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THE ROLE OF DISTURBANCE IN COMMUNITY DYNAMICS AND STRUCTURING OF TROPICAL RAINFOREST STREAM COMMUNITIES

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in October 1998

for the degree of Doctor of Philosophy
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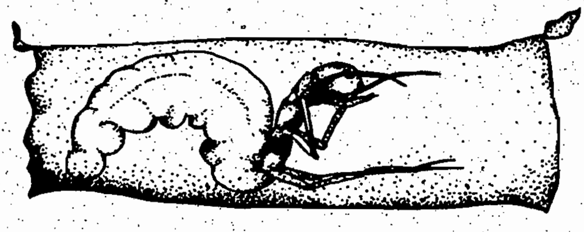
This is dedicated to Arthur and Carol – the most wonderful, supportive and loving parents



ABSTRACT

This study examined the role of disturbance in the community dynamics of benthic macroinvertebrates in tropical rainforest streams, incorporating sites in the Australian Wet Tropics and Papua New Guinea. The focus was on physical disturbance through the movement of the substratum, as this is likely to be the most ecologically relevant measure of disturbance to benthic stream fauna. The approach combined long-term sampling following severe, natural floods, with smaller-scale experimental manipulations, permitting faunal response to disturbance to be examined at three spatial scales: stream-wide, stream section and individual stone.

Streams within the Australian Wet Tropics are characterised by strongly seasonal patterns of stream flow, with high and variable flows during the summer wet season and low and relatively stable flows during the dry season. Continuous, long-term sampling of macroinvertebrate stone fauna within the major habitats, riffles and pools, revealed that the influence of disturbance on the temporal variation in benthic community structure is dependent on the magnitude of the flood and differs between habitats. When floods are severe, resulting in substantial alteration to the habitat, seasonal cycles in community structure are most distinct, with a relatively distinct, highly resilient fauna (i.e. able to recover rapidly following disturbance) present during the wet season shifting to less resilient assemblages during the dry season. During years where the magnitude of disturbance by floods is reduced, the temporal shift in assemblage dominance is less marked, and highly fluctuating communities (e.g. species turnover – indicated by multivariate ordinations) suggest increased prominence of biotic interactions as habitats contract during the dry season. The fauna on stones was remarkably resistant, particularly in pool habitats, and

recovered rapidly (within 21 days in the pool and 45 days in the riffle) to pre-flood densities and richness following substratum-moving floods. The relatively high resistance and resilience in pool habitats compared to riffles may not only reflect intrinsic characteristics of the assemblages (which were relatively distinct), but also the reduced impact of floods in pool habitats, which tended to accumulate fauna. This suggests an important refugial role of pools, and the subsequent redistribution from these areas is very likely an essential part of the recovery process following flood disturbance in these streams.

As the spatial scale of disturbance is reduced to the stream section and individual stone, faunal recovery becomes more rapid (2 days – 24 hrs), reflecting the proximity of colonists to the disturbed patch, and small-scale rather than large-scale recolonisation processes are likely to increase in importance (e.g. benthic movements rather than drift). The composition and recolonisation characteristics of the fauna are influenced by the position of the disturbed patch within the stream. Along a longitudinal gradient, incorporating headwater, mid-reach and lower-reach sites, faunal resistance and resilience was highest at the lower-reach site, corresponding to longitudinal differences in the natural flood regime and stability characteristics of the surrounding substratum.

The temporal frequency of disturbance influenced faunal responses as indicated by experiments which directly manipulated the frequency of substratum disturbance, and by comparisons between streams with different historical patterns of natural disturbance. Increasing disturbance frequency *per se* – the number of times individual stones are tumbled – increased the susceptibility of macroinvertebrates to disturbance. The influence of different historical frequencies of disturbance was examined by comparing faunal response to experimental disturbance in aseasonal streams in Papua New Guinea, characterised by a high annual frequency of natural flood disturbance, with a seasonal stream in the Wet Tropics which had a low annual frequency of disturbance. Sites in PNG, with a short inter-flood period (i.e. frequently disturbed), supported a fauna that was much more resistant and resilient to disturbance, compared with the streams in the Wet Tropics. The historical pattern of disturbance is likely to provide a strong selective force for the fauna inhabiting the frequently disturbed PNG streams, promoting characteristics such as high mobility and species turnover, which are likely to enhance persistence in these environments.

Disturbance is likely to play an important role in the maintenance of the very high benthic diversities observed in streams of the Australian Wet Tropics. The results of this study show that at all spatial scales, disturbance tends to increase the spatial variability of individuals on stones, which may create opportunities for the coexistence of rarer species. The combination of abiotic disturbance during the wet season and increasing biotic interactions during the dry season may provide the basis for the particularly high diversity in these streams.

In summary, disturbance involving the physical movement of the substratum is clearly a major factor influencing the dynamics of benthic communities in tropical streams. However, the results of this study indicate that macroinvertebrate response to disturbance is strongly influenced by the characteristics of the disturbance, such as magnitude and frequency and also by the intrinsic nature of the habitat.

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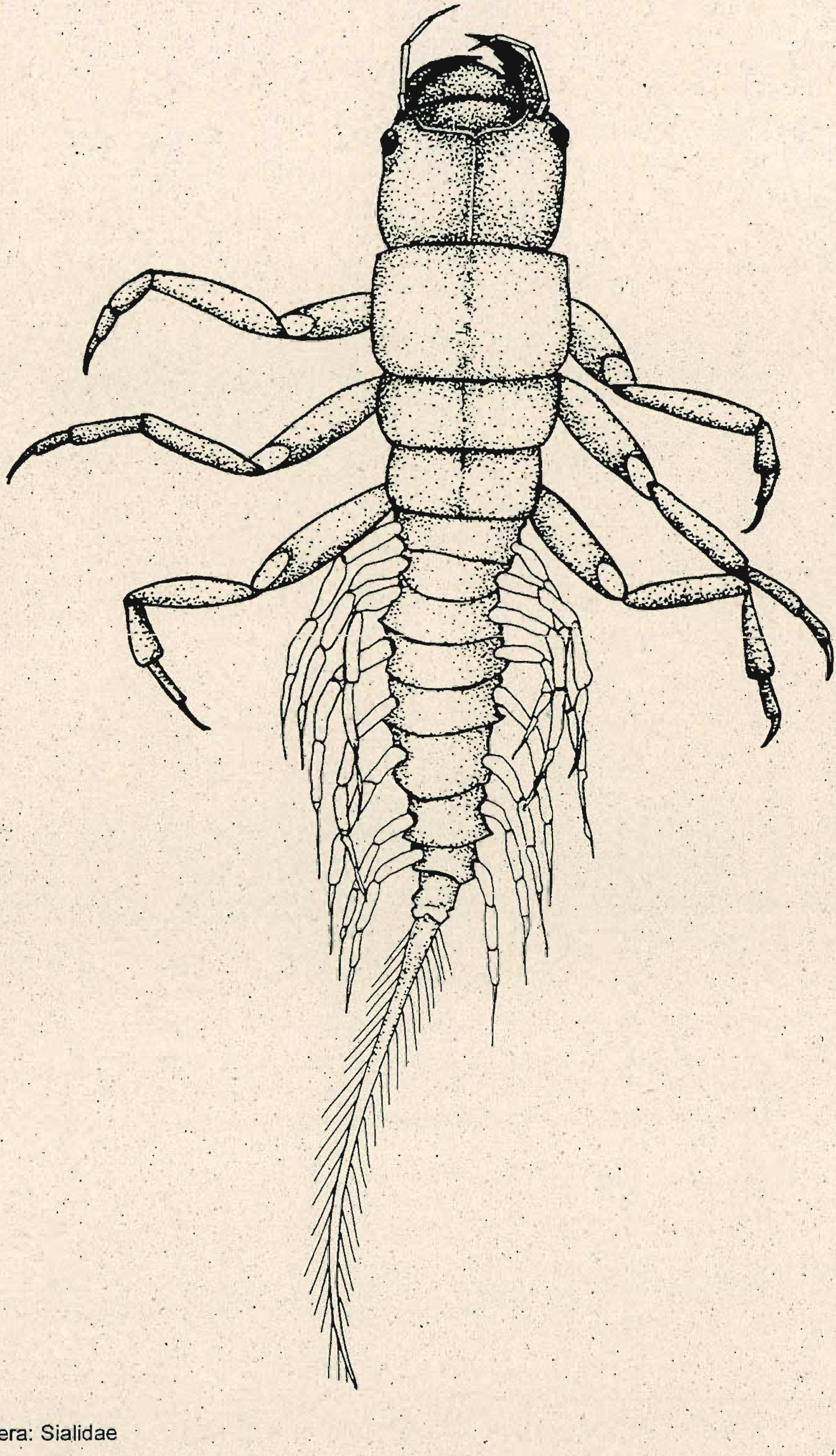


Megaloptera: Sialidae

Artist: Andi Cairns

CHAPTER 1: INTRODUCTION

1.1 Introduction

This study investigates the role of disturbance in tropical rainforest stream communities. Information on ecological processes and long-term community dynamics within tropical stream ecosystems is lacking, with the majority of research both in Australia and overseas conducted in temperate regions. As such, the incorporation of disturbance into theoretical concepts of stream ecosystem structure and functioning derives its empirical basis almost exclusively from temperate-zone studies. As the number of studies within the tropics increases (e.g. reviews by Dudgeon 1992, Pearson 1994) it is clear that generalisations based on work in temperate regions are not always directly applicable to the tropics, and that more information from the tropics will improve general paradigms of stream ecology.

This chapter (Chapter 1) briefly reviews what is known about disturbance and its role in communities, particularly in streams, with the major focus being the effects of physical disturbance associated with extreme (high) flows, and outlining major differences between temperate and tropical systems. Following this review, an outline of this study is given, detailing its aims and how they are addressed by this thesis.

1.2 Community organisation: pattern, process and scale

A major goal of community ecology is to explain the processes that generate or maintain the spatial and temporal patterns observed in natural communities (Table 1.1). Studies of communities, defined here as all species at all trophic levels at a particular location in a given habitat (Menge 1982), provide valuable insights into the structure and function of ecological systems. Patterns are causally connected with processes (Fisher 1994) and occur at characteristic spatial and temporal scales.

Table 1.1 Examples of ecological patterns and processes.

Patterns	Processes
Community structure	Disturbance
Species diversity	Competition
Distribution	Predation
Abundance	Colonisation/recruitment
Habitat patchiness	Nutrient cycling
Biomass/production	Habitat selection
Life history events	Growth

In 1978 Connell published results of his research on the role of disturbance in structuring communities which reset the thinking of many ecologists. Prior to 1978, theoretical community ecology was dominated by equilibrial competition theory and its notions of predictable structuring through biotic interactions, resource limitation and feedback loops (although Hutchinson (1961) presented an early view of a non-equilibrial community). Equilibrium models presume that biotic interactions are the key determinants of community structure (Table 1.2). The community is the direct result of the competitive, mutualistic, and predator-prey relationships among and between species. High species diversity was often explained using spatial heterogeneity and predator-mediated coexistence.

Traditional theory treated disturbances as small perturbations in the neighbourhood of local equilibria (e.g. Levins 1975). However, the realisation that natural communities are dynamic in nature and are impacted to varying degrees by a suite of disturbing factors operating across a wide range of temporal and spatial scales (Sousa 1984) has promoted the need to de-emphasise the equilibrial viewpoint. Equilibrial conditions should be considered as a special case (Palmer and Poff 1997) or as a framework whose usefulness depends critically on the scale of study (DeAngelis and Waterhouse 1987). Emphasis on a non-equilibrium view of communities has increased the focus on stochastic processes, habitat heterogeneity and patchiness (Diamond and Case 1986, Petraitis *et al.* 1989, Kolasa and Rollo 1991, Palmer and Poff 1997) and the degree to which they influence ecological patterns and processes. This has promoted the development of an alternative conceptual framework and methods for studying disturbed, dynamic communities and the refinement of non-equilibrium theory.

Table 1.2 Proposed properties of equilibrial and non-equilibrial communities (after Wiens 1984).

Equilibrial communities	Non-equilibrial communities
Biotic processes regulate populations	Abiotic processes regulate populations
Species highly interdependent	Species relatively independent
Temporally predictable patterns of community development	Temporally unpredictable patterns of community development
High persistence	Low persistence
Density dependent populations	Density independent populations
High resistance to environmental change	Low resistance to environmental change
High resilience following disturbance	Low resilience following disturbance

In his seminal study, Connell (1978) investigated the ability of equilibrial and non-equilibrial theory to explain the high species diversity observed in tropical rainforests and coral reefs. He examined three equilibrial hypotheses, invoking niche partitioning, circular networks (Gilpin 1975), and compensatory mortality, as well as three non-equilibrial hypotheses invoking intermediate levels of disturbance, the size of the regional pool of species and local densities (equal chance hypothesis), or gradual environmental changes. He concluded that frequent disturbances or more gradual climatic changes “maintain local diversity by preventing the elimination of inferior competitors” and that most local assemblages are kept far from equilibrial conditions by these changes.

The ‘intermediate disturbance hypothesis’ proposed by Connell (1978), as a non-equilibrial explanation for high species diversity, presumes a competitive hierarchy of species. In the absence of disturbance, superior competitors (assumed to be more efficient occupiers of space) will eliminate inferior ones, reducing overall species richness. If the magnitude and frequency of disturbances are too high, the resident competitors will be eliminated and colonising species (inferior competitors) will dominate the system, with a reduction in overall richness. Under a disturbance regime that is intermediate in frequency and intensity, resident species will persist in the system along with a continuing supply of colonising species that exploit the disturbed areas.

Similarly, disturbance was incorporated into Huston's (1979) 'dynamic equilibrium' model of community structure where diversity is determined by the influence of the environment on the net outcome of competitive interactions. Community structure is regarded as a trade-off between growth rates, rates of competitive exclusion, and frequency of population reductions. If the recurrence interval of disturbance was shorter than the time necessary for competitive exclusion, poorer competitors would be able to persist in the system. This may lead to increased species richness, unless the frequency or severity of disturbances was sufficient to eliminate species with long life cycles. As in the intermediate disturbance hypothesis, species diversity may be viewed as a nonlinear function of the frequency of disturbance.

The role of disturbance in community ecology is now regarded as the result of a combination of equilibrial and non-equilibrial dynamics with the classification of whole systems as either deterministic or stochastic as an oversimplification (Grossman 1982, Wiens 1984, Dodds and Henebry 1996). Natural communities should be viewed as intrinsically variable, composed of mosaics of species assemblages, some adapted to predictable equilibrial conditions and others to non-equilibrial conditions. Importantly, the continuum of biological and physical process influencing community dynamics occurs at characteristic spatial and temporal scales (Schneider 1994). The cause-effect relationship between process and pattern can be complex, given that many ecological patterns are the result of multiple causation. Problems often arise when attempting to infer process from pattern as causation may be indirect, have undetermined flow-on effects, or may propagate effects across scales (Loehle 1991, Fisher 1994). The success of ecological studies will therefore depend not only on the development and use of appropriate, spatially and temporally explicit models that incorporate heterogeneity (Palmer and Poff 1997), but on the careful selection of biologically meaningful parameters.

1.3 Community organisation in stream environments

It is generally accepted that environmental variability and disturbance are an integral part of stream ecosystems, maintaining communities in a non-equilibrial state (Reice 1994, Lake 1995). Disturbance is most commonly regarded as an externally imposed event (i.e. allogenic) (e.g. Pickett *et al.* 1989, Lake 1990) although some authors include biotic processes generated within the ecosystem (i.e. autogenic) in their classification (e.g. Fisher and Grimm 1991) (Table 1.3). The present study follows the traditional view that disturbance *sensu stricto* applies to external abiotic processes and regards biotic factors such as competition and predation separately. The term disturbance, as used in this study, is therefore defined as an externally imposed, discrete event that disrupts population, community or ecosystem structure, through the removal of organisms, changes in resources, and alterations to the physical environment (Sousa 1984, Resh *et al.* 1988, Hildrew and Giller 1994).

Table 1.3 Examples of autogenic and allogenic disturbance within stream ecosystems.

Types of disturbance	Reference
Autogenic:	
Algal grazing	Poff and Nelson-Baker (1997)
Predation	Crowl *et al.* (1997)
Herbivorous fishes	Flecker (1997)
Omnivorous fishes	Pringle and Hamazaki (1997)
Allogenic:	
Drying	Stanley *et al.* (1994)
Flood	Grimm and Fisher (1989), Townsend *et al.* (1997a, 1997b)
Catchment logging	Golladay *et al.* (1992)
Volcanic eruption	Rushforth *et al.* (1986), Turner *et al.* (1997)
Fire	Minshall *et al.* (1989), Turner *et al.* (1997)
Hurricanes	Turner *et al.* (1997)

In some streams, equilibrial processes (strong biotic interactions) are likely to occur, especially where the interval between disturbance is long or where relatively constant environmental conditions prevail, such as in some spring-fed streams (Minshall and Petersen

1985, Minshall *et al.* 1985). Deterministic control of community structure, typified by strongly interactive, specialist species limited by stable resources, can therefore be regarded as a function of habitat stability (e.g. Death and Winterbourn 1994). In some cases competition for space among less mobile (sedentary) species promotes conditions for strong interspecific interactions (Hildrew and Townsend 1987, Townsend 1989, Dudley *et al.* 1990). Coexistence between such sedentary species often relies on small-scale disturbances that open up space for less competitive species (Hemphill 1991).

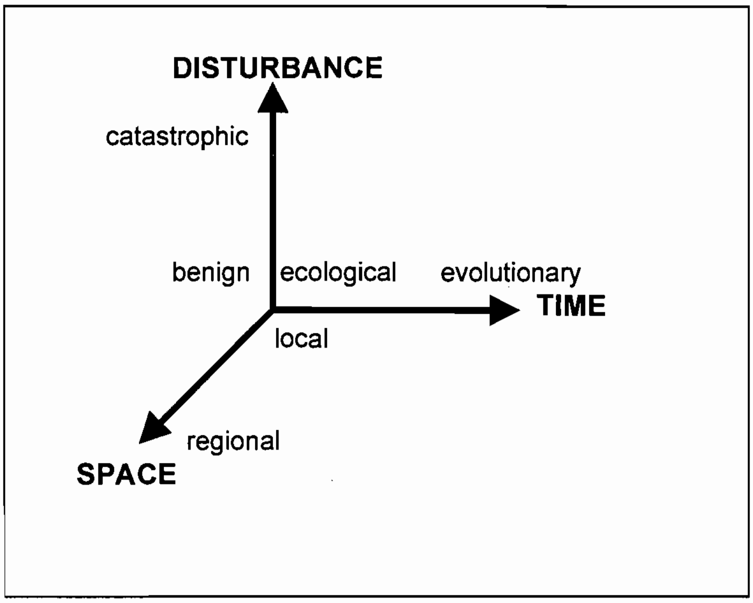
Physical disturbance or fluctuating environments are believed to weaken the strength of biotic interactions (Lancaster 1996) and should be characterised by an assemblage of weakly interactive opportunists with generalised strategies for exploiting frequently changing resources (Poff and Allan 1995). In streams, space is rarely limiting for most species as the majority are highly mobile and utilise a complex set of resources (Downes 1990), and species coexistence may be mediated through the temporal and spatial heterogeneity in resource states (Kohler 1992) and the physical habitat generated by disturbance.

Fisher and Grimm (1991) propose a conceptual model describing the temporal shift in control of ecosystem functioning in streams influenced by both flooding and drying, which may have applicability to many systems. This model may be particularly relevant in Australian streams which are characterised by high variability in flow (McMahon 1982), and many of which flow intermittently (Lake 1995). It is suggested that overall control of the ecosystem is dependent on the regime of disturbance (either flood or drought). If floods are frequent, variance in the system state will be best explained by time elapsed since disturbance. If floods are rare, biotic interactions will predominate (as the organism-to-resource ratio rises), and resource-related variables may be the best predictor of community control. Stream communities may therefore undergo complex temporal shifts between abiotic and biotic controls, generated autogenically or allogenically (e.g. Peterson and Grimm 1992), reflecting the degree of environmental variability. Therefore, in highly seasonal streams (e.g. those in most of tropical Australia, including the majority of sites in the present study), abiotic controls would be expected to predominate during the wet season when high and variable flows occur, while biotic interactions may increase in relative importance during the low and relatively stable flows of the dry season as habitats contract (Pearson *et al.* 1986). Alternatively, macroinvertebrate communities in aseasonal, frequently disturbed streams (e.g. sites in Papua New Guinea in the current study) may rarely experience conditions suitable for the development of strong interactions and are therefore likely to be primarily controlled by disturbance-related factors, and mechanisms promoting persistence may assume greater relative importance (see section 1.6).

1.4 Disturbance and Heterogeneity

Disturbance in streams may occur over a range of temporal and spatial scales (Figure 1.1) and may act on stream organisms either directly (through mortality or removal) or indirectly (e.g. disruption of nutrient cycling), creating variability in process and patterns (heterogeneity) at multiple scales (Palmer and Poff 1997).

Figure 1.1 Diagram illustrating that the disruptive effect of disturbance varies along temporal and spatial scales (after Karlson and Hurd 1993).



The creation and maintenance of spatio-temporal heterogeneity in physical (habitat) features has important implications for stream fauna (Hildrew and Giller 1994). Heterogeneity firstly acts to modify the outcome of local species interactions (Pickett and White 1985, Shorrocks 1990) and, secondly, determines community response to disturbance, providing areas which may ameliorate disturbance impacts (refugia) (Sedell *et al.* 1990, Lancaster and Hildrew 1993, Robertson *et al.* 1995, Palmer *et al.* 1996, Townsend, *et al.* 1997a).

Streams and rivers are heterogeneous in nature, share characteristics of unidirectional flow and linkages with adjacent terrestrial systems, and tend to be dominated by relatively short-lived and highly mobile biota. Variability of stream environments in space and time is dominated by factors such as stream flow, temperature, light, substratum and resource availability. Stream habitat features may be viewed in a hierarchical way (Table 1.4), incorporating a number of levels nested at successively smaller scales and decreased temporal persistence (Frissell *et al.* 1986, Bayley and Li 1992, Hawkins *et al.* 1993, Townsend and Hildrew 1994); however, interaction between scales may occur (Downes *et al.* 1993, Downes *et al.* 1997), suggesting that strict hierarchical models may not be applicable in all situations.

Table 1.4 The hierarchical classification of stream habitats showing approximate linear spatial and temporal scales (persistence) (after Frissell *et al.* 1986, Ward 1989).

Habitat	Spatial scale (m)	Persistence (years)
STREAM SYSTEM	10^3	$10^5 - 10^6$
↓		
STREAM SEGMENT	10^2	$10^3 - 10^4$
↓		
STREAM REACH	10^1	$10^1 - 10^2$
↓		
POOL/ RIFFLE SYSTEM	10^0	$10^0 - 10^1$
↓		
STREAM MICROHABITAT	10^{-1}	$10^{-1} - 10^0$

1.5 Hydraulic forces and substratum characteristics

Stream flow, which can vary substantially over a range of temporal and spatial scales (Davis and Barmuta 1989, Poff and Ward 1989, Biggs *et al.* 1990, Poff and Allen 1993), is the major architect of physical patchiness on the stream bed. Flow (a product of climate, relief, geology, and land use) varies from the microhabitat (sub-millimetre) to entire drainage basin scales.

Hydrologic extremes, including floods and droughts, may directly influence local community structure for fishes (Bain *et al.* 1988, Jowett and Duncan 1990, Fausch and Bramblett 1991) and invertebrates (Fisher 1983, Resh *et al.* 1988, Poff and Ward 1989, Niemi *et al.* 1990, Fisher and Grimm 1991, Giller *et al.* 1991) through severe population losses. As well as direct mortality effects, variability in stream flow may influence community structure through the indirect alteration of habitat, in-stream productivity and food availability, and the cycling of nutrients (Schlosser 1990). Low flows may influence stream communities through silt deposition, decreases in oxygen concentration, increased temperature, shrinking habitat and desiccation (Delucchi 1989, Stanley *et al.* 1994), while high flows are usually accompanied by chemical and nutrient changes, increased shear stress (hydraulic force acting on the substrate), and movement of particles within the stream bed (e.g. Niemi *et al.* 1990, Giller *et al.* 1991).

Movement of the substratum associated with high flows provides the primary source of disturbance to benthic fauna (Townsend *et al.* 1997b) as this comprises their physical habitat. During periods of high flow, individuals and attached algae and associated organic material (e.g. detritus) may be removed as surfaces of the substrata are scoured and stones are overturned and moved downstream, thus creating unoccupied patches.

Stability of the substratum (or degree of resistance to movement) as an index of disturbance frequency, is a function of particle size, degree of particle packing within the stream bed, and slope and depth of water (Minshall 1984, Downes *et al.* 1997). At the regional scale, substratum characteristics (and therefore disturbance) of streams vary predictability (depending on geology, gradient and climate) along a longitudinal profile (e.g. Vannote *et al.*

1980). At the headwaters, bedrock, boulder and cobble predominate, replaced by an alluvial gravelbed with distinct riffle and pool structure in the mid-reaches, and, downstream, an alluvial sandbed. Small, non-cohesive particles (e.g. sands) may be moved by small increases in discharge, while larger particles (e.g. boulders and cobbles) require much larger forces to initiate motion, resulting in temporal and spatial variability in disturbance among channel forms and substratum types (Resh *et al.* 1988, Cobb *et al.* 1992).

1.6 Resistance and resilience

The effects of disturbance on ecosystem structure and function are determined by the capacity of individuals to avoid change (resistance) and the ability to recover rapidly following disturbance (resilience) (Lake and Barmuta 1986, Grimm and Fisher 1989, Boulton *et al.* 1992, Golladay *et al.* 1992). Stream communities commonly show low resistance to disturbance events, in terms of severe reductions in abundance and biomass (Table 1.5), although this response is variable, depending on differences in the disturbance regime (type, magnitude and timing), structural complexity (heterogeneity) of the impacted ecosystem, the taxonomic groups and life history stages of the biota, and the scale of measurement (Fisher and Grimm 1991).

The effect of disturbance on the flora and fauna of streams may be severe, with almost total mortality or complete removal from an area (e.g. Grimm and Fisher 1989). Streams that are higher in structural complexity are less impacted by disturbance, as heterogeneous habitats potentially harbour a higher proportion of refugia, helping to 'incorporate' the event (*sensu* Urban *et al.* 1987). Some taxonomic groups possess characteristics that confer high resistance to disturbance (Townsend *et al.* 1997c), such as the ability to swim strongly, burrow rapidly into the substratum, or cling to exposed surfaces. Larval stages or smaller sized individuals appear to be more susceptible to flow disturbance (lower resistance), and some species avoid being in vulnerable life history stages when the probability of flooding is highest (Gray 1981). However, small individuals may recover rapidly following disturbance as there is a general relationship between resilience and organism size (Fisher and Grimm 1991).

Table 1.5 Resistance (measured as percent change of stream biota to a variety of disturbance events) (modified from Fisher and Grimm 1991).

Disturbance	Stream biota	Reduction (%)	Reference
Flood	Bacteria	0^b	Goulder 1986
Flood	Algae	$68\text{-}96^b$	Power and Stewart 1987
Flood	Algae	$0\text{-}100^b$	Grimm and Fisher 1989
Volcano	Algae	100^b	Rushforth *et al.* 1986
Flood	$CPOM^+$	$10\text{-}80^b$	Fisher 1977
Flood	Macroinvertebrates	$0\text{-}99^b$	Grimm and Fisher 1989
Flood	Macroinvertebrates	90^a	Matthaei *et al.* 1997a
Flood	Macroinvertebrates	94^b	Molles 1985
Flood	Macroinvertebrates	$66\text{-}72^a$	Angradi 1997
Flood	Macroinvertebrates	$> 90^a$	Miller and Golladay 1996
Substrate raking	Macroinvertebrates	92^a	Matthaei *et al.* 1997a
Substrate raking	Macroinvertebrates	$83\text{-}87^a$	Matthaei *et al.* 1996
Siltation	Chironomidae	$> 90^b$	Gray and Ward 1982

a = abundance, b = biomass, + = coarse particulate organic matter.

Recovery, most commonly assessed as the re-establishment of structure or function to pre-disturbance conditions (Wallace 1990, Fisher and Grimm 1991), is facilitated through environmental heterogeneity (conferring differential survival), and the dispersal abilities of individuals (Dunning *et al.* 1992, Lancaster 1996). Stream communities show considerable resilience to disturbance (Table 1.6), with most recovery times, even following severe disturbance, completed in less than three years (see review by Niemi *et al.* 1990).

Table 1.6 Resilience (measured as recovery time to pre-disturbance conditions) of stream biota to floods (modified from Fisher and Grimm 1991).

Stream biota	Recovery time (days)	Reference
Bacteria	10-12	Cooper 1983
Algae	21	Power and Stewart 1987
Algae	21-30	Fisher *et al.* 1982
Algae	20-78	Grimm and Fisher 1989
Macroinvertebrates	30-40	Fisher *et al.* 1982
Macroinvertebrates	20-40	Grimm and Fisher 1989
Macroinvertebrates	19-22	Matthaei *et al.* 1997a

Reported recovery rates, although rapid, are highly variable, due both to different selection criteria used for the detection of endpoints, and to natural factors. Recovery of disturbed communities is influenced by the magnitude of the disturbance (spatial scale of the affected area), its frequency (relative to the generation time of the fauna), as well as disturbance-related modification of physical and chemical habitat characteristics. The intrinsic ability of the fauna to recover from a given disturbance will be a function of their dispersal abilities, both at local and regional scales (e.g. ability to enter the drift), life history characteristics (e.g. generation time), and historical exposure to disturbance (may provide a selective force for disturbance-related traits).

Recovery is most rapid following localised, small-scale disturbance events (Sheldon 1984, Niemi *et al.* 1990) with recolonisation from adjacent undisturbed patches or refugia. Refugia may be broadly defined as areas (or times) where the negative effects of disturbance are lower compared with surrounding ares (or times) (Lancaster and Belyea 1997). During disturbance, fauna utilising refugia have a relatively high probability of survival, and are subsequently able to recolonise disturbed areas. Two major refugial categories have been identified within streams: the interstitial region in the stream bed (hyporheic zone), and microhabitat patches with reduced hydraulic stress during high and variable flows (flow refugia) (e.g. Townsend *et al.* 1997a). Although empirical support exists for the movement of stream fauna into identified refugium patches during hydrological extremes (Dole-Oliver and Marmonier 1992, Lancaster and Hildrew 1993, Clinton *et al.* 1996, Winterbottom *et al.* 1997), utilisation is highly species and size specific (Lancaster and Hildrew 1993, Robertson *et al.* 1995). The role of refugia in reducing the impact of disturbance on overall community characteristics therefore depends on several factors (Townsend and Hildrew 1994): firstly, the ease of movement, either active or passive, into the refugium and subsequent retainment of organisms; secondly, the proportion of the total population utilising refugia; and finally, the effectiveness of recolonisation from the refugia following disturbance.

Intense disturbances, which are less frequent, affect much larger spatial scales, disrupting ecosystem-level processes (Biggs and Close 1989, Entwistle 1989, Grimm and Fisher 1989, Poff and Ward 1990) resulting in much slower recovery times (e.g. Fisher 1990, Malmquist *et al.* 1991). Such disturbances may cause long-term physical and chemical changes to the habitat and effectively isolate the disturbed area from sources of potential colonists (Giller *et* *al.* 1991). As disturbance increases (in magnitude or frequency), the relative importance of regional (*cf.* local) dispersal strategies will therefore increase, including aerial dispersal by adult stages and the downstream transport of individuals in the water column via drift.

Southwood (1977, 1988), in his habitat templet model, proposed the view that habitat forms the basis for the evolutionary shaping of life history strategies. The levels of spatial and temporal variation inherent in an environment act as selective forces for survival and reproductive ability. Over evolutionary time scales, the life history traits selected for will therefore reflect the disturbance regime and degree to which heterogeneity interacts to modify its influence (Townsend and Hildrew 1994) (Table 1.7). High resilience following floods has been attributed to life history characteristics such as rapid growth and short generation times (Grimm and Fisher 1989, Miller and Golladay 1996). In particular, timing of disturbance and stage of development is an important factor influencing resilience in stream communities (Resh *et al.* 1988). Slower recovery (lower resilience) may occur at times of the year when rates of recruitment (e.g. low numbers of ovipositing adults) are reduced, and water temperatures are low (reducing growth rates) (Grimm and Fisher 1989, Miller and Golladay 1996).

Table 1.7 Life history traits proposed as determinants of high resistance and resilience of freshwater macroinvertebrates to disturbance (after Townsend *et al.* 1997c).

	Species traits
i) resistance	Firm attachment mechanisms Streamlined / flattened body form Invulnerable life stages
ii) resilience	Early age at first reproduction Short reproductive cycles Potential for regeneration Ability to recolonise from refugia

In the tropics, for example, warmer temperatures (*cf.* temperate regions) result in rapid development times, with many species breeding year-round, thereby producing multiple, overlapping cohorts (Dudgeon 1992, Jackson and Sweeney 1995) and enhancing recovery potential following disturbance (Nolen and Pearson 1992). Where streams are frequently disturbed, life histories may incorporate effective dispersal or resistant stages. For example, frequent exposure to severe flash flooding in desert streams, combined with warm temperatures, has selected for rapid development, continuous emergence and diapausing eggs that facilitate rapid recovery (Gray and Fisher 1981, Fisher *et al.* 1982).

The collective properties of resistance and resilience of component species together provide an index of community persistence, or the tendency for stability in species composition over time (Fisher and Grimm 1991). In spite of low overall resistance to disturbance, a high degree of community persistence has been demonstrated for stream invertebrates (Meffe and Minckley 1987, Giller *et al.* 1991) and fishes (Ross *et al.* 1985, Meffe and Minckley 1987) through high resilience. However, assemblages may be less predictable (i.e. show low persistence) with increased environmental variation, such as increased variability in flow (Meffe and Minckly 1987), decreased habitat stability (Wallace *et al.* 1988), and fluctuating water levels (Boulton and Lake 1992a, 1992b).

1.7 Tropical Stream Ecosystems

Although the importance of disturbance in stream ecosystem functioning and community dynamics is well documented in temperate streams (e.g. Resh *et al.* 1988, Reice 1994, Lake 1995), disturbance is also likely to be a fundamental process in the ecology of tropical freshwater ecosystems.

Disturbance, associated with hydrologic extremes, may result in dramatic fluctuations in the densities of macroinvertebrates, reported from a range of tropical localities including Ghana (Hynes 1975), Hong Kong (Dudgeon 1993), India (Arunachalam *et al.* 1991), Kenya (Mathooko and Mavuti 1992), Malaysia (Bishop 1973), Papua New Guinea (Yule and Pearson 1996), Venezuela (Flecker and Feifarek 1994), Costa Rica (Pringle and Hamazaki 1997), and Australia (Rosser and Pearson 1995). However, few of these studies give detailed accounts at the population and community level, and relatively little detailed information exists on the mechanisms by which benthic communities persist in the face of exposure to severe physical disturbance by hydrological extremes.

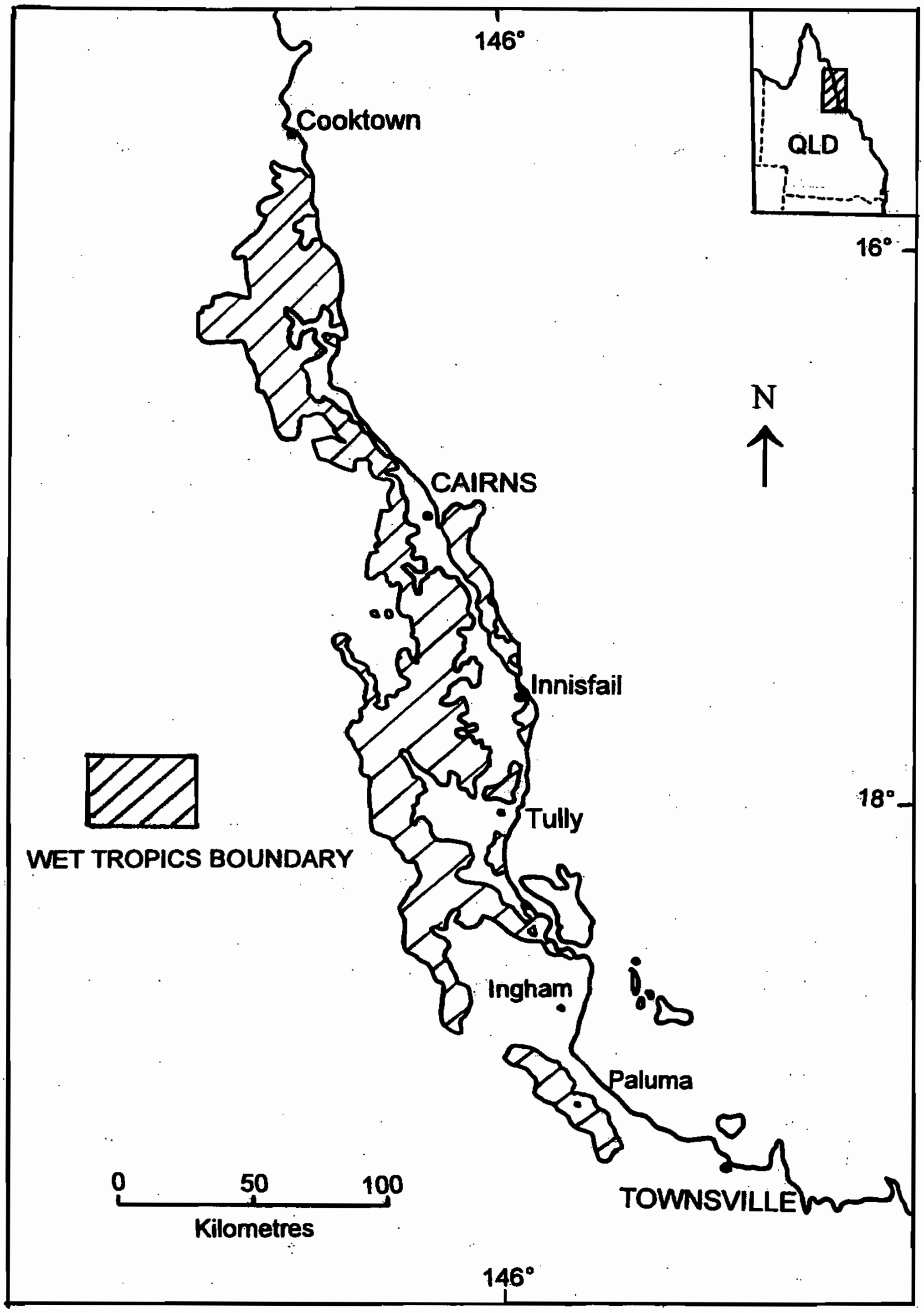
This study was conducted primarily in the Australian Wet Tropics (Figure 1.2), a biogeographic region roughly encompassing the area between Townsville and Cooktown, extending from the coast to the western edge of the wet sclerophyll forests (Webb and Tracey 1981). Freshwater ecosystems in the Wet Tropics (see Pearson 1994), and the Alligator Rivers Region in the Northern Territory (Outridge 1987, 1988; Humphrey and Dostine 1994) comprise the only areas within the Australian tropics that have been the focus of long-term investigations. The present study is therefore complementary to previous stream research in the region (Table 1.8), contributing to a more complete understanding of these tropical freshwater systems. Studies of disturbance in these streams are not only important for the contribution they make to the ecological knowledge of tropical ecosystems, but also to disturbance theory in general, broadening the basis for the formulation of generalised models.

Table 1.8 Examples of stream-related ecological studies carried out in the Wet Tropics of north Queensland.

Study Description	Reference
Faunal diversity	Pearson *et al.* 1986, Lake *et al.* 1994
Detrital dynamics	Benson and Pearson 1993
Dietary studies	Hearnden and Pearson 1990
Resource partitioning	Hearnden and Pearson 1991
Community food webs	Cheshire 1997
In-stream litter processing	Nolen and Pearson 1993
Litter inputs	Benson and Pearson 1993
Ecology of waterfall fauna	Clayton 1995
Drift and upstream movement	Benson and Pearson 1987a
Colonisation processes	Benson and Pearson 1987b
Disturbance/colonisation dynamics	Rosser and Pearson 1995
Disturbance/colonisation dynamics	This study

In addition, streams within the Australian Wet Tropics have a number of features that distinguish them ecologically from those in temperate regions and are likely to influence response to disturbance. These are:

Figure 1.2 Map indicating the Australian Wet Tropics biogeographic region.


146°
Cooktown
QLD
16°
N
CAIRNS
Innisfail
18°
Tully
WET TROPICS BOUNDARY
Ingham
Paluma
0
50
100
Kilometres
TOWNSVILLE
146°

- Temperature – Higher ambient temperatures in the tropics leads to shortened development times for the majority of the fauna (Nolen and Pearson 1992, R.G. Pearson, pers. comm.), and are likely to have significant effects on many in-stream processes, such as microbial action and leaf litter breakdown (Nolen and Pearson 1993).

- Allochthonous inputs – Inputs into the stream from the surrounding vegetation appear to be of primary importance to the energetics of these systems (Cheshire 1997) and they differ from temperate regions in both composition and timing. Material entering these streams is derived from a highly diverse rainforest community (*cf.* dominance by *Eucalyptus* spp.) and falls year-round, with a peak in summer, when water temperature and discharge are highest (*cf.* low discharge) (Benson and Pearson 1993).

