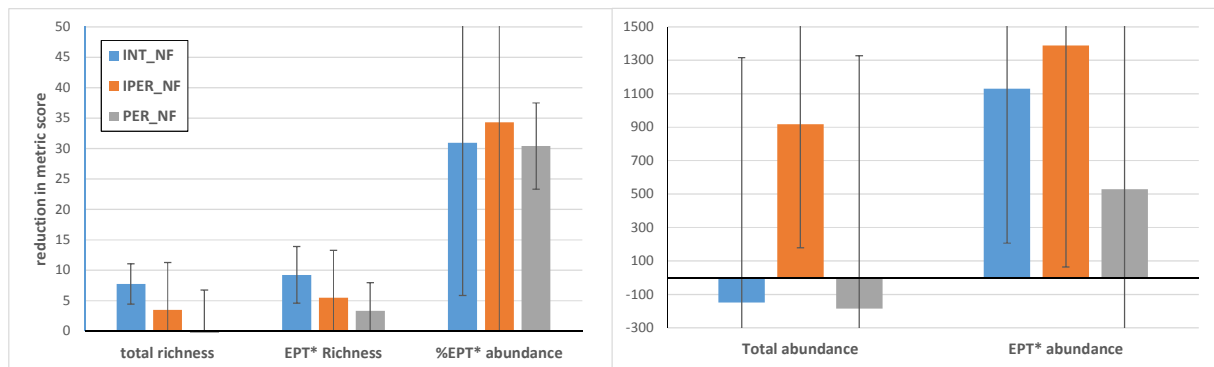


Figure 7: Differences in the values of invertebrate richness and abundance metrics between the wettest year (2012) and the driest year (2009) at native forest reaches with differing intermittency. A positive difference means a higher value in 2012 than in 2009. Intermittent headwater sites (INT_NF) are compared with intermittent mid-reaches (have perennial headwaters; IPER_NF) and perennial sites (PER_NF). Error bars are standard deviations.

3.8 Forested vs. pasture intermittent streams

The average reduction in total taxon richness, EPT* richness and EPT* abundance between driest and wettest years was slightly less in INT_P than in INT_NF sites (Fig. 8). Total abundance appeared to be greater in the driest year than the wettest year at both types of site, and the increase appeared to be greater at INT_P sites. But the increase was highly variable among sites.

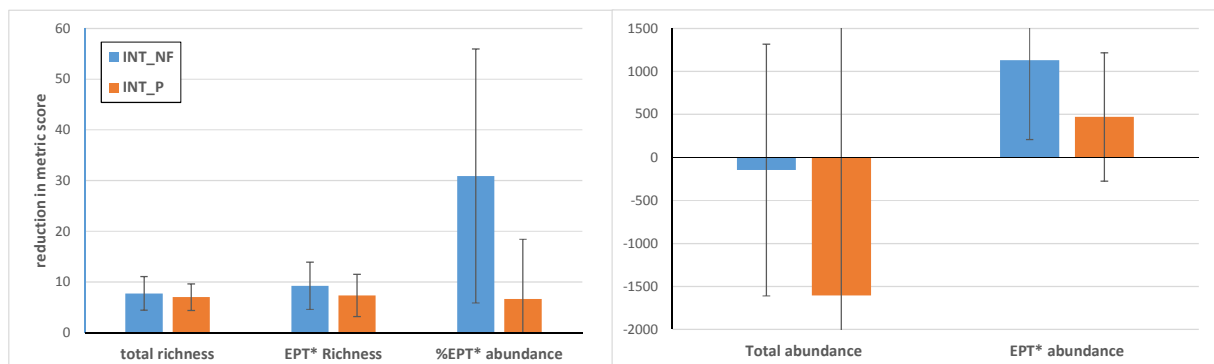


Figure 8. Differences in the values of invertebrate richness and abundance metrics between the wettest year (2012) and the driest year (2009) at intermittent stream reaches in pasture and native forest. A positive difference means a higher value in 2012 than in 2009. Forested intermittent sites (INT_NF) are compared with pasture intermittent sites (INT_P). Error bars are standard deviations.

3.9 Community composition

3.9.1 Differences among flow types and land uses

The macroinvertebrate community composition at the intermittent sites (INT_NF and INT_P) was different from that at IPER and PER sites, as indicated by the separation between these flow types on MDS axes 1 and 2 (Fig. 9). PER and IPER sites are not clearly separated from each other in this plot, indicating little difference in composition between them. Among the intermittent sites, forested sites are separated from pasture sites on MDS axis 2.