- Hydrological regime – Streams in the Wet Tropics form a unique hydrological group in that they differ in the magnidude and timing of hydrological extremes (see below), and are subject to extremely high flows during the summer wet season. However, although seasonal, the interannual variability is high, and the precise timing of flood events is highly unpredictable, being dependent on the formation of cyclones and rain depressions.

The major focus of the present study is on physical disturbance of stream habitats associated with high flows, and in particular, the movement of the substratum at the scale of individual stones. Individual (cobble-sized) stones are an appropriate unit for the following reasons:

1. It has been suggested that the degree of bed movement provides the most meaningful measure of disturbance to the benthic fauna of streams (Townsend *et al.* 1997b), many of which are closely associated with the substratum. Movement of particles within the stream bed by high flows (hereafter referred to as floods), resulting in alterations to community composition (e.g. Death and Winterbourn 1994), therefore provides a significant source of disturbance to the fauna associated with these substrata.

2. Thus, the focus of this study is likely to be at a scale of ecological relevance to the fauna (Downes *et al.* 1993, Downes *et al.* 1997), and is also at the scale at which models incorporating disturbance into ecological theory are based (e.g. involving patchiness at small spatial scales and concepts of local stability) (Death 1996).

3. While floods may disturb entire streams, experiments involving marked stones suggest that rocks are moved individually (i.e. selectively entrained – Lake and Schreiber 1991).

4. Individual stones are readily colonised and utilised as a primary habitat by a diverse range of fauna (e.g. Lake and Schreiber 1991), they are easy to sample accurately as a discrete unit, and they are readily manipulated for experimental purposes.

5. Stones comprise substantial habitat patches in streams of the Wet Tropics and elsewhere (for comparison), are found within a range of habitat types, and are rearranged and displaced downstream by floods (see Chapter 2).

In Australia, and the tropics in particular, disturbance due to hydrological extremes (floods and droughts) may be especially relevant to stream communities (reviews by Pearson 1994, Lake 1995) because:

1. Australian streams and rivers, in general, comprise a distinct hydrological group which are more variable (high coefficient of variation of annual flow) when compared with similar world streams and world arid-zone streams, and the peak floods are generally much higher than in world average streams (McMahon 1982). These characteristics may be more pronounced in the Australian tropics, where the variation in annual flows is very high (see Chapter 4) and is close to the range of values for Australian arid-zone streams and exceeds values reported for non-arid streams in Australia (McMahon 1982). Furthermore, discharge in tropical Australian streams is generally high compared with similar streams in temperate regions. Therefore, flow-related disturbance is likely to be highly important to the fauna in tropical north Queensland.

2. Conditions of high variability within Australian streams is likely to have existed for a long period of time, at least since the mid Miocene (~ 10 m.y.B.P.) and this may have

enhanced the selection of mechanisms promoting persistence despite variable flow conditions (Lake *et al.* 1985b).

3. Streams of the Australian Wet Tropics have been found to support very high diversities of benthic macroinvertebrates (e.g. Pearson *et al.* 1986, Lake *et al.* 1994) compared with temperate streams, and this may be true of the tropics in general (Stout and Vandermeer 1975, Outridge 1987, Yule 1995). There is a long-held belief that disturbance is an important mechanism in the creation and maintenance of local diversity, for example by the prevention of competitive exclusion (Connell 1978). Thus, it is of considerable ecological interest to investigate factors, such as disturbance, which may be important in these streams and contribute to the maintenance of the observed high diversity.

1.8 Aims and approach

This study investigated both natural events and experimental manipulations to examine the response of the macroinvertebrate fauna of stones to disturbance in tropical streams. This permitted faunal responses to three spatial scales of disturbance to be examined. The overall aims were to:

1. Examine the response of stone fauna, in terms of resistance and resilience, to i) large-scale, severe (stream-wide, substratum-moving) disturbance by wet season floods, ii) experimental disturbance (raking of the substratum) of a stream section and iii) overturning and scouring of individual stones.

   Response to these different spatial scales of disturbance was assessed at the community level and the level of the individual species.

2. Determine the influence of disturbance frequency (which , together with magnitude, defines the temporal and spatial axes of the disturbance regime) in shaping the faunal response to disturbance.

This was examined from two perspectives. Firstly, the effect of frequency *per se* was investigated by experimentally manipulating the number of times individual stones were tumbled and observing the effect on characteristics of resistance and resilience. Secondly, the influence of *historical* differences in disturbance frequency in shaping (in evolutionary time) response to disturbance was examined. This was achieved by comparing response to experimental disturbance (i.e. magnitude held constant) in streams with a high temporal frequency of natural disturbance (Papua New Guinea) with those with a low temporal frequency of disturbance (north Queensland). Although the two regions differ in terms of climate, a difference reflected in the hydrological regime, they share close geological and biological links (Williams and Allen 1987) following a prolonged Quaternary connection (Kikkawa *et al.* 1981). In terms of the aquatic fauna, both Papua New Guinea and north Queensland share strong affinities with south-east Asia, and to a lesser degree, elements of Gondwanan origin (Mackerras 1970).

3. Determine the influence of habitat on macroinvertebrate response to disturbance in terms of modifying the impact of disturbance and the recolonisation process.

To achieve this, the impacts of large-scale (flood) disturbance and the subsequent recovery of benthic communities in the major habitats (riffle and pool) were examined. Also, experimental disturbance of individual stones (bricks) was carried out in these habitats and along a longitudinal stream gradient which differed in habitat features (e.g. substratum characteristics) predicted to influence response to substratum disturbance.

Within this general framework, detailed aims are given in each chapter, which are broadly organised on the basis of different spatial scales of disturbance, as follows:

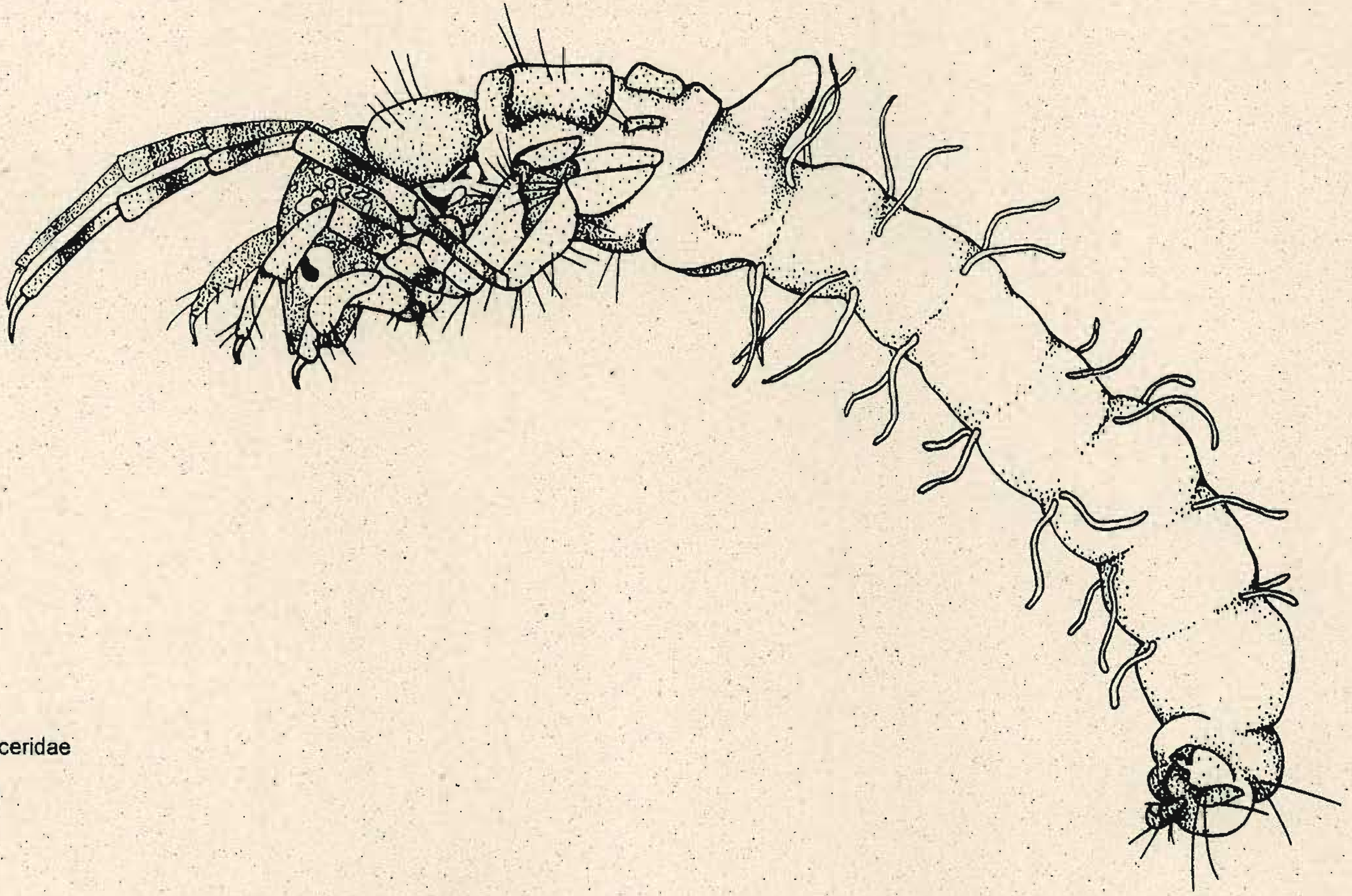
Chapter 2 investigates the response of stone fauna to natural flood disturbance (i.e. scale of the whole stream) in the context of seasonal variations in flow including high and fluctuating flows during the wet season and low and relatively stable flows during the dry season. This was examined by the long-term collection of benthic samples in Birthday Creek, and incorporated the two major habitats, riffle and pool, common to streams of the Australian Wet Tropics. Birthday Creek, an upland rainforest stream, was chosen for this aspect of the study because: i) this site is readily accessible from

Townsville, ii) this stream type is common to the Wet Tropics biogeographic region and, iii) the study site and nearby areas have been the focus of previous ecological research (e.g. Lake *et al.* 1994, Rosser and Pearson 1995).

Chapter 3 describes the results of experimental manipulations to determine response to physical disturbance (i.e. substratum tumbling) at the scale of individual stones, assessed within different habitats predicted to influence resistance and resilience. This was addressed by performing experimental manipulations within three sites in the Wet Tropics – permitting the generality of response to disturbance to be determined. These sites included upland (Birthday Creek, north of Townsville; and Yuccabine Creek, north-west of Cardwell), and lowland (Pixies Creek, west of Tully) rainforest streams. The experimental disturbance involved tumbling and scrubbing of individual substrata, with different treatments reflecting different intensities of natural disturbance. The effect of longitudinal position within a stream on the faunal response to disturbance was examined at Yuccabine Creek, as headwater, mid-reach, and lower-reach sites were accessible, and ecological information existed for this stream as the result of previous research (Pearson *et al.* 1986, Benson and Pearson 1987a, b, Lake *et al.* 1994). Pixies Creek was originally chosen for comparison with Birthday Creek to examine whether faunal response to disturbance within riffle and pool habitats was influenced by the higher rainfall, and therefore higher discharge at the Pixies Creek site. However, incorporation of the Papua New Guinea sites into this study in 1993 and 1994 meant that the influence of hydrological regime on community response to disturbance could be examined in greater detail, as the streams chosen in Papua New Guinea, while sharing a similar faunal inheritance (see above), provided considerable hydrological contrasts to those in the Australian Wet Tropics (see next Chapter).

Chapter 4 therefore investigates the faunal response to physical disturbance of a stream section (i.e. raking of the substratum at the riffle scale) in the context of different historical patterns of natural disturbance. This was examined by comparing macroinvertebrate response to identical experimental disturbance (i.e. magnitude held constant) in similar habitats within hydrologically different streams in Papua New Guinea and the Australian Wet Tropics. Importantly, streams in Papua New Guinea were carefully chosen to share as many physical characteristics (stream order, size of the substratum, degree of shading by riparian vegetation) with the site in North Queensland as possible to minimise other factors confounding the results when comparing streams in different geographical regions.

Chapter 5 provides the general discussion, drawing the results together, viewing them in relation to the proposed aims and in the context of general disturbance theory, and suggesting directions for future research on disturbance.



Trichoptera: Leptoceridae

Artist: Andi Cairns

CHAPTER 2: TEMPORAL DYNAMICS OF THE MACROINVERTEBRATE FAUNA OF STONES AT BIRTHDAY CREEK, A TROPICAL RAINFOREST STREAM

2.1 Introduction

This study investigates the temporal variation in the structural and functional characteristics of macroinvertebrate communities on stream stones in Birthday Creek, a tropical rainforest stream in north Queensland. This stream, as with other upland streams of the Australian Wet Tropics (e.g. Pearson *et al.* 1986), is characterised by distinctly seasonal variations in flow. The occurrence of floods during the summer months (December-March) contrasts with the relatively low and stable flows over the remainder of the year. The magnitude and precise timing of floods are unpredictable, as they are associated with the formation of tropical cyclones and monsoon-driven rain depressions. Although disturbance by floods during the summer wet season has been implicated as a major structuring force in these tropical streams (Pearson *et al.* 1986, Lake *et al.* 1994), little is known of the specific mechanisms promoting community persistence (but see Rosser and Pearson 1995) and high diversity (Pearson *et al.* 1986, Lake *et al.* 1994) despite seasonal, often severe disturbance by floods.

Disturbance, in the form of hydrologic extremes, may dramatically affect macroinvertebrate community structure through significant reductions in abundance and diversity, reported in tropical streams from a range of localities including Malaysia (Bishop 1973), Hong Kong (Dudgeon 1993), Ghana (Hynes 1975), India (Arunachalam *et al.* 1991), Venezuela (Flecker and Feifarek 1994), and Australia (Pearson *et al.* 1986, Outridge 1988). High discharge events disturb stream fauna by direct dislodgement, through high shear; by crushing, through mobilisation of the substratum; and by abrasion by entrained particles. Although the effects of floods on stream fauna and flora may be severe, post-flood recovery is typically rapid (Niemi *et al.* 1990, Stevenson 1990).

Within seasonal streams such as Birthday Creek, it is predicted that during the wet season, when flow is high and variable, communities will be closer to non-equilibrial states (Wiens

1977), with populations limited primarily by abiotic factors, and possessing low resistance to, and resilience following disturbance (Lake and Barmuta 1986). In contrast, during the dry season, when hydrological variability is low, biotic controls may exert greater influence on community regulation (Peckarsky 1983, Power *et al.* 1988, Resh *et al.* 1988, Lancaster 1990, Dudgeon 1993). In addition, many taxa in seasonal tropical streams have rapid development times, relative to the inter-flood periods, and this may permit biotic interactions to intensify over time (Fisher and Grimm 1991). By examining temporal change in macroinvertebrate communities over consecutive wet and dry seasons, the extent to which the community conforms to non-equilibrial predictions may be determined.

As floods within streams of the Australian Wet Tropics can be severe and may result in substantial alterations to the physical habitat, it was predicted that the benthic assemblages at Birthday Creek would show low resistance, but would persist in the system through high resilience following disturbance by wet season flooding. The variation in assemblage structure was expected to be high initially, reflecting stochastic recolonisation following flood disturbance, decline as the assemblage develops, and increase again as biotic interactions intensify over the dry season. This response should be modified by habitat (e.g. Resh *et al.* 1988), and provision of refugia (Palmer *et al.* 1995), so this study examined responses to disturbance in two habitat types – riffle and pool – common to streams in this region.

The response of macroinvertebrate communities on stream stones to large-scale disturbance was examined in Birthday Creek in the context of temporal changes in flow by addressing the following questions:

i) Does the temporal variation in benthic communities in riffle and pool habitats reflect the seasonal pattern of flow, characterised by high and variable flows in the wet season and low and relatively stable flows during the dry season?

ii) Is the faunal response (i.e. characteristics of resistance and resilience) to disturbance by floods during the wet season modified within these (riffle and pool) habitats in this stream? In addition, what are the mechanisms by which benthic communities in these two habitats persist over time despite severe disturbance by floods?

iii) How does the seasonal pattern of flow affect the availability of potential food resources (particulate organic matter and chlorophyll *a*, as an index of algal biomass) on stone surfaces?

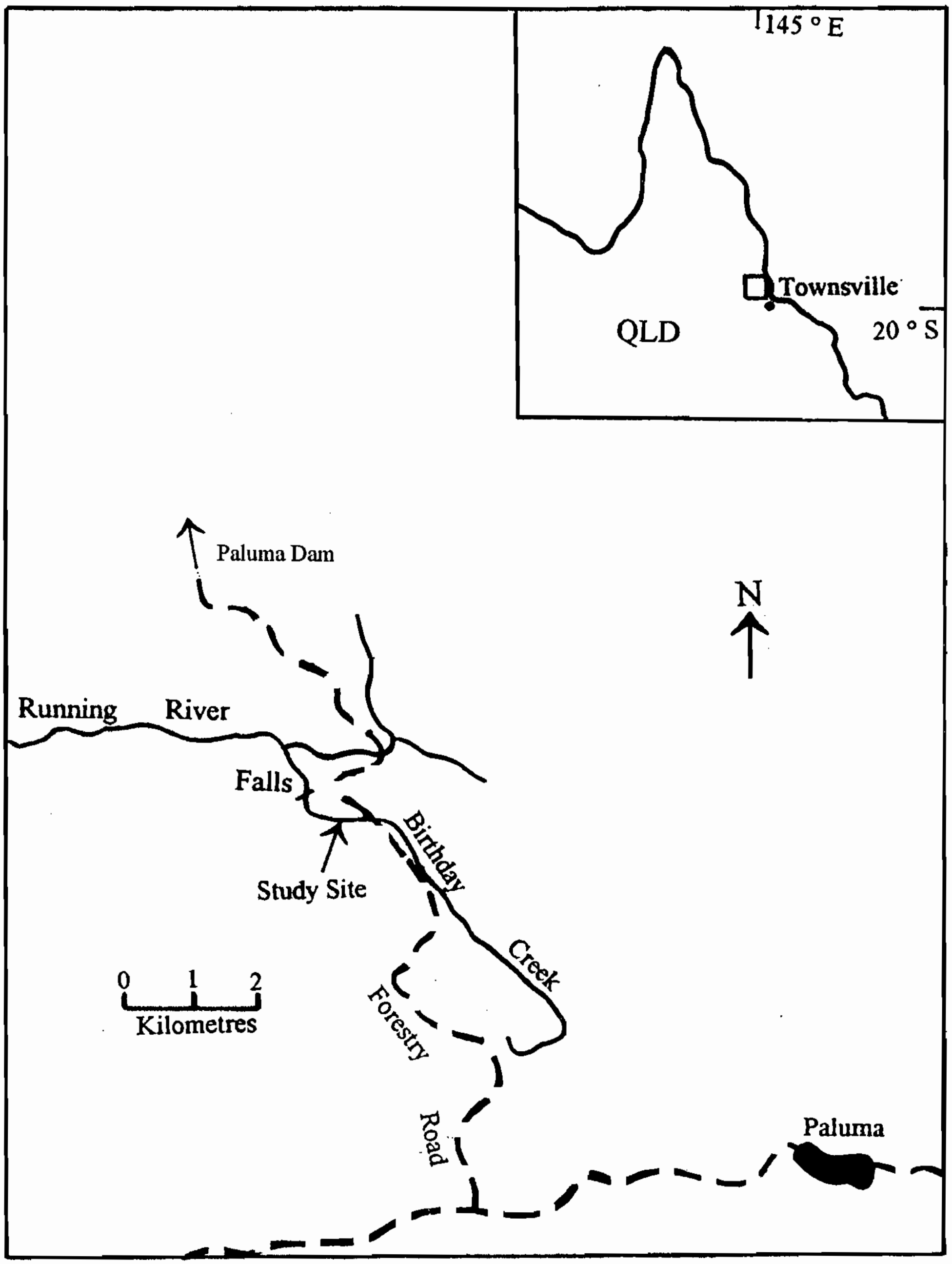
2.2 Methods

Study Site

The study was conducted in Birthday Creek (19°00′S, 146°15′E), an upland rainforest stream originating in the Paluma Range, which is situated northwest of Townsville, and about 15 km from the coast (Figure 2.1). Birthday Creek at the study site is a third-order stream, at an altitude of 800 m, and consists of an alternating series of rocky riffles and pools. The catchment is located within State Forest near the small township of Paluma, and forms one of the headwater catchments of the Burdekin River. The forest was selectively logged in 1964-65. This system is the focus of continuing ecological investigation (reviewed by Pearson 1994).

Chemically, Birthday Creek is similar to other low-order forested streams in the Australian Wet Tropics (Pearson *et al.* 1986, Rosser 1991, Clayton 1995) and other tropical streams (e.g. Bishop 1973). The water is low in conductivity, hardness, and total dissolved solids, with a dominance of sodium and chloride ions, and has stable, slightly acid pH. Riparian vegetation comprises rainforest species, forming a largely closed canopy (estimated at 80 % cover) over the stream at the study site. The climate of the region is dominated by strongly seasonal patterns of rainfall and temperature. The wet season occurs over the summer months (December - February), sometimes extending into early autumn (March, April), when around 70 % of the total annual rainfall occurs. Rainfall is closely correlated with stream discharge in Birthday Creek (Clayton, 1995), with rapid response to the onset and cessation of rainfall within the catchment.

Figure 2.1 Map indicating the location of the Birthday Creek study site in north Queensland.


145 ° E
Townsville
20 ° S
QLD
Paluma Dam
N
Running River
Falls
Birthday Creek
Study Site
0 1 2
Kilometres
Forestry Road
Paluma

Stream discharge data for this study was recorded at a gauging station approximately two kilometres upstream of the study site (A.Pomeroy, unpublished data). Although Birthday Creek is perennial, stream flow can be reduced to a trickle at the end of the dry season (September-November). During the period of this study (October, 1992 – April, 1995), 1992 was a particularly dry year, as a result of El Ninõ, with well below average rainfall during the summer months (pers. comm., Townsville Bureau of Meteorology). Annual patterns of discharge in this stream are predictable (predictability with contingency, Colwell 1974), but superimposed with high levels of short-term variability of discharge during the summer wet season. The timing and magnitude of particularly large flood events, caused by the formation of tropical cyclones during the summer, are highly unpredictable. Flood events are characterised by steeply rising discharge hydrographs, with flow diminishing almost as rapidly following cessation of rainfall. The sampling period incorporated two major flood events of different magnitude, in January, 1994 and February, 1995.

To examine the extent of substratum movement due to flood disturbance at the study site, the displacement of marked bricks was monitored. This technique has been used in other studies (Lake and Schreiber 1991, Death and Winterbourn 1994, Townsend *et al.* 1997a, 1997b) and reflects flood magnitude. Bricks of three different sizes (quarter, half and whole ("standard house brick")), encompassing the size of natural stones sampled, were aligned in rows within the study riffle prior to the 1995 flood. Following the flood, the downstream displacement of individual bricks from their pre-flood position was measured using a tape-measure.

Water temperature was monitored over the study period using maximum/minimum thermometers placed within a riffle and a pool, with readings taken monthly at the time of benthic sampling.

Macroinvertebrate Sampling

Benthic samples were taken from a 100 m section of riffle habitat (Plate 1) and an adjacent 25 m pool section (Plate 2). Stones were removed monthly from the riffle over a 43 month

Plate 1 Riffle site at Birthday Creek, north Queensland, looking downstream.

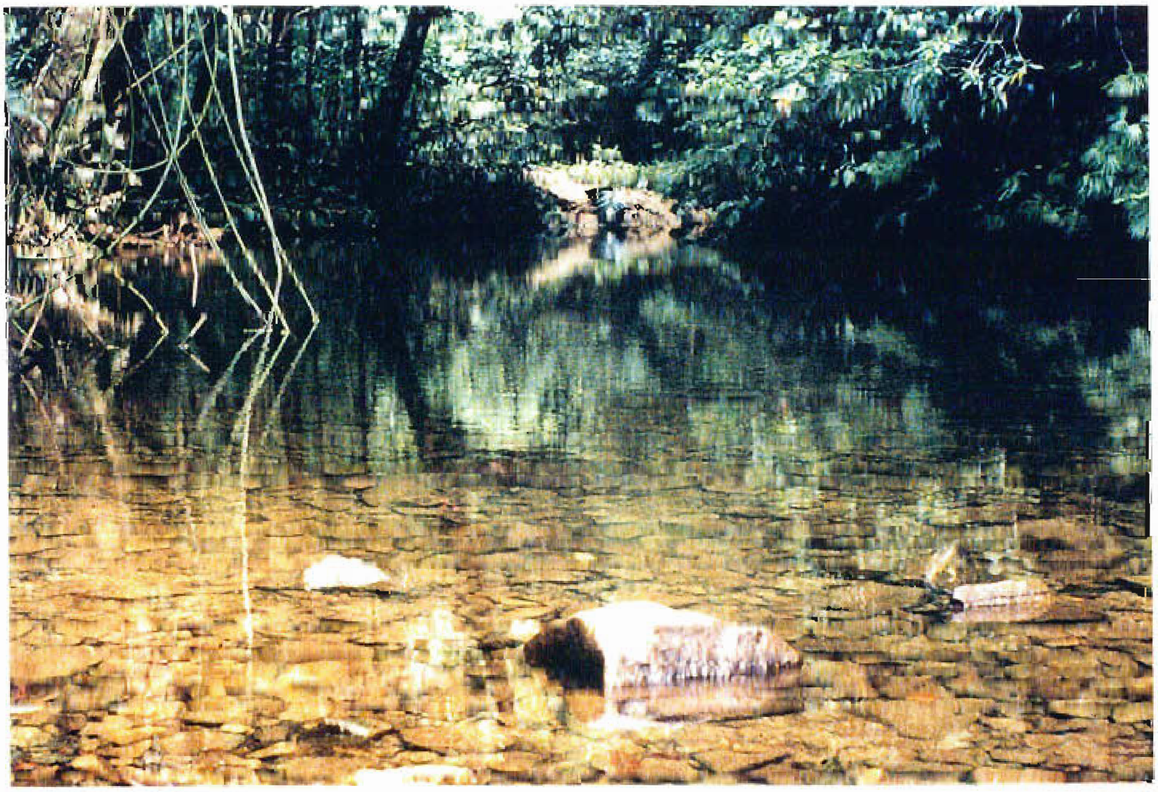


Plate 2 Pool site at Birthday Creek, north Queensland, looking upstream.

period, from October, 1991 to April, 1995. Pool samples were only included for comparison towards the end of the study, and therefore represented a reduced data set of the final 16 months of the study (January, 1994 to April, 1995). Nevertheless, this sampling regime included pre-flood and post-flood samples following each of the major flood events in both habitats. Post-flood samples were collected 21 days following the largest flood (1994), and six days following the second event (1995). Each month, eight stones, of roughly half-brick size were sampled from each habitat. Individual stones were lifted, while a dip net (250 μm mesh), held downstream, was brought forwards and upwards to surround the stone. Macroinvertebrates were then brushed from the surface of each stone into the net using a test-tube brush, after which the contents of the net were preserved in 70% ethanol and returned to the laboratory the study (January, 1994 to April, 1995). Nevertheless, this sampling regime included pre-flood and post-flood samples following each of the major flood events in both habitats. Post for processing.

Each stone was weighed in the field. The surface area for each stone was then determined from a predetermined regression of weight and (measured) surface area, determined for 30 stones (Rosser and Pearson 1995), using plastic film to determine area, following Doeg and Lake (1981). This is a practical and accurate method for the determination of substrate surface area (with < 5 % recorded error), particularly when selecting rocks of similar shape, as was the case in this study. To overcome slight variations in dimensions of natural stones sampled in this study, and to permit direct comparisons with results from experimental manipulations using artificial substrata (Chapter 3), data were standardised to individuals/number of taxa per 0.08 m^2 (= surface area of artificial substrata). It had previously been determined that within the narrow size range of stones sampled, there was no measureable relationship between surface area and total abundance or richness ($r^2 = 0.019$, $p = 0.468$, $n = 30$; $r^2 = 0.020$, $p = 0.455$, $n = 30$ respectively, Rosser 1991).

Macroinvertebrates were counted and identified under a stereo dissecting microscope. Most taxa were identified to genus, and species where possible, using published keys and the reference collection held by the Australian Centre for Tropical Freshwater Research, James Cook University. Where species names were unavailable, numeric designations (e.g. sp. 1, sp. 2) were given. Some groups were identified only to higher taxonomic levels such as family (e.g. Chironomidae), or order (e.g. Oligochaeta). Early instar stages which could not be confidently separated were pooled (e.g. Trichoptera: Hydroptilidae).

Macroinvertebrates were assigned to functional feeding groups based on previous work in temperate Australian streams (Boulton and Lake 1992d), as well as a recent study of trophic food webs in Birthday Creek (Cheshire 1997). Although viewing communities in a functional perspective provides a useful adjunct in stream ecological studies to the more commonly used structural view, cautious interpretation is required (Mihuc 1997). Many stream animals do not adhere to strict feeding categories, and instead may exhibit generalised diets, or show shifts in feeding categories during development (Yule 1986). This is particularly true for those species utilising particulate organic matter (POM) and algae. However, predatory species and those that feed on vascular plant tissue (shredders), are generally more consistent in their diet (Cheshire 1997). With these reservations in mind, however, assignment to functional feeding groups permits response to disturbance to be assessed from both a structural and functional perspective, as recovery may also be defined as restoration of functional integrity (see review by Niemi *et al.* 1990).

Chlorophyll a and Benthic Organic Matter

Between April, 1994 and April, 1995, portions of stone surfaces in riffle and pool habitats were sampled for the determination of chlorophyll *a* levels. Individual stones were lifted from the bottom and surrounded by a dip net (as outlined above) to prevent loss of fauna. Stones were then carefully placed in a bucket of water where a scourer (surface area = 28.3cm^2) was used to remove algae from the upper surface of each stone. The scouring disk was then agitated for 3 minutes in a jar containing 30 ml of solvent (ethanol 95 %, methanol 5 %) to release algal fragments. Samples were kept in the dark and on ice prior to processing. Stones were then scrubbed (using a test-tube brush), and the resultant animals and organic material were added to the contents of the net, and transferred to containers of 70% alcohol and returned to the laboratory.

Chlorophyll *a* was determined following the method outlined in Lorenzen (1967). Within 12 hours of collection, the fraction retained for chlorophyll *a* was concentrated by washing through a glass fibre filter paper (Whatman GF / A) using distilled water. The filter was then mechanically ground in 2 ml of acetone (90 %) using a mortar and pestle until thoroughly macerated. Disrupting the cells in this manner ensures the complete extraction of the pigments. The sample was rinsed into a centrifuge tube, and the final volume made up to 10 ml with acetone. Samples were steeped for 2 hours at 4 ° C in the dark to extract pigments, after which they were centrifuged for 5 minutes at 5000 rpm. 3.0 ml of clarified extract was then decanted into a 1 cm glass cuvette in preparation for spectrophotometric determination of chlorophyll. The optical density (OD) was read at 750 and 665 nm before and after acidification with 2 drops of 1 *N* HCl. Chlorophyll *a* may be overestimated by including phaeopigments that absorb near the same wavelengths. Acidification of the sample converts chlorophyll *a* to phaeophytin, therefore allowing the chlorophyll *a* measurement to be corrected in the presence of phaeophytin. The readings obtained at 665 nm before and after acidification, corrected for the 750 nm reading, were entered into the following equations (Lorenzen 1967):

$$\text{Chlorophyll } a \text{ (mg / m}^3\text{)} = \frac{A \times K \times (665_o - 665_a) \times v}{V_f \times l}$$

$$\text{phaeophytin (mg / m}^3\text{)} = \frac{A \times K \times (R\,[665_a] - 665_o) \times v}{V_f \times l}$$

where A = absorption coefficient of chlorophyll *a* = 11.0, K = factor to equate the reduction in absorbancy to initial chlorophyll concentration = 2.43, 665_o = absorbance before acidification, 665_a = absorbance after acidification, v = volume of acetone used for extraction (ml), V_f = litres of water filtered, l = path length of cuvette (cm), R = maximum ratio of 665_o : 665_a in the absence of phaeopigments = 1.7.

Macroinvertebrates were separated from the particulate organic material under a stereo dissector microscope and were retained for identification. Particulate organic matter (>250 µm) was concentrated, using vacuum filtration, on to pre-dried (to standard weight), glass fibre filter papers (Whatmans GF / A). To determine organic content, samples were then oven dried (60 °C) for two days, weighed, ashed at 550 °C for 5 h, and reweighed.

The riffle could not be sampled for chlorophyll *a* and particulate organic material in November 1994, when stone surfaces were insufficiently submerged due to very low flow levels.

Data analysis

Prior to analysis, counts of invertebrates were transformed to log (x + 1), as recommended by Elliot (1977). Temporal variation in overall density, richness, and density of common taxa over the study period were determined using one-way ANOVAs using the statistical package SPSS™ for windows. Where significant (α=0.05), multiple comparison tests (Tukey HSD) were used to discriminate between consecutive months. Species richness is known to depend on sample size, and many of the diversity patterns reported in the literature may be arithmetic consequences of variations in the number of individuals (Rosenzweig 1995). Therefore, temporal change in Fisher's α, an index of diversity independent of sample size (Williams 1947), were calculated to determine whether observed changes in richness were real or artifacts of changes in abundance. To detect annual patterns in overall community structure, transformed data were ordinated using semi-strong hybrid multidimensional scaling (SSH, Faith 1991) using PATN software (Belbin 1988), using the reduced data matrix of those taxa comprising $\geq$ 0.05 % of total abundance over all samples, as rare species are capable of distorting the results (Gauch 1982). The recommended coefficient of dissimilarity between samples (Kulzynski) was used (Faith *et al.* 1987), with 100 random starting configurations for each analysis to reduce the chance of local optima (Faith 1990). Selection of the appropriate number of dimensions for the HMDS was based on the stress parameter which goves a measure of the "goodness of fit" of the ordination solution. This study follows the recommendations of Clarke (1993), where stress values $\leq$ 0.1 were used as a valid ordination configuration "with no real risk of drawing false inferences".Following the approach used by Boulton and Lake (1992b), time trajectories linking the centroids of groups of samples from consecutive months were plotted in ordination space to provide a visual representation of relative rate of change in community structure. To determine whether patterns evident from the ordinations were due to changes in species representation or species abundance, ordinations were also performed on presence/absence data. Pearson and Kendall correlations were computed between independent variables (water temperature, discharge, particulate organic matter, chlorophyll *a*, and days post-flood), and the first three ordination axes of multidimensional scaling plots using the PC-ORD package (McCune and Mefford 1995).

Resilience to flood disturbance was examined using a range of criteria: i) by comparing pre- and post-flood densities (overall, and densities of common taxa) and richness; non-significant differences, between the pre- and post-flood samples, or significant increases in the post-flood samples, were regarded as indicative of high resilience; ii) similarity in community structure (taxonomic composition and relative abundance) between pre- and post-flood assemblages was assessed using the proportional similarity index (PSI), recommended by Schoener (1968):

$$\mathrm{PSI}_{xy} = 1 - 0.5 \sum_{i=1}^{s} |p_{ix} - p_{iy}|$$

where p_{ix} and p_{iy} are the proportional abundances of species i in samples x and y; values range from 0 (no species common to both samples) to 1 (identical species lists and relative abundances); in this study, assemblages were considered to share high similarity when values of PSI ≥ 0.65 (represents the lowest PSI value among control samples); and iii) assemblage resilience was assessed by the degree of displacement of community structure in ordination space following flooding.

2.3 Results

Stream temperature and discharge data reflected the seasonal pattern of warm water and high discharge over the summer months, and cool water and low, stable discharge during the remainder of the year (Figure 2.2).

The discharge hydrographs for the two flood events which occurred during the study are presented in Figure 2.3. The first, peaking on January 31, 1994, was of much greater magnitude (>3x) than the second, which peaked on February 11, 1995. Both floods were characterised by a rapid increase in discharge.

Figure 2.2 Monthly water temperature ranges and total monthly discharge (A. Pomeroy, unpublished data) at Birthday Creek during the period of study (October, 1991-April 1995).

Discharge data prior to March, 1992 were unavailable; other breaks in the data were due to equipment failure.

Note that flow did not cease throughout the sampling period.

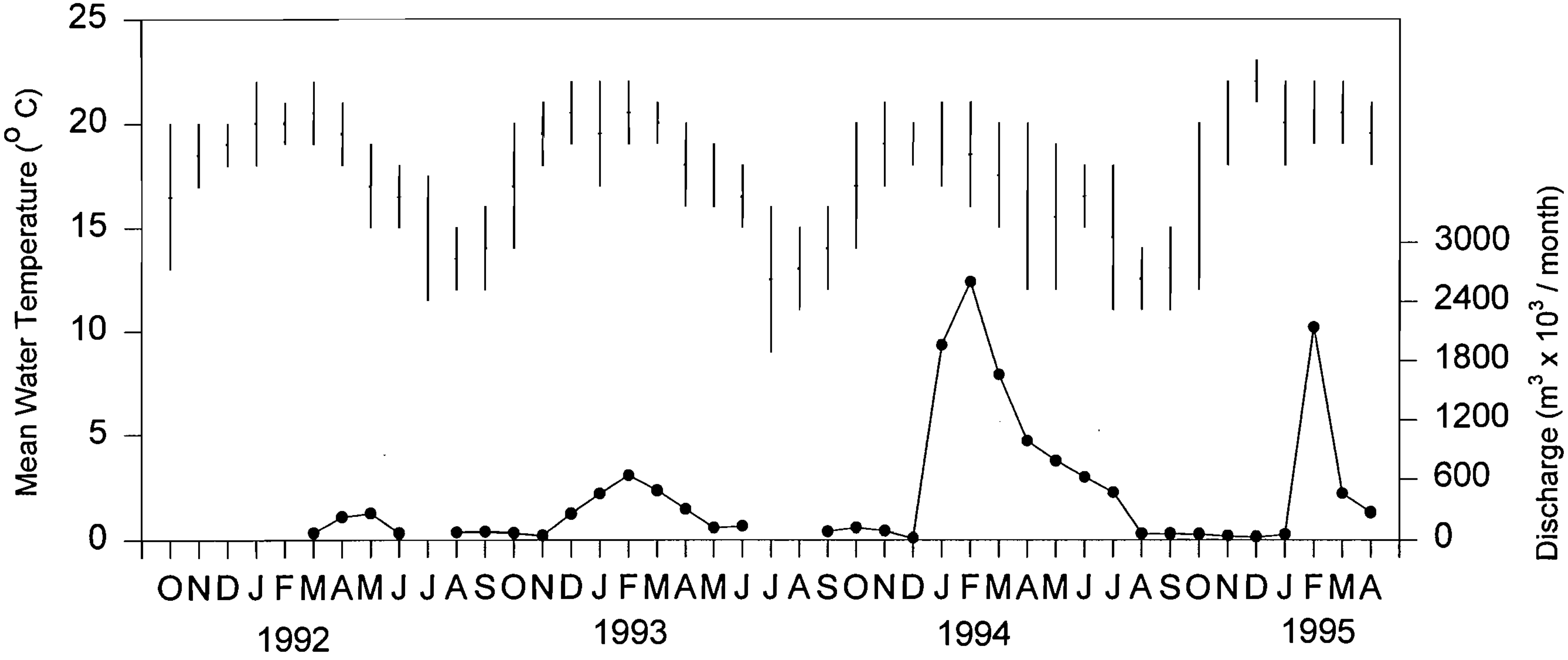
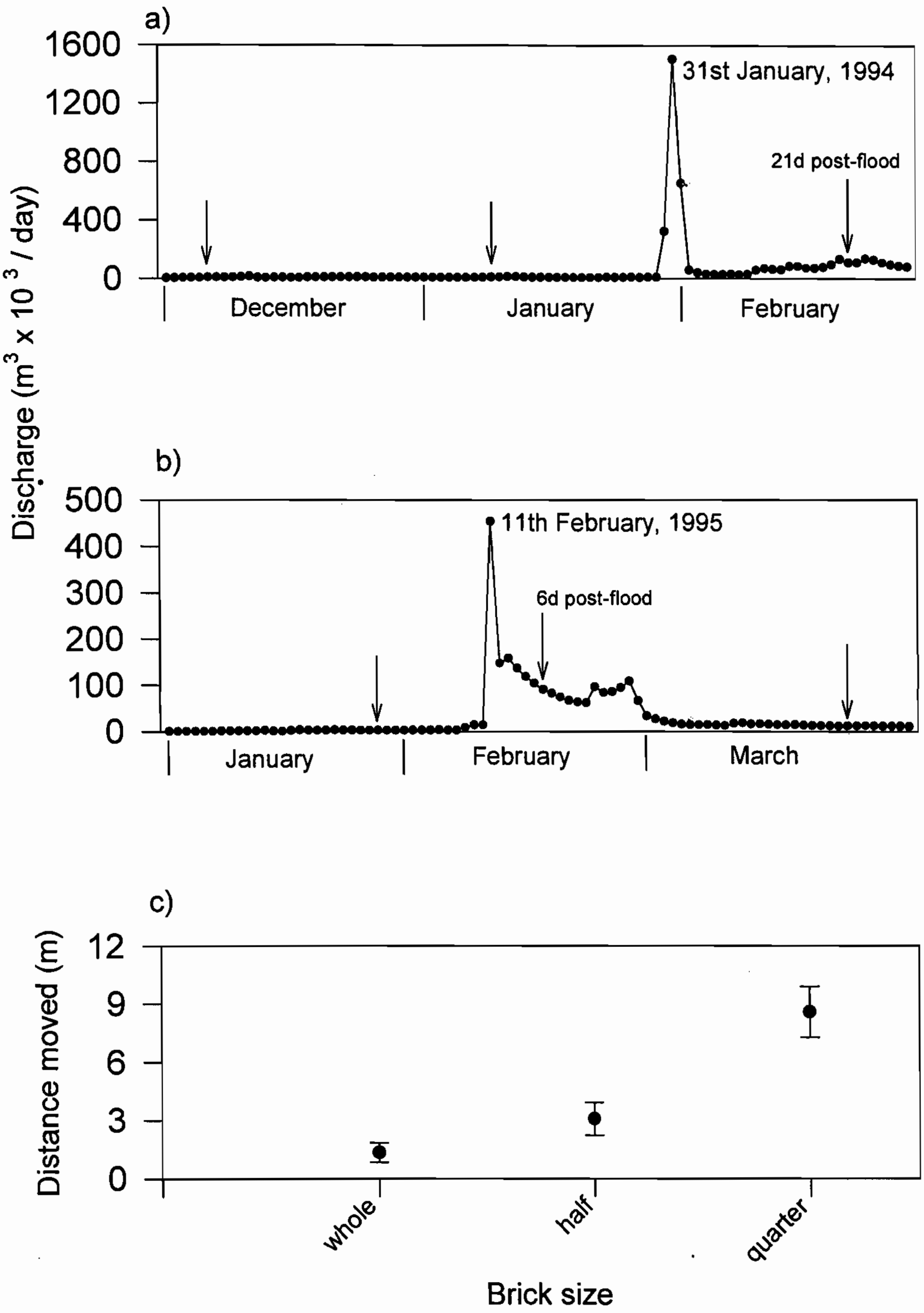

Mean Water Temperature (° C)
25
20
15
10
5
0
Discharge (m^3 x 10^3 / month)
3000
2400
1800
1200
600
0
O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A
1992
1993
1994
1995

Figure 2.3 Hydrographs of the two major floods at Birthday Creek during the study period, occurring in a) January, 1994, and b) February, 1995; and c) the resultant mean displacement (± 1 SE) of different sized bricks downstream following the February, 1995 flood.

The half-bricks correspond to the size range of natural stones sampled in this study.

Arrows indicate the day of sampling.


a)
1600
1200
800
400
0
31st January, 1994
21d post-flood
December
January
February
Discharge (m^3 x 10^3 / day)
b)
500
400
300
200
100
0
11th February, 1995
6d post-flood
January
February
March
c)
Distance moved (m)
12
9
6
3
0
whole
half
quarter
Brick size

In 1994, streamflow returned to base levels rapidly (within two days), while flow remained elevated for approximately three weeks following the 1995 flood. The flood in 1995 resulted in the downstream displacement of quarter-, half- and whole-bricks, with the distance moved highly size-dependent (Figure 2.3). This indicates that this, and presumably the flood of higher magnitude (1994), were of sufficient intensity to mobilise the substratum. Of particular interest was the movement of the half-bricks, which correspond to the size range of the natural stones sampled in this study.

The stone fauna of riffle and pool habitats

A total of 75 taxa/species were collected from the riffle and 51 taxa from the pool over the study period at Birthday Creek (Table 2.1), the overwhelming majority of which were insects.

The most common riffle taxa were the dipterans *Simulium* sp. (filterers), Chironomidae (collector-gatherers, collector-filterers, predators), Oligochaeta (collector-gatherers), *Kingolus* sp. (collector-scrapers) and *Dinotoperla* sp. (collector-scrapers). Chironomids, oligochaetes and *Kingolus* sp. were also common in the pool, as were the mayflies *Austrophlebioides* sp. 1 and *Baetis* sp. (both collector-scrapers).

Variance in monthly densities, expressed as the coefficient of variation (CV = standard deviation/mean) was used as a comparative measure of population variability (Pearson *et al.* 1986, Grossman *et al.* 1990, Palmer *et al.* 1997). Following the classification scheme proposed by Freeman *et al.* (1988), all common taxa from both habitats may be regarded as having moderately ($50\ \% < CV \leq 75\ \%$) to highly fluctuating ($CV \geq 76\ \%$) population sizes (Figure 2.4)

Although the total number of comparable temperate Australian studies which have sampled individual stones is limited (Table 2.2) it is evident that the total number of taxa collected from the riffle in Birthday Creek is relatively high. This is despite the fact that the highly diverse Chironomidae, as well as less diverse groups (e.g. Oligochaeta) were unresolved in the current study.

Table 2.1: Macroinvertebrate taxa collected from stones at Birthday Creek over the sampling period from riffle (October, 1991 – April, 1995) and pool (January, 1994 – April, 1995) habitats and their allocation to functional feeding groups (FFG). Mean abundance (mean), standard error (se), and coefficient of variation (CV) over all samples (area = 0.08 m^2) during this period is given for each taxon. Taxa listed in boldface were those comprising the reduced species data matrix for the ordination procedure (see data analysis section).

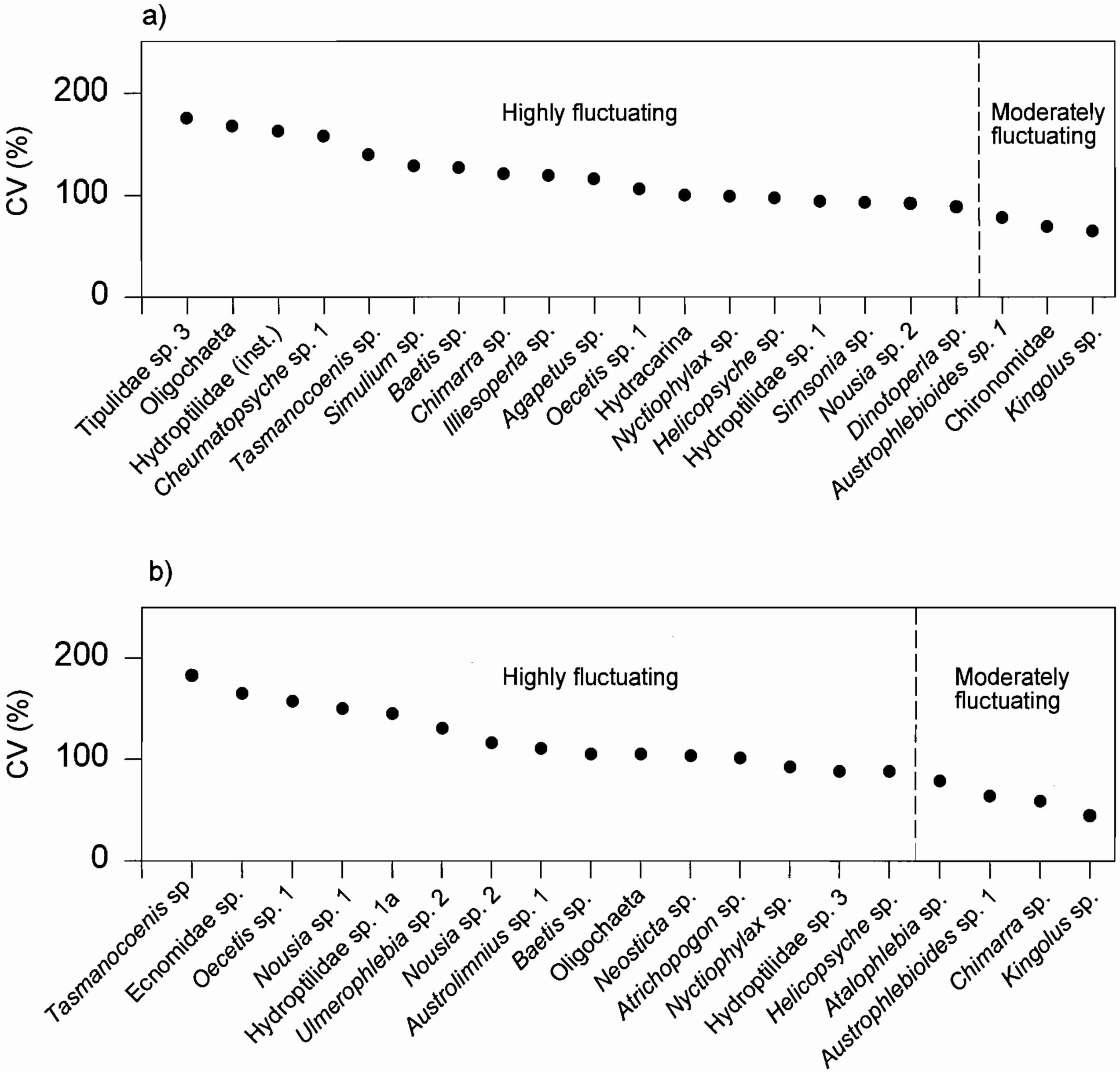
	FFG	Riffle				Pool			
			mean	SE	CV		mean	SE	CV
Insect orders:									
Coleoptera									
(a) 'horn'	Cscr	X	0.003	0.003	6.56				
(a) sp. 3	Cscr	X	0.032	0.024	4.89	X	0.126	0.089	2.80
(a) sp. 4	Cscr	X	0.228	0.057	1.63	X	0.008	0.008	4.00
(a) sp. 8	Cscr	X	0.012	0.012	6.56				
***Austrolimnius* (a) sp. 1**	Cscr	X	0.167	0.046	1.82	X	**0.401**	**0.110**	**1.10**
Austrolimnius (a) sp. 4	Cscr	X	0.006	0.006	6.56	X	0.031	0.031	4.00
Elmidae (l) sp. 1	Cscr	X	0.131	0.040	1.98	X	0.024	0.024	4.00
Elmidae (l) sp. 1a	Cscr	X	0.076	0.039	3.37				
Elmidae (l) sp. 2a	Cscr	X	0.432	0.108	1.64	X	0.094	0.041	1.72
***Kingolus* sp.**	Cscr	X	**4.805**	**0.477**	**0.65**	X	**7.753**	**0.871**	**0.45**
Kingolus sp. 2	Cscr	X	0.093	0.070	4.91				
Kingolus sp. 3	Cscr	X	0.026	0.018	4.59				
Helodidae sp.	Cg	X	0.160	0.045	1.87				
***Simsonia* sp.**	Cscr	X	**2.881**	**0.409**	**0.93**	X	0.008	0.008	4.00
Psephenidae sp. 1	Cscr	X	0.130	0.024	1.20	X	0.016	0.011	2.73
Ptilodactylidae (l)	Shr	X	0.003	0.003	6.56				
Diptera									
***Atrichopogon* sp.**	Cscr	X	0.271	0.129	3.12	X	**0.471**	**0.119**	**1.01**
Berosus sp.	Cscr					X	0.008	0.008	4.00
Ceratopogonidae sp. 2	Cscr	X	0.158	0.042	1.74				
Chironomidae	Cg/Cf	X	**24.954**	**2.621**	**0.69**	X	**20.218**	**3.002**	**0.59**
Dixa sp.	Cg	X	0.190	0.050	1.72	X	0.048	0.028	2.36
Empididae sp.	Cg	X	0.650	0.120	1.21	X	0.032	0.018	2.29
***Simulium* sp.**	Cf	X	**41.803**	**8.217**	**1.29**	X	0.024	0.017	2.88
Tipulidae sp. 2	Pred					X	0.016	0.011	2.73
Tipulidae sp. 3	Pred	X	**1.240**	**0.333**	**1.76**	X	0.008	0.008	4.00
Ephemeroptera									
***Atalophlebia* sp.**	Cg	X	0.058	0.032	3.64	X	**0.674**	**0.134**	**0.79**
Atalomicria sp.	Cg	X	0.053	0.018	2.21	X	0.008	0.008	4.00
***Austrophlebioides* sp. 1**	Cscr	X	**1.505**	**0.180**	**0.78**	X	**1.823**	**0.293**	**0.64**
Austrophlebioides sp. 2	Cscr	X	0.082	0.044	3.58	X	0.039	0.028	2.80
***Baetis* sp.**	Cscr	X	**4.093**	**0.790**	**1.27**	X	**1.103**	**0.289**	**1.05**
***Nousia* sp. 1**	Cscr	X	0.203	0.089	2.88	X	**0.259**	**0.097**	**1.50**
***Nousia* sp. 2**	Cscr	X	**0.900**	**0.127**	**0.92**	X	**0.783**	**0.227**	**1.16**
Mirawara sp.	Pred	X	0.009	0.006	4.81				
***Tasmanocoenis* sp.**	Cg	X	**1.866**	**0.397**	**1.40**	X	**0.250**	**0.114**	**1.83**
Ulmerophlebia sp.	Cg					X	**0.384**	**0.124**	**1.30**
Lepidoptera									
sp. 1	Shr	X	0.123	0.058	3.11	X	0.008	0.008	4.00
sp. 2	Shr	X	0.094	0.041	2.85				
Megaloptera									
Archichauliodes sp.	Pred	X	0.030	0.015	3.34	X	0.048	0.032	2.71
Odonata									
Aeshnidae	Pred	X	0.042	0.013	2.07				

Table 2.1 continued

	FFG	Riffle				Pool			
		taxa	mean	SE	CV	taxa	mean	SE	CV
Corduliidae	Pred	X	0.050	0.018	2.34	X	0.047	0.025	2.15
Chorismagrion risi	Pred	X	0.003	0.003	6.56				
Diphlebia euphaeoides	Pred	X	0.124	0.029	1.51	X	0.018	0.070	2.38
Episynlestes cristatus	Pred	X	0.009	0.006	4.81	X	0.180	0.123	2.74
Eusynthemis nigra	Pred	X	0.003	0.003	6.56	X	0.016	0.011	2.73
Gomphidae sp.	Pred	X	0.023	0.010	2.92	X	0.024	0.017	2.88
Neosticta fraseri	Pred	X	0.003	0.003	6.56	X	**0.558**	**0.144**	**1.03**
Synlestes tropicus	Pred	X	0.047	0.020	2.73	X	0.024	0.024	4.00
Plecoptera									
***Dinotoperla* sp.**	Cscr	X	**4.198**	**0.057**	**0.89**	X	0.032	0.018	2.29
***Illiesoperla* sp.**	Cg	X	**0.710**	**0.129**	**1.19**				
Trinotoperla sp.	Csgr	X	0.056	0.032	3.73				
Trichoptera									
***Agapetus* sp.**	Cscr	X	**2.142**	**0.378**	**1.16**				
Anisocentropus	Shr	X	0.044	0.016	2.31				
***Cheumatopsyche* sp. 1**	Cf	X	**1.272**	**0.306**	**1.58**	X	0.008	0.008	4.00
***Chimarra* sp.**	Pred	X	**2.509**	**0.462**	**1.21**	X	0.016	0.011	2.73
Ecnomidae sp.	Pred	X	0.085	0.040	3.09	X	**0.306**	**0.126**	**1.65**
***Helicopsyche* sp.**	Cscr	X	**1.953**	**0.288**	**0.97**	X	**0.558**	**0.123**	**0.88**
Hydrobiosinae sp. 1	Pred	X	0.147	0.034	1.54				
Hydroptilidae, early instars	Cscr	X	0.556	0.156	1.83				
Hydroptilidae sp. 1	Cscr	X	**2.965**	**0.423**	**0.94**				
Hydroptilidae sp. 1a	Cscr	X	**1.693**	**0.421**	**1.63**	X	**0.376**	**0.136**	**1.45**
Hydroptilidae sp. 2	Cscr	X	0.388	0.106	1.80	X	0.016	0.011	2.73
Hydroptilidae sp. 3	Cscr	X	0.089	0.033	2.44	X	**0.308**	**0.068**	**0.88**
Hydroptilidae sp. 5	Cscr	X	0.018	0.008	2.94	X	0.008	0.008	4.00
Hydroptilidae sp. 6	Cscr	X	0.012	0.009	5.13				
Hydroptilidae sp. 7	Cscr	X	0.003	0.003	6.56	X	0.048	0.028	2.36
Leptoceridae sp. 1	Cscr	X	0.009	0.009	6.56				
Leptoceridae sp. 2	Cscr	X	0.015	0.010	4.68				
***Nyctiophylax* sp.**	Pred	X	**3.869**	**0.586**	**0.99**	X	**0.643**	**0.148**	**0.92**
Odontoceridae sp.	Cscr	X	0.015	0.015	6.56				
***Oecetis* sp. 1**	Pred	X	**0.868**	**0.140**	**1.06**	X	**0.353**	**0.139**	**1.57**
Oecetis sp. 2	Pred	X	0.050	0.036	4.72	X	0.056	0.032	2.33
Philorheithridae	Pred	X	0.015	0.010	4.26				
Plectrocnemia sp.	Pred	X	0.003	0.003	6.56	X	0.032	0.025	3.08
Polycentropidae sp. 5	Pred	X	0.003	0.003	6.56				
Rhyacophilidae	Pred	X	0.006	0.006	6.56				
Stenopsychodes sp.	Pred	X	0.006	0.006	6.56				
Non-insect orders:									
Gastropoda									
Ferrissia sp.	Cscr	X	0.006	0.006	6.56				
Hydracarina	Pred	X	**0.597**	**0.091**	**1.00**	X	0.032	0.018	2.29
Oligochaeta	Cg	X	**5.909**	**1.512**	**1.68**	X	**1.784**	**0.467**	**1.05**
Turbellaria									
Dugesia sp.	Pred	X	0.044	0.018	2.63				
Total number of taxa		75				51			

Figure 2.4 Coefficient of variation (expressed as a percentage) between mean monthly densities of the common taxa in a) riffle and b) pool habitats over the full study period at Birthday Creek. Riffle samples were collected between October, 1991 and April, 1995; pool samples between January, 1994 and April, 1995.

The distinction between moderately and highly fluctuating population sizes (dashed line) follows that proposed by Freeman *et al.* (1988) and represents CV values ≥ 76.0 %.


a)
CV (%)
200
100
0
Highly fluctuating
Moderately fluctuating
Tipulidae sp. 3
Oligochaeta
Hydroptilidae (inst.)
Cheumatopsyche sp. 1
Tasmanocoenis sp.
Simulium sp.
Baetis sp.
Chimarra sp.
Illiesoperla sp.
Agapetus sp.
Oecetis sp. 1
Hydracarina
Nyctiophylax sp.
Helicopsyche sp.
Hydroptilidae sp. 1
Simsonia sp.
Nousia sp. 2
Dinotoperla sp.
Austrophlebioides sp. 1
Chironomidae
Kingolus sp.
b)
CV (%)
200
100
0
Highly fluctuating
Moderately fluctuating
Tasmanocoenis sp
Ecnomidae sp.
Oecetis sp. 1
Nousia sp. 1
Hydroptilidae sp. 1a
Ulmerophlebia sp. 2
Nousia sp. 2
Austrolimnius sp. 1
Baetis sp.
Oligochaeta
Neosticta sp.
Atrichopogon sp.
Nyctiophylax sp.
Hydroptilidae sp. 3
Helicopsyche sp.
Atalophlebia sp.
Austrophlebioides sp. 1
Chimarra sp.
Kingolus sp.

Groups such as the Chironomidae are typically very diverse in Wet Tropics streams (e.g. Pearson *et al.* 1986). Current work on the taxonomy of chironomids in Birthday Creek has revealed very high diversity, with 42 species identified so far from drift sampling, the majority of which also occur on stone surfaces (B. McKie, pers. comm.). Further taxonomic resolution of the freshwater fauna, the Chironomidae in particular, is therefore likely to greatly increase the estimate of the total number of species on stones in Birthday Creek.

Table 2.2 Total number of taxa/species collected on stream stones in riffles in this study compared with other regions.

Location	Number of taxa / species	Reference
Temperate		
Victoria, Australia	55	Lake *et al.* 1985a
Acheron River	34-38	Lake *et al.* 1985b
Toorongo River	42-66	Lake *et al.* 1985b
Taggerty and Steavenson Rivers	161	Downes *et al.* 1993
Idaho, USA	59	Minshall 1981
New Zealand	52	Towns 1979
Tropics		
North Queensland, Australia		
Birthday Creek	75[a]	This study

a = conservative value

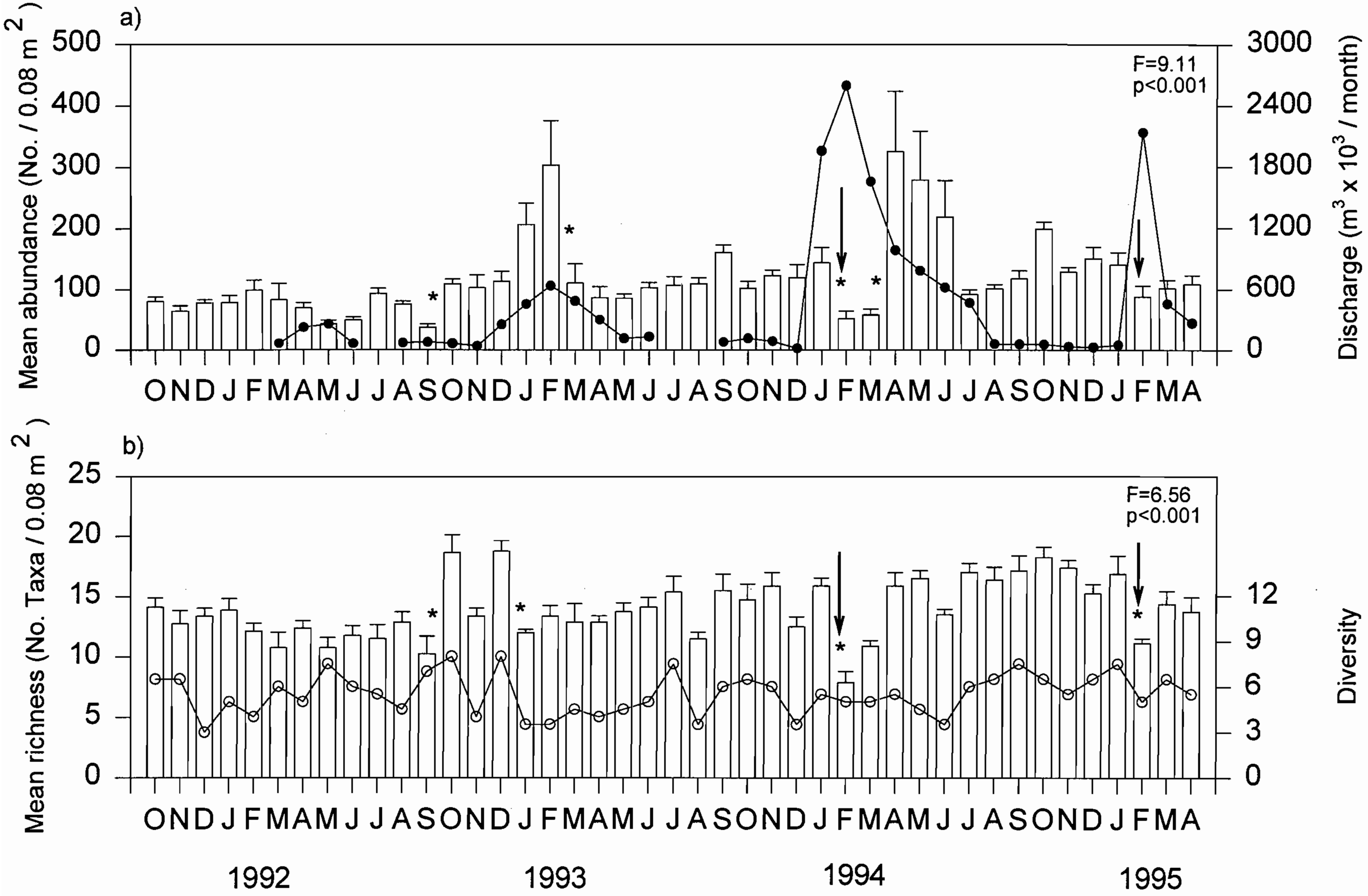
Temporal variation of macroinvertebrate riffle fauna

There was significant temporal variation in total numbers of macroinvertebrates on stones in the riffle (one-way ANOVA, d.f.=42, F=9.11, $p<0.001$) (Figure 2.5a). Highest benthic densities over the sampling period were observed in late summer (1993) and autumn (1994), coinciding with the time of high and variable flows or as flow was declining following the wet season. Numbers were low during the dry season, when flow was low and stable, tending to increase in the late dry season. Mean richness on stones in the riffle (Figure 2.5b) also displayed temporal variation (one-way ANOVA, d.f.=42, $p<0.001$), tending to increase in the late dry/early wet, particularly during the driest year of this study (1992).

Figure 2.5 Mean (± 1 SE) a) abundance and b) richness of macroinvertebrates on stream stones sampled monthly from a riffle at Birthday Creek (October, 1991-April, 1995). The total monthly discharge is shown in solid circles (a), with arrows indicating the timing of the two major floods.

Results of one-way ANOVAs (effect of time) on abundance and richness are given (d.f. = 42, $\alpha = 0.05$), with asterisks indicating significant differences between consecutive months (Tukey's HSD multiple comparison test, $\alpha = 0.05$) (significant differences between non-consecutive months are not indicated).

Changes in Fisher's diversity index (α) over the study period are shown in open circles (b).


a)
Mean abundance (No. / 0.08 m^2)
0
100
200
300
400
500
Discharge (m^3 x 10^3 / month)
0
600
1200
1800
2400
3000
F=9.11
p<0.001
*
O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A
b)
Mean richness (No. Taxa / 0.08 m^2)
0
5
10
15
20
25
Diversity
0
3
6
9
12
F=6.56
p<0.001
O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A
1992
1993
1994
1995

The largest flood (January-February, 1994) sampled 21 days following the peak in discharge, significantly reduced overall densities in the riffle (Tukey HSD, $p<0.05$), while the smaller flood in 1995, sampled closer to the peak (six days) had little effect on numbers (Tukey HSD, $p>0.05$). Both floods significantly reduced overall richness in the riffle (Tukey HSD, $p<0.05$ in both cases), although Fisher's α (Figure 2.5b) indicates that much of the decrease in richness following the 1994 flood was a consequence of a drop in numbers. In 1995, however, the reduction in richness was mirrored by a reduction in diversity. This indicates that 21 days and six days, respectively, were insufficient periods for the recovery of density and richness of riffle fauna to pre-flood levels following floods of these magnitudes. Densities had recovered to pre-flood levels within 45 days, while richness was similar within 45 and 40 days following the 1994 and 1995 floods, respectively (Tukey HSD, $p>0.05$ in all cases).

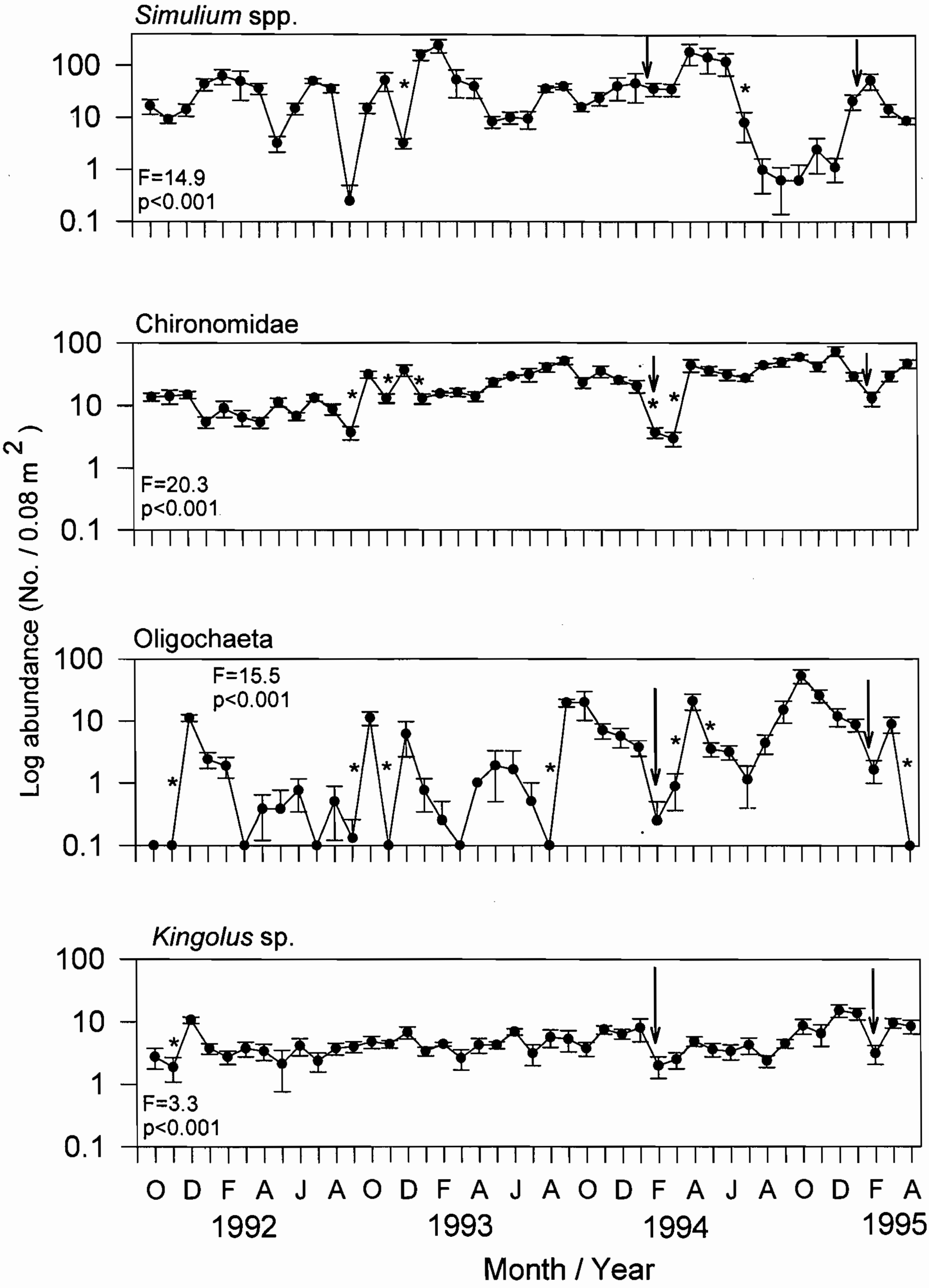
The common riffle taxa (Figure 2.6) all exhibited significant temporal changes in abundance (one-way ANOVA, d.f.=42, $p<0.001$ in all cases). Much of the observed pattern in overall densities during the wet season was due to increases in abundance of the blackfly larvae, *Simulium* sp. (e.g. responsible for 60% of increase in total numbers in early autumn, 1994). Late dry season increases in densities of Chironomidae, Oligochaeta, and *Nyctiophylax* sp. contributed to the significant increase in overall density in 1992, which was a particularly dry year. During 1992, these taxa displayed greater annual fluctuations in densities, especially during the dry season, compared with the annual pattern observed in 1994 following the largest flood.

The common taxa showed a range of responses to the floods (Table 2.3). Many had high resilience, with post-flood densities not significantly different from pre-flood levels; recovery for these taxa was completed by day 21 (1994) and day six (1995). Most species had a consistent response to the two floods. Only the Chironomidae showed a different response, being significantly reduced in numbers following the largest flood (1994), but recovering to pre-flood levels six days after the smaller flood (1995), which may be a reflection of flood magnitude or indicate a different suite of species involved. Two of the common taxa, the plecopteran, *Dinotoperla* sp. and the trichopteran, *Nyctiophylax* sp., showed relatively low resilience, being significantly lower in numbers following both floods.

Figure 2.6 Mean abundance (± 1 SE) of the common macroinvertebrate taxa on stream stones sampled monthly from a riffle at Birthday Creek (October, 1991-April, 1995).

Arrows indicate the timing of the two major floods.

Results of one-way ANOVAs (effect of time) on abundance are given (d.f. = 42, $\alpha = 0.05$), with asterisks indicating significant differences between consecutive months (Tukey's HSD multiple comparison test, $\alpha = 0.05$) (significant differences between non-consecutive months are not indicated).



Simulium spp.
F=14.9
p<0.001
Chironomidae
F=20.3
p<0.001
Oligochaeta
F=15.5
p<0.001
Kingolus sp.
F=3.3
p<0.001
100
10
1
0.1
*
Log abundance (No. / 0.08 m 2)
O D F A J A O D F A J A O D F A J A O D F A
1992
1993
1994
1995
Month / Year

continued.....

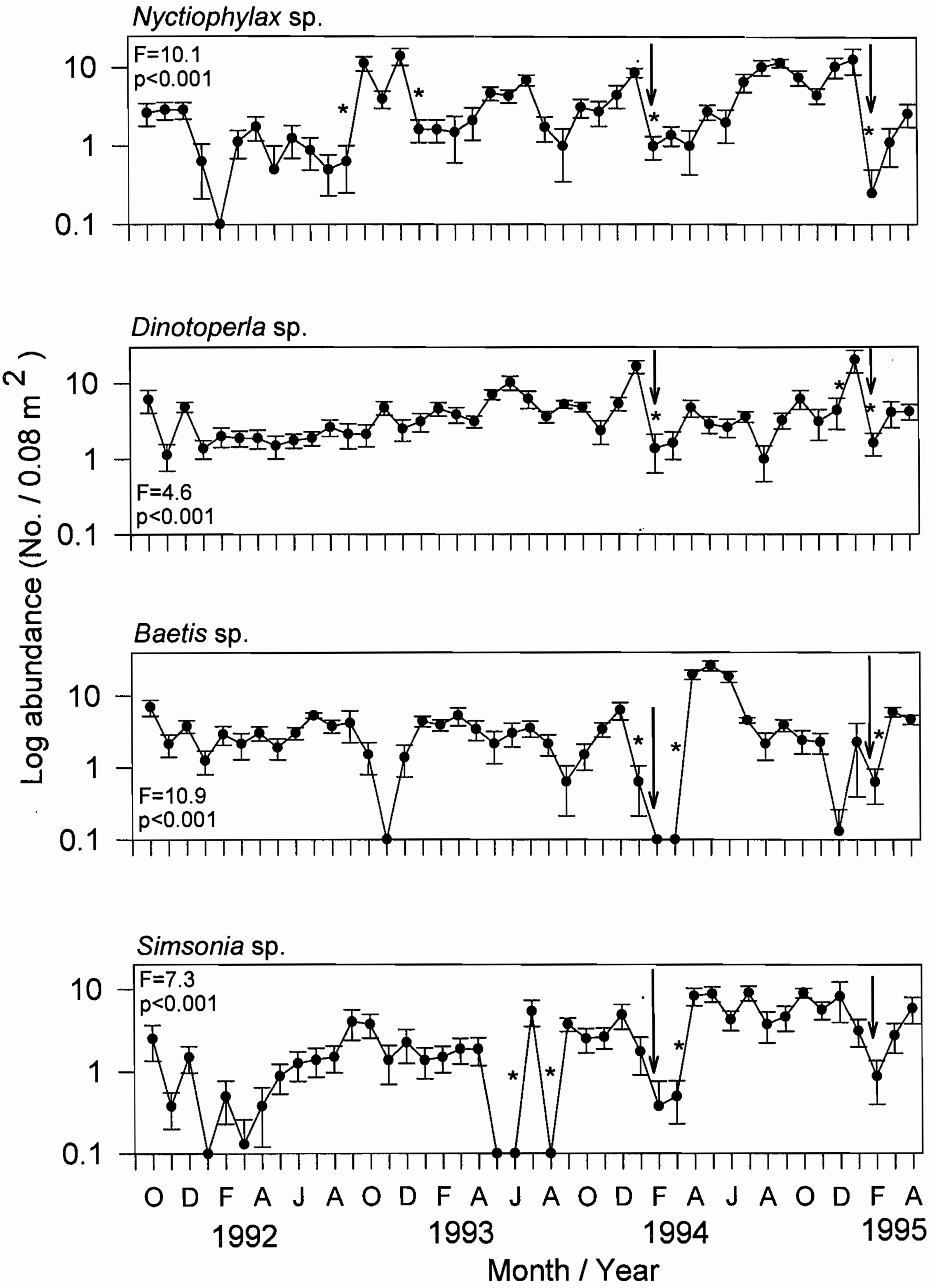

Nyctiophylax sp.
F=10.1
p<0.001
Dinotoperla sp.
F=4.6
p<0.001
Baetis sp.
F=10.9
p<0.001
Simsonia sp.
F=7.3
p<0.001
10
1
0.1
*
Log abundance (No. / 0.08 m 2)
O D F A J A O D F A J A O D F A J A O D F A
1992
1993
1994
1995
Month / Year

Table 2.3 Comparison of pre- and post-flood total abundance, richness, and densities of the common riffle taxa in response to the 1994 and 1995 flood events. n.s. = non-significant difference between pre- and post-flood samples, ↓ = significantly lower densities in the post-flood samples. Samples were discriminated using Tukey HSD test performed on the entire data set ($p<0.05$). Within-sample variance, indicated by the coefficient of variation (CV) before and after each flood are given, with post-flood increases indicated in boldface.

Taxa	1994 Flood (recovery period = 21d)			1995 Flood (recovery period = 6d)		
	Density	CV pre-	CV post-	Density	CV pre-	CV post-
Simulium sp.	n.s.	1.62	0.81	n.s.	0.93	**0.97**
Oligochaeta	n.s.	0.82	**2.88**	n.s.	0.65	**1.14**
Kingolus sp.	n.s.	1.21	**1.27**	n.s.	0.61	**0.94**
Baetis sp.	n.s.	1.90	**2.14**	n.s.	2.34	1.47
Simsonia sp.	n.s.	1.36	**2.83**	n.s.	1.03	**1.55**
Chironomidae	↓	0.56	0.42	n.s.	0.36	**0.66**
Nyctiophylax sp.	↓	0.38	**0.93**	↓	1.03	**2.83**
Dinotoperla sp.	↓	0.55	**2.83**	↓	0.93	**0.94**
Total abundance	↓	0.49	**0.67**	n.s.	0.40	**0.57**
Total richness	↓	0.11	**0.33**	↓	0.25	0.11

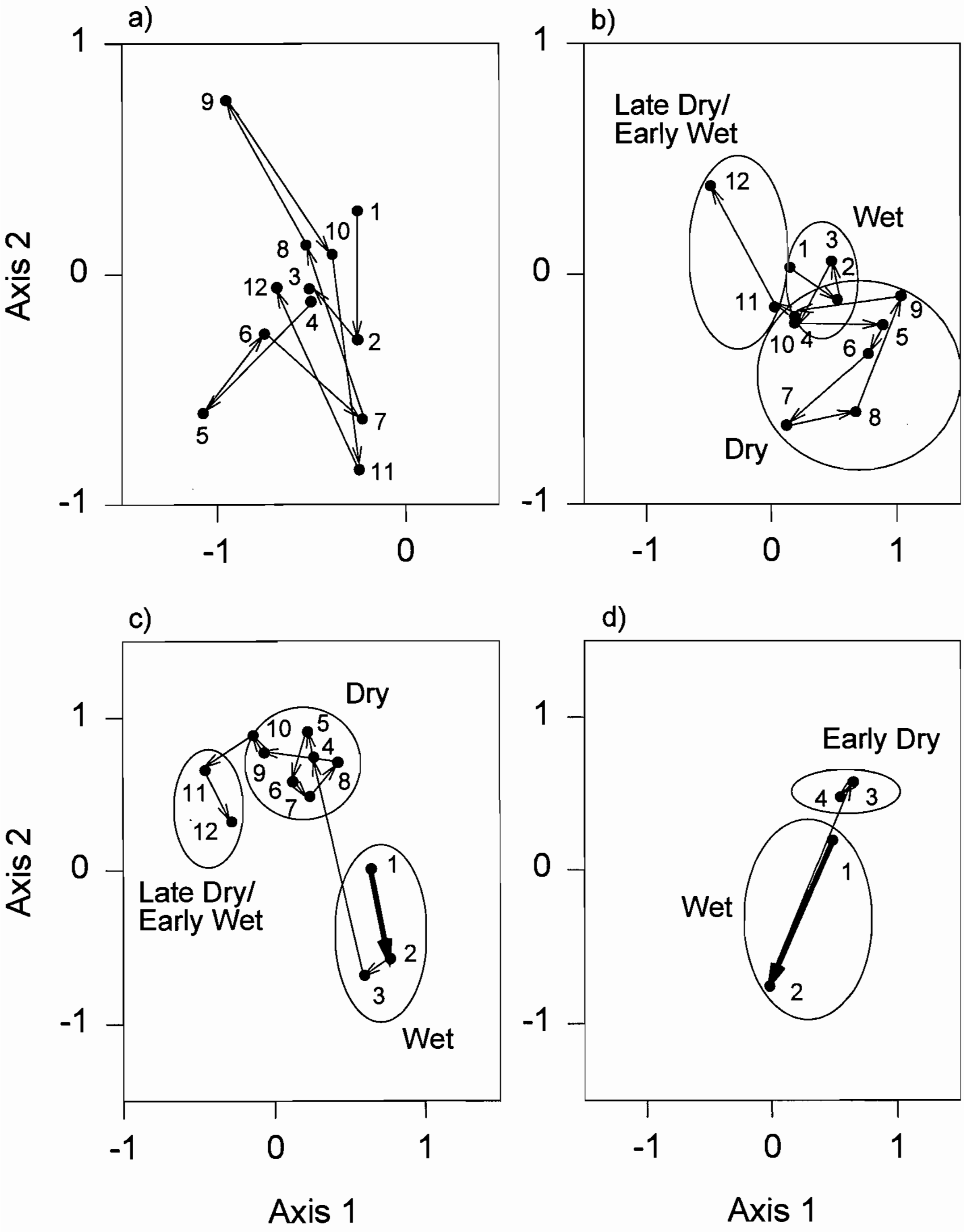
Within-sample variation (indicated by the coefficient of variation) increased following both floods for the majority of taxa, regardless of whether resilience was high or low.