The main taxa responsible for separating the intermittent from perennial sites were greater abundances of the snail *Potamopyrgus*, the chironomid midge *Naonella*, and oligochaete worms, and lower abundances of the mayflies *Coloburiscus* and *Deleatidium*, the riffle beetle family Elmidae, the caddisflies *Pycnocentroides* and *Olinga*, and the chironomid midge *Stictocladus* in the intermittent sites. The main taxa responsible for separating the forested from pasture intermittent sites were greater abundances of the caddisfly *Polypsectropus*, the stonefly *Acroperla*, the mayfly *Zephlebia* and the chironomid Tanypodinae, and lower abundances of the chironomids *Cricotopus*, *Eukiefferiella*, *Tanytarsus* and *Corynoneura*, the caddisflies *Oxyethira* and *Hydrobiosis*, and nematode worms in the forested sites.

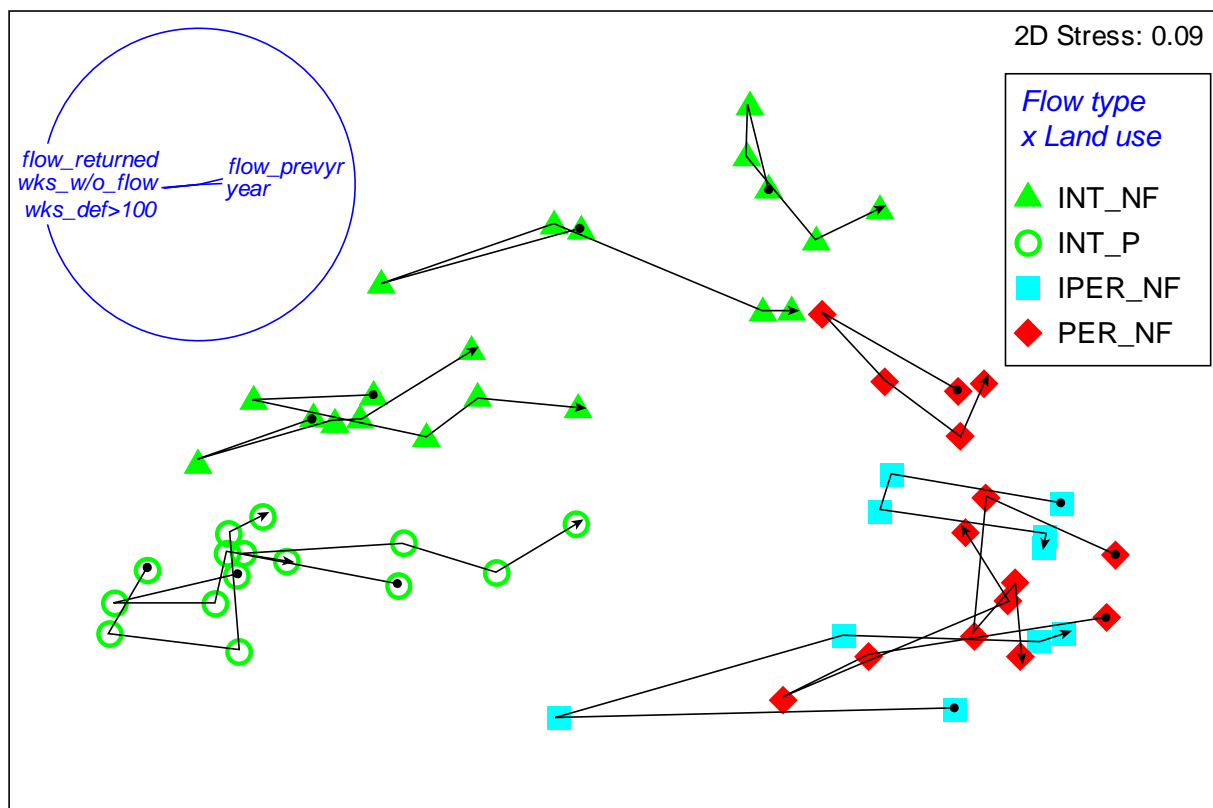


Figure 8: Multidimensional scaling (MDS) plot of macroinvertebrate community composition (as $\log(x+1)$ -transformed abundance) at the different flow and landuse types over the five-year monitoring period. Arrows show the direction of change at each monitoring site by year from 2008 to 2012. Vectors show correlations between MDS axes and dryness measures. Abbreviations are: flow_returned: number of weeks after 1 Jan that flow returned; wks_w/o_flow = number of weeks without flow; wks_def>100 = number of weeks when soil moisture deficit was >100 mm; flow_prev_yr = number of weeks with flow during the previous year; year = calendar year.