Ordination of the samples shows that temporal variation in community structure on stones in the riffle was evident among years at Birthday Creek (Figure 2.7). In years where major flooding occurred (1994 and, to a lesser degree, 1995), distinct wet and dry season assemblages were observed in the first three dimensions in ordination space. Ordination of presence/absence data yielded similar solutions in the first three dimensions and seasonal cycles persisted (less distinct in drier years). Therefore, the major annual and seasonal changes in assemblage composition reflected changes in species representation more than changes in relative abundance. A major transition between wet and dry season assemblages ocurred in the late wet (early autumn), coinciding with a shift in dominance by *Simulium* sp. following flooding, to dominance by Chironomidae in the dry season assemblage.

Figure 2.7 Ordination plot of the first two dimensions of SSH (semi-strong hybrid multidimensional scaling) of macroinvertebrate communities on stream stones from a riffle at Birthday Creek sampled monthly between January, 1992 and April, 1995.

For clarity, years are presented in separate plots (a, b, c, d = 1992, 1993, 1994 and 1995 respectively) and months are represented by numbers (1=January, 2=February, etc.), with arrows linking consecutive months.

Note that 1992 (a), and to a lesser degree 1993 (b), were very dry years, while 1994 (c) and 1995 (d) were characterised by severe, substratum-moving floods. Boldface arrows link pre- (January) and post-flood (February) samples.



a)
b)
c)
d)
Axis 2
Axis 2
Axis 1
Axis 1
1
0
-1
Late Dry/
Early Wet
Wet
Dry
Early Dry
9
10
8
1
12
3
4
2
6
5
7
11

This transition period was the time of maximum turnover of taxa (indicated by the inter-centroid distance between consecutive months), while turnover during the dry season was relatively low, increasing slightly in the late dry/early wet (Figure 2.7c). In drier years (1992 and 1993), seasonal shifts in community structure became increasingly difficult to distinguish, with greater overlap between wet and dry season assemblages (Figure 2.7a and 2.7b, respectively), particularly evident in 1992, the driest year of the study. Species turnover also appeared to be linked to the amount of rainfall during the wet season, with the highest inter-monthly turnover observed in the driest years (1992 and 1993), and was relatively high during the dry season. In contrast, where large wet season floods occurred, dry season turnover of species was relatively low (Figure 2.7c). Correlations between environmental variables and ordination axes of multidimensional scaling plots indicate the importance of discharge (axes 2 and 3), days post-flood (axis 3), and levels of particulate organic matter (axis 3), with many of the common taxa showing significant correlations with axes 2 and 3 (Table 2.4). Of the variables measured, chlorophyll *a* and temperature did not show significant correlations with the first three axes.

Table 2.4 Pearson and Kendall correlations of the first three axes (% variation explained by each axis is given in parentheses) of multidimensional scaling ordination with five independent variables and selected riffle taxa. Significant correlations ($p < 0.05$) are indicated in boldface.

	Axis 1 (48.67 %)	Axis 2 (26.89 %)	Axis 3 (11.06 %)
Discharge	-0.230	**-0.587**	**-0.626**
Days post-flood	0.210	0.484	**0.696**
POM	-0.454	0.322	**0.623**
Chlorophyll *a*	-0.317	0.068	0.361
Temperature	0.280	-0.095	0.002
Illiesoperla sp.	0.317	-0.515	**-0.894**
Tasmanocoenis sp.	0.040	**0.845**	**0.623**
Baetis sp.	0.202	-0.324	**-0.715**
Nousia sp. 2	0.240	0.275	**0.605**
Chironomidae	0.001	**0.566**	0.437
Simulium sp.	0.462	**-0.648**	**-0.965**
Empididae sp.	0.002	**0.789**	**0.588**
Agapetus sp.	0.021	-0.484	**-0.620**
Nyctiophylax sp.	0.047	**0.666**	**0.798**
Chimarra sp.	0.331	**-0.735**	**-0.731**
Cheumatopsyche sp. 1	0.041	-0.549	**-0.759**
Hydroptilidae sp. 1	0.075	**0.717**	**-0.629**
Hydroptilidae sp. 1a	0.360	**0.860**	0.082

In the riffle, both the 1994 and 1995 floods had little effect on the rankings of the two dominant taxa, *Simulium* sp. and Chironomidae (Table 2.5). However, many of the remaining taxa showed substantial fluctuations in rank abundance following both substratum-moving floods, with the proportional similarity values (PSI) indicating little overlap between pre- and post-flood assemblages, in terms of overall community composition and relative abundance. Lowest similarity was observed following the 1995 flood (PSI = 0.46), which may reflect the fact that samples were taken only 6 days following the flood peak, compared with 21 days following the 1994 event.

Table 2.5 Common taxa (ranked in order of abundance) on stones in the riffle before and after the two major flood events, and comparison of overall community similarity (Proportional Similarity Index, PSI). PSI values ≥ 0.65 indicate high overlap (similarity) between assemblages. "–" indicates taxon absent in post-flood samples.

	1994			1995	
	Ranking			Ranking	
	pre-flood	post-flood		pre-flood	post-flood
Simulium sp.	1	1	Chironomidae	1	2
Chironomidae	2	2	*Simulium* sp.	2	1
Dinotoperla sp.	3	4	*Dinotoperla* sp.	3	6
Nyctiophylax sp.	4	7	*Kingolus* sp.	4	4
Kingolus sp.	5	3	*Nyctiophylax* sp.	5	14
Tasmanocoenis sp.	6	15	Oligochaeta	6	7
Tipulidae sp. 3	7	6	*Tasmanocoenis* sp. 1	7	14
Cheumatopsyche sp. 1	8	15	*Simsonia* sp.	8	10
Oligochaeta	9	14	*Cheumatopsyche* sp. 1	9	–
Chimarra sp.	10	15	*Chimarra* sp. 1	10	3
	PSI=0.54			PSI=0.46	

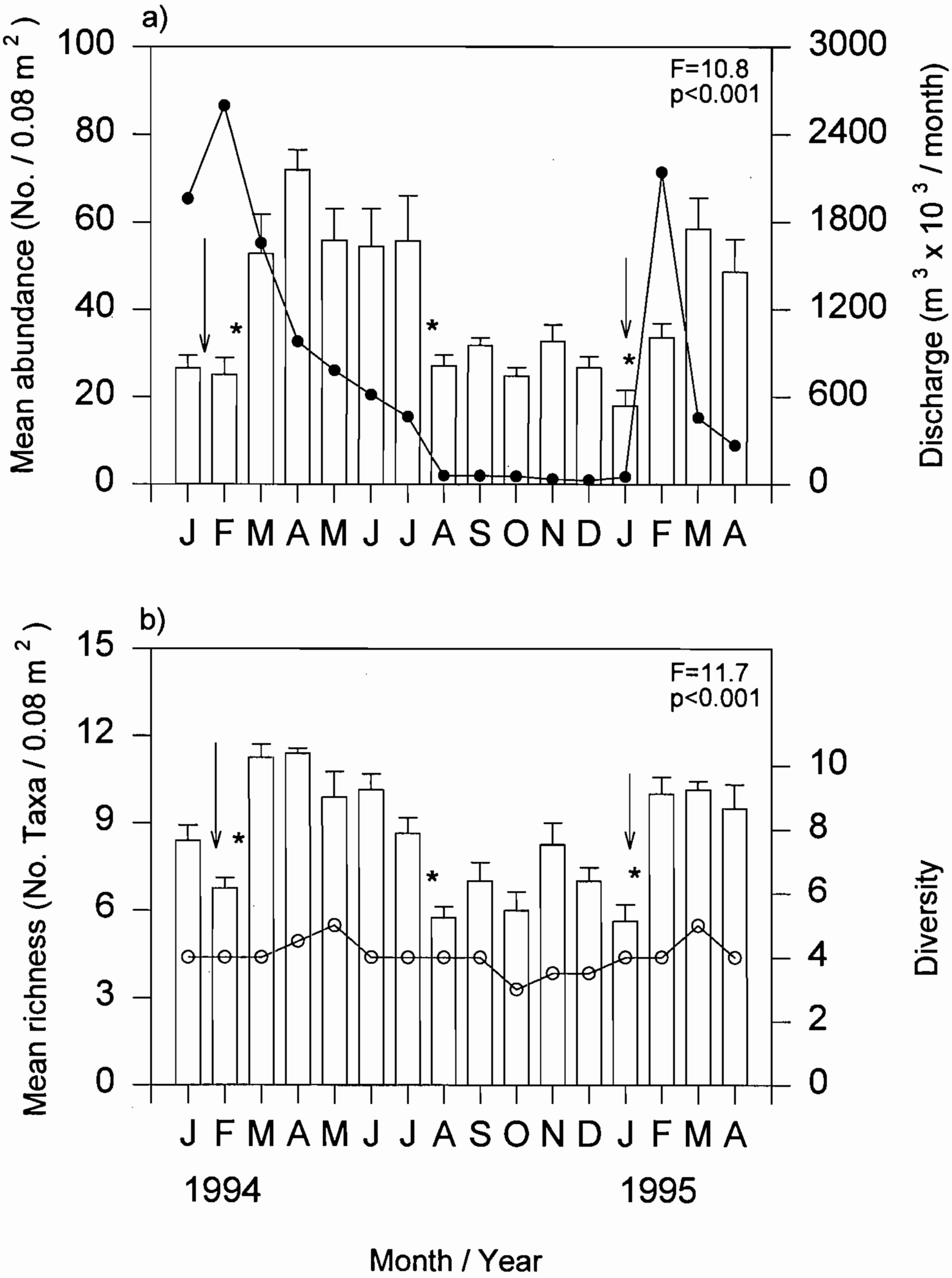
Temporal variation of macroinvertebrate pool fauna

In the pool, there was significant temporal variation in total densities on stones over 16 months, incorporating the two major flood events (one-way ANOVA, d.f.=15, F=10.8, $p<0.001$) (Figure 2.8a). Benthic densities were highest late in the wet season as flow was declining, and lowest in the late dry season.

Figure 2.8 Mean (± 1 SE) a) abundance and b) richness of macroinvertebrates on stream stones sampled monthly from a pool at Birthday Creek (January, 1994-April, 1995). The total monthly discharge is shown in (a), with arrows indicating the timing of the two major floods.

Results of one-way ANOVAs (effect of time) on abundance and richness are given (d.f. = 15, $\alpha = 0.05$), with asterisks indicating significant differences between consecutive months (Tukey's HSD multiple comparison test, $\alpha = 0.05$).

Changes in Fisher's diversity index (α) over the study period are given in (b).


a)
Mean abundance (No. / 0.08 m ^{2})
100
80
60
40
20
0
F=10.8
p<0.001
Discharge (m ^{3} x 10 ^{3} / month)
3000
2400
1800
1200
600
0
*
*
*
J F M A M J J A S O N D J F M A
b)
Mean richness (No. Taxa / 0.08 m ^{2})
15
12
9
6
3
0
F=11.7
p<0.001
Diversity
10
8
6
4
2
0
*
*
*
J F M A M J J A S O N D J F M A
1994
1995
Month / Year

Overall richness also varied over time (one-way ANOVA, d.f.=15, F=11.7, $p<0.001$), peaking in the wet/late wet, and low during the dry season although this pattern appears to be largely a consequence of variations in density, with diversity showing little temporal variation (Figure 2.8b).

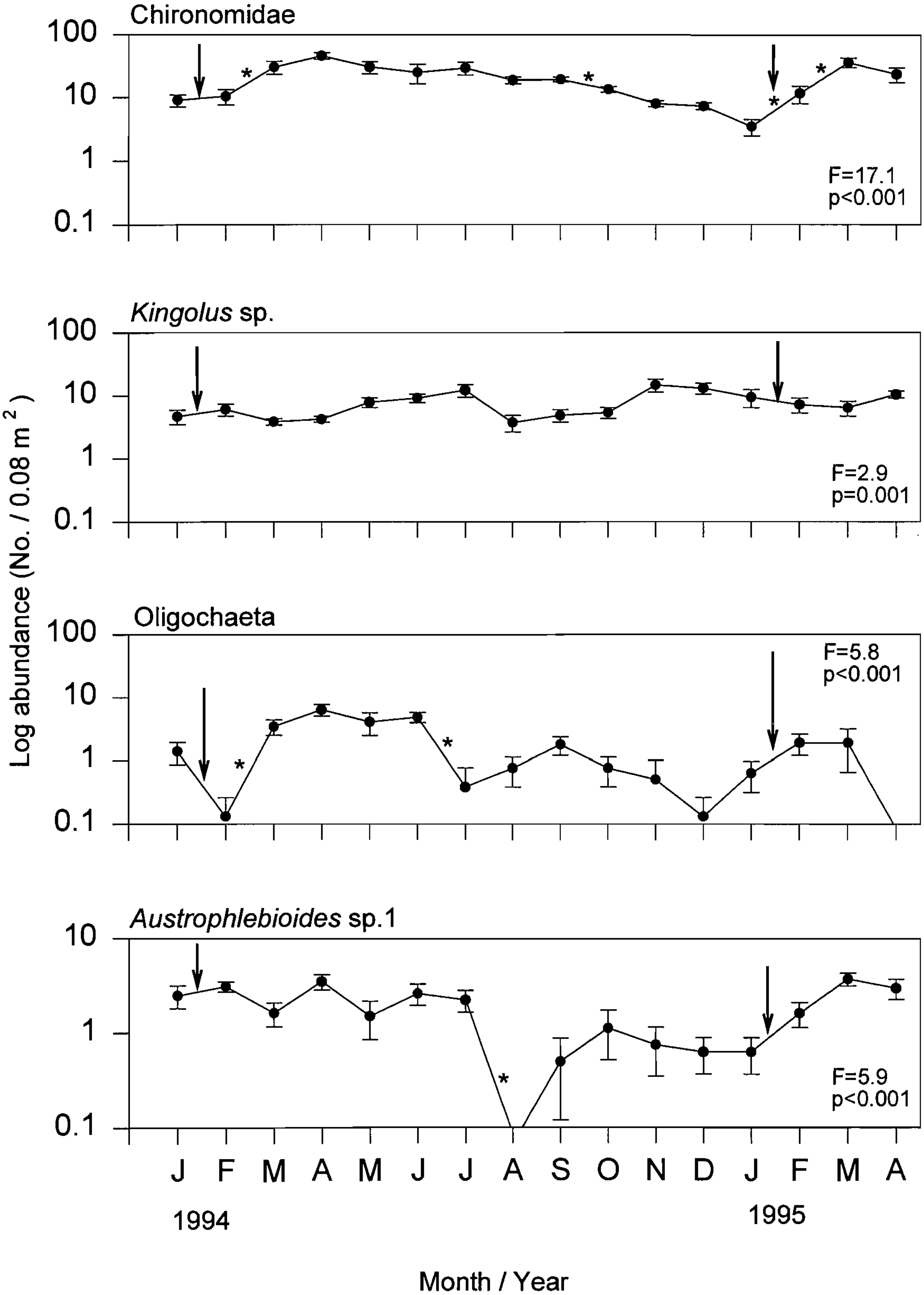
Resilience to both major flood events was exceptionally high in the pool, with density and richness not significantly different (Tukey HSD, $p > 0.05$ in both cases) following the largest flood, sampled 21 days later, and significantly higher (Tukey HSD, $p < 0.05$) following the relatively smaller flood, sampled six days post-flood (Figure 2.8). Temporal variation in the abundance of common pool taxa was evident (one-way ANOVA, d.f. = 15, $p \leq 0.001$ in all cases) (Figure 2.9). Changes in the densities of Chironomidae (1994 and 1995) and Oligochaeta (1994) contributed to much of the pattern in total density observed in the pool, increasing significantly during the wet season/late wet season months (Tukey HSD, $p<0.05$). Common pool taxa reflected the very high overall resilience (Table 2.6) to both floods, with pre- and post flood densities not significantly different, regardless of magnitude (1994 vs. 1995), or time since flooding (21 days vs. six days). Chironomidae significantly increased in abundance when sampled six days after the 1995 flood. In contrast to the pattern observed in the riffle, within-sample variability rarely increased in the post-flood samples, tending to be lower or similar to the pre-flood values.

Ordination of samples shows that temporal shifts in community structure in the pool habitat between 1994 and 1995 were evident (Figure 2.10), with distinction between the wet and early dry season assemblages (1994). As with the riffle fauna, this pattern was influenced more by the presence/absence of individual taxa than changes in their relative abundance. The transition between the late wet and early dry (February-March), characterised by high turnover, coincided with a significant increase in numbers of Chironomidae and Oligochaeta. Turnover again increased in the late dry season (September-November).

Figure 2.9 Mean abundance (± 1 SE) of the common macroinvertebrate taxa on stream stones sampled monthly from a pool at Birthday Creek (January, 1994-April, 1995).

Arrows indicate the timing of the two major floods.

Results of one-way ANOVA's (effect of time) on abundance are given (d.f. = 15, $\alpha = 0.05$), with asterisks indicating significant differences between consecutive months (Tukey's HSD multiple comparison test, $\alpha = 0.05$).


Chironomidae
100
10
1
0.1
F=17.1
p<0.001
Kingolus sp.
100
10
1
0.1
F=2.9
p=0.001
Oligochaeta
100
10
1
0.1
F=5.8
p<0.001
Austrophlebioides sp.1
10
1
0.1
F=5.9
p<0.001
Log abundance (No. / 0.08 m 2)
J F M A M J J A S O N D J F M A
1994
1995
Month / Year

continued.....

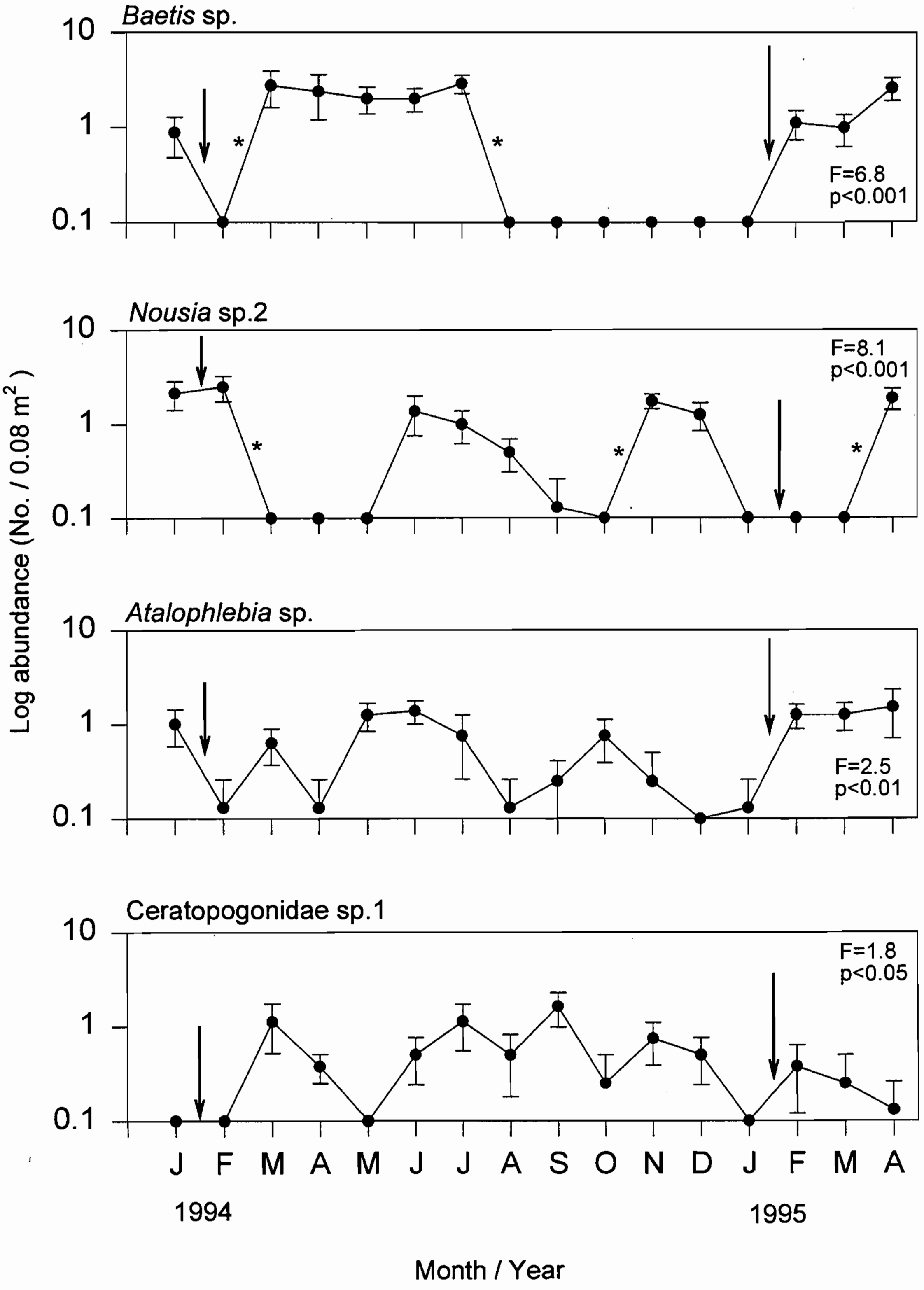

Baetis sp.
F=6.8
p<0.001
Nousia sp.2
F=8.1
p<0.001
Atalophlebia sp.
F=2.5
p<0.01
Ceratopogonidae sp.1
F=1.8
p<0.05
10
1
0.1
Log abundance (No. / 0.08 m2)
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
1994
1995
Month / Year

Figure 2.10 Ordination plot of the first two dimensions of SSH (semi-strong hybrid multidimensional scaling) of macroinvertebrate communities on stream stones from a pool at Birthday Creek sampled monthly between January, 1994 and April, 1995.

Months are represented by numbers (1=January, 2=February, etc.), with arrows linking consecutive months.

This period incorporated two severe, substratum-moving floods, with pre- (January) and post-flood (February) samples linked with boldface arrows.

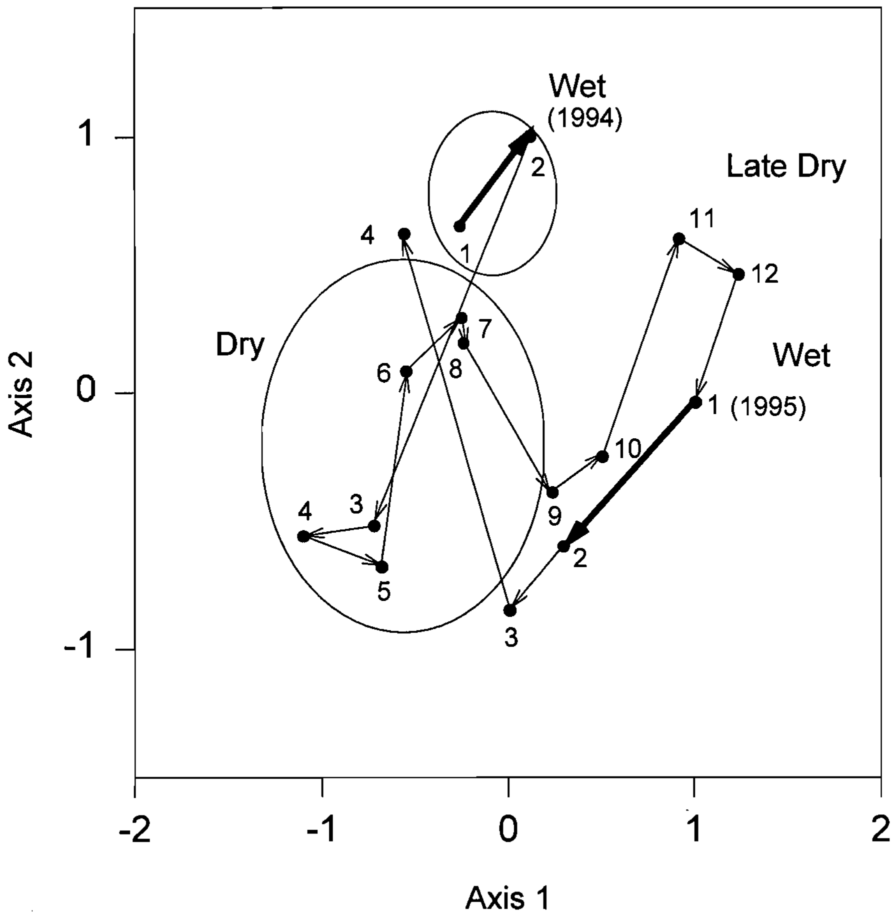

Wet
(1994)
Late Dry
Dry
Wet
1 (1995)
Axis 1
Axis 2
1
0
-1
-2
-1
0
1
2
1
2
3
4
5
6
7
8
9
10
11
12
1
2
3
4

Table 2.6 Comparison of pre- and post-flood total abundance, richness, and densities of the common pool taxa to the 1994 and 1995 flood events. n.s. = non-significant difference between pre- and post-flood samples, ↑ = significantly higher densities in the post-flood samples. Samples were discriminated using Tukey HSD test performed on the entire data set ($p<0.05$). Within-sample variance, indicated by the coefficient of variation (CV) before and after each flood is given, with post-flood increases indicated in boldface.

Taxa	1994 Flood (recovery period = 21d)			1995 Flood (recovery period = 6d)		
	Density	CV pre-	CV post-	Density	CV pre-	CV post-
Kingolus sp.	n.s.	0.73	0.61	n.s.	0.91	0.76
Oligochaeta	n.s.	1.10	**2.83**	n.s.	1.47	1.05
Austrophlebioides sp. 1	n.s.	0.77	0.36	n.s.	1.19	0.87
Baetis sp.	n.s.	1.29	0.76	n.s.	0.37	**1.00**
Nousia sp. 2	n.s.	0.96	0.86	n.s.	0.25	0.13
Atalophlebia sp.	n.s.	1.20	**2.83**	n.s.	2.83	0.83
Chironomidae	n.s.	0.61	0.60	↑	0.70	**0.87**
Total abundance	n.s.	0.31	**0.44**	↑	0.55	0.27
Total richness	n.s.	0.17	0.15	↑	0.28	0.16

Succession rate (i.e. change in community composition following disturbance, *sensu* Fisher 1987), indicated by the relative distance between pre- and post-flood samples, was higher following the smaller flood in 1995, and is likely to be a reflection of the sample being taken sooner after the flood (i.e. six days compared to 21 days), rather than an indication of the effect of flood magnitude.

Pearson and Kendall correlations between the first three ordination axes of multidimensional scaling plots and a range of independent variables indicate significant correlations with discharge (axis 3), days post-flood (axes 1 and 3), and temperature (axis 3) within the pool habitat, with many of the common taxa correlated significantly with axes 1 and 3 (Table 2.7).

Table 2.7 Pearson and Kendall correlations of the first three axes (% variation explained by each axis is given in parentheses) of multidimensional scaling ordination with five independent variables and selected pool taxa. Significant correlations ($p < 0.05$) are indicated in boldface.

	Axis 1 (43.79 %)	Axis 2 (21.48 %)	Axis 3 (9.11 %)
Discharge	0.314	-0.162	**0.556**
Days post-flood	**0.677**	0.192	**0.668**
POM	-0.069	-0.339	-0.433
Chl. a	-0.270	-0.040	-0.397
Temperature	0.230	-0.008	**-0.708**
Tasmanocoenis sp.	**-0.680**	0.317	**0.692**
Baetis sp.	**-0.784**	0.231	**0.763**
Austrophlebioides sp. 1	**-0.572**	-0.023	**0.739**
Chironomidae	**-0.757**	0.522	**0.860**
Nyctiophylax sp.	0.237	-0.469	**-0.598**
Helicopsyche sp.	**-0.773**	0.047	**0.764**
Austrolimnius sp. 1	**-0.840**	0.019	**0.806**
Oligochaeta	**-0.801**	0.363	**0.817**
Hydroptilidae sp. 1a	0.424	-0.444	**-0.685**

In contrast to the riffle, the substratum-moving floods had little effect on the rank abundance of the common taxa in the pool (Table 2.8). This is also reflected in the high PSI values, indicating a high degree of overlap in pre- and post-flood assemblage structure. Again, similarity values were lower in 1995, suggesting that time since disturbance is important for the development of similar community structure.

Temporal change in macroinvertebrate functional feeding groups, benthic particulate organic matter and chlorophyll a

Filterers, mainly *Simulium* sp. and some chironomids, dominated the riffle assemblage over the summer wet season (Figure 2.11). As flow declined in the late wet, scrapers increased, becoming the dominant feeding group in the dry season, while shredders, although uncommon, peaked in the early dry.

Floods reduced the numbers (and proportions) of scrapers, gatherers, shredders and predators, while filterers showed a dramatic proportional increase.

Table 2.8 Common taxa (ranked in order of abundance) on stones in the pool before (January) and after (February) the two major flood events, and comparison of overall community similarity (Proportional Similarity Index, PSI). PSI values ≥ 0.65 indicate high overlap (similarity) between assemblages.

1994	Ranking		**1995**	Ranking	
	pre-	post-		pre-	post-
Chironomidae	1	1	*Kingolus* sp.	1	2
Kingolus sp.	2	2	Chironomidae	2	1
Austrophlebioides sp. 1	3	3	*Nousia* sp. 1	3	15
Nousia sp. 2	4	4	Jappa sp.	4	8
Oligochaeta	5	7	*Austrophlebioides* sp. 1	5	4
Atalophlebia sp.	6	7	Oligochaeta	6	3
	PSI=0.80			PSI=0.65	

In contrast to the riffle, the pool habitat (Figure 2.12) was dominated by scrapers during the wet season, with gatherers and filterers most abundant in the late wet/early dry, and declining during the late dry season. Gatherers and filterers showed a similar temporal pattern, peaking in the early/mid dry and declining in the late dry season. There was little change following the biggest flood in density or relative abundance of particular functional groups in the pool, while in 1995 gatherers and filterers increased in post-flood samples.

Levels of particulate organic matter (POM) showed a general build-up up during the late dry/early wet season in the riffle and pool (Figures 2.13a, 2.13b). The flood in January-February, 1995 did not significantly reduce levels of POM, although there was a significant drop in the early wet season in the riffle and pool (Tukey HSD, $p<0.05$). Chlorophyll *a* levels, in contrast, did not show clear seasonal trends, being highly variable throughout the year in both habitats (Figures 2.13b, 2.13c). Flooding significantly reduced chlorophyll *a* levels in the pool (Tukey HSD, $p<0.05$), but not in the riffle.

Figure 2.11 Temporal change (October, 1991 - April, 1995) in the abundance (mean ± 1 SE) of invertebrates in the different functional feeding categories in the riffle at Birthday Creek.

Arrows indicate the timing of the two major floods.

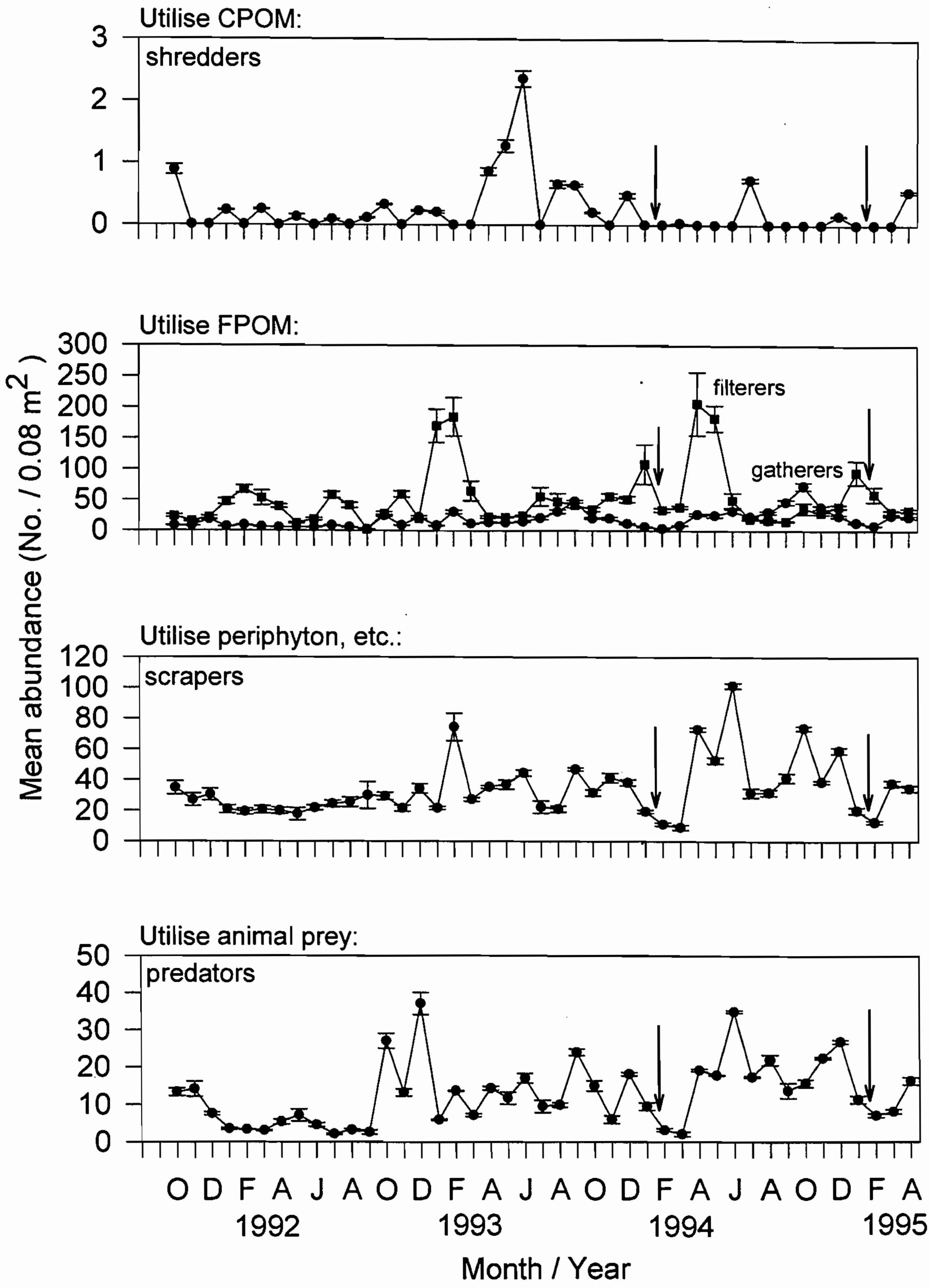

Utilise CPOM:
shredders
3
2
1
0
Utilise FPOM:
filterers
gatherers
300
250
200
150
100
50
0
Utilise periphyton, etc.:
scrapers
120
100
80
60
40
20
0
Utilise animal prey:
predators
50
40
30
20
10
0
Mean abundance (No. / 0.08 m²)
O D F A J A O D F A J A O D F A J A O D F A
1992
1993
1994
1995
Month / Year

Figure 2.12 Temporal change (January, 1994 - April, 1995) in the abundance (mean ± 1 SE) of invertebrates in the different functional feeding categories in the pool at Birthday Creek.

Arrows indicate the timing of the two major floods.

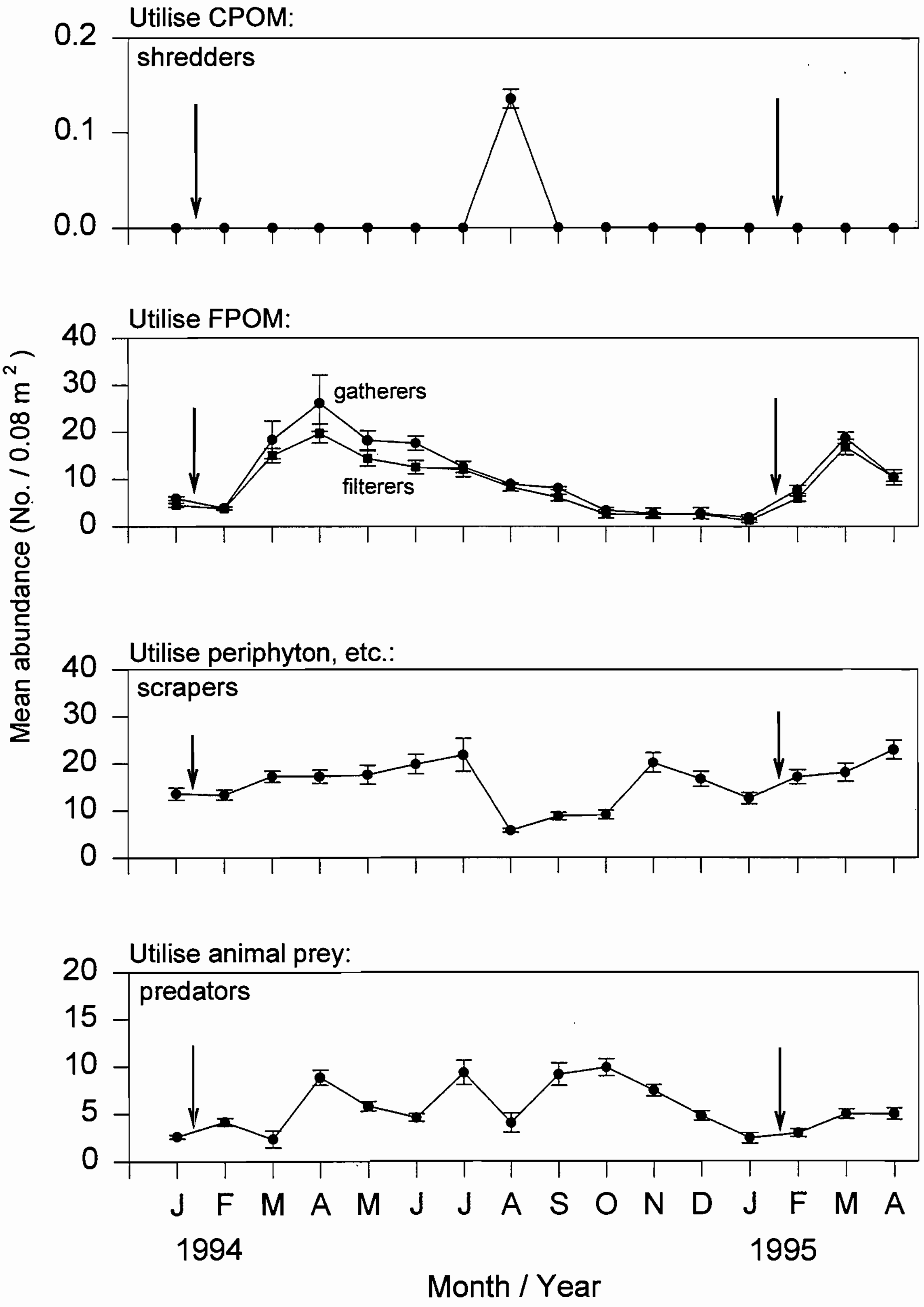

Utilise CPOM:
shredders
0.2
0.1
0.0
Utilise FPOM:
gatherers
filterers
40
30
20
10
0
Utilise periphyton, etc.:
scrapers
40
30
20
10
0
Utilise animal prey:
predators
20
15
10
5
0
Mean abundance (No. / 0.08 m 2)
J F M A M J J A S O N D J F M A
1994
1995
Month / Year

Figure 2.13 Temporal change in the levels of particulate organic matter (POM) in a) riffle and b) pool and chlorophyll *a* levels in c) riffle and d) pool on stone surfaces at Birthday Creek (April, 1994 - April, 1995). Data are means ± 1 SE.

The arrow indicates the timing of the flood in February 1995.

Results of one-way ANOVAs (effect of time) are given (d.f. = 12, $\alpha = 0.05$), with asterisks indicating significant differences between consecutive months (Tukey's HSD multiple comparison test, $\alpha = 0.05$).

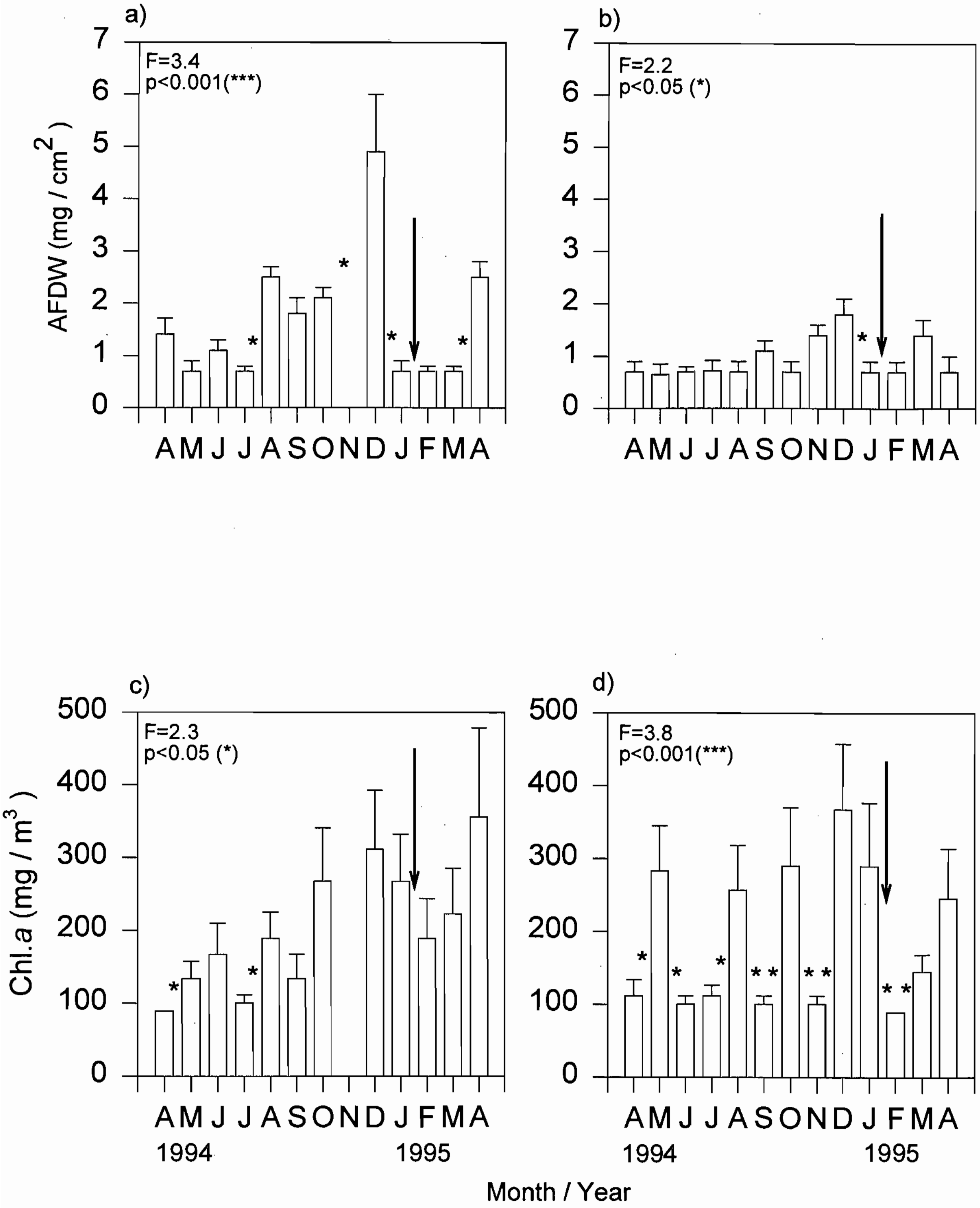

a)
F=3.4
p<0.001(***)
AFDW (mg / cm^2)
0
1
2
3
4
5
6
7
A M J J A S O N D J F M A
b)
F=2.2
p<0.05 (*)
0
1
2
3
4
5
6
7
A M J J A S O N D J F M A
c)
F=2.3
p<0.05 (*)
Chl.*a* (mg / m^3)
0
100
200
300
400
500
A M J J A S O N D J F M A
1994
1995
d)
F=3.8
p<0.001(***)
0
100
200
300
400
500
A M J J A S O N D J F M A
1994
1995
Month / Year

Table 2.9 shows that community persistence of both wet and dry season assemblages, in terms of composition and relative abundance, was high among years in the riffle, and very high for wet season assemblages in the pool.

Table 2.9 Persistence of wet and dry season assemblages over time, assessed in terms of proportional similarity (PSI). Values approaching 1.0 indicate increasing similarity of community structure, in terms of composition and relative abundance. PSI values ≥ 0.65 indicate high overlap (similarity) between assemblages. "–" indicates comparison could not be made.

	1992 vs.1993	1993 vs.1994	1994 vs.1995
Riffle			
Wet season (December-February)	0.76	0.71	0.70
Dry season (June-August)	0.73	0.70	–
Pool			
wet season (December-February)	–	–	0.84

2.4 Discussion

The physical environment of Birthday Creek, like similar streams within the Australian Wet Tropics (Pearson *et al.* 1986) is dominated by seasonal variations in discharge. The wet season, occurring during the summer months, is characterised by high and variable flows, the precise timing and magnitude of which are highly unpredictable, while during the remainder of the year, flow tends to be low and stable or gradually diminishing. These components of variability, comprising predictable seasonal variation in discharge superimposed by high levels of short-term variability due to floods, define the temporal axis of the disturbance regime (Poff and Ward 1989) within this stream.

Temporal variation of stone fauna in riffle and pool habitats

The observed temporal variation in macroinvertebrate densities on stream stones in riffle and pool habitats reflected seasonal changes in the flow regime at Birthday Creek. In the riffle, highest benthic densities were observed in late summer/early autumn following flooding, due largely to the positive response of the seasonally dominant blackfly larvae, *Simulium* sp., to high and variable flows; a similar pattern was also observed by Mathooko and Mavuti (1992) in a Kenyan River. Blackfly larvae are well suited to the conditions prevailing during the wet season, favouring i) elevated flow levels (Schlosser 1992, Clayton 1995), and ii) reduced densities of other taxa, as they are poor competitors (Hemphill and Cooper 1983). In addition, their ability to maintain position on stone surfaces exposed to strong currents through morphological adaptations such a ventral adhesive disc means that they can exploit the increased concentration of suspended food particles in the water column during elevated flows (Growns and Davis 1994). Blackfly larvae are also capable of very rapid recolonisation (Mackay 1992) for, although they are not highly mobile, they posses silken "safety lines," enabling rapid recovery should dislodgement occur.

Pools generally support lower densities and richness of macroinvertebrates compared with riffles (Brown and Brussock 1991, Miller and Golladay 1996, Cheshire 1997), as was found in the present study. In Birthday Creek, increased structural components (aquatic mosses) on the surface of stones in the riffle may enhance diversity through increased habitat complexity (Downes *et al.* 1995) or by trapping detritus (Glime and Clemons 1972, Arunachalam *et al.* 1991, see below). Temporal variation in benthic densities within the pool showed a similar pattern to the riffle, reaching a peak in the late wet season as flow declined, and being lowest during the late dry season, driven largely by changes in abundance of Chironomidae and, to a lesser extent, Oligochaeta. Similarly, in a study of seasonal variation in pools of a tropical lowland river (India), Arunachalam *et al.* (1991) observed peak macroinvertebrate densities following monsoon-related flooding in two of three pools examined and suggested this was related to post-monsoon increases in algal biomass. An alternative explanation, and that proposed here, is that individuals are displaced from upstream sources during floods and accumulate in pools (see below).

Resistance and resilience to flood disturbance

Substratum-moving floods provide an obvious source of disturbance to stream benthic communities, with associated increases in water velocity and hydraulic forces resulting in high levels of mortality or the downstream displacement of individuals (Yount and Niemi 1990, Giller *et al.* 1991, Boulton *et al.* 1992, Flecker and Feifarek 1994, Angradi 1997). The knowledge that disturbance effects vary spatially, even at the scale of microhabitat patches (Lancaster and Belyea 1997), has generated considerable interest in the mechanisms responsible for the remarkable resilience and, in the longer term, high persistence of stream communities in the face of such severe disturbances. Areas of refugium within the stream, where the negative effects of floods are reduced relative to surrounding areas, are likely to provide a crucial source of colonists following disturbance (Townsend and Hildrew 1994). The availability of refugia within Birthday Creek is dependent on the stability of substratum particles (Death and Winterbourn 1994) and the proportion of low flow areas (flow dead zones – Lancaster and Hildrew 1993) during flooding, and is likely to vary among the habitat types (i.e. riffle and pool) examined in this study. Depositional, low-flow areas (e.g. pools) may experience negligible substratum movement during floods, and retain or accumulate fauna, while erosional, higher flow areas, with a predominance of coarser substratum particles may experience much higher flow forces and consequently lose fauna (Palmer *et al.* 1995). There is some evidence in this study to suggest that pools have the potential to act as flow refugia in Birthday Creek. There was an accumulation of animals (i.e. a significant increase in total abundance) in the pool following the 1995 flood, with at least two of the taxa (Elmidae sp. 2 and the megalopteran, *Archichauliodes* sp.) previously found only in the riffle. Accumulation of individuals in refugial patches (i.e. where the negative effects of disturbance are reduced relative to surrounding areas – Lancaster and Belyea, 1997) during or following floods has previously been found (Palmer *et al.*1996, Winterbottom et al. 1997), and may fit the "directional flux" model proposed by Lancaster and Belyea (1997). This model, which involves active or passive movements of individuals into (and out of) refugia in response to individual disturbance events, has received the strongest support from empirical studies (Lancaster and Belyea 1997), and is the likely mechanism of refugial use in Birthday Creek. Relative to riffles, pool habitats in Birthday Creek retain a greater range of habitat features which may reduce the impact of hydraulic forces during flood disturbance. For example, the increased substratum particle size range (Townsend and Scarsbrook 1997), large accumulations of leaf litter and woody debris (Palmer *et al.* 1996), and a more extensive hyporheic habitat (Palmer *et al.* 1992) in pools compared with riffles, would be expected to translate to a higher proportion of potential refugial sites during floods. In addition, the proportion of low flow areas is likely to be relatively high, particularly at pool margins, which are not in a direct line with the main flow. The suggestion that pools are less affected than riffle habitats during flood disturbance in these streams (*cf.* Brown and Brussock 1991, Scarsbrook and Townsend 1993, Miller and Golladay 1996) is supported by the negligible effects on density, richness (largely a reflection of density) and diversity. Whether the movement into pools is a consequence of active short-term avoidance of high hydraulic forces (Lancaster *et al.* 1990) or simply the passive downstream displacement of individuals (Winterbottom *et al.* 1997), the end result is the same, and highlights the importance of pools in arresting some of the downstream displacement of individuals during extreme flow disturbances, or under normal flow conditions (Benson and Pearson 1987a). This suggests that pools may play a vital role in the recolonisation dynamics following disturbance within streams such as Birthday Creek, characterised by a riffle-pool geomorphology.

Although it is likely that pools serve as important refuge areas during floods in Birthday Creek, the relative importance of refugial use by stream fauna may depend on the magnitude of the disturbance (Palmer *et al.* 1996). In this study, only the largest flood resulted in a significant reduction in benthic densities in the riffle, which occurred despite the longer time interval between the flood and the time of sampling (21 days), compared with the smaller event (six days). It is likely that the greater intensity of disturbance, as well as resulting in increased mortality and displacement of individuals, may also render previously utilised refugia as inoperative (e.g. the hyporheic habitat may be scoured to a greater depth), thereby extending recovery times. Where the habitat is less altered, and population reductions less severe (1995 flood), recovery of riffle fauna to pre-flood densities occurs rapidly at Birthday Creek (within six days), indicating a resilient fauna (see review by Niemi *et al.* 1990). High resilience in Birthday Creek following flooding may not only occur through the utilisation of flow refugia (i.e. flux among habitat patches), but may also depend on the flux of individuals between the streambed and drift. Drift appears to be the major mechanism of recolonisation by stream fauna (e.g. Williams and Hynes 1976), particularly during periods of high flow (Moser and Minshall 1996). Regional dispersal processes such as drift tend to become increasingly important to recovery as the scale of disturbance increases (Palmer *et al.* 1996, Matthaei *et al.* 1997b; but see Doeg *et al.* 1989) and are likely to provide a significant source of colonists following flood disturbance in Birthday Creek. In Yuccabine Creek, Benson and Pearson (1987b) concluded that drifting animals could account for the total supply of colonists during the wet season. A reproductive peak in early summer, reflected in the drift in the late wet season, permits maximum recolonisation of habitat patches newly created following flooding. In Birthday Creek, as with other seasonal streams, some fauna, particularly those which are large and long-lived, may synchronise aspects of their life history to coincide with seasonal variations in patterns of flow (e.g. Flecker and Fiefarek 1994). However, the emerging pattern from studies within tropical streams suggests that the most common life history strategy involves rapid development (enhanced by higher temperatures) with multiple, overlapping cohorts (Dudgeon 1992, Nolen and Pearson 1992, Jackson and Sweeney 1995, Yule and Pearson 1996), particularly for the smaller larvae (Dudgeon 1995). The presence of all life stages through the year combined with rapid development times in tropical streams, compared with univoltine life histories common to many species in temperate regions, enables extended recruitment, enhancing recovery following disturbance.

Richness of macroinvertebrates on stones in the riffle habitat, although less variable compared with total numbers, showed some temporal variation, tending to increase in the late dry season and early wet season, with significant reductions during the wet season following flooding. The apparent reduction in 1994, however, was due largely to a reduction in overall density, rather than number of taxa *per se*. Dominance by fewer taxa (especially *Simulium* sp.) in summer when flow is high and variable, contrasts with the pattern found in seasonal streams of West Australian jarrah forests (Bunn *et al.* 1986) where fewer taxa were present when flow was low. Flood magnitude appears to influence the turnover of taxa, with greatest turnover occurring during years when magnitude was relatively low, and lowest following the largest flood. Although richness appears relatively stable, diversity within the riffle fluctuated greatly during the year, which contrasts with the pattern observed in the pool, where diversity was remarkably stable.

Temporal variation in food resource levels

The expectation of a strong temporal pattern in particulate organic matter (POM) in Birthday Creek, reflecting seasonal variation in discharge, as found in other Australian seasonal streams (Bunn 1986, Pearson *et al.* 1986), received only limited support in this study. However, these other studies examined total POM within the benthos rather than on the surface of individual stones. Although sampling of stone surfaces may only provide a partial picture of total benthic POM, levels of particulate organic matter on stones is likely to be of direct ecological relevance to the fauna of interest in this study.

Only the riffle habitat appeared to accumulate POM during the low flow conditions of the late dry season, while a similar seasonal pattern, although suggested, was not significant in the pool. The reasons for the higher seasonal accumulation, as well as higher overall levels of POM in the riffle, rather than in the depositional (pool) habitat are unclear. A contributing factor, as mentioned earlier, may be the presence of additional surface topography features such as pupal cases of *Simulim* sp. and aquatic mosses (both of which are reasonably common, personal observation), and may assist in the retention of POM on stone surfaces within the riffle (Arunachalam *et al.* 1991). Such increases in surface complexity (= microhabitat diversity) may also contribute to the higher overall richness (Douglas and Lake 1994), and diversity in the riffle compared with the pool.

In the riffle, the peak in gatherer abundance coincided with the late dry season (low flow) accumulation of particulate organic matter. In the pool, however, gatherers peaked in the early dry, before the time of maximum amounts of POM, which was in the late dry season. Boulton and Lake (1992c) found strong positive correlations between amounts of benthic organic matter and detritivores in riffle habitats in intermittent streams, while the association was much weaker in pools. These authors suggest that non-significant correlations in pools may reflect an over-abundance of organic material in these depositional habitats. Except for the March sample, the results of the present study suggest that levels of POM, at least within the size range of > 250 μm, were higher in the riffle, although it is expected that the smaller particle sizes (< 250 μm), which were not sampled, would be higher in pool habitats due to the more benign flow environment, and total POM may conform to the pattern by Boulton and Lake (1992c). Tropical upland streams such as Birthday Creek derive the majority of their energy from allochthonous inputs, rather than in-stream primary production, much of which enters as leaf-fall throughout the year (*cf.* compared with temperate Australian streams, Boulton and Lake 1992c). Consequently, it may be that levels of particulate organic matter are rarely limiting in this stream (Cheshire 1997), except when extensive flushing by floods occur. However, the substratum-moving flood in 1995 did not significantly reduce the levels of POM in either the riffle or pool, and it may be that this flood imported organic material from upstream sources, as suggested by Boulton and Lake (1990).

High abundance of *Simulium* sp., when flow is high and variable, leads to filterers dominating the riffle community during the summer months. With declining flow, filterers decrease in abundance and scrapers increase, becoming the dominant feeding group during the dry season. As flow declines and densities of other taxa increase, it is likely that conditions for the filtering *Simulium* sp. become less favourable, and competitive exclusion may occur, with space being the limiting resource (Hemphill and Cooper 1983). However, (Downes and Lake 1991) suggest that the requirement for minimum flow levels are likely to be the overriding factor influencing blackfly colonisation. Both floods, of different magnitude, decreased the abundance of all feeding groups, although there was a large proportional increase in filterers.

Algal biomass (reflected in chlorophyll *a* levels) on stream stones in Birthday Creek appears to be very patchy in both riffle and pool habitats, with no clear seasonal patterns. A slight temporal trend towards higher (although variable) levels of chlorophyll *a* in the late dry/early wet season in the pool coincides with increased abundance of scrapers. Similarly in the riffle, increases in chlorophyll *a* levels over the dry season may explain the increased densities of scrapers such as the elmid larva, *Kingolus* sp. Seasonal peaks in scraper densities correlating with peaks in periphyton levels have been demonstrated in intermittent Victorian streams (Boulton and Lake 1992c). The expectation that the substratum-moving flood in 1995 would result in significant reductions in algal biomass, and hence chlorophyll *a* levels, was only supported in the pool habitat. In their long-term study of streams in the Australian sub-tropics, Mosisch and Bunn (1997) found that floods significantly reduced chlorophyll *a* levels, but recovery occurred within 10-30 days in the absence of further disturbance. Although high discharge events may significantly alter algal communities on stone surfaces (Steinman and McIntire 1990, Arunachalam *et al.* 1991, Mosisch and Bunn 1997), assemblages that develop in areas of relatively slow flow may be more susceptible than those from regions of faster flow (Holling 1973), which may contribute to the disparity between habitat types observed in this study. It is becoming increasingly apparent that the relationship between epilithic algae in streams and flow-related disturbance is related to the magnitude of the disturbance; however, this relationship is complex. While severe substratum-moving flows and periods of low flow commonly have detrimental effects on algal communities (Mosisch and Bunn 1997), minor events may have beneficial effects including flushing of the stream (Deniseger *et al.* 1986), removal of dead components (Stevenson 1990) and enhanced nutrient inputs (Power and Stuart 1987). Furthermore, increases in stream flow which are gradual rather than sudden, may promote the growth and productivity of epilithon, reflected in chlorophyll *a* and biomass values (Mosisch and Bunn 1997).

Flood disturbance and community structure

Differences in flood magnitude among years at Birthday Creek resulted in different temporal sequences in community structure in the riffle habitat. Wet and dry season communities were most distinct from each other, and displayed high persistence during years when major flooding occurred (1994 and 1995). Major transition between wet and dry season assemblages coincided with a shift from a post-flood *Simulium* sp. dominated community to one dominated by chironomids in the dry season. Variation in community structure is high during the wet season, possibly reflecting stochastic colonisation following disturbance, low during the early/mid dry, increasing again in the late dry. Other studies within Australia, including temperate Victorian streams (Lake *et al.* 1985a) and streams within the jarrah forests of Western Australia (Bunn *et al.* 1986) have found seasonal shifts in macroinvertebrate assemblages reflecting variations in the flow regime, with a relatively distinct fauna associated with periods of high discharge.

During drier years in Birthday Creek, when the magnitude of flood events was reduced (1992 and to a lesser degree 1993), there is increasing overlap between wet and dry season assemblages. It may be that when the magnitude of temporal change in flow is reduced, seasonal shifts in assemblage structure are less evident, as was also shown by Bunn *et al.* (1986). In addition, drier years appear to be characterised by increased temporal variation in assemblage structure, particularly during the dry season, when environmental conditions are relatively benign (*sensu* Peckarsky 1983). In the absence of severe wet season disturbance by floods, and during prolonged periods of relatively stable conditions, it is predicted that biotic interactions would intensify, particularly in riffles as habitat size is reduced. In streams such as Birthday Creek, with strongly seasonal discharge patterns, low densities of invertebrates during the dry season, when the habitat is physically stable and available area is reduced (thereby increasing contact between individuals), are often attributed to increased biotic interactions such as predation and competition. This has been reported in both tropical (Pearson *et al.* 1986, Hearnden and Pearson 1991, Flecker and Feifarek 1994, Nolte *et al.* 1997) and temperate streams (Fisher and Grimm 1991, Boulton and Lake 1992b). In Birthday Creek, predator densities were generally highest during the dry season and lowest during the wet season in both the riffle and pool, which supports this scenario. Furthermore, a recent study by Cheshire (1997) found that predator biomass in Birthday Creek (riffles and pools) is highest in the late dry (November) and is reduced in the early wet (February). The interaction between abiotic and biotic controls of community structure were observed by Dudgeon (1993) in a Hong Kong headwater stream, who found that deterministic influences (fish predation), although not eliminated, were significantly reduced during periods of hydrologic variability and were highest during the dry season when predators and prey were in close contact. Such seasonal shifts in abiotic and biotic controls of macroinvertebrate community structure are likely in Birthday Creek.

In Birthday Creek, disturbance by floods during the summer months which resulted in the removal of individuals and increased the patchiness of individuals on stones, particularly in riffles may be an important mechanism enhancing benthic diversity. The particularly high levels of spatial heterogeneity in tropical streams have been emphasised previously (Stout and Vandermeer 1975, Lake *et al.* 1994). Outridge (1987) suggests that density-independent eliminations (rarefaction) in environments regulated by seasonal variations in flow is a likely mechanism promoting high diversity in tropical freshwater ecosystems. The results obtained in Birthday Creek further supports the views of previous researchers (Stout and Vandermeer

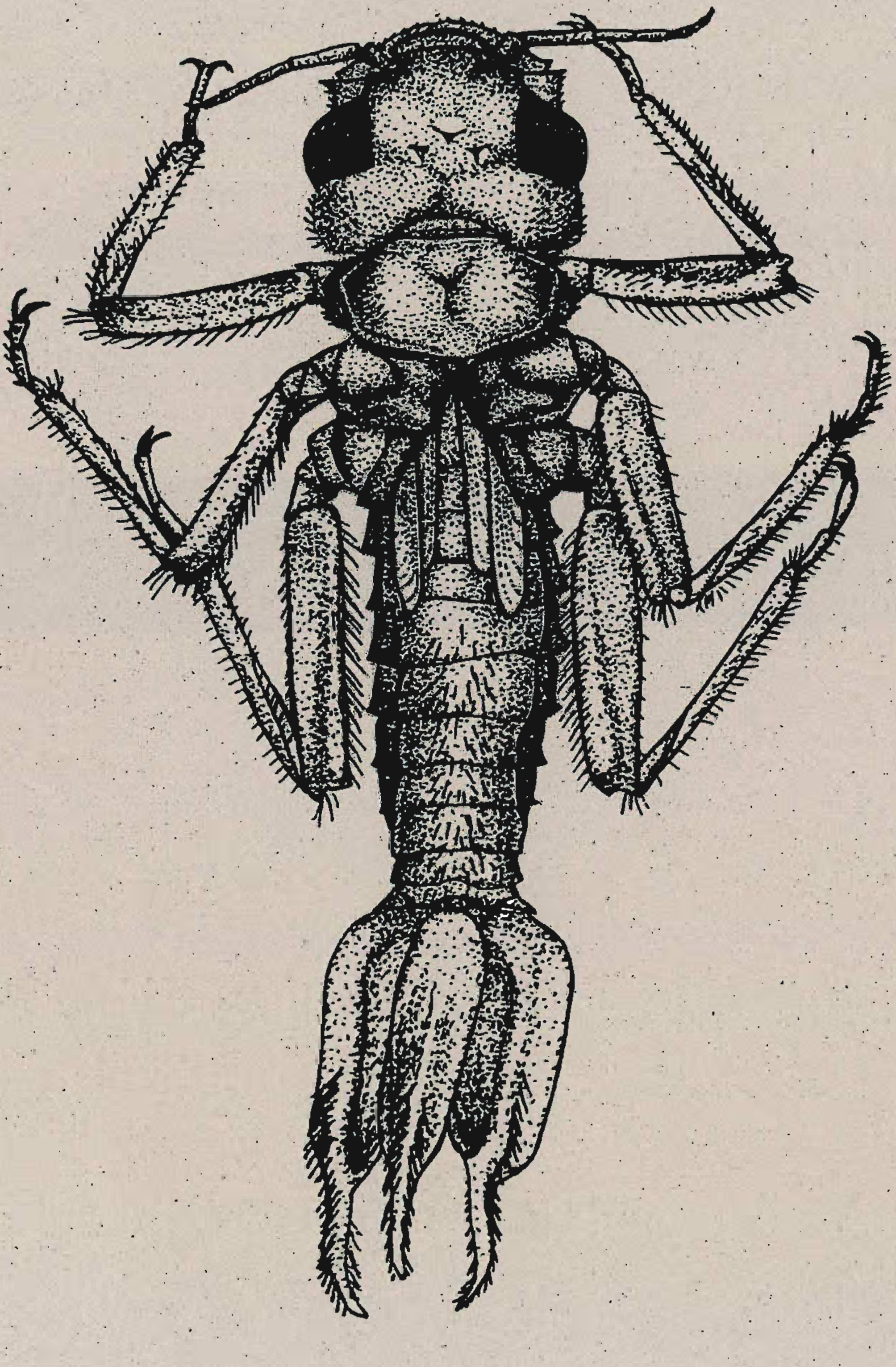
1975, Pearson *et al.* 1986, Lake *et al.* 1994, Yule 1995) that tropical streams are particularly diverse when compared with similar temperate systems.

In summary, 43 months sampling of the riffle stone fauna and 16 months of the pool stone fauna at Birthday Creek has demonstrated that:

- There was a temporal shift in macroinvertebrate community structure, reflecting annual variations in stream flow, and the magnitude of the disturbance. A relatively distinct, highly resilient fauna during the time of high and variable flows (summer), shifts to a less resilient assemblage during the dry season. It is suggested that stochastic controls dominate community structure during the wet season and biotic controls may increase in importance during the dry season as the habitat contracts.

- Stream fauna on stones are remarkably resistant (pools) and recover rapidly (high resilience) in both riffle and pool habitats following severe, habitat-altering floods. The high resistance to disturbance in pool habitats may not only reflect characteristics of the fauna (which was relatively distinct from that in riffles), but may also reflect the reduced impact of floods in these habitats which tended to accumulate rather than lose fauna. Accumulation of individuals in pools (displaced from upstream sources and adjacent riffles) suggests an important refugial role of these habitats, and thus redistribution from these areas is likely to be important in the recovery process following flood disturbance in these streams.

- There is some evidence to suggest that the effects of disturbance have the potential to influence diversity at the local scale, particularly in species-rich riffles, through the creation of increased patchiness of individuals.



Odonata: Amphypterygidae

Artist: Linda Davis

CHAPTER 3: MACROINVERTEBRATE RESPONSES TO EXPERIMENTAL DISTURBANCE AT THE INDIVIDUAL ROCK SCALE

3.1. Introduction

Stream environments are spatially complex from regional (whole drainage basins) to local (riffle/pool) and micro-scales (individual stones) (Frissell *et al.* 1986, Carter *et al.* 1996). The degree of complexity and heterogeneity between and within habitats influences community composition and overall richness (Douglas and Lake 1994, Downes *et al.* 1995) and may determine the nature and impact of disturbance (Palmer *et al.* 1996).

This study investigated the response of macroinvertebrates to disturbance at the scale of individual stones by posing the following questions:

i) What effect does physical disturbance (tumbling and scouring) of individual stones have on the macroinvertebrates living on their surfaces?

As substratum-moving disturbance is a feature of these streams, it is hypothesised that the macroinvertebrate fauna will possess mechanisms for persistence in the face of such physical disturbance, through characteristics of high resistance and/or resilience. Studies involving experimental disturbance of artificial substrata or small substratum patches (e.g. Malmqvist and Otto 1987, Boulton *et al.* 1988, Lake and Schreiber 1991), provide valuable insight into recovery processes at the local scale, the scale at which many ecological models are based. Spatial differences in survival and subsequent dispersal within local patch/habitat types will determine recovery following disturbance and may explain regional community persistence (DeAngelis and Waterhouse 1987). At the local scale, physical outcomes of flooding involve tumbling and shifting of individual stones (see Chapter 2), which may dislodge associated fauna and scour attached algae; at this scale the intensity and frequency of bed movement may provide the most relevant measure of disturbance to benthic organisms (e.g. Townsend *et al.* 1997b). Therefore a range of treatments, reflecting different intensities of disturbance was used in this study. In addition, the effect of increasing the frequency of disturbance on the response of fauna to substratum movement was determined. The problem of rock-to-rock variation in features such as surface complexity (e.g. variations in roughness, presence of cracks and depressions), known to strongly influence community structure and richness at this scale (Downes *et al.* 1995), was controlled for by the use of standardised clay bricks, of a size comparable to natural stones common to streams of the region.

ii) Secondly, how is the macroinvertebrate response to tumbling disturbance modified within different habitats? In this study, riffle and pool habitats were examined, as well as riffles at different positions along a longitudinal stream gradient.

Stony, upland streams of the Australian Wet Tropics have a channel form characterised by alternating riffle and pool habitats which can be distinguished primarily by depth and flow, with riffles being shallow and turbulent, while pools are characterised by deeper water, and barely discernible, non-turbulent flow. Riffles and pools also differ in their disturbance regime: some authors regard pools as having a higher disturbance frequency compared with riffles (Reice 1985, Frissell *et al.* 1986, Brown and Brussock 1991, Scarsbrook and Townsend 1993), while others suggest that the impact of flood disturbance may be reduced in pools (i.e. function as flow refugia) (Palmer *et al.* 1995, see Chapter 2). These features are likely to vary depending on the intensity of the disturbance and characteristics of individual pools such as depth, size, particle size distribution of the substratum, and position in relation to the flow trajectory.

Along longitudinal gradients from headwater to lower reaches, the interaction of stream flow with substratum particles of different sizes provides an index of habitat stability, and will determine the frequency of disturbance in streams (Cobb *et al.* 1992). It is recognised that longitudinal positional within a stream reach and the associated sediment type are major determinants of the frequency and intensity of flow-induced disturbance (see review by Reice *et al.* 1990). There exists a general relationship between sediment particle size and the critical velocity required for movement, although the degree to which particles are packed together will influence this relationship (Downes *et al.* 1997). Generally, mobilisation of sand (0.05-0.5mm) requires the lowest force, with the required velocity increasing as particle size increases (e.g. cobble, boulder), due to greater mass. At the other end of the size spectrum, increased adhesive forces in silts and clays again increases the critical velocity required for mobilisation (Middleton and Southard 1977). The given hydrological regime within a stream will therefore disturb different sediment types at different frequencies. The degree of physical instability of the substratum will have direct consequences for the benthic fauna, for which the substratum constitutes the physical habitat. Because large-scale hydrological events, required to move silts and boulders, are less frequent relative to smaller events, it is predicted that sands will have the highest frequency of disturbance, and consequently contain communities most able to cope with disturbance (Reice *et al.* 1990). Three sites along a longitudinal gradient were examined in this study, each of which differed in the predominant substratum particle size, reflecting longitudinal differences in the disturbance regime, and hypothesised to influence the resistance and resilience characteristics of the local colonising fauna.

As temporal variation in response to large scale disturbance by natural floods had been described previously (Chapter 2), a subsidiary aim was to examine how the faunal response varied across different spatial scales of disturbance. Previously, Brooks and Boulton (1991) found that the rates and pathways of recolonisation following small-scale, experimental disturbance differed from those following large-scale floods, while, in contrast, Matthaei *et al.* (1997a) found similar recovery patterns following experimental and natural disturbance.

3.2 Methods

Study Sites

Three rainforest streams, Birthday Creek (see Chapter 2, Figure 2.1), Pixies Creek (Figure 3.1), and Yuccabine Creek (Figure 3.2), all within the Wet Tropics, were sampled during the wet season (December-March) in 1993. Experimental disturbance within pool and riffle habitats was examined at Birthday Creek and Pixies Creek, with the influence of disturbance frequency in these two habitats determined at Birthday Creek. The response of macroinvertebrates to disturbance at different sites along a longitudinal gradient was examined at Yuccabine Creek. Comparative details of the study sites are given in Table 3.1.

Figure 3.1 Map indicating the location of the Pixies Creek study site in north Queensland.

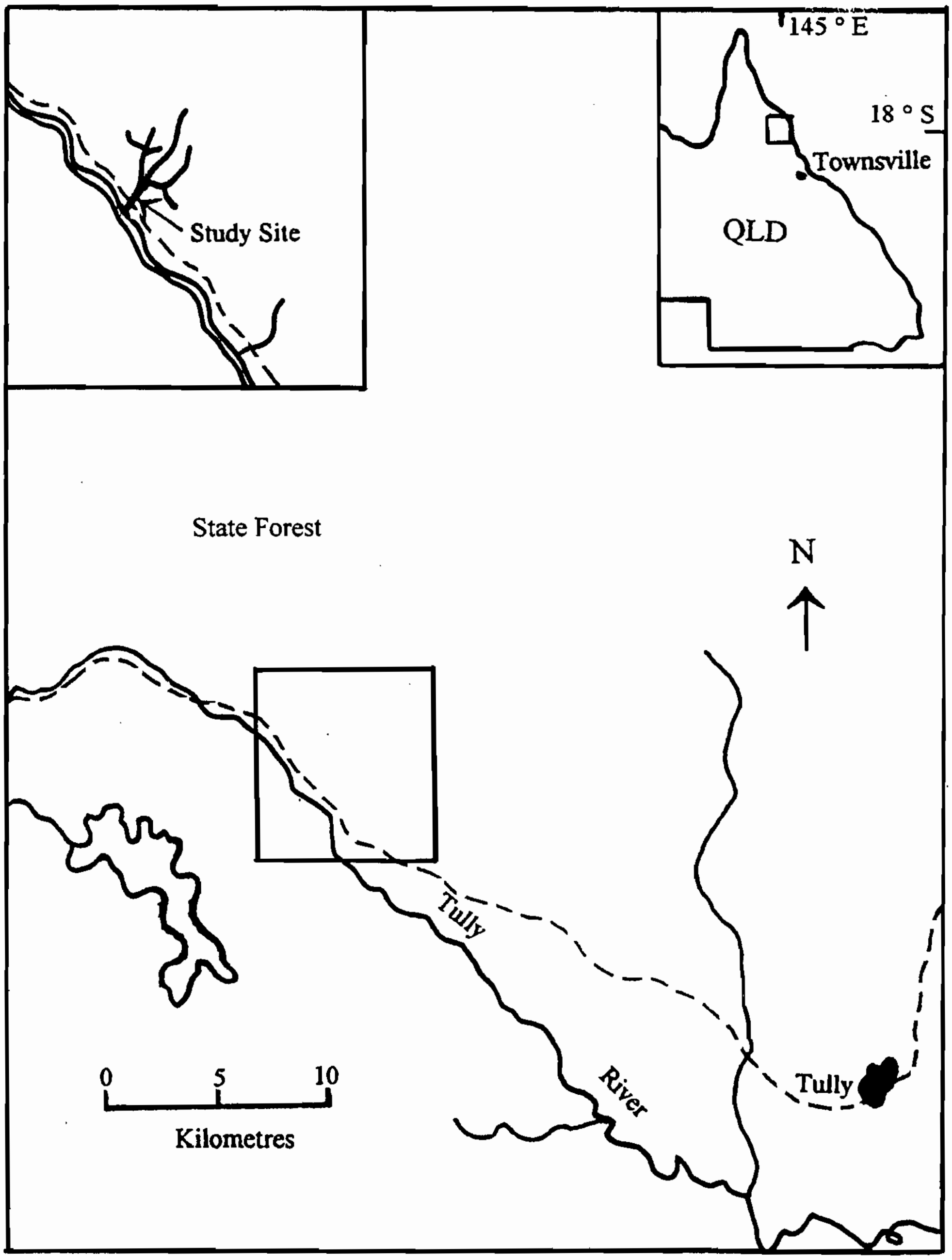
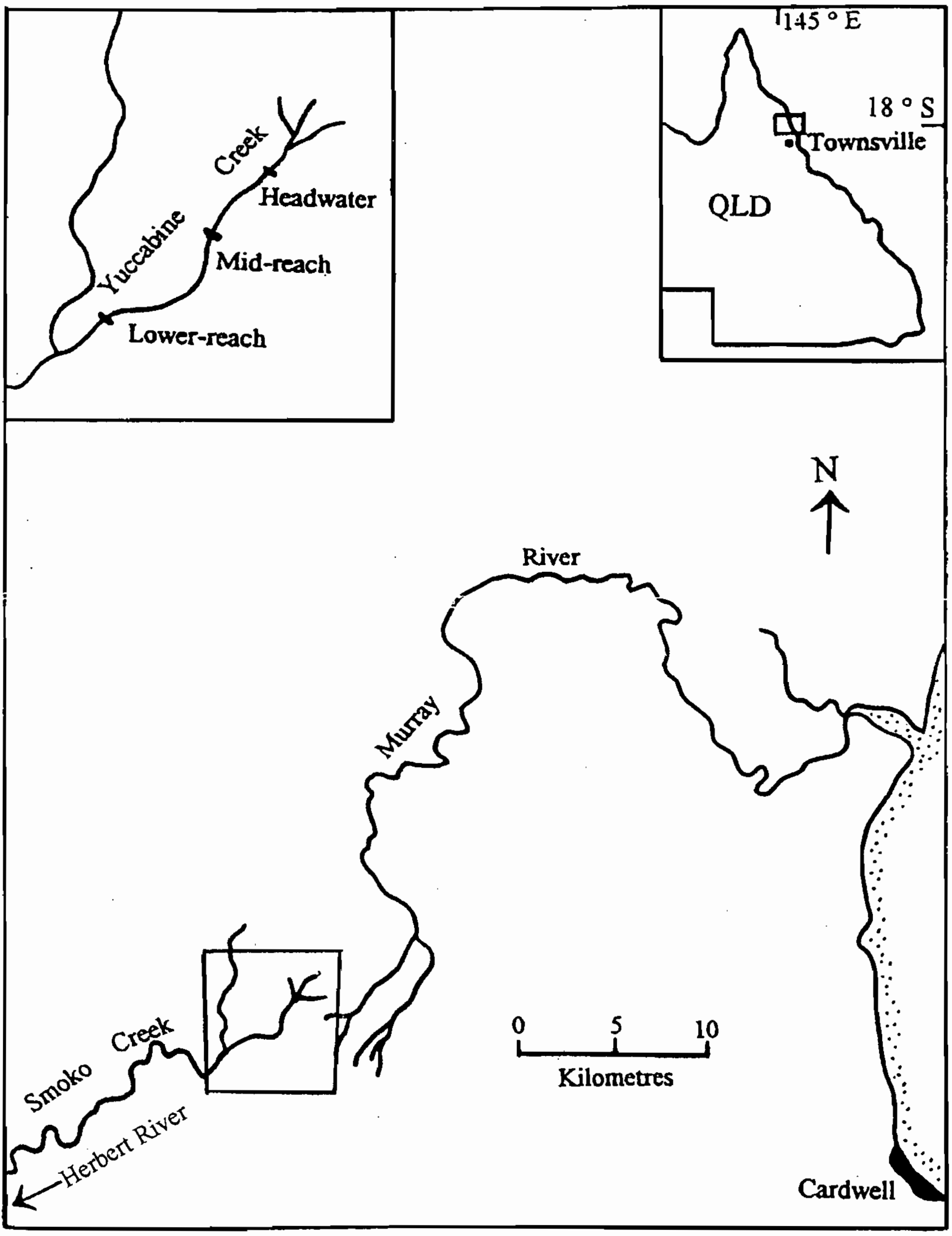

145 ° E
18 ° S
Townsville
QLD
Study Site
State Forest
N
Tully
River
Tully
0
5
10
Kilometres

Figure 3.2 Map indicating the location of the headwater, mid-reach and lower-reach sites along Yuccabine Creek in north Queensland.


Yuccabine
Creek
Headwater
Mid-reach
Lower-reach
145 ° E
18 ° S
Townsville
QLD
N
River
Murray
0
5
10
Kilometres
Smoko
Creek
Herbert River
Cardwell

Similar physical characteristics at the mid-reach site at Yuccabine Creek permit comparisons of riffle fauna on natural stones between this site and Birthday Creek and Pixies Creek (in February). Pixies Creek (17°47'S, 145°41'E), a tributary of the Tully River, is a third-order stream at the study site with a catchment of mixed rainforest species. Macroinvertebrate samples were collected from a 45 m section of riffle habitat (Plate 3) and a 30 m pool section (Plate 4).

All three sites are characterised by seasonal rainfall patterns (Figure 3.3), with most rain falling over the summer months (December - February) (For a detailed description of seasonal patterns of rainfall, stream flow and temperature, refer to that given for Birthday Creek in Chapter 2). Of the three sites, highest rainfall occurs at Tully, which is near the Pixies Creek study site.

Table 3.1 Physical characteristics of the Birthday Creek, Yuccabine Creek, and Pixies Creek study sites.