3.9.2 Changes with year

At most sites, the greatest difference in community composition occurred between 2009 (the driest year) and 2012 (the wettest year), while the composition in 2008, 2010 and 2011 was intermediate between those (Fig. 9, Table 10). This was true of all the intermittent sites (except INT_NF4), in which the separation between years was mostly correlated with MDS axis 1. Among PER and IPER sites, the differences among years were more variable, and were correlated with either axis 1 or axis 2. At most sites, the most similar two years were 2011 and 2012 (Table 10). 2011 had a relatively short but intense dry period (Tables 1, 2).

Taxa that were present during wet years but absent during dry years at two or more INT_NF sites included the mayflies *Austroclima*, *Deleatidium*, *Neozephlebia* and *Zephlebia*, the caddisflies *Helicopsyche*, *Olinga*, *Orthopsyche*, *Polyplectropus*, *Pycnocentria*, *Pycnocentrodes*, the “toe-biter” *Archichauliodes*, amphipods and Sphaeriid clams. Taxa that showed the strongest negative correlation between abundance and length of dry period included the mayflies *Neozephlebia* and *Acanthophlebia*, the stoneflies *Austroperla*, *Zelandobius* and *Acroperla*, the caddisflies *Aoteapsyche*, *Pycnocentrodes*, *Helicopsyche*, *Orthopsyche* and *Psilochorema*, the midge *Stictocladius*, amphipods, and the damselfly *Xanthocnemis*. Taxa showing the strongest positive correlation between abundance and length of dry period were springtails (Collembola), the chironomids *Tanytarsus*, *Chironomus*, Podonominae, *Cricotopus* and unidentified Orthoclaadiinae, the microcrustaceans *Daphnia*, Chydoridae and calanoid copepods, the snail *Gyraulus*, oligochaete families Enchytraeidae and Naididae, the caddisfly *Oxyethira* and mosquitoes (Culicidae). Except for *Oxyethira*, all the taxa showing positive correlations with length of dry period were either dipterans or non-insects.

Table 10: Bray-Curtis similarities among years at each of the monitoring sites.

Stream type	Similarity 2009-2012	Min similarity among all years	Max similarity among all years	Most similar 2 years
INT_NF1	51.4	51.4	84.6	2011-2012
INT_NF2	61.4	61.4	86.1	2010-2011
INT_NF3	62.2	62.2	83.3	2011-2012
INT_NF4	75.6	74.2	81.8	2011-2012
INT_P1	65.8	65.8	87.1	2011-2012
INT_P2	74.3	74.4	82.5	2008-2011 (2011-2012)
INT_P3	57.8	57.8	81.4	2008-2011 (2010-2011)
IPER_NF1	53.6	53.6	82.5	2011-2012
IPER_NF2	77.8	75	90.5	2011-2012
PER_NF1	74.5	61.7	80.6	2011-2012
PER_NF2	73.0	73	84.7	2010-2012
PER_NF3	73.9	72.3	87.6	2011-2012

3.9.3 Correlations with dryness measures

At the intermittent sites (both NF and P), year-to-year changes in community composition were strongly correlated with three dryness measures – “number of weeks without flow,” “number of weeks after 1 Jan that flow returned” and “number of weeks with soil moisture deficit >100 mm” (Figs. 9, 10). These correlations were all significant ($p < 0.05$), according to a randomisation test (Fig. 10, Table 11), and overall were stronger than the correlations at

IPER and PER sites. However, the two IPER sites and PER_NF3 were also significantly correlated with the dryness measures. This implies either that flow reduction as well as stream drying affect macroinvertebrate community composition, or that another environmental factor associated with dryness affected the invertebrate community composition at these sites.