	Birthday Creek	Yuccabine Creek			Pixies Creek[b]
		Headwater	Mid-reach[a]	Lower-reach	
Stream order	3	1	3	4	3
Mean width (m)	7.5	5.0	7.0	10.0	7.0
Mean depth (m)	0.45	0.4	0.45	0.35	0.5
Mean water temperature (°C)	20.5	19.5	20.0	20.5	20.5
Dominant substratum	cobble	boulder/ cobble	cobble	sand	cobble
Altitude (m above sea level)	800	750	600	500	60
Mean annual rainfall (mm)[c]	2497	2073	2073	2073	3865

[a] Yuccabine Creek site used in comparison with Birthday Creek and Pixies Creek.
[b] Ungazetted name.
[c] Rainfall for the period January, 1969 - December, 1997.

Three riffle sites (stream orders 1-4) were chosen along Yuccabine Creek (18°79'S, 145°45'E) to investigate longitudinal differences in macroinvertebrate response to disturbance corresponding to differences in geomorphology and (inferred) flood frequency. The headwater site (Plate 5), less than one kilometre from the source, was narrow, relatively high gradient, and drained a small catchment; the mid-reach site (Plate 6) was intermediate in size, gradient and catchment area; while the lower-reach site (Plate 7) was relatively wide, with a low gradient, and drained a larger catchment in comparison with the other sites.

Plate 3 Riffle site at Pixies Creek, north Queensland, looking upstream.

Plate 4 Pool site at Pixies Creek, north Queensland, looking downstream.

Figure 3.3 Monthly rainfall totals (December, 1992-November, 1993) and long-term averages for a) Paluma (near Birthday Creek), b) Cardwell (near Yuccabine Creek), and c) Tully (near Pixies Creek).

Long-term averages are calculated for the period between January, 1969 and December, 1997.

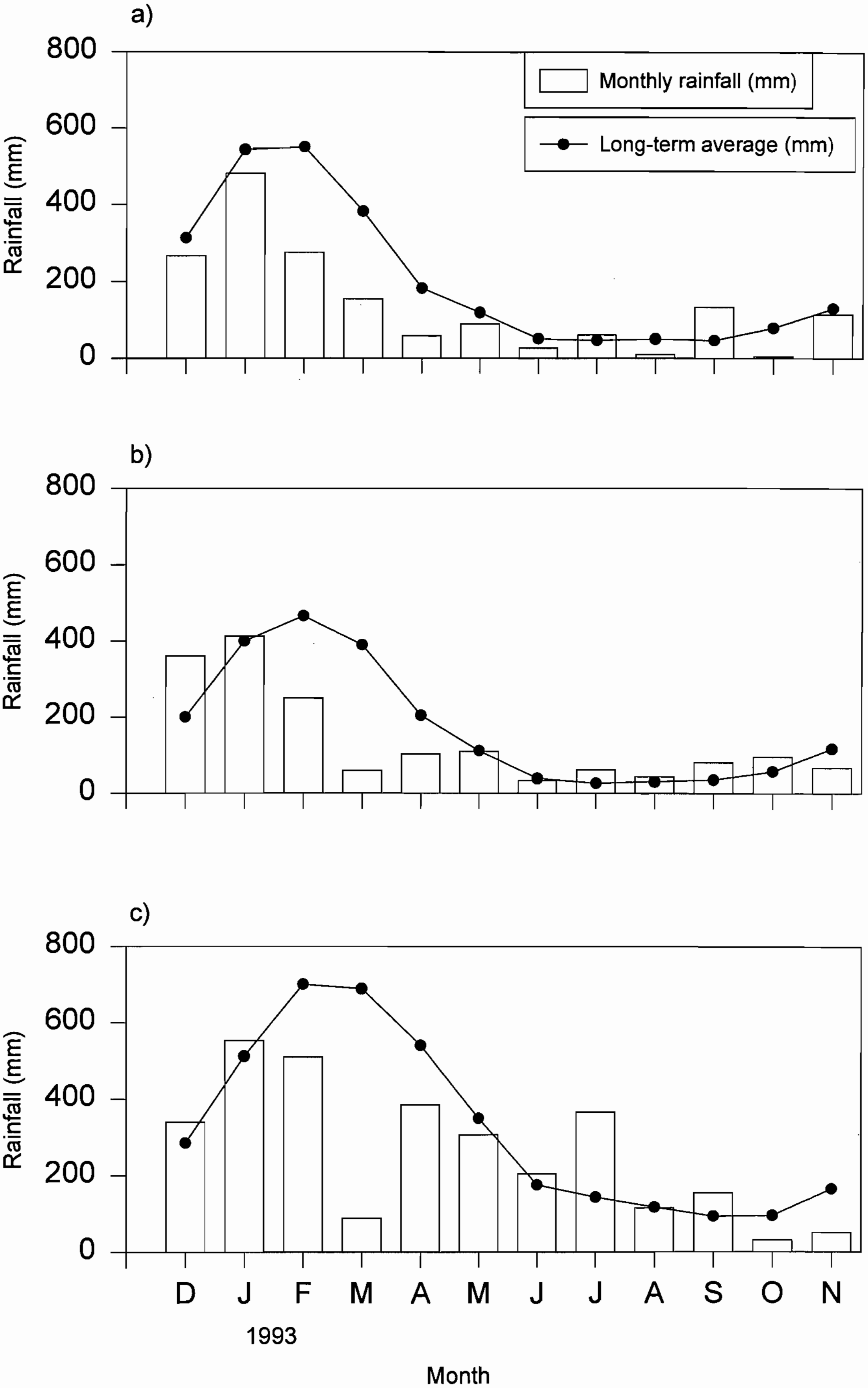

a)
b)
c)
Rainfall (mm)
800
600
400
200
0
Monthly rainfall (mm)
Long-term average (mm)
D
J
F
M
A
M
J
J
A
S
O
N
1993
Month

Plate 5 Headwater site at Yuccabine Creek, north Queensland, looking upstream.

Plate 6 Mid-reach site at Yuccabine Creek, north Queensland, looking upstream.

Plate 7 Lower-reach site at Yuccabine Creek, north Queensland, looking upstream.

The mid-reach site has been the focus of previous studies (Pearson *et al.* 1986, Lake *et al.* 1994). The distribution of the substratum particle size was estimated visually at ten 10 m intervals within riffles along a 100 m stream section at each site. The pooled results and proportions within each category are summarised in Table 3.2. The proportional composition of the different substratum shows that although cobble-sized substrata (corresponding to the size of the bricks used in manipulations) were present at each of the three sites, these sites differed in terms of the predominant substratum particle size. The headwater sites contained a high proportion of boulder/cobble substrata, the mid-reach site was dominated by cobbles, while at the lower-reach site finer sands were common (Table 3.2).

Table 3.2 Substratum particle size distribution (% composition) at headwater, mid-reach and lower-reach sites at Yuccabine Creek. "-" indicates particle size not recorded.

Substratum type (size)	Headwater	Mid-reach	Lower-reach
Bedrock (> 330mm)	15	-	-
Boulder (256-330mm)	40	10	-
Cobble[a] (64-256mm)	45	65	15
Gravel (2-64mm)	-	15	25
Sand (< 2mm)	-	10	60

[a] Note that cobbles correspond with the brick size used in the disturbance experiments

Experimental disturbance procedure

Substrate units for the experimental manipulations were standardised by using half clay bricks (Nubrik, tan). These had been previously used successfully as a substitute for natural rocks (Rosser and Pearson 1995). The surface area available on each brick was 0.08 m^2. Thirty-two bricks were placed in riffles at each site and were disturbed according to the procedure outlined below.

During high flow disturbances, individual particles may be moved considerable distances downstream, rolling and tumbling against other particles. In addition, surfaces may be scoured by suspended particles (Hynes 1970). The experimental treatments, designated low (L), medium (M), and high (H), were intended to encompass a range of disturbance intensities within Birthday Creek (see Rosser 1991) and simulate the physical movement (tumbling) of the substratum and surface scouring (brushing – high treatment) during periods of high flow (Table 3.3). Undisturbed bricks were used as controls (C).

Bricks were randomly placed in the stream at each site and were left to condition for a period of four weeks prior to experimental manipulations. This period had been shown previously to provide an adequate development time for surface organic layers (Rosser and Pearson 1995), an important factor in the use of artificial substrata as representatives of natural stones. To assess whether the fauna on the (control) bricks reflected that on natural stones, eight stones were sampled in conjunction with the bricks at each site. Unless otherwise stated, 32 bricks were used in each experiment (i.e. eight replicates each of control (undisturbed) and three treatments). Following disturbance, bricks were left for 24 hours before sampling.

Table 3.3 Description and of the experimental disturbance treatments used with brick substrata. (note: tumbling involved rolling against the streambed)

Treatment	Description
Low (L)	each brick tumbled twice
Medium (M)	each brick tumbled ten times
High (H)	each brick tumbled ten times and surfaces scrubbed with a test-tube brush

During sampling of the fauna on the bricks, the effect of each disturbance treatment was quantified to permit the separation of components of resistance and resilience.

Each brick was lifted from the streambed and surrounded by a dip net (250 μm mesh) taking care not to include any accumulations of organic material underneath the brick. In the dip net, the brick was disturbed according to one of the three levels of disturbance. Animals which were dislodged from the brick surface as a result of the treatment were retained in the net and termed "portion removed." The brick was then placed into a container of 70 % ethanol for five minutes and surfaces were scrubbed with a test tube brush to remove all macroinvertebrates and thus determine the "portion remaining." The two fractions were then compared enabling treatments to be assessed in terms of the proportion of the total macroinvertebrates removed. The effectiveness of faunal removal by each treatment therefore indicated the relative importance of resistance and resilience characteristics following disturbance. The presence of macroinvertebrates on bricks after experimental manipulation could thus be regarded as due to components of resistance (high treatment) or a combination of resistance and resilience (low and medium treatments) (see *Quantification of the experimental disturbance treatments*, below).

Disturbance frequency

In addition to the collection of invertebrates following a single disturbance, the effect of multiple disturbances (i.e. increasing the frequency) was determined at Birthday Creek. Pre-conditioned bricks, which were labelled according to their designated treatments (i.e. control, low, medium, and high) were placed in riffle (N = 160) and pool (N = 64) habitats at this site. Bricks were disturbed following the experimental disturbance procedure previously outlined (above) on a weekly basis for five weeks (D1 –D5). Therefore, D1 represents one disturbance, D2, two disturbances (one week apart), D3, three disturbances, and so on. The sampling procedure over this period was as follows:

D1 (week 1) – all bricks disturbed (according to their treatment) ($N_{riffle} = 160$, $N_{pool} = 64$).
24 hrs after disturbance, 8 randomly selected bricks from each treatment (i.e. a total of 32) were sampled from the riffle.

D2 (week 2) – all bricks disturbed ($N_{riffle} = 128$, $N_{pool} = 64$).
32 bricks sampled from riffle.

D3 (week 3) – all bricks disturbed ($N_{riffle} = 96$, $N_{pool} = 64$).
32 bricks sampled from riffle and pool.

D4 (week 4) – all bricks disturbed ($N_{riffle} = 64$, $N_{pool} = 32$).
32 bricks sampled from riffle.

D5 (week 5) – all bricks disturbed ($N_{riffle} = 32$, $N_{pool} = 32$).
32 bricks sampled from riffle and pool.

Therefore, the fauna was sampled following each of the five disturbances in the riffle, and following the third and fifth disturbance in the pool. This sampling strategy was designed to permit comparisons between responses of riffle and pool faunas midway and at the end of the experiment. Also, the cumulative effects of disturbance, if present, could be determined in both habitats.

Data analysis

Where natural stones were examined (i.e. to determine the representativeness of the bricks used in experimental manipulations), data were standardised to the surface area of bricks (0.08 m^2, see Chapter 2). The effect of disturbance treatments on macroinvetebrate abundance and richness were determined using univariate techniques (t-tests and ANOVAs) on log (x + 1) transformed data. Where a significant effect was obtained using one-way ANOVAs, treatment means were discriminated using Tukey's HSD multiple comparison test (Zar 1984). Disturbance effects on community structure were assessed using the proportional similarity index of Schoener (1968) and multivariate ordinations (semi-strong hybrid multidimensional scaling) on the reduced data matrix (i.e. only those taxa comprising > 0.05 % of overall totals, Faith and Norris 1989). Details of these procedures have previously been outlined in Chapter 2.

3.3. Results

Characteristics of the stone fauna at each site

There were distinct differences in the macroinvertebrate communities on natural stones at the three sites. Birthday Creek showed consistently higher benthic densities compared with Pixies Creek and Yuccabine Creek (Figure 3.4), peaking in February. Species richness was similar at Birthday Creek and Pixies Creek in December, higher at Pixies Creek in January, and higher at Birthday and Yuccabine Creeks in February. In a comparison of all three sites (February), richness was similar at Birthday Creek and Yuccabine Creek, and higher than at Pixies Creek. The temporal dynamics of the stone fauna at Birthday Creek has been described in detail in Chapter 2.

Ordination of the communities at the three sites over the 1992-1993 wet season (Figure 3.5), shows a temporal shift in community structure along the second axis at Birthday Creek and Pixies Creek.

Figure 3.4 Macroinvertebrate a) abundance and b) richness on stream stones from riffles at Birthday Creek, Yuccabine Creek and Pixies Creek over the summer wet season (December, 1992 - February, 1993). Data are means ± 1 SE.

Significant differences between sites (two sites, t-test, $\alpha = 0.05$; three sites, one-way ANOVAs, d.f. = 2, $\alpha = 0.05$) are indicated with an asterisk with the following significance levels:

n.s. = non-significant,
* = $p \leq 0.05$,
** = $p \leq 0.01$,
*** = $p \leq 0.001$.

In February, different letters indicate means which were significantly different from each other (Tukey's HSD multiple comparison test, α = 0.05).

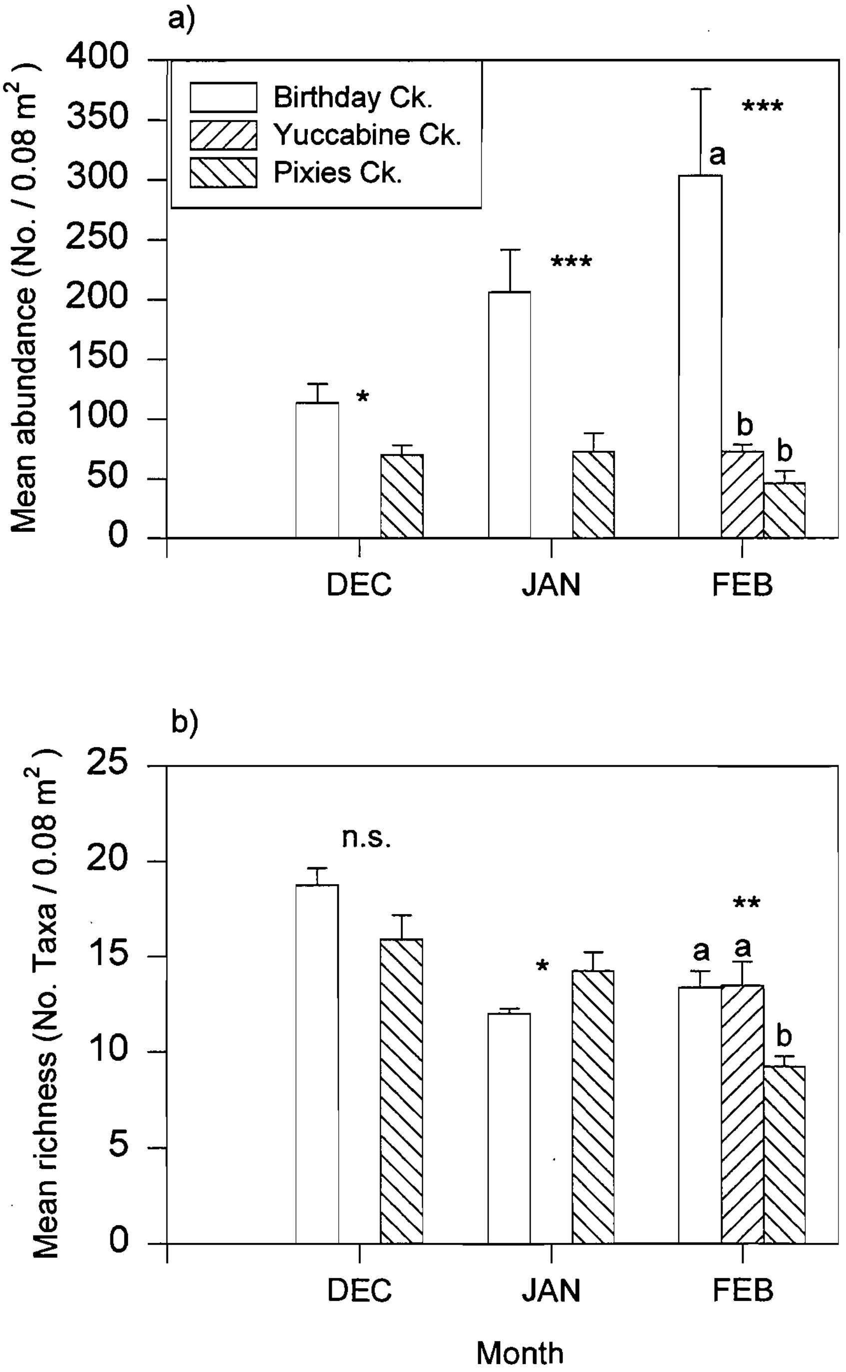
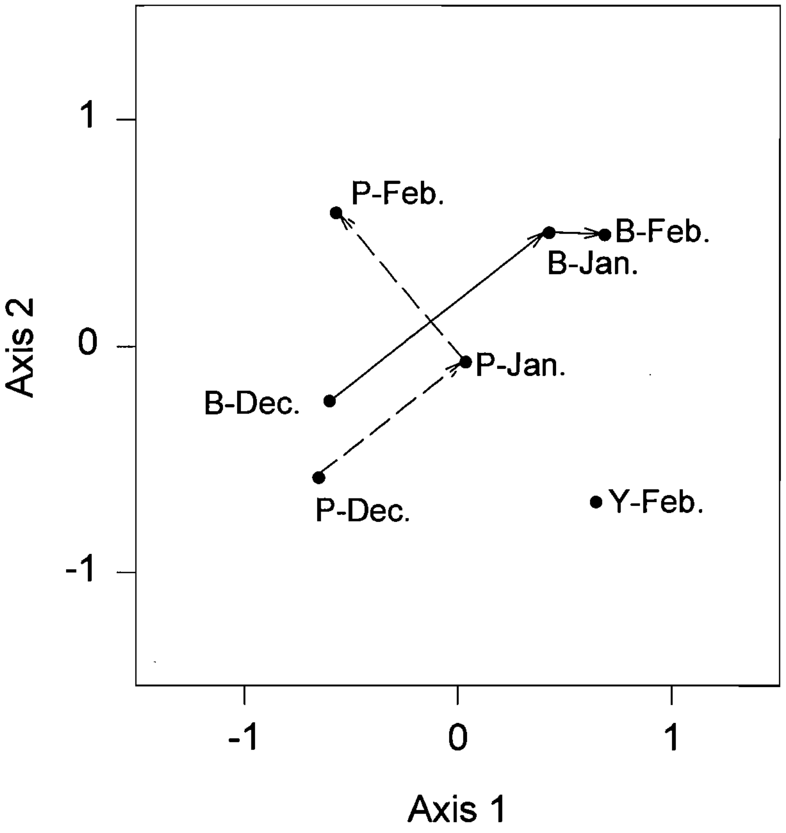

a)
Mean abundance (No. / 0.08 m^2)
400
350
300
250
200
150
100
50
0
Birthday Ck.
Yuccabine Ck.
Pixies Ck.
*
***
***
a
b
b
DEC
JAN
FEB
b)
Mean richness (No. Taxa / 0.08 m^2)
25
20
15
10
5
0
n.s.
*
**
a
a
b
DEC
JAN
FEB
Month

Figure 3.5 Plot of the first two dimensions of SSH ordination (semi-strong hybrid multidimensional scaling) of macroinvertebrate communities on stream stones from riffles at Birthday Creek (B), Yuccabine Creek (Y) and Pixies Creek (P) over the summer wet season (December, 1992 - February, 1993).

Arrows link the consecutive monthly samples (Birthday and Pixies Creek only).


Axis 2
1
0
-1
-1
0
1
Axis 1
P-Feb.
B-Feb.
B-Jan.
P-Jan.
B-Dec.
P-Dec.
Y-Feb.

Community change at Birthday Creek (as indicated by the distance between consecutive centroids), was greatest in early summer (December-January), with little change between January and February; at Pixies Creek changes between samples were of similar magnitude. Community structure at Yuccabine Creek in February was similar to Birthday Creek along the first axis.

Community composition on natural stones in the February samples is shown in Table 3.4. Birthday Creek was numerically dominated by *Simulium* sp., which comprised 82 % of total numbers. As a result, the remaining taxa only contributed to a small proportion of overall numbers.

Table 3.4 Composition of the communities on natural stones from riffles at Birthday Creek, Yuccabine Creek (mid-reach), and Pixies Creek, sampled in February, 1993. The mean abundance ± 1 SE of the common taxa is given with the relative abundance of each indicated in brackets (rounded to the nearest percentage). "-" indicates rare or absent at this site.

Taxa	Birthday Creek	Yuccabine Creek	Pixies Creek
Simulium sp.	247.5 ± 71.32 (82 %)	1.75 ± 0.7 (2 %)	10.75 ± 3.93 (23 %)
Chironomidae	15.38 ± 1.22 (5 %)	33.4 ± 4.19 (46 %)	7.88 ± 2.27 (17 %)
Hydroptilidae sp. 1	5.88 ± 0.77 (2 %)	1.38 ± 0.26 (2 %)	-
Dinotoperla sp.	4.63 ± 0.93 (2 %)	2.25 ± 1.05 (3 %)	-
Agapetus sp.	4.38 ± 1.16 (1 %)	-	-
Kingolus sp.	4.38 ± 0.32 (1 %)	1.88 ± 0.72 (3 %)	-
Chimarra sp.	2.38 ± 0.71 (1 %)	-	5.38 ± 4.06 (12 %)
Cheumatopsyche sp. 1	2.13 ± 0.52 (1 %)	3.5 ± 0.96 (5 %)	1.63 ± 0.96 (4 %)
Helicopsyche sp.	2.13 ± 0.67 (1 %)	-	-
Baetis sp.	-	11.5 ± 2.38 (16 %)	8.0 ± 3.92 (17 %)
Cheumatopsyche sp. 2	-	3.88 ± 1.72 (5 %)	-
Illiesoperla sp.	-	1.88 ± 0.58 (3 %)	-
Dugesia sp.	-	1.75 ± 0.65 (2 %)	2.75 ± 1.22 (6 %)
Hydroptilidae sp.6	-	1.25 ± 0.41 (2 %)	-
Psephenidae sp. 1	-	1.63 ± 0.84 (2 %)	-
Psephenidae sp. 2	-	1.13 ± 0.52 (2 %)	-
Helminthidae sp. 13	-	-	2.75 ± 2.75 (6 %)
Austrophlebioides sp. 1	-	-	1.38 ± 0.53 (3 %)
Lepidoptera sp. 1	-	-	1.38 ± 0.60 (3 %)
Proportion of total	**96 %**	**93 %**	**91 %**

Numerical dominance was much less evident at both Yuccabine Creek and Pixies Creek. Chironomidae (many species) comprised just under half the overall numbers at Yuccabine Creek, while *Baetis* sp. was also common. At Pixies Creek, *Simulium* sp., *Baetis* sp., Chironomidae and *Chimarra* sp. were the most common taxa and contributed similarly to overall densities.

Quantification of the experimental disturbance treatments

As the intensity of the experimental disturbance increased from low to high, the treatments were more effective at removing individual taxa (Table 3.5). Both the low and medium disturbance treatments removed a proportion of the total individuals (40.0 % – 87.0 %, respectively), and therefore the presence of individuals at the time of sampling is likely to be a combination of resistance (i.e. those individuals remaining) and resilience (i.e. individuals which have colonised within 24 hours), with resilience characteristics of the fauna assuming greater importance on medium treatments.

The addition of surface scrubbing (high treatment) proved very effective at removal of macroinvertebrates (98 % removed), so individuals present on the high treatments represent those with high resilience (i.e. ability to recolonise within 24 hours). The treatments were effective at removing taxa, or causing taxa to leave the substrata, including both highly mobile taxa (e.g. *Baetis* sp.) and more sedentary forms (e.g. *Helicopsyche* sp.). Only in two cases was the abundance of taxa unaffected by the experimental disturbance, both at the low intensity treatment. All individuals of Lepidoptera sp. 1 and Tipulidae sp. 3 remained on the bricks as they were tumbled (twice), suggesting that the strategy for these taxa is to "cling on" rather than leave the substratum as it is moved, in contrast to the majority of taxa. As the intensity of disturbance increased, more taxa were totally removed by the treatments, ranging from 35 % (low treatment) to 75 % (high treatment) of total numbers of taxa.

Table 3.5 Effect of the experimental disturbance treatments on common macroinvertebrate taxa and the overall assemblage, expressed as the proportion of individuals of each taxon removed from the bricks following each treatment. "-" indicates taxon rare or absent from treatment.

	Low (tumbled twice)	**Medium** (tumbled 10 x)	**High** (tumbled 10 x plus surface scrubbed)
Lepidoptera sp. 1	0 %	-	-
Tipulidae sp. 3	0 %	-	98 %
Helicopsyche sp.	100 %	-	-
Austrophlebioides sp. 1	75 %	100%	-
Baetis sp.	100 %	100 %	100 %
Tasmanocoenis sp.	96 %	100 %	100 %
Hydroptilidae, early instars	71 %	96 %	93 %
Simulium sp.	60 %	100 %	100 %
Oecetis sp. 1	60 %	100 %	100 %
Nyctiophylax sp.	30 %	-	-
Hydroptilidae sp. 1a	-	75 %	100 %
Hydroptilidae sp. 2	-	86 %	100 %
Hydroptilidae sp. 3	50 %	83 %	94 %
Oligochaeta	34 %	99 %	100 %
Chironomidae	30 %	81 %	97 %
Helminthidae (l) sp. 2a	-	82 %	100 %
Kingolus sp.	-	89 %	94 %
Dinotoperla sp.	-	50 %	100 %
% reduction in overall abundance	**40.0 ± 6 %**	**87.0 ± 9 %**	**98.0 ± 1%**
number of taxa totally removed by the treatment	**7 / 20 (35.0 %)**	**14 / 28 (50.0 %)**	**24 / 32 (75 %)**

Experimental disturbance in riffle and pool habitats at Birthday Creek and Pixies Creek

In the stream riffle, macroinvertebrate abundance and richness on the undisturbed (control) bricks was higher at Birthday Creek compared to Pixies Creek (Figure 3.6). In contrast, overall abundance and richness of pool fauna was higher at Pixies Creek (Figure 3.7). At Birthday Creek, there was no significant change in overall abundance in the riffle or richness in the riffle and pool as disturbance intensity increased, while abundance was significantly reduced by all treatments in the pool (Figures 3.6, 3.7). None of the common riffle taxa were affected by disturbance at Birthday Creek indicating a combination of high resistance and resilience.

Figure 3.6 a) Abundance and b) richness of riffle fauna on experimentally disturbed bricks at Birthday Creek and Pixies Creek. Data are means ± 1 SE.

Significant differences within sites (effect of treatment) were determined using one-way ANOVAs (d.f. =3, $\alpha = 0.05$), and are indicated with an asterisk with the following significance levels:

n.s. = non-significant,
* = $p \leq 0.05$,
** = $p \leq 0.01$,
*** = $p \leq 0.001$.

Within each site, different letters indicate treatment means which were significantly different from each other (Tukey's HSD multiple comparison test, $\alpha = 0.05$).

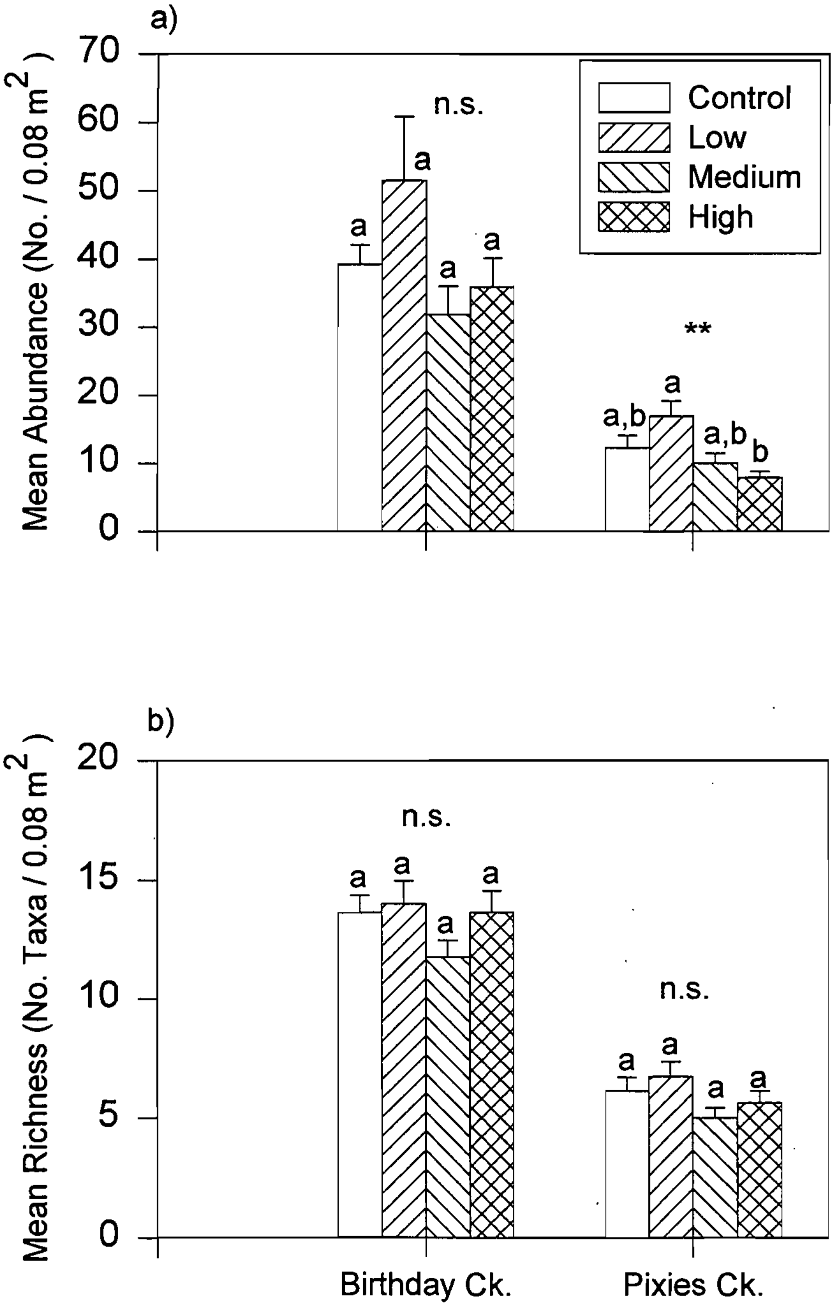
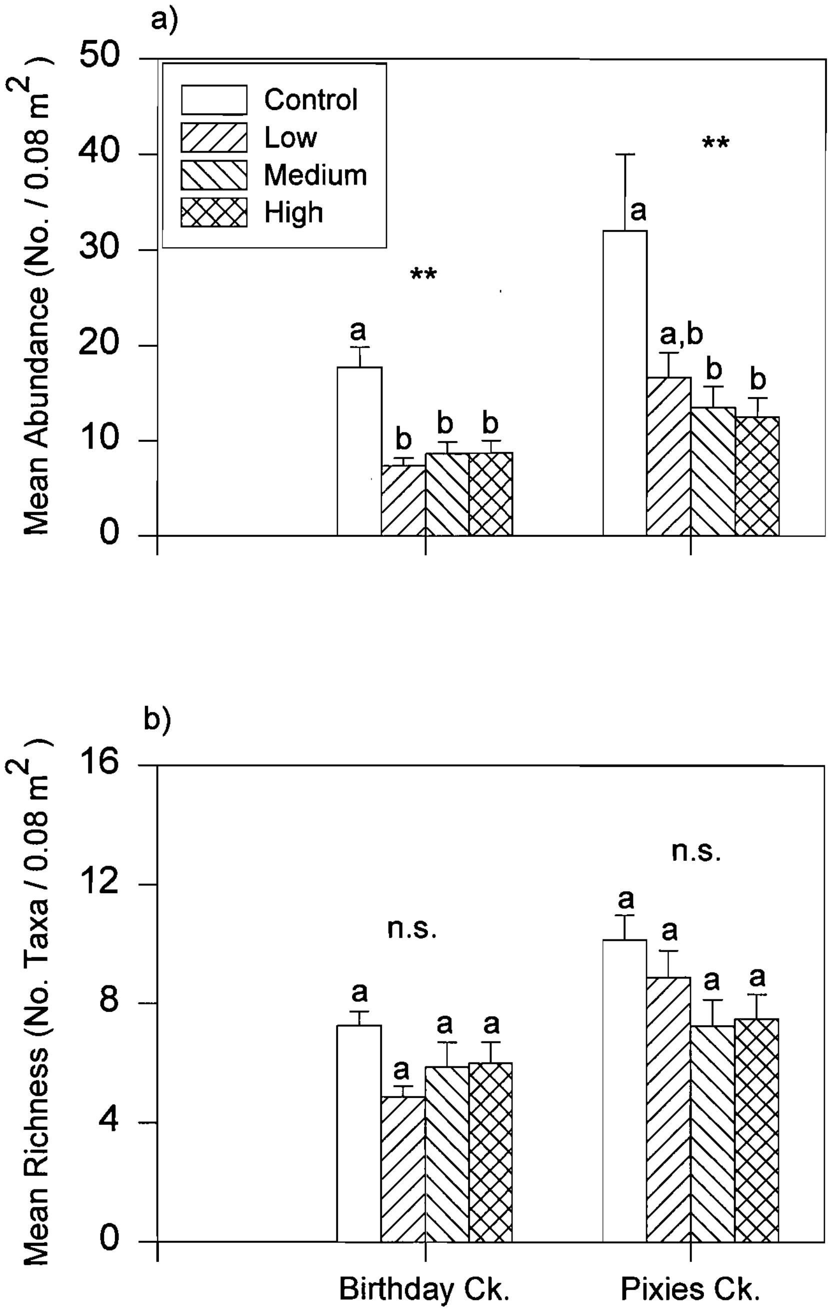

a)
Mean Abundance (No. / 0.08 m^2)
70
60
50
40
30
20
10
0
Control
Low
Medium
High
n.s.
a
a
a
a
**
a,b
a
a,b
b
b)
Mean Richness (No. Taxa / 0.08 m^2)
20
15
10
5
0
n.s.
a
a
a
a
n.s.
a
a
a
a
Birthday Ck.
Pixies Ck.

Figure 3.7 a) Abundance and b) richness of pool fauna on experimentally disturbed bricks at Birthday Creek and Pixies Creek. Data are means ± 1 SE.

Significant differences within sites (effect of treatment) were determined using one-way ANOVAs (d.f. = 3, $\alpha = 0.05$), and are indicated with an asterisk with the following significance levels:

n.s. = non-significant,
* = $p \leq 0.05$,
** = $p \leq 0.01$,
*** = $p \leq 0.001$.

Within each site, different letters indicate treatment means which were significantly different from each other (Tukey's HSD multiple comparison test, $\alpha = 0.05$).


a)
Mean Abundance (No. / 0.08 m^2)
0
10
20
30
40
50
Control
Low
Medium
High
**
a
b
b
b
**
a
a,b
b
b
b)
Mean Richness (No. Taxa / 0.08 m^2)
0
4
8
12
16
n.s.
a
a
a
a
n.s.
a
a
a
a
Birthday Ck.
Pixies Ck.

Of the common taxa in the pool, most were also unaffected, the exceptions being chironomids (reduced by all treatments) and the trichopteran *Nyctiophylax* sp. (reduced by low and high treatments) (Table 3.6).

Abundance of riffle fauna was significantly reduced at Pixies Creek by the surface scrubbing (compared to the low treatment), while in the pool, abundance was significantly lower on the medium and high treatments. Richness was unaffected in both habitats across disturbance treatments (Figures 3.6, 3.7). All common riffle taxa were reduced by disturbance at Pixies Creek, while *Helicopsyche* sp. was the only common pool taxon affected by the disturbance, being reduced by all treatments.

Table 3.6 Summary of one-way ANOVAs testing the effect of disturbance treatments on the abundance of common taxa from riffle and pool habitats at Birthday Creek and Pixies Creek ($\alpha = 0.05$, d.f. = 3). n.s. = non-significant, * = $p \le 0.05$, ** = $p \le 0.01$, *** = $p \le 0.001$. For each taxa, different letters indicate treatment means which were significantly different from each other (Tukey's HSD multiple comparison test, $\alpha = 0.05$). C=control, L=low, M=medium, and H=high.

Taxa	Birthday Creek		Pixies Creek	
	Riffle	Pool	Riffle	Pool
Chironomidae	n.s.	*** $C^{a}L^{b}M^{b}H^{b}$	** $C^{a}L^{a}M^{b}H^{a,b}$	n.s.
Hydroptilidae sp. 1a	n.s.	-	-	-
Nyctiophylax sp.	n.s.	* $C^{a}L^{b}M^{a,b}H^{b}$	-	-
Oecetis sp. 1	n.s.	-	-	n.s.
Helicopsyche sp.	-	n.s.	-	* $C^{a}L^{b}M^{b}H^{b}$
Austrophlebioides sp. 1	-	n.s.	* $C^{a}L^{b}M^{b}H^{b}$	-
Baetis sp.	-	n.s.	-	-
Kingolus sp.	-	-	* $C^{a}L^{b}M^{a,b}H^{b}$	-
Simulium sp.	n.s.	-	* $C^{a,b}L^{a}M^{a,b}H^{b}$	n.s.
Hydracarina	-	-	-	n.s.

A measure of the overall turnover of taxa on the bricks as disturbance intensity increased (i.e. across treatments) at Birthday Creek and Pixies Creek, provided a comparison (adjusted by the mean) between sites and habitats (Table 3.7). Turnover was generally higher in the pool than the riffle at Birthday Creek and in the riffle at Pixies Creek. Relative to the controls, highest turnover occurred on the low treatments (rolled twice) in the riffles and the medium treatments (rolled ten times) in the pool habitat at both sites, suggesting that in some instances, the treatments may enhance the turnover of individuals relative to undisturbed substrata.

Table 3.7 Number of taxa lost, gained and remaining the same on bricks as the intensity of disturbance increases (i.e. across treatments). An indication of species turnover is calculated as: turnover = spp. lost + spp. gained/total spp x 100 (%).

Site	Control vs. Low	Control vs. Medium	Control vs. High
Birthday Creek			
Riffle:			
species lost	3	5	2
species gained	5	1	5
same species	27	23	28
TOTAL spp.	30	25	34
Turnover (%)	26.6	24.0	20.5
Pool:			
lost	4	5	4
gained	2	5	6
same	9	9	10
TOTAL spp.	11	14	16
Turnover (%)	54.5	71.4	62.5
Pixies Creek			
Riffle:			
lost	7	7	7
gained	8	2	5
same	13	12	12
TOTAL spp.	20	15	18
Turnover (%)	75.0	60.0	66.7
Pool:			
lost	5	9	8
gained	8	2	4
same	19	16	16
TOTAL spp.	27	19	21
Turnover (%)	48.1	57.9	57.1

Ordination of experimentally disturbed communities from the riffle (Figure 3.8) and the pool (Figure 3.9) revealed distinct assemblages at each site, and reflect the trends observed by the common taxa in response to disturbance. In the riffles, changes in community structure resulting from the disturbance treatments and indicated by the distance between ordination centroids were greater at Pixies Creek. In contrast, community structure was little altered by disturbance at Birthday Creek. In the pools this contrast did not occur, and in both cases there was a trend towards increased change in community structure (shift away from controls) as disturbance intensity increased; however, some of these shifts occurred in opposite directions at the two sites. Similar results were obtained using presence/absence data in both habitats at the two sites, indicating that the pattern of community response to disturbance is driven more by species representation rather than individual abundances.

Disturbance frequency

Within times (i.e. each week), there was a general pattern of a decline in abundance and richness relative to the controls as the intensity of disturbance increased, from low to high (Figure 3.10). The reduction across the treatments was less pronounced in the pool; in most cases the treatments, although lower than the controls, were not significantly different from each other (Tukey's HSD multiple comparison test, $p > 0.05$). The only exception was at week five (D5), where there was no significant difference in richness of macroinvertebrates on the control and disturbed bricks.

The interactive effects of disturbance with time were significant for total abundance and richness of riffle fauna (Table 3.8). The response of the common taxa to increased frequency of disturbance was varied. When the responses are compared to those following a single disturbance (see Table 3.6), a number of the common taxa (Chironomidae, *Nyctiophylax* sp., *Oecetis* sp. 1) shifted from a non-significant response to a significant reduction in abundance with increased frequency of disturbance. Other taxa showed a non-significant response to an increased frequency of disturbance (e.g. *Baetis* sp., *Austrophlebioides* sp. 1, and in particular, the numerically dominant *Simulium* sp.), suggesting high resistance and/or resilience.

Figure 3.8 Plot of the first two dimensions of SSH ordinations (semi-strong hybrid multidimensional scaling) of macroinvertebrate riffle communities in terms of a) abundance and b) presence/absence on experimentally disturbed bricks at Birthday Creek and Pixies Creek over the summer wet season (December, 1992 - February, 1993).

Arrows link the different disturbance treatments (C = control, L = low, M = medium, H = high).

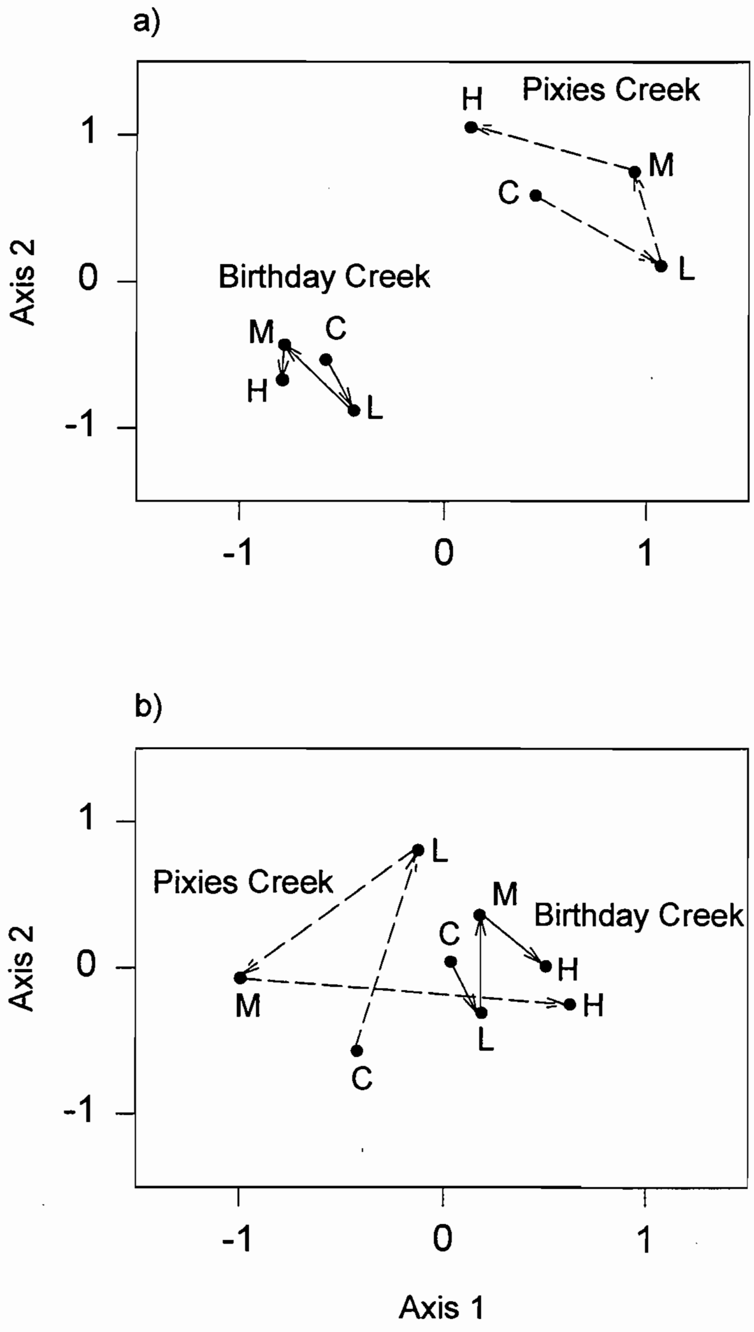
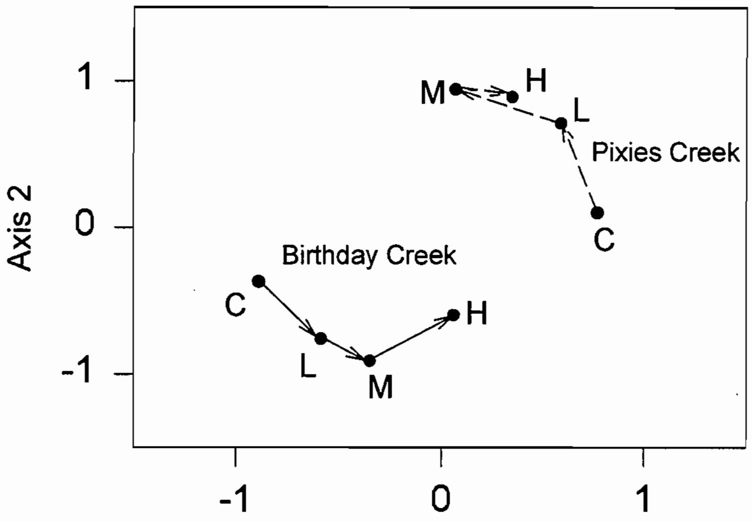

a)
Pixies Creek
H
M
C
L
Birthday Creek
M
C
H
L
1
0
-1
-1
0
1
Axis 2
b)
Pixies Creek
L
M
C
H
Birthday Creek
M
C
H
L
1
0
-1
-1
0
1
Axis 2
Axis 1

Figure 3.9 Plot of the first two dimensions of SSH ordinations (semi-strong hybrid multidimensional scaling) of macroinvertebrate pool communities in terms of a) abundance and b) presence/absence on experimentally disturbed bricks at Birthday Creek and Pixies Creek over the summer wet season (December, 1992 - February, 1993).

Arrows link the different disturbance treatments (C = control, L = low, M = medium, H = high).

a)


Axis 2
1
0
-1
-1
0
1
M
H
L
Pixies Creek
C
Birthday Creek
C
L
M
H

b)

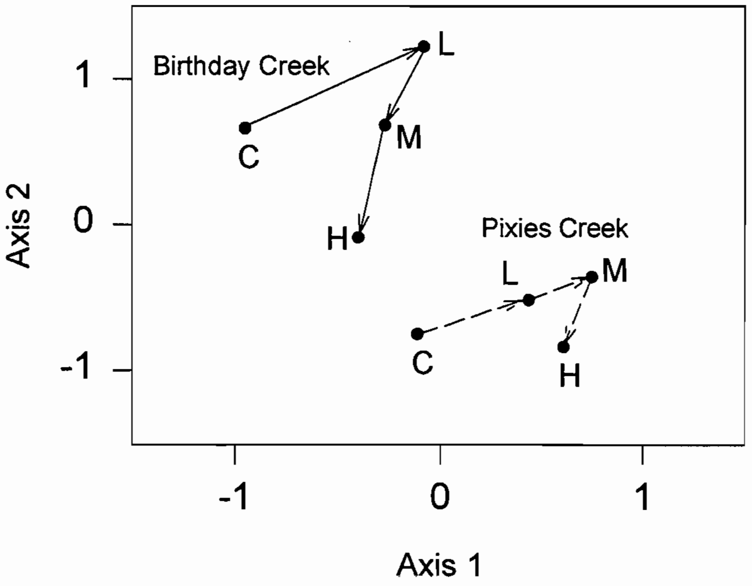

Axis 2
1
0
-1
-1
0
1
Axis 1
Birthday Creek
L
C
M
H
Pixies Creek
L
M
C
H

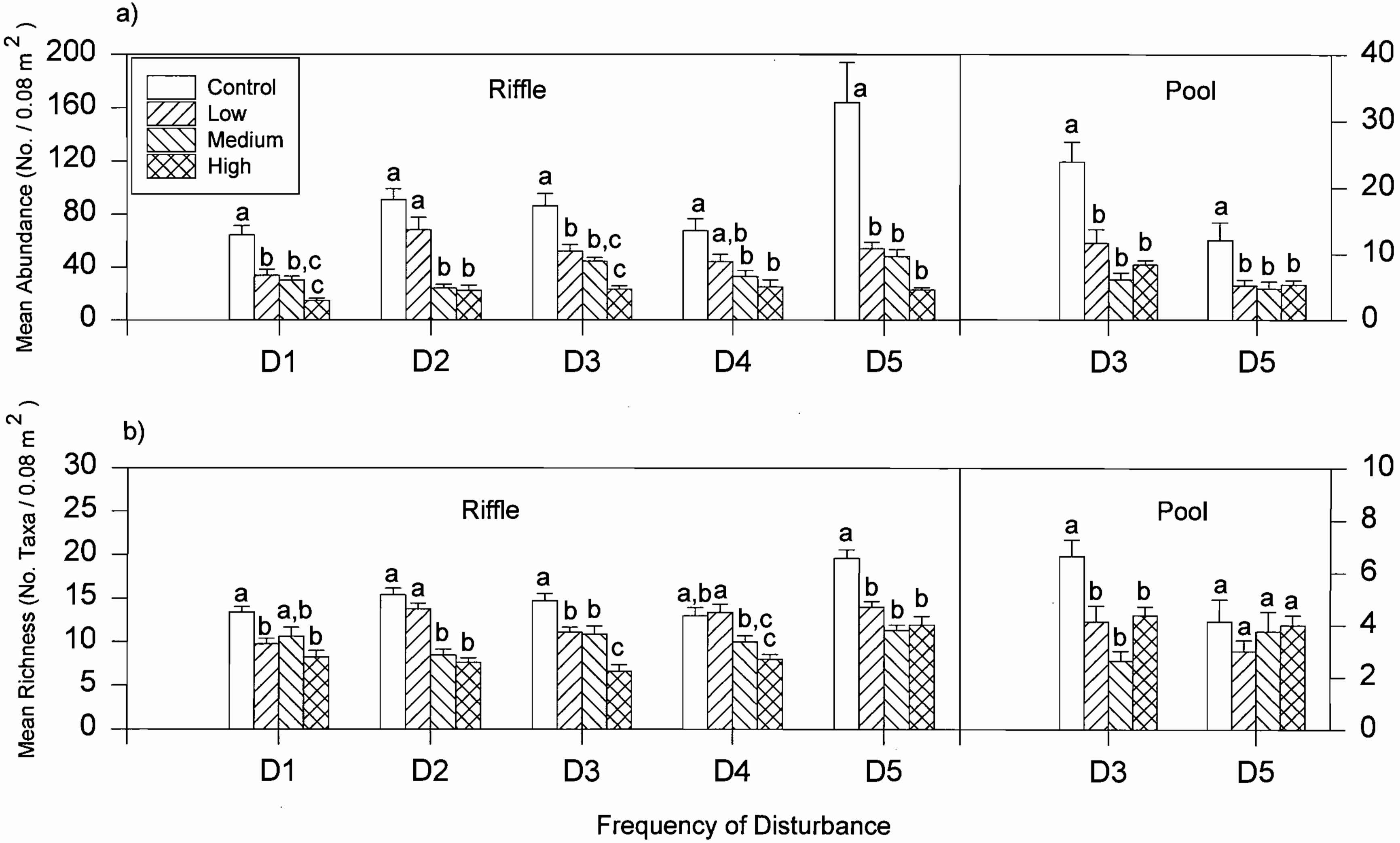
Figure 3.10 The effect of increased disturbance frequency (cumulative weekly disturbance) on a) abundance and b) richness of macroinvertebrates on experimentally disturbed bricks in riffle and pool habitats at Birthday Creek. D1 = single disturbance, D2 = D1 + second disturbance, D3 = D1 + D2 + third disturbance, etc. Data are means ± 1 SE.

Significant differences within times (effect of treatment) were determined using one-way ANOVAs (d.f. = 3, $\alpha = 0.05$), and are indicated with an asterisk with the following significance levels:

n.s. = non-significant,
* = $p \leq 0.05$,
** = $p \leq 0.01$,
*** = $p \leq 0.001$.

Summary of one-way ANOVAs (within-times) are given in Appendix 1, Table A3.1.

At each time, different letters indicate treatment means which were significantly different from each other (Tukey's HSD multiple comparison test, $\alpha = 0.05$).


a)
Mean Abundance (No. / 0.08 m 2)
200
160
120
80
40
0
Control
Low
Medium
High
Riffle
Pool
40
30
20
10
0
a
b
b,c
c
a
a
b
b
a
b
b,c
c
a
a,b
b
b
a
b
b
b
a
b
b
b
a
b
b
b
D1
D2
D3
D4
D5
D3
D5
b)
Mean Richness (No. Taxa / 0.08 m 2)
30
25
20
15
10
5
0
Riffle
Pool
10
8
6
4
2
0
a
b
a,b
b
a
a
b
b
a
b
b
c
a,b
a
b,c
c
a
b
b
b
a
b
b
b
a
a
a
a
D1
D2
D3
D4
D5
D3
D5
Frequency of Disturbance

In the pool, there was a slight significant effect ($p<0.05$) of disturbance frequency on overall richness and numbers of Chironomidae, while overall abundance and the abundance of *Austrophlebioides* sp. 1 were unaffected (Table 3.8).

Table 3.8 Summary of two-way ANOVAs testing disturbance treatment by time for total abundance, richness, and the most common taxa within pool and riffle habitats. n.s. = non-significant, *** = $p \leq 0.001$, ** = $p \leq 0.01$, * = $p \leq 0.05$. (For details, refer to Appendix 1, Table A3.2).

	Main Effects		Interaction
	Treatment	Time	Treatment x Time
Riffle			
Total abundance	***	***	**
Total richness	**	***	**
Baetis sp. 1	**	***	n.s.
Austrophlebioides sp. 1	**	***	n.s.
Simulium sp.	n.s.	**	n.s.
Hydroptilidae (I) sp. 1a	**	**	n.s.
Chironomidae	***	**	*
Helicopsyche sp.	**	***	*
Oecetis sp. 1	***	***	***
Nyctiophylax sp.	***	***	**
Pool			
Total abundance	***	***	n.s.
Total richness	**	n.s.	*
Austrophlebioides sp. 1	n.s.	***	n.s.
Chironomidae	**	n.s.	*

There was little evidence to suggest a cumulative effect of disturbance frequency on community similarity, at least in the riffle (Table 3.9). Instead of declining with increased frequency of disturbance (i.e. D1 – D5), proportional similarity index values indicate high overlap in composition and relative abundance between control and treatment assemblages. In the pool however, proportional similarity after five disturbances (D5) was generally lower relative to values after three disturbances (D3), suggesting a possible cumulative effect of disturbance.

Table 3.9 The effect of disturbance frequency (performed weekly) on the proportional similarity (PSI index) between control and treatment assemblages in riffle and pool habitats. PSI values ≥ 0.65 indicate high overlap (similarity) between assemblages. D1 = one disturbance, D2 = two disturbances, etc. Pools were sampled after three and five disturbances (D3, D5 respectively)

Frequency	Control vs. Low	Control vs. Medium	Control vs. High
Riffle			
D1	0.74	0.73	0.65
D2	0.74	0.74	0.76
D3	0.77	0.75	0.69
D4	0.73	0.69	0.73
D5	0.81	0.74	0.65
Pool			
D3	0.75	0.74	0.62
D5	0.64	0.58	0.63

Longitudinal gradient

The composition of the benthic fauna (stones and undisturbed bricks) at each of the three sites along Yuccabine Creek is summarised in Table 3.10. The headwater site was numerically dominated by Ephemeroptera, particularly the highly mobile *Baetis* sp. The Ephemeroptera and the Chironomidae together comprised approximately 60 % of total numbers on stones, and 70 % of totals on bricks. The Chironomidae was the most abundant taxa and, with *Baetis* sp., comprised 63 % of totals on stones and 86 % of totals on bricks. The most common taxa at the lower reaches of Yuccabine Creek were *Baetis* sp., Chironomidae, and *Cheumatopsyche* sp. 2, comprising 57 % of totals on stones. In contrast, on bricks, numbers, and relative proportions of *Simulium* sp. were higher, contributing 81 % of the total numbers.

Similarity in community composition on stones and bricks was most similar at the headwater site, with total abundance, richness, and the abundance of all but one of the common taxa not significantly different between stones and bricks. The elmid larva, *Kingolus* sp., was under-represented on the bricks at this site.

Table 3.10 Comparison of macroinvertebrates on natural stones (S) and artificial bricks (B) at headwater, mid-reach and lower-reach sites along Yuccabine Creek. Mean abundance ± 1 SE of the common taxa are given (abundance on stones expressed per 0.08 m^2 and so are directly comparable to bricks), with their relative abundance (%) in parentheses. Proportion of total numbers comprised by the major orders is indicated in bold. Significant differences between substrata were determined using t-tests ($\alpha = 0.05$, d.f. = 14) where: n.s. = non-significant, * = $p \le 0.05$, ** = $p \le 0.01$, *** = $p \le 0.001$. Where significant, the substratum type with the highest abundance is indicated in parentheses.

Taxa		**Headwater**			**Mid-reach**			**Lower-reach**	
	Stones (%)	Bricks (%)	S vs. B	Stones (%)	Bricks (%)	S vs. B	Stones (%)	Bricks (%)	S vs. B
Baetis sp.	20.38 ± 4.37 (33.3)	15.75 ± 1.87 (41.0)	n.s.	11.5 ± 2.34 (17.4)	28.38 ± 3.71 (13.8)	** (Brick)	29.13 ± 4.17 (21.6)	18.63 ± 5.15 (10.0)	n.s.
Austrophlebioides sp. 1	0.75 ± 0.36 (2.0)	0.75 ± 0.41 (1.2)	n.s.	-	-		5.38 ± 1.39 (4.8)	1.25 ± 0.45 (1.0)	** (Stone)
Total Ephemeroptera	**(35.3 %)**	**(44.0 %)**		**(17.4 %)**	**(14.0 %)**		**(33.5 %)**	**(11.0 %)**	
Chironomidae	16.25 ± 3.61 (26.5)	11.0 ± 4.02 (28.7)	n.s.	33.63 ± 4.19	149.25 ± 21.66 (72.1)	*** (Brick)	27.13 ± 6.25 (24.3)	4.88 ± 1.05 (2.5)	*** (Stone)
Simulium sp.	1.13 ± 0.35 (1.9)	3.25 ± 1.32 (8.5)	n.s.	(45.8)	1.0 ± 0.63 (1.9)		4.88 ± 0.97 (4.4)	149.25 ± 79.86 (80.9)	*** (Brick)
Total Diptera	**(28.4 %)**	**(35.0 %)**		**(48.5 %)**	**(74.0 %)**		**(29.0 %)**	**(83.4 %)**	
Cheumatopsyche sp. 1	1.25 ± 0.56 (2.0)	-	-	3.5 ± 0.96 (4.8)	4.88 ± 2.24 (2.4)	n.s.	4.0 ± 0.94 (3.6)	1.25 ± 0.41 (1.0)	* (Stone)
Cheumatopsyche sp. 2	-	-	-	3.88 ± 1.72 (5.3)	1.13 ± 0.67 (1.0)	n.s.	12.5 ± 4.56 (11.2)	-	-
Helicopsyche sp.	2.63 ± 1.03 (4.3)	0.88 ± 0.4 (2.3)	n.s.	-	-	-	3.0 ± 1.0 (3.0)	-	** (Stone)
Chimarra sp.	0.88 ± 0.88 (1.4)	0.25 ± 0.25 (4.3)	n.s.	-	-	-	5.63 ± 1.95 (5.0)	-	-
Total Trichoptera	**(10.4 %)**	**(7.0 %)**		**(15.0 %)**	**(7.3 %)**		**(28.4 %)**	**(1.1 %)**	
Kingolus sp.	10.38 ± 4.64 (17.0)	0.75 ± 0.31 (2.0)	* (Stone)	1.88 ± 0.71 (2.5)	-	-	1.13 ± 0.4 (1.0)	-	-
Total Coleoptera	**(18.0 %)**	**(2.5 %)**		**(9.3 %)**	**(0.1 %)**		**(2.5 %)**	**(0.2 %)**	
Dinotoperla sp.	2.25 ± 0.88 (3.7)	2.25 ± 1.05 (6.0)	n.s.	2.25 ± 0.67 (3.1)	1.25 ± 0.49 (0.6)	n.s.	3.13 ± 1.39 (3.0)	-	-
Illiesoperla sp.	2.25 ± 1.40 (3.8)	1.75 ± 0.8 (4.5)	n.s.	1.88 ± 0.58 (2.3)	1.38 ± 0.53 (0.7)	n.s.	3.25 ± 1.29 (3.0)	7.13 ± 1.23 (3.9)	* (Brick)
Total Plecoptera	**(7.5 %)**	**(10.5 %)**		**(5.4 %)**	**(1.3 %)**		**(6.0 %)**	**(4.0 %)**	
Total other	**(0.4 %)**	**(1.0 %)**		**(4.4 %)**	**(3.3 %)**		**(0.6 %)**	**(0.3 %)**	
Overall abundance	**61.25 ± 10.85**	**38.38 ± 5.72**	n.s.	**72.88 ± 5.88**	**207.13 ± 25.63**	*** (Brick)	**111.5 ± 9.67**	**184.75 ± 80.35**	n.s.
Overall richnes	**8.75 ± 0.67**	**7.13 ± 0.64**	n.s.	**13.5 ± 1.25**	**12.13 ± 0.64**	n.s.	**13.75 ± 0.37**	**7.63 ± 0.68**	*** (Stone)

Macroinvertebrate richness at the mid-reach was not significantly different on the stones and bricks; however, total abundance was significantly higher on the bricks, due largely to greatly increased numbers of chironomids and many of the less common taxa. Notable exceptions were two species of *Cheumatopsyche*, which were of similar abundance on natural and artificial substrata. The greatest differences between natural stones and bricks were observed at the lower-reach site where the proportion of cobble-sized particles in the streambed was relatively low (comprising only 15 % of totals) compared with headwater and mid-reach sites (45 % and 65 % respectively). At this site only total abundance was similar on stones and bricks, due largely to the over-representation of *Simulium* sp. on the bricks, as many of the remaining taxa were significantly lower in abundance on the bricks. Similarly, overall richness was lower on the bricks compared to the natural stones.

On the undisturbed bricks, the headwater site had the lowest overall abundance, was similar in richness to the lower reach, both of which were significantly lower in richness than the mid-reach site. The experimental disturbance had little effect on abundance and richness at the headwater site and only the addition of surface scrubbing (high treatment) resulted in a significant reduction (Figure 3.11). The mid-reach site was the most impacted by the experimental disturbance, with the greatest reductions in abundance and richness. The medium and high treatments resulted in a significant drop in total abundance, while richness was significantly reduced by all treatments. The disturbance treatments did not result in a significant drop in abundance at the lower reach site. Richness was significantly lower on the medium and high treatments.

Ordination of the disturbed communities reflects compositional differences between the sites along the primary axis with some overlap between headwater and lower-reach sites, and little overlap between these two sites and the mid-reach site (Figure 3.12). Surprisingly, the sequence of sites along Axis 1 didn't reflect the sequence along the stream. The second axis, which represented a gradient of disturbance intensity, reveals that community structure is most altered by disturbance at the mid-reach site (i.e. greatest distance between treatment centroids), and least altered at the lower-reach site. This indicates that in terms of overall resistance and resilience to the disturbance treatments, from highest to lowest, the sites follow the pattern: lower-reach > headwater > mid-reach.

Figure 3.11 a) Abundance and b) richness of macroinvertebrates on experimentally disturbed bricks at headwater, mid-reach, and lower-reach sites along Yuccabine Creek. Data are means ± 1 SE.

Significant differences within sites (effect of treatment) were determined using one-way ANOVAs (d.f. = 3, $\alpha = 0.05$), and are indicated with an asterisk with the following significance levels:

n.s. = non-significant,
* = $p \leq 0.05$,
** = $p \leq 0.01$,
*** = $p \leq 0.001$.

At each site, different letters indicate treatment means which were significantly different from each other (Tukey's HSD multiple comparison test, $\alpha = 0.05$).

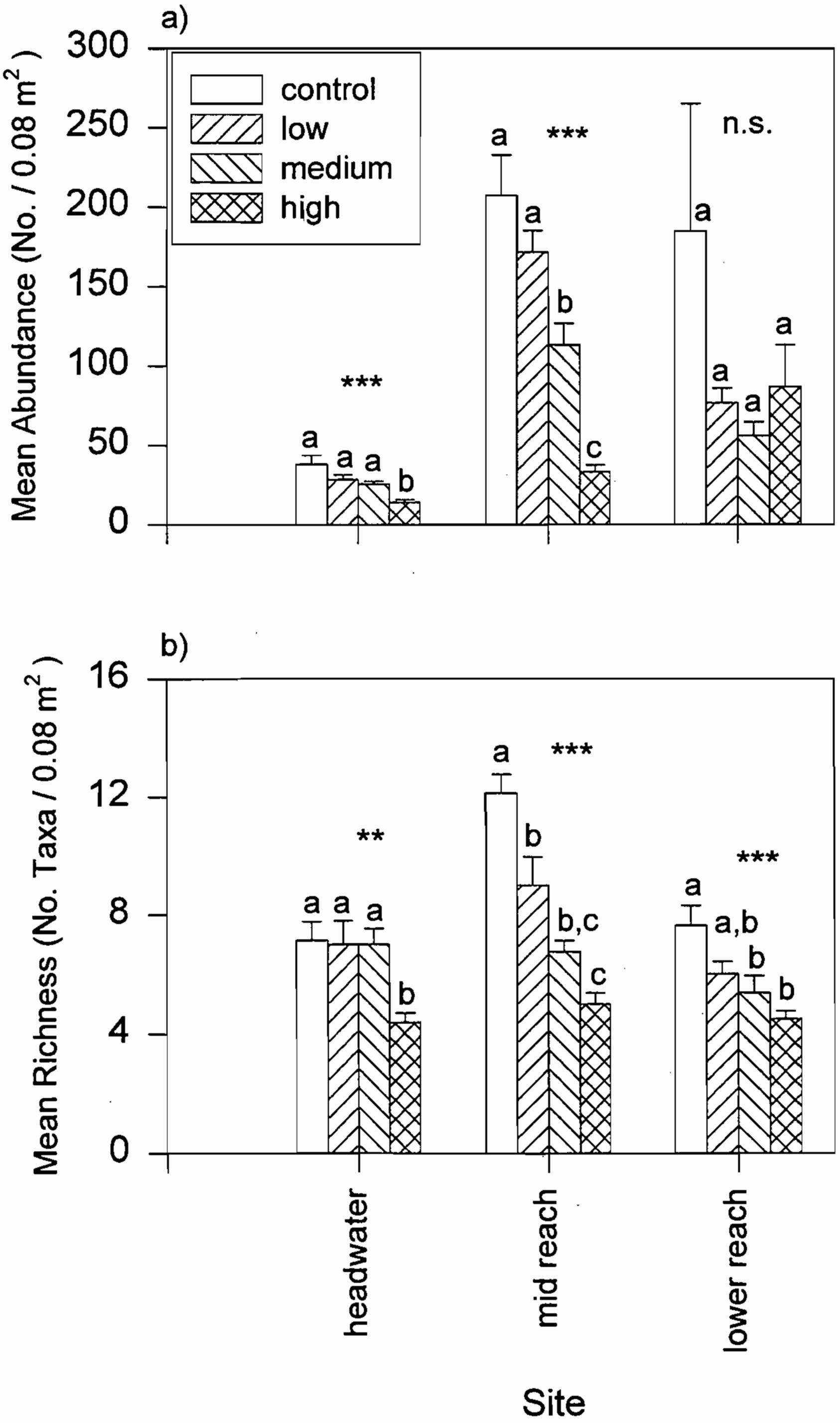
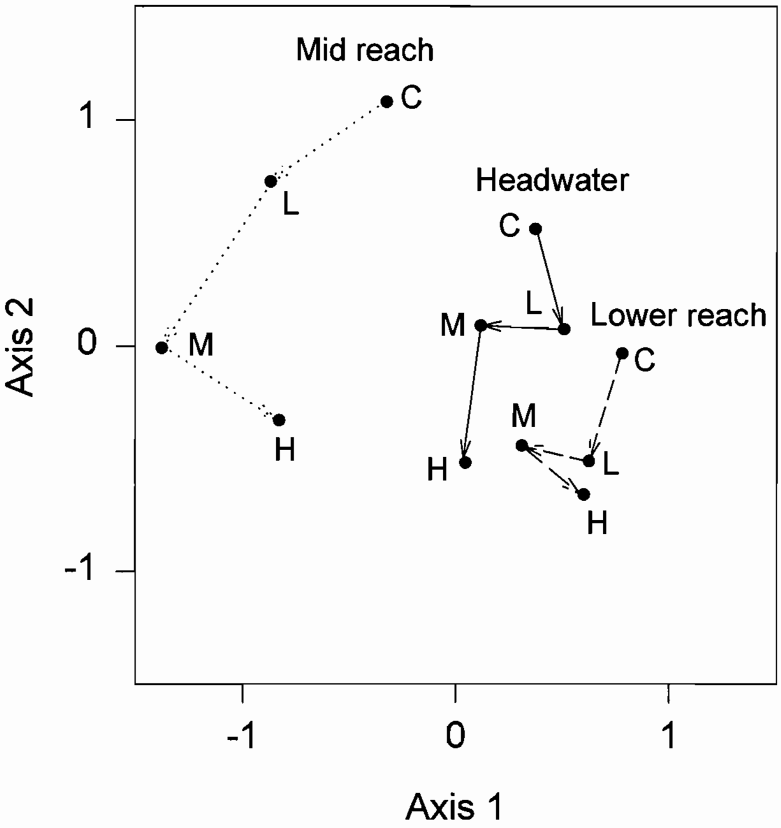

a)
Mean Abundance (No. / 0.08 m^2)
300
250
200
150
100
50
0
control
low
medium
high
***
a
a
a
b
a
***
a
b
c
n.s.
a
a
a
a
b)
Mean Richness (No. Taxa / 0.08 m^2)
16
12
8
4
0
**
a
a
a
b
a
***
b
b,c
c
***
a
a,b
b
b
headwater
mid reach
lower reach
Site

Figure 3.12 Plot of the first two dimensions of SSH ordination (semi-strong hybrid multidimensional scaling) of macroinvertebrate communities on experimentally disturbed bricks at headwater, mid-reach, and lower-reach sites along Yuccabine Creek.

Arrows link the different disturbance treatments (C = control, L = low, M = medium, H = high).


Mid reach
C
L
M
H
Headwater
C
L
M
H
Lower reach
C
M
L
H
Axis 2
1
0
-1
-1
0
1
Axis 1

The responses of individual taxa to the experimental disturbance were variable across the three sites (Table 3.11). Some common patterns were evident in the response of common taxa to disturbance. Taxa with low resistance and/or resilience were: *Dinotoperla* sp. (headwater, mid reach) and *Illiesoperla* sp. (mid reach); *Kingolus* sp. (headwater); *Cheumatopsyche* sp. 1 and *Cheumatopsyche* sp. 2 (mid reach); Hydroptilidae (larvae), early instars and sp. 1a (mid reach); and *Austrophlebioides* sp. 1 (lower reach). In contrast, taxa with characteristics of high resistance and/or resilience (i.e. no significant difference across all treatments) were: *Simulium* sp. (all three sites); *Helicopsyche* sp. (headwater); *Illiesoperla* sp. (headwater); Hydracarina (mid reach); *Baetis* sp. (lower reach); and Chironomidae (lower reach).

Table 3.11 Summary of one-way ANOVAs testing the effect of disturbance treatments on the abundance of common taxa from headwater, mid-reach, and lower-reach sites along Yuccabine Creek ($\alpha = 0.05$, d.f. = 3). n.s. = non-significant, * = $p \le 0.05$, ** = $p \le 0.01$, *** = $p \le 0.001$. For each taxa, different letters indicate treatment means which were significantly different from each other (Tukey's HSD multiple comparison test, $\alpha = 0.05$). C=control, L=low, M=medium, and H=high.

Taxa	Headwater	Mid-reach	Lower-reach
Dinotoperla sp.	** $C^aL^aM^bH^b$	** $C^aL^{a,b}M^bH^b$	n.s.
Chironomidae	*** $C^aL^bM^bH^b$	*** $C^aL^aM^bH^b$	n.s.
Baetis sp.	** $C^aL^aM^bH^c$	* $C^aL^{a,b}M^aH^b$	n.s.
Simulium sp.	n.s.	n.s.	n.s.
Illiesoperla sp.	n.s.	** $C^aL^bM^aH^b$	*** $C^aL^bM^bH^b$
Helicopsyche sp.	n.s.	-	-
Oligochaeta	-	*** $C^aL^bM^bH^b$	-
Hydroptilidae (l) sp. 1a	n.s.	-	-
Hydracarina	-	n.s.	-

3.4. Discussion

Overturning of stream stones disturbs stream benthic communities through the removal of individuals and the creation of patches of space with altered densities of other taxa and levels of resources (Boulton *et al.* 1988, Resh *et al.* 1988, Lake *et al.* 1989). The response by the stream fauna to such micro-scale changes provides considerable insight into the mechanisms responsible for the creation and maintenance of the high levels of patchiness observed in benthic communities at this scale (Downes *et al.* 1995). In this study, tumbling of stream substrata to varying degrees, simulating some of the physical effects of floods of different intensities, affected the communities on substratum surfaces within different habitat types (riffle and pool) and within the same habitat (riffles) at different positions along a longitudinal gradient.

Experimental disturbance of benthic fauna in riffle and pool habitats

Riffles and pools supported a relatively distinct fauna in these streams, with only a small number of taxa common to both habitats. Therefore, pools cannot generally be regarded as simply a subset of riffle communities, as was found by Brown and Brussock (1991). Within riffles and pools, however, inter-site differences in the pattern of response to disturbance was observed. Within sites, highest resistance and resilience were observed in habitats with greatest abundance and richness. At Birthday Creek, this was in riffles, while at Pixies Creek, highest abundance and richness of macroinvertebrates were found in the pool. These differences may contribute to the observed differences in resistance and resilience between sites. Higher community complexity (of which species richness is a measure) may confer enhanced resistance to disturbance, while the presence of greater numbers of individuals in the surrounding streambed should enhance recovery. Previous work in Australian upland streams indicates that absolute rates of colonisation of individual stones (Lake and Schreiber 1991), and small patches (1 - 4 m^2) of substrata following disturbance (Marchant *et al.* 1991) are closely related to ambient abundance and number of taxa. Species richness of macroinvertebrates is commonly found to be higher in riffles compared to pools (Barmuta 1990, Brown and Brussock 1991, Miller and Golladay 1996, Cheshire 1997), and this may contribute to relatively higher resistance to disturbance, at least when disturbed patches are small. However, when the scale of disturbance is increased to encompass the whole stream (i.e. floods), additional factors, such as the presence of refugia and mechanism of recolonisation may assume greater relative importance (Brooks and Boulton 1991; see Chapter 2).

Taxon richness was little affected by experimental disturbance, indicated by the array of non-significant results across habitats and sites. There are two likely explanations for this: either the treatments affected all components of the community equally, resulting in a negligible effect on richness, or that the treatments had little effect on factors which influence species richness at the local scale. The first is unlikely as response to disturbance is highly species specific, and may even vary within a given species. For example, the trichopteran *Helicopsyche* sp. showed a non-significant response to disturbance at Birthday Creek, while response to the same treatments was significant at Pixies Creek. Species richness on stream stones may be regulated by microhabitat complexity (Douglas and Lake 1994, Downes *et al.* 1995) and levels of surface resources such as epilithon (Lake *et al.* 1989, Lake 1990), both of which may be modified by disturbance. The results of the current experiments suggest that simple overturning of substrata, or scrubbing of substratum surfaces did not alter either factor. The use of artificial substrata in these experiments essentially overcomes the problems encountered when using natural substrata of between-stone variation in microscale features such as pits and crevices or surface roughness. In addition, tumbling and brushing of the substratum are unlikely to have pronounced effects on surface epilithic layers, a food resource for many macroinvertebrates. Boulton *et al.* (1988) suggested that following brushing, a thick "lawn" of epilithon remains intact on stone surfaces, revealed by examination with scanning electron microscopy.

Although overturning stones may significantly reduce macroinvertebrate densities (e.g. Boulton *et al.* 1988), recovery of many of the common taxa was complete within 24 hours, indicated by an array of non-significant results as disturbance intensity increased across habitats and sites. As the experimental treatments were effective at removing individuals, (particularly with the addition of surface scrubbing, i.e. the "high" treatment), this result is indicative of the high resilience of the fauna.

The recovery process is strongly influenced by the size of the disturbed area and the relative proximity of undisturbed areas providing a source of potential colonists. At the scale of these experiments, high resilience is likely to be enhanced greatly by the close proximity of colonists in the surrounding undisturbed streambed. Animals only had to move small distances to be present on the disturbed substrata, and thus recolonisation of these patches represents a redistribution of the benthos (Townsend and Hildrew 1976) rather than representing the process of colonisation following natural flood events (Chapter 2) where large areas of the surrounding streambed are also disturbed. Therefore, as expected, the processes involved in the colonisation of individually tumbled substrata are likely to differ from those observed following natural flooding (Chapter 2). Two studies, Brooks and Boulton (1991) and Matthaei *et al.* (1997a) have directly compared the response of invertebrate assemblages within streams to large scale (flooding) and small scale (experimental) disturbance. Although Matthaei *et al.* (1997a) found that general patterns of recovery following disturbance were similar across scales, the recolonisation mechanisms of the fauna appear to be very different (Brooks and Boulton 1991). However, in both studies, increasing the magnitude, and therefore the spatial scale of disturbance, resulted in slower recovery rates. When the scale of disturbance is small, and recovery involves simple redistribution of the benthos, characteristics of mobility of the fauna assume primary importance. After large scale disturbance the presence of refugia and mode of colonisation, and the interaction of these factors with individual characteristics of mobility, may determine the recovery process (Brooks and Boulton 1991).

Response of macroinvertebrates in riffle and pool habitats to increased frequency of disturbance

Increasing the frequency of disturbance was expected to i) result in a greater negative impact of the treatments on overall abundance and numbers of individual taxa (Reice 1985), and ii) reduce species richness through the exclusion of taxa which could not re-establish in the period of time between disturbances (Townsend *et al.* 1997c). Disturbing the bricks weekly for five weeks compared with a single event greatly increased the impact of disturbance for a number of species, particularly in the riffle. Many of the common taxa in the riffle shifted from a non-significant response to the treatment to a significant decrease in abundance with increased frequency of disturbance (e.g. Chironomidae, *Nyctiophylax* sp.). There was also a significant reduction in overall abundance, compared with a non-significant result after a single event.

The pool fauna was also impacted by increases in disturbance frequency; however, three weekly disturbances had a greater impact on richness than five weekly disturbances.

Increasing the number of disturbance events had the greatest effect on community structure in pools. Reice (1985) found that more taxa were significantly reduced in abundance with increased frequency of disturbance, and overall abundance was lower following the second disturbance than following a single disturbance with only one group, the Oligochaeta, peaking after a single disturbance.

Disturbance frequency significantly affected macroinvertebrate richness in both habitats. The one week interval between disturbances may be insufficient time for the colonisation of some taxa, particularly those with reduced mobility (Townsend *et al.* 1997c). Although multiple disturbances in general appear to have greater impact on numbers and richness of macroinvertebrates compared with a single disturbance event, this effect is not necessarily cumulative, and varies among the common taxa.

The influence of different historical frequencies of natural disturbance on macroinvertebrate characteristics of resistance to and resilience following experimental disturbance are examined in the next chapter.

Response to experimental disturbance along a longitudinal gradient

The responses of macroinvertebrates to experimental disturbance were influenced by their longitudinal position within the stream, as the composition of the colonising fauna varied with location, thereby influencing characteristics of resistance and resilience. There was some evidence to suggest that at the three locations in this study (i.e. headwater, mid reach, and lower reach), relative resistance and resilience reflect aspects of substratum stability and frequency of natural disturbance. Highest resistance and resilience were evident at the lower-reach site, predicted to have the highest frequency of natural disturbance due to the high proportion of small substratum particles. Sandy substrata, predominant at the lower-reach site, are unstable under relatively minor flows, and are indicative of a high frequency of disturbance (Reice 1985). In addition, downstream sites such as this may experience more extended floods than upstream sites, as they drain a greater area (Marchant *et al.* 1991). The high proportion of taxa such as *Baetis* sp. and *Simulium* sp., commonly regarded as possessing characteristics conferring high resistance and/or resilience (Mackay 1992, Townsend *et al.* 1997c), may be a reflection of an unstable and frequently disturbed substratum at this site. However, it is unlikely that instability of the substratum is the only factor responsible for the longitudinal differences in composition, as the headwater site, physically the most stable, had close faunal affinities with the lower-reach site. Although physically stable, and experiencing floods of relatively short duration, this site had an assemblage that was like the lower-reach site, dominated by *Baetis* sp. and *Simulium* sp., resulting in high resistance and resilience to substratum-tumbling disturbance.

Benthic crawling has previously been shown to be an important mechanism for recolonisation in this stream (Benson and Pearson 1987b). Brooks and Boulton (1991) found that small disturbed patches, of a scale comparable to this study (0.05 m^2), were largely colonised by movement from adjacent intact areas. Therefore, the relatively high proportion of mobile taxa (e.g. *Baetis* sp.) at the lower-reach and headwater sites should enhance recovery on to individual stones through small-scale lateral movements within the benthos (Mackay 1992).