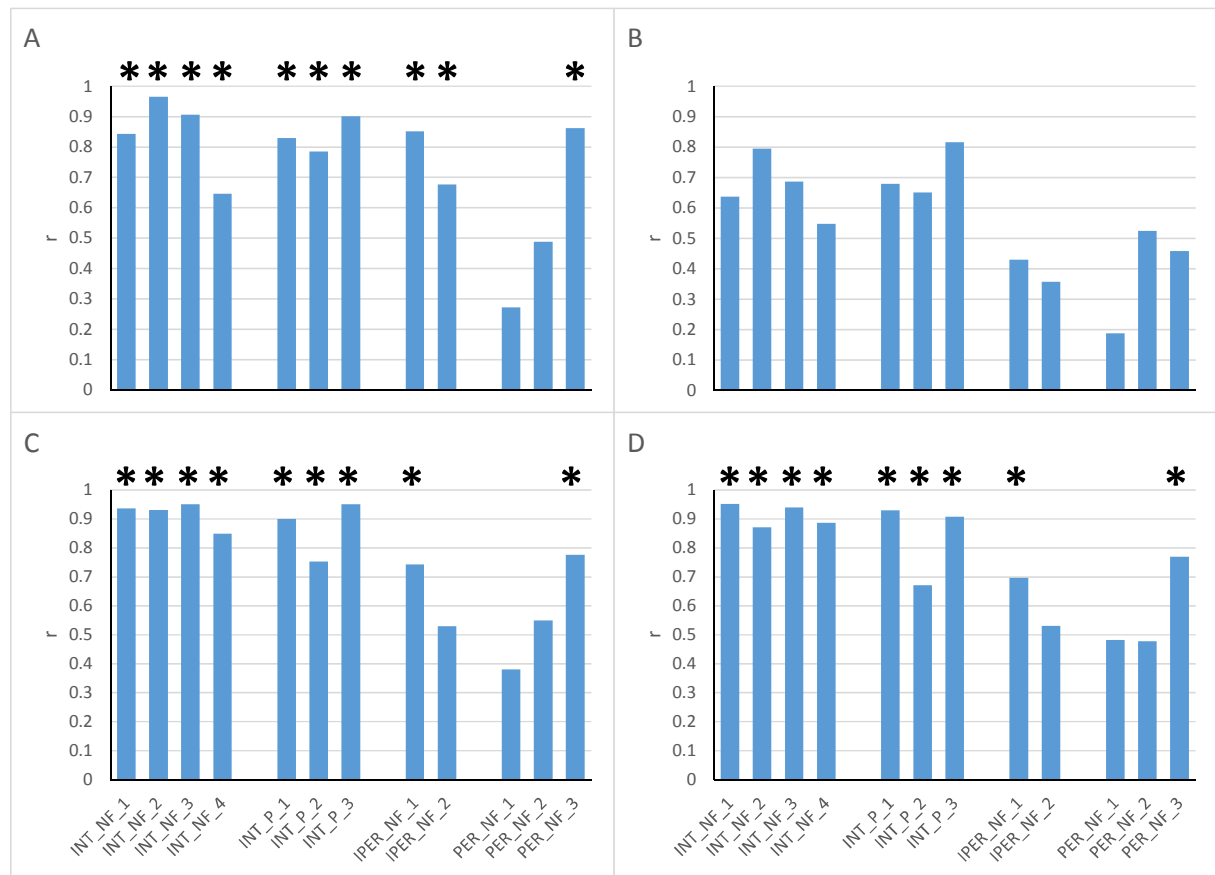


Figure 9: Correlations between MDS axis 1 and four dryness measures at each monitoring site r is the Pearson correlation coefficient. Asterisk means that the correlation was significant (at $\alpha=0.05$) in a randomisation test. Panel A: number of weeks without flow; Panel B: number of weeks with flow during the previous year; Panel C: number of weeks after 1 January when flow began; Panel D: number of weeks when soil moisture deficit was >100 mm).

Table 11: Tests for significance of correlations between MDS axis 1 and the four dryness measures for each monitoring site. Values are Z statistic, with asterisk indicating statistical significance at $\alpha=0.05$ ($Z>1.65$).

Stream type	Number of weeks without flow	Number of weeks with flow in previous year	Number of weeks after 1 Jan when flow returned	Number of weeks with soil moisture deficit >100 mm
INT_NF1	2.39*	1.21	2.62*	2.66*
INT_NF2	2.63*	1.16	2.56*	2.43*
INT_NF3	2.57*	1.2	2.68*	2.65*
INT_NF4	1.77*	1.11	2.26*	2.35*
INT_P1	2.35*	1.36	2.53*	2.6*
INT_P2	1.94*	0.76	1.88*	1.72*
INT_P3	2.43*	1.25	2.53*	2.44*
IPER_NF1	2.25*	0.54	2.02*	1.92*
IPER_NF2	1.84*	0.6	1.5	1.5
PER_NF1	0.39	0.48	0.6	0.79
PER_NF2	1.23	0.6	1.34	1.21
PER_NF3	2.43*	0.77	2.23*	2.21*

4 Discussion

4.1 Assumptions

In applying dryness data from INT_NF3 to all analyses, I assumed that rainfall patterns were reasonably similar across all sites, and that there was a constant relationship between INT_NF3 and each of the other sites in terms of dry period length. This was not completely true. For example, INT_NF2 dried 4 weeks before INT_NF3 in 2009, while in 2011 it dried in the same week as INT_NF3. However, provided the rank order among years with respect to “dryness” is the same at each site, correlations between invertebrate metrics and dryness measures should be fairly accurate. Since most sites were geographically close, it is very likely that the rank order of years was the same at each site. INT_NF1 and PER_NF1 were the only sites in a different catchment that could have experienced slightly different weather conditions.

I also assumed that a short period of flow in the middle of the dry period will not benefit the invertebrate community, therefore such periods were counted as having no flow.

4.2 Responses of intermittent stream invertebrates to duration and intensity of stream drying

The first aim was to determine whether the length, intensity or timing of the dry period affects the abundance, diversity and community composition of benthic macroinvertebrates in intermittent headwater streams. Overall, the invertebrate community of intermittent streams showed a clear difference between the driest and wettest years (2009 and 2012 respectively). This was seen as a reduction in taxon richness, EPT* richness, EPT* abundance, %EPT* abundance and a shift in community composition at all intermittent sites except INT_P1. Total invertebrate abundance was not well correlated with any of the dryness measures, though five of the seven intermittent sites showed greater total abundance in 2012 than in 2009.

Most of the invertebrate metrics showed a rank order of 2012>2011>2008>2010>2009, i.e., their rank order followed the rank order of dryness as measured by “number of weeks after 1 Jan that flow began” and “number of weeks with soil moisture deficit >100 mm”. Therefore, the data suggest that either the absence of flowing water during the autumn, or the length of time with extremely dry conditions, may be more important than the length of the no-flow period. However, the importance of the former must remain uncertain, as it is not known exactly when flow returned at all intermittent sites during all years. In addition, while soil moisture deficit may relate to moisture conditions in dry stream bed sediments, it is a measure of surface conditions, and its relationship to presence/absence of flow is not known. Therefore, although it appeared to “work” in this study as a measure combining the length and intensity of drought, it may not perform well at other places or times.

In this data set, peak intensity of drought did not seem to be the strongest influence on the invertebrate community. 2011 had a relatively short but intense dry period (it was the only year apart from 2009 when surface water disappeared completely at INT_NF1). However, 2011 was the most similar of all years to the wettest year (2012) in terms of invertebrate richness, abundance and community composition. The presence of remnant pools during the dry season (another indicator of drought intensity) was not found to significantly affect invertebrate richness or abundance, though the data suggested that EPT* richness and

abundance may be higher during years with remnant pools. Summer storms may serve to reduce the intensity of drought by increasing sediment moisture content. As with presence of remnant pools, no significant difference in invertebrate richness or abundance was found between years with and without summer storms, though EPT* richness and abundance were higher in years when summer storms occurred.

Summer storms did not seem to represent a false start to the flow season, causing catastrophic mortality of larvae that hatched then perished during the subsequent dry period.

“Number of weeks with flow in the previous year” was analysed with respect to invertebrate metrics to test whether there are legacy effects in intermittent streams, i.e., whether a longer flow period leads to larger invertebrate populations that result in greater recruitment in the following year. The data gave little evidence of this effect – correlations with this measure were almost always the weakest among the four dryness measures.

4.3 Stream drying vs. flow reduction

It was expected that the effects of dry vs. wet years would be much greater for benthic invertebrate communities experiencing stream drying (intermittent sites) than those experiencing only a reduction in flow (perennial sites). This appeared to be true in terms of total richness, EPT* richness, EPT* abundance and community composition, for which the difference between the driest and wettest years was greater at intermittent than at perennial sites. However, the invertebrate communities in perennial streams clearly showed some of the same relationships with dryness as those in intermittent streams, suggesting that flow reduction has the same kinds of effects on benthic invertebrates as stream drying, though to a lesser degree.

4.4 Response of intermittent mid-reaches vs. intermittent headwaters

The second aim was to determine whether intermittent streams with perennial headwaters are affected by wet/dry period length as greatly as intermittent headwater streams. It was expected that because they receive invertebrate drift from upstream, intermittent streams with perennial headwaters (IPER sites) would be less affected by the length or intensity of the dry period than would intermittent headwater streams (those without perennial headwaters; INT sites). The data did suggest that drift from upstream perennial reaches plays a significant role in structuring the invertebrate community at IPER sites, as the community composition of these sites showed a strong resemblance to the PER sites and a distinct difference from INT sites. Some of the invertebrate metrics (total taxon richness and EPT* richness) showed the expected response to dry period length, i.e., the decline in richness at IPER sites was midway between that of INT and PER sites. However, with only two IPER sites in the study, this comparison was not statistically significant due to high variability within each stream type. The invertebrate abundance and composition metrics (total, EPT* and %EPT* abundance) did not show the expected response, but again, results were highly variable. Therefore we may tentatively conclude that in dry years, intermittent sites with perennial headwaters show loss of fewer taxa than intermittent headwater sites, and show no decline in total or EPT* abundance. However, further research with a greater number of sites and years would be needed to be confident of this.

4.5 Response of pasture vs. forested intermittent streams

The third aim was to determine whether the benthic invertebrate community in pasture intermittent streams is affected by dry period length as greatly as that of forested intermittent streams. The answer appears to be no – the average reduction in total taxon richness, EPT* richness and EPT* abundance between driest and wettest years was slightly less in INT_P than in INT_NF sites. Taxa inhabiting pasture streams experience several forms of environmental stress, e.g., siltation, elevated temperatures, reduced oxygen (especially during the pool phase) besides stream drying. The number of taxa (and the number of EPT* taxa) inhabiting pasture streams was slightly less than that inhabiting forested streams, whereas the average EPT* abundance was very similar at INT_P and INT_NF sites. Therefore, it appears that the fewer taxa able to survive the stresses associated with pasture are also more tolerant of additional stressors (such as longer or more intense stream drying) than those inhabiting the more benign forested streams.

4.6 Implications for climate change and flow abstractions

The results described here suggest that the longer and more intense dry periods predicted to accompany global climate change are likely to cause significant changes to the benthic macroinvertebrate communities of intermittent streams. In particular, reductions in the richness and abundance of EPT taxa are likely. However, the invertebrate community response to climate change may be greater than that recorded here for two reasons. First, increases in the length and intensity of drought with climate change are likely to be greater than the differences between dry and wet years during this monitoring period. Second, the effects on invertebrate populations of year-to-year changes in weather patterns may be less than those of long-term changes to stream drying/wetting regimes associated with climate change. During individual dry years, a few individuals of drought-sensitive taxa may be able to persist in isolated damp refuges and recolonize streams once conditions become favourable. Repeated droughts, however, may eliminate all individuals in a population, preventing recolonisation.

While preventing or mitigating climate change is beyond the ability of a regional council, some actions may be taken to reduce the impact of climate change on stream invertebrate communities. Riparian shading has been shown to reduce mortality of over-summering invertebrates in dry streambed sediments (Storey and Quinn 2013), therefore riparian planting is one potential tool to mitigate climate change effects. The conclusion of this report that pasture intermittent streams are less affected by dry season length than forested intermittent streams does not imply that riparian forest has no value, since the forested streams had richer and more abundant invertebrate communities than the pasture streams.

The results described here also have implications for flow management of intermittent streams. Perennial streams typically are protected from over-abstraction of water by minimum flow requirements set on the basis of scientific models. Intermittent streams also are subject to requests for water abstraction, but councils have little scientific data on which to base limits to water abstraction. The results presented here indicate that abstractions that increase the length of the dry period of intermittent streams by several weeks would have an impact on the benthic invertebrate fauna.

4.7 Recommendations for further research

In Hawke's Bay the summer of 2012-13 was estimated by various sources as the strongest drought in nearly 70 years. Flow did not begin in the study streams until July 2013, making it a longer dry period than any of those from 2008-2012. The conclusions of this study would be greatly strengthened by adding another year of data at the extreme end of the dryness gradient.

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