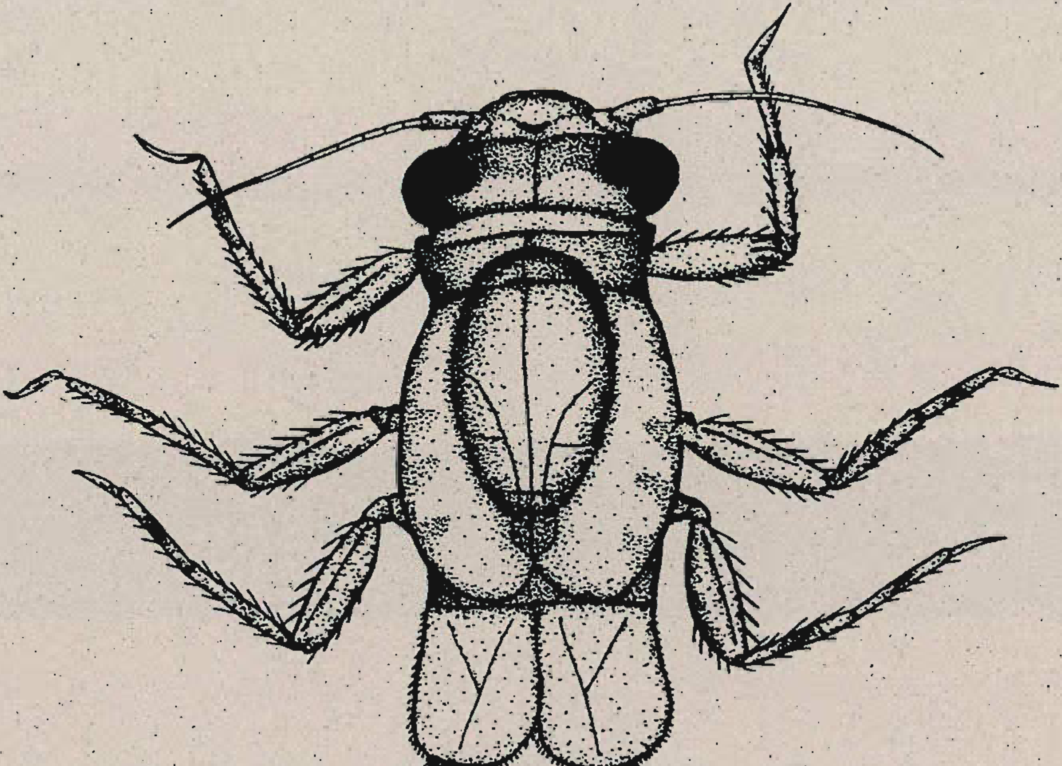
The response to disturbance, however, was not always consistent within a taxon. For example, *Baetis* sp. was not significantly affected by the high treatment at the lower-reach site, indicating high resilience, while at both headwater and mid-reach sites, abundance was reduced significantly (50% in both cases), suggesting relatively low resilience. This variability of response to disturbance of a given magnitude, as reported in other studies (e.g. Boulton *et al.* 1992b) may indicate that this does not depend solely on colonising ability or resistance characteristics, but rather may reflect the interaction of these characteristics with other factors, such as habitat.

In summary, this study has shown that:

- Overturning of individual stones (bricks) provided a significant source of disturbance to macroinvertebrates. The proportion of individuals removed, and therefore the creation of patches was related to the intensity of the disturbance. This indicates that macroinvertebrates are influenced directly by habitat stability.

- Recovery following overturning of stones was rapid, and was often complete within twenty-four hours. Recolonisation at this small spatial scale, which is closely related to ambient levels, reflects the capacity of the fauna for rapid redistribution through small-scale movements from local sources in comparison to recovery following large-scale disturbance by floods (Chapter 2), where large-scale dispersal mechanisms and use of refugia assume greater relative importance and contribute to longer recovery times.

- Position within the stream, both along a longitudinal gradient and within pool and riffle habitats, influenced resistance and resilience of the fauna. Fauna from sandy, lower reaches and headwater sites was most resistant and resilient to disturbance, possibly reflecting the relative instability of the substratum (lower reach) and high hydrologic forces such as shear stress during natural disturbance by floods (headwater) at these sites, compared with the more stable mid-reach site.



Ephemeroptera: Caenidae

Artist: Andi Cairns

CHAPTER 4: EFFECTS OF PHYSICAL DISTURBANCE IN STREAMS OF CONTRASTING HYDROLOGICAL REGIMES

4.1. Introduction

The characterisation of stream environments along axes of disturbance frequency and predictability (Hughes and James 1989, Poff and Ward 1989, Jowett and Duncan 1990), disturbance frequency and productivity (Hildrew and Townsend 1987), and disturbance frequency and spatial heterogeneity (Scarsbrook and Townsend 1993, Townsend and Hildrew 1994), has provided a framework for the prediction of species' attributes in relation to temporal environmental variability. Following the premise of Southwood (1977, 1988), spatial and temporal characteristics of the physical environmental provide strong selective forces for "ecological strategies" which promote local persistence. Therefore, the long-term regime of natural disturbance experienced by the biota may constrain the nature and range of response mechanisms available following disturbance (Poff and Ward 1990). As environmental stability declines (i.e. variability increases), traits of species that enhance survival are predicted to increase (e.g. Levins 1968, Townsend and Hildrew 1994). For example, responses to high levels of unpredictability and temporal variability may include high mobility, small size, and rapid growth and development (e.g. Gray 1981). Populations and communities from more variable and unpredictable environments may therefore be relatively less susceptible to disturbance compared with those from more constant environments (Connell and Sousa 1983, Poff and Ward 1990) and may show high persistence (stability of assemblage structure over time) through rapid recolonisation (Grossman 1982).

The northern Wet Tropics of Australia and neighbouring Papua New Guinea (PNG), provide considerable contrasts climatically and hydrologically, particularly with regard to disturbance frequency. Rainfall in tropical north Queensland is seasonally constrained, with most rain occurring during the summer months, influenced by the formation of tropical cyclones and rain depressions, while rainfall during the remainder of the year is relatively low. This seasonal pattern is reflected in stream discharge, with summer being the time of intense, temporally unpredictable flows (in terms of precise timing during summer), followed by low and stable flows (Chapter 2). A framework for the classification of streams based on variability of natural flows has been proposed by Haines *et al.* (1988) and Poff and Ward (1989), the latter of which is used in this study as it contains categories most applicable to both the PNG and north Queensland study sites. Within this framework, the north Queensland stream may be regarded as "summer rain" (as opposed to the "winter rain" of the authors' US streams). This stream type is characterised by a low flood frequency (i.e. long interflood periods) and a high seasonal predictability. The time of sampling in the present study coincided with the season of predictably low daily flows (dry season). In contrast, rainfall in the region of study in PNG is very high (8 000 – 10 000 mm annually), and occurs throughout the year (i.e. it is aseasonal), driven largely by convective thunderstorms and the influence of topography (Hall 1984). PNG is dominated by a series of high mountain ranges, extending 2 500 km and rising to 4 500 m, interspersed by wide valleys and coastal plains. This topography, together with the maritime influence of warm, moist air over the equatorial Western Pacific, contribute to the increased frequency of intense rainfall activity over much of its area. High rainfall, produced by intense storms of short duration occurring throughout the year, means that streams in PNG may be regarded as "perennial flashy" (Poff and Ward 1989), with a high flood frequency (i.e. short interflood periods), and high variability of daily flows. These components of variability define the temporal axis of the disturbance regime within these streams and such contrasts provide an ideal opportunity to test hypotheses relating characteristics of resistance and resilience of the fauna to historical frequencies of disturbance.

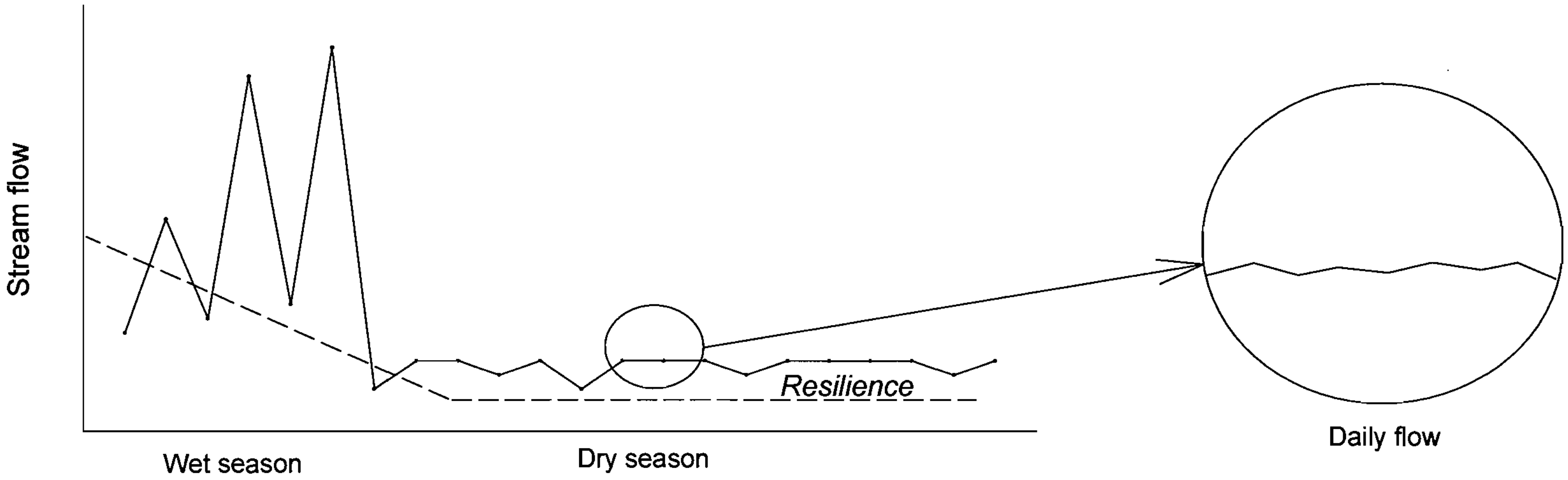
This aim of this study was, therefore, to compare the response to experimental disturbance of the substratum between benthic macroinvertebrate assemblages which had been historically exposed to very different disturbance regimes. Figure 4.1 indicates the temporal differences in the flow environments in the two streams and gives predictions of resistance and resilience of the fauna in relation to the variations in flow. Specifically, I aimed to compare the nature and pattern of response to disturbance in an aseasonal stream (PNG), which had a high (within-year) frequency of natural disturbance, to that of a seasonal stream in the Wet Tropics, with a low (approximately annual) frequency of disturbance.

Figure 4.1 Stylised diagram indicating the temporal differences in the annual (x-axis) and daily (insert) flow regimes at the north Queensland and Papua New Guinea sites at the time of sampling.

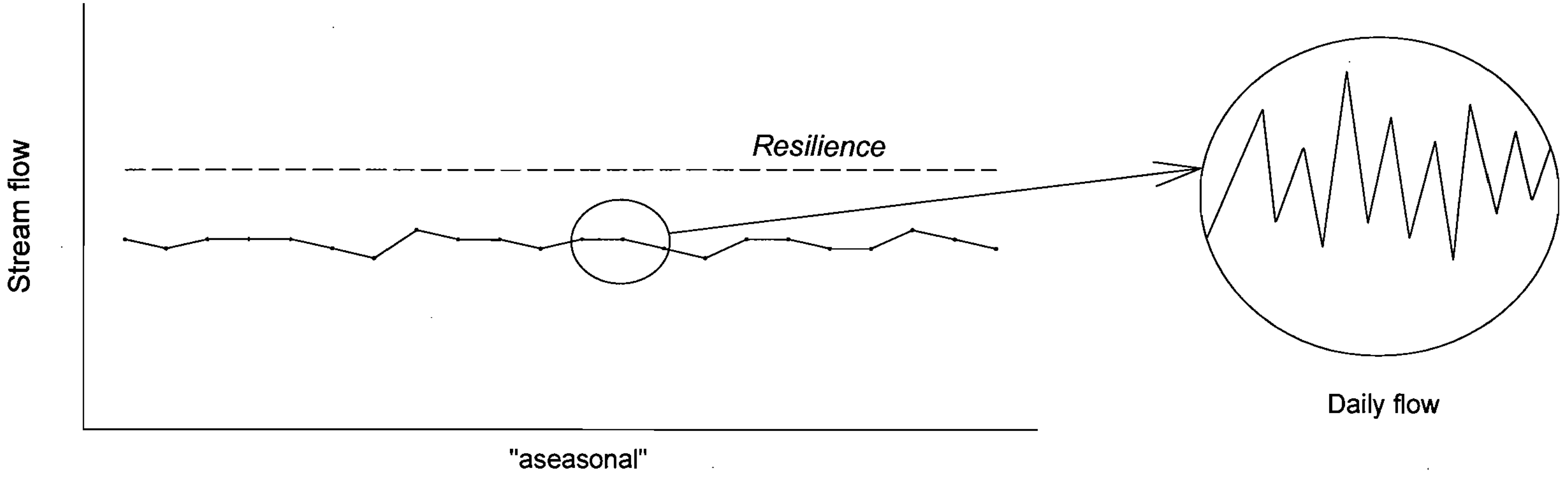
The high temporal variability of daily flows at the PNG sites is predicted to result in relatively high resilience of the benthic macroinvertebrate community following disturbance. In contrast at the north Queensland site, while resilience is predicted to be high over the summer wet season, during the time of sampling (dry season) when daily flows are low and stable, resilience to substratum disturbance is predicted to be low.

Macroinvertebrate resistance at the time of sampling is predicted to be higher at the PNG sites.

i) Low (within-year) frequency of natural disturbance - Birthday Creek, north Queensland.



ii) High (within-year) frequency of natural disturbance - Tam Creek and Creek 115, PNG.



Comparisons were made during the dry season of the Wet Tropics streams, as this is the time of relatively stable hydrological conditions when the fauna are not "expecting" substratum disturbance, and differences in response to disturbance between sites were likely to be most pronounced (Figure 4.1).

The aims were addressed by the following questions:

i) Do benthic assemblages from an aseasonal, frequently disturbed stream possess characteristics of high resistance to and resilience following disturbance compared with a seasonal stream with a relatively low frequency of natural disturbance? In other words, does the historical pattern of disturbance constrain the ecological response shown by the fauna to disturbance? Is the response to disturbance in the aseasonal stream temporally (year to year) and spatially (stream to stream) consistent?

ii) Do the results fit the prediction of relatively low community persistence at the more frequently disturbed site compared with the infrequently disturbed stream?

4.2. Methods

Study Sites

Experiments were conducted during August 1993 (Tam Creek, PNG), October 1993 (Birthday Creek, north Queensland), and December 1994 (Tam Creek and Creek 115, PNG).

A description of the study reach at Birthday Creek is given in Chapter 2. Experiments were carried out downstream from the area where monthly rock samples were collected in a riffle section 14 m long and 4 m wide. Rainfall is strongly seasonal in this region with > 70 % of annual totals occurring during the summer months (December-February), reflected in the inter-annual coefficient of variation (CV = 109.1 %). During the dry season months, which was the time of sampling of the present study, mean flow is typically low and stable.

During the month prior to this study, only 5 mm of rain fell at Birthday Creek, and no rainfall was recorded during the experimental manipulations (Townsville Bureau of Meteorology).

Both Tam Creek and Creek 115 are small tributaries of the Ok Tedi River (Figure 4.2). The Ok Tedi forms part of the Fly River system, the second largest river network of PNG (catchment area of 76 000 km^2). Rainfall in the Fly River catchment is very high, ranging from 10 000 mm per annum in the upper catchment to 3 000 mm per annum near the coast (OTML 1988). The area of this study (upper Ok Tedi region), receives around 8 000 mm of rain annually, distributed throughout the year (Brown 1983). This pattern of continuous rainfall throughout the year is reflected in the low inter-annual coefficient of variation at nearby Tabubil (CV = 26.4 %). In contrast to Birthday Creek, spates (of relatively low magnitude) are frequent in streams of this region, occurring at any time of the year, reflected the daily rainfall values. For example, daily rainfall during the month of in study in both 1993 and 1994, fluctuated greatly (Figure 4.3).

Tam Creek (5°22'S, 141°17'E) is a third order stream at the study site, with an elevation of 340 m (Plate 8). The stream bed was partly shaded (about 20 % cover), with riparian vegetation consisting of closed rainforest. The riffle used for the colonisation and experimental disturbance study was 17 m long and 4 m wide, with a maximum depth of 0.40 m. Control samples were taken from a nearby riffle. Current velocity ranging from 0.20 - 0.40 ms^{-1} were recorded during the study. Water temperatures ranged from 22 – 26 °C. The substratum was predominantly medium cobbles, with no large patches of detritus.

Creek 115 (5°27'S, 141°16'E) is a fourth order stream at the study site, with an elevation of 240 m (Plate 9). The riparian rainforest vegetation formed a partial canopy (about 40 % cover) over the stream. The study riffle was 15 m long and 4 m wide, with an average depth of less than 0.35 m. Current velocity ranged from 0.20 - 0.43 ms^{-1}, while water temperature was 21 - 27 °C. The major substratum type was cobbles.

Figure 4.2 Map indicating the location of the a) Tam Creek and b) Creek 115 study sites in Papua New Guinea.

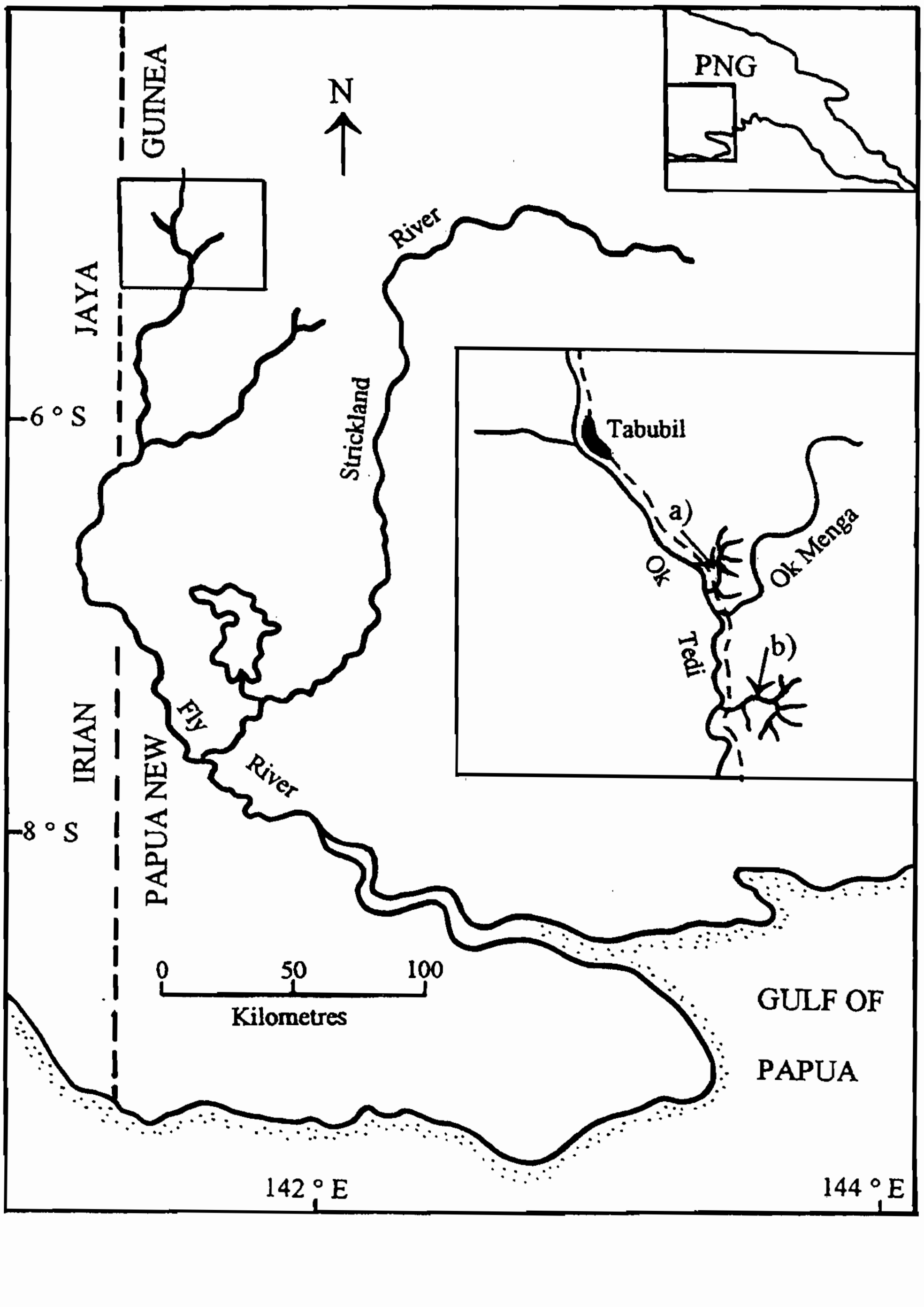

PNG
N
GUINEA
JAYA
IRIAN
PAPUA NEW
River
Strickland
Tabubil
a)
Ok
Ok Menga
Tedi
b)
-6 ° S
-8 ° S
Fly
River
0
50
100
Kilometres
GULF OF
PAPUA
142 ° E
144 ° E

Figure 4.3 Total daily rainfall (mm) recorded at Tabubil, Western Province, PNG, near Tam Creek and Creek 115 during a) August, 1993, and b) November-December, 1994. The sampling period is indicated by the interval between the dashed line.

Note that daily rainfall for Paluma, near Birthday Creek, is not included as no rainfall was recorded during the sampling period, and only 5 mm fell during the month prior to sampling.

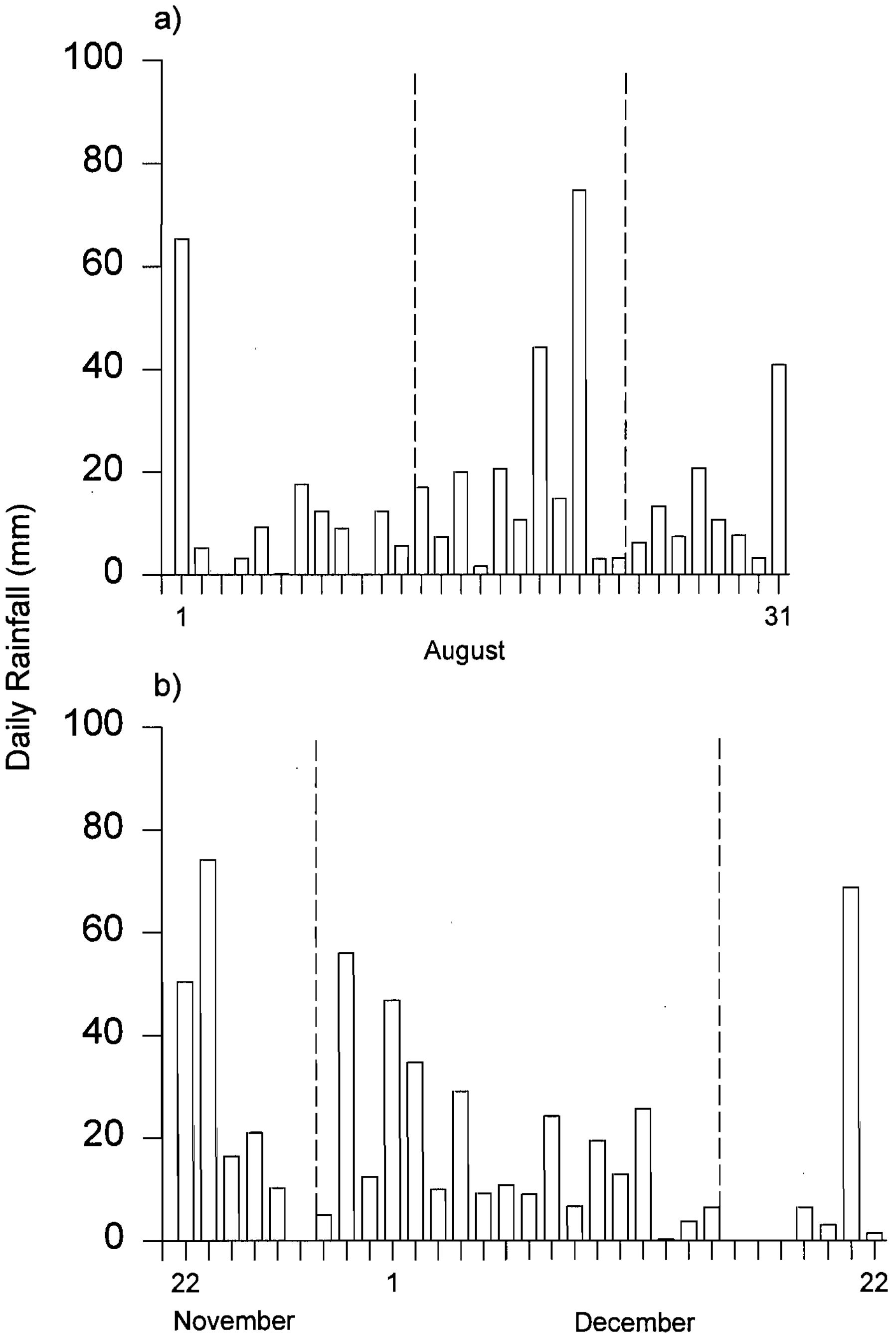

a)
Daily Rainfall (mm)
100
80
60
40
20
0
1
31
August
b)
100
80
60
40
20
0
22
1
22
November
December

Plate 8 Riffle site at Tam Creek, Papua New Guinea, looking upstream.

Plate 9 Riffle site at Creek 115, Papua New Guinea, looking downstream.

On the last day of collection (day 14) at both Tam Creek and Creek 115, flow levels were elevated from an overnight spate, with a mean current speed of 1.2 ms^{-1} at Tam Creek and 1.5 ms^{-1} at Creek 115 at the time of sampling. There was evidence that higher flow levels had been reached, with six of the colonisation stones moved downstream at Creek 115 (maximum of 12 m), ending up in a large pool. These six stones were excluded from the experiment, as their fauna would be influenced by being in a pool habitat. Three of the marked colonisation stones had been displaced a short distance from their original position (maximum of 0.5 m) at Tam Creek; however, they remained within the study riffle and were therefore included in the analyses.

Colonisation of scrubbed substrata

To investigate colonisation on to conditioned stones which were free of invertebrates, forty stones (of a similar size) were removed from each site. Stones were scrubbed, then labelled (with coloured tape), and weighed to determine surface area (following the procedure outlined in Chapter 2, as the stones sampled from both sites were similar in density). Individual stones were then placed randomly within the disturbed riffle immediately following raking and tumbling of the substratum. Eight stones were removed after four hours (day 0), then every two days until all were removed. For experiments performed in 1993 (Tam Creek and Birthday Creek), the exposure period for colonisation was 0, 2, 4, 6 and 8 days; the following year (Tam Creek and Creek 115) this was extended to 0, 2, 4, 6, 8, 10, 12, and 14 days' exposure.

Macroinvertebrate colonisation and extinction rates were calculated following Dickson and Cairns (1972) and Boothroyd and Dickie (1991). The total number of taxa, the number of new taxa, the number of recurring taxa (eliminated and subsequently reappearing), and the number of taxa eliminated (occurred in previous sample, but now absent), were recorded for each sampling date at each site. Colonisation rate (CR) was calculated as the number of new taxa plus the number of recurring taxa divided by the time (days) between the sampling periods. Similarly, extinction rate was calculated by dividing the number of taxa eliminated by the time (days) between sampling dates.

Turnover rates were calculated as: $(CR + ER)/(S_1 + S_2)$, where CR = colonisation rate, ER = extinction rate, and S_1 and S_2 are the number of taxa at the beginning and end of the sampling period.

Experimental Disturbance

The experimental disturbance involved raking and tumbling the substratum within the riffle area at each site with a steel-toothed rake, working downstream. This method also removed any leaf pack accumulations from the riffle. Larger stones, which could not be tumbled, had their surfaces brushed (by hand). Disturbance of the entire riffle took approximately 20 minutes. Eight individual stones were sampled immediately following the experimental disturbance (day 0), then at days 2, 4, 6 and 8 (1993 samples), and days 2, 4, 6, 8, 10,12, and 14 (1994 samples). Sampling involved enclosing each stone within a dip net and scrubbing the surface with a test-tube brush. Samples taken concurrently from an undisturbed riffle acted as controls. All samples were preserved in ethanol and returned to the laboratory for identification. The identification of macroinvertebrates followed the procedure outlined in Chapter 2.

Macroinvertebrate Drift

In conjunction with the experimental disturbance of the riffle, drift was sampled over a 24 hr period which included the disturbance (Table 4.1). It is important to note that the pre-(dawn) and post-disturbance comparisons occurred at different times of the day. Nevertheless, as the densities of drifting fauna increase overnight (e.g. Benson and Pearson 1987a), significant differences detected between the two time periods reflect even more strongly the post-disturbance change.

Drift was sampled using three nets placed at upper, middle, and lower positions in the main flow of the study riffle. Each sampler consisted of a metal frame with a 0.02 m^2 inlet, connected to a conical collecting net (250 μm mesh).

Table 4.1 Summary of drift sampling regime at Birthday Creek and Tam Creek.

Time interval	Description
1400 - 1800	dusk
1830 - 2230	night
2300 - 0300	night
0330 - 0730	dawn
1030 - 1100[a]	disturbance
1130 - 1530	post-disturbance

[a] nets removed immediately following the experimental disturbance

The opening of each net was positioned in the water column, fixed to metal stakes, 10 cm above the substratum (to prevent entry of crawling invertebrates). Drift was expressed as density (number per m^3 of water filtered). Volume was estimated from the product of area of net opening, current velocity at the opening, and duration of the sampling period. Three measurements of current velocity were taken adjacent to the opening of each net at the time of sampling, using an OSS model flow meter, with the mean value used in the water volume calculations. The contents of each sample were preserved in 70 % ethanol and returned to the lab for processing.

Data Analysis

Data analysis followed the same methodology as described in Chapter 2. Abundance and richness values were standardised to individuals/0.08 m^2. Means were compared using univariate tests (t-tests and ANOVAs) on log (x + 1) transformed data (Elliot 1977). Similarity in community structure between macroinvertebrates colonising bare stones and concurrently sampled controls, and fauna on stones following disturbance and undisturbed controls was assessed using the proportional similarity index (Schoener 1968) (see Chapter 2). As in previous chapters, PSI values ≥ 0.65 were considered high as this was the lowest value obtained for within-control comparisons. Proportional similarity of the communities, together with other measures (see below), indicated when colonisation and recovery following disturbance were complete.

Changes in community structure during colonisation and recovery following disturbance were also examined by ordinations using semi-strong hybrid multidimensional scaling (SSH) with the input data matrix for each ordination excluding the rare taxa (i.e. those comprising < 0.05 % of overall totals – Faith and Norris 1989). Time trajectories linking the centroids of groups of samples from consecutive collection dates were plotted in ordination space for both the colonisation series and following experimental disturbance at each stream with the distance between the centroids providing a visual representation of relative rate of change (Boulton *et al.* 1992).

Resistance and resilience were assessed using a range of criteria. Resistance, at the community level, was quantified as the percent change in overall abundance and richness (Fisher and Grimm 1988) caused by the experimental disturbance, and by assessing the magnitude of change in community structure (comparison of the PSI and degree of displacement in ordination space) between disturbed and control stones. In addition, resistance to disturbance of each of the common taxon was determined at each site. Individual taxa were considered resistant if their numbers were not significantly reduced, or if their numbers significantly increased, immediately following disturbance. Conversely, low resistance was attributed to those taxa which showed significant reductions following disturbance. Community-level resilience (rate of recovery following disturbance – Stanley *et al.* 1994) was measured as the time taken to attainment of comparable abundance and richness on disturbed and control stones, as well as time taken for the development of similar community structure (as assessed by PSI and ordination plots). Resilience characteristics of the most abundant taxa at each site were also determined.

4.3. Results

Characteristics of the stone fauna at each site

The macroinvertebrate fauna on stones from the two streams in Papua New Guinea (Tam Creek and Creek 115) differed substantially from that at Birthday Creek (North Queensland)

(Appendix 2, Table A4.1). Of the more abundant taxa at each site (Table 4.2), only the dipteran, Tipulidae sp. 3, and the trichopteran *Cheumatopsyche* sp. 1 were common to both Tam Creek and Birthday Creek. Although representatives from the family Chironomidae were abundant at all sites, many from the New Guinea streams were different species from those in Birthday Creek.

Table 4.2 Relative abundance (%) of common riffle taxa on stones from Tam Creek, Birthday Creek and Creek 115. "-" indicates taxon rare or absent.

Taxa	Tam Creek (1993)	Birthday Creek (1993)	Tam Creek (1994)	Creek 115 (1994)
Austrophlebioides sp. 1	-	3	-	-
Austrophlebioides sp. 2	-	2	-	-
Baetis sp.	-	2	-	-
Baetis sp. 1	-	-	10	2
Baetis sp. 2	2	-	11	2
Baetis sp. 3	61	-	11	3
Tasmanocoenis sp.	1	-	2	-
Chironomidae	29	28	46	33
Simulium sp.	-	21	-	-
Simuliidae	-	-	1	2
Tipulidae sp. 3	3	8	4	-
Agapetus sp.	-	1	-	-
Agapetus sp. 1	-	-	-	45
Cheumatopsyche sp. 1	2	1	4	4
Cheumatopsyche sp. 3	-	-	-	3
Helicopsyche sp.	-	2	-	-
Hydroptilidae sp. 1a	-	7	-	-
Nyctiophylax sp.	-	4	-	-
Dinotoperla sp.	-	5	-	-
Kingolus sp.	-	5	-	-
Simsonia sp.	-	3	-	-
Lepidoptera sp. 1	-	-	5	-
Oligochaeta	-	4	-	-
% of Total	98	96	94	94

Tam Creek was dominated by several species of mayflies (family Baetidae in particular) and chironomid larvae. While these same mayfly taxa were common at nearby Creek 115, a glossosomatid trichopteran (*Agapetus* sp. 1), together with the chironomids, were numerically dominant. The most common taxa at Birthday Creek were dipteran larvae (Chironomidae and Simuliidae). Plecoptera, notably absent from the PNG samples, were quite abundant in Birthday Creek (e.g. *Dinotoperla* sp.).

Macroinvertebrate colonisation of bare stones

At all sites, the number of macroinvertebrate taxa colonising bare stones increased over time (Figure 4.4). Cumulative species curves were very asymptotic, with very high rates of accrual initially at all sites followed by a decline. Birthday Creek had higher richness compared to the two PNG streams, and also had higher colonisation rates through most of the colonising period (Table 4.3). After only four hours' exposure, there were 19 taxa on the previously bare stones at Birthday Creek, compared with 10-11 at the PNG sites. After eight days, Birthday Creek had accumulated the most taxa (47), even when compared with a longer exposure period (14 days) at the two PNG sites. There was a very similar colonisation pattern in both years, in terms of number of taxa accrued, at Tam Creek over the first eight days (Table 4.3). The higher colonisation rate at Birthday Creek was not reflected in the turnover rate, with Tam Creek (1993) having almost double the turnover of the other sites, and of itself in 1994.

When compared with controls, both total numbers (Figure 4.5) and number of taxa (Figure 4.6) on the bare stones were significantly lower after four hours' exposure (t-test, $p < 0.05$ in all cases). Overall abundance was similar to levels on the natural stones by day two at Tam Creek in 1993, and by day four in the following year (Table 4.4).

Abundance was similar to the controls by day two at Birthday Creek, but similar abundances did not occur until day eight at Creek 115. The attainment of comparable richness on the scrubbed and control stones was most rapid at the two PNG sites. This occurred after two days' exposure at Tam Creek in 1993, four days in 1994, and two days at Creek 115. At Birthday Creek, richness was significantly lower relative to the controls until day eight.

Figure 4.4 Cumulative number of taxa colonising bare stones at Tam Creek (1993 and 1994), Birthday Creek (1993), and Creek 115 (1994).

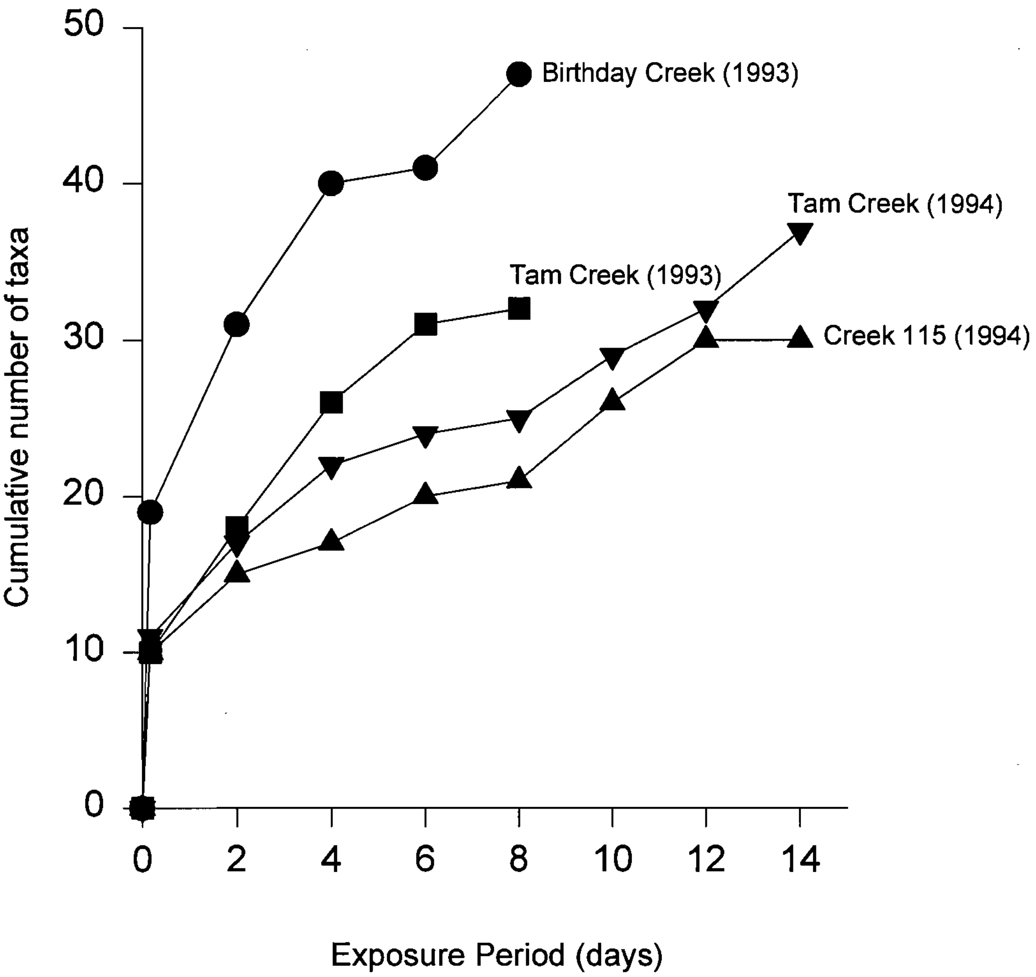

Cumulative number of taxa
50
40
30
20
10
0
0
2
4
6
8
10
12
14
Exposure Period (days)
Birthday Creek (1993)
Tam Creek (1994)
Tam Creek (1993)
Creek 115 (1994)

Table 4.3 Macroinvertebrate colonisation of scrubbed stones at Tam Creek, Birthday Creek and Creek 115. Colonisation rate (CR) = NT + RT / time (days between sampling periods); Extinction rate (ER) = ET / time; and Turnover rate (TR) = (CR + ER) / (S_1 + S_2), where S_1 and S_2 are the number of taxa at the beginning and end of the sampling period, respectively (Dickson and Cairns 1972, Boothroyd and Dickie 1991).

Exposure period (days)	Total taxa	New taxa (NT)	Recurring taxa (RT)	Eliminated taxa (ET)	Colonisation rate (CR) (taxa/day)	Extinction rate (ER) (taxa/day)	Turnover rate (TR)
Tam Creek (1993)							
0.17	10	10	0	0	60	0	6
2	13	8	0	5	4	2.5	0.28
4	18	8	2	5	5	2.5	0.24
6	14	5	2	11	3.5	5.5	0.28
8	17	1	8	6	4.5	3	0.24
Birthday Creek (1993)							
0.17	19	19	0	0	114	0	6
2	25	12	0	6	6	3	0.2
4	29	9	0	5	4.5	2.5	0.13
6	27	1	4	7	2.5	3.5	0.11
8	36	6	8	5	7	2.5	0.15
Tam Creek (1994)							
0.17	11	11	0	0	66	0	6
2	16	6	0	5	3	2.5	0.2
4	15	5	0	6	2.5	3	0.18
6	16	2	1	2	1.5	1	0.08
8	17	1	3	4	2	2	0.12
10	18	4	1	4	2.5	2	0.13
12	21	3	3	1	3	0.5	0.09
14	24	5	3	4	4	2	0.13
Creek 115 (1994)							
0.17	10	10	0	0	60	0	6
2	13	5	0	1	2.5	0.5	0.13
4	12	2	1	4	1.5	2	0.14
6	15	3	2	2	2.5	1	0.13
8	12	1	0	4	0.5	2	0.09
10	21	5	4	0	4.5	0	0.14
12	20	4	1	6	2.5	3	0.13
14	13	0	0	7	0	3.5	0.11

Figure 4.5 Mean abundance (± 1 SE) of macroinvertebrates colonising bare stones (●) compared with controls (■) at a) Tam Creek, 1993; b) Birthday Creek, 1993; c) Tam Creek, 1994; and d) Creek 115.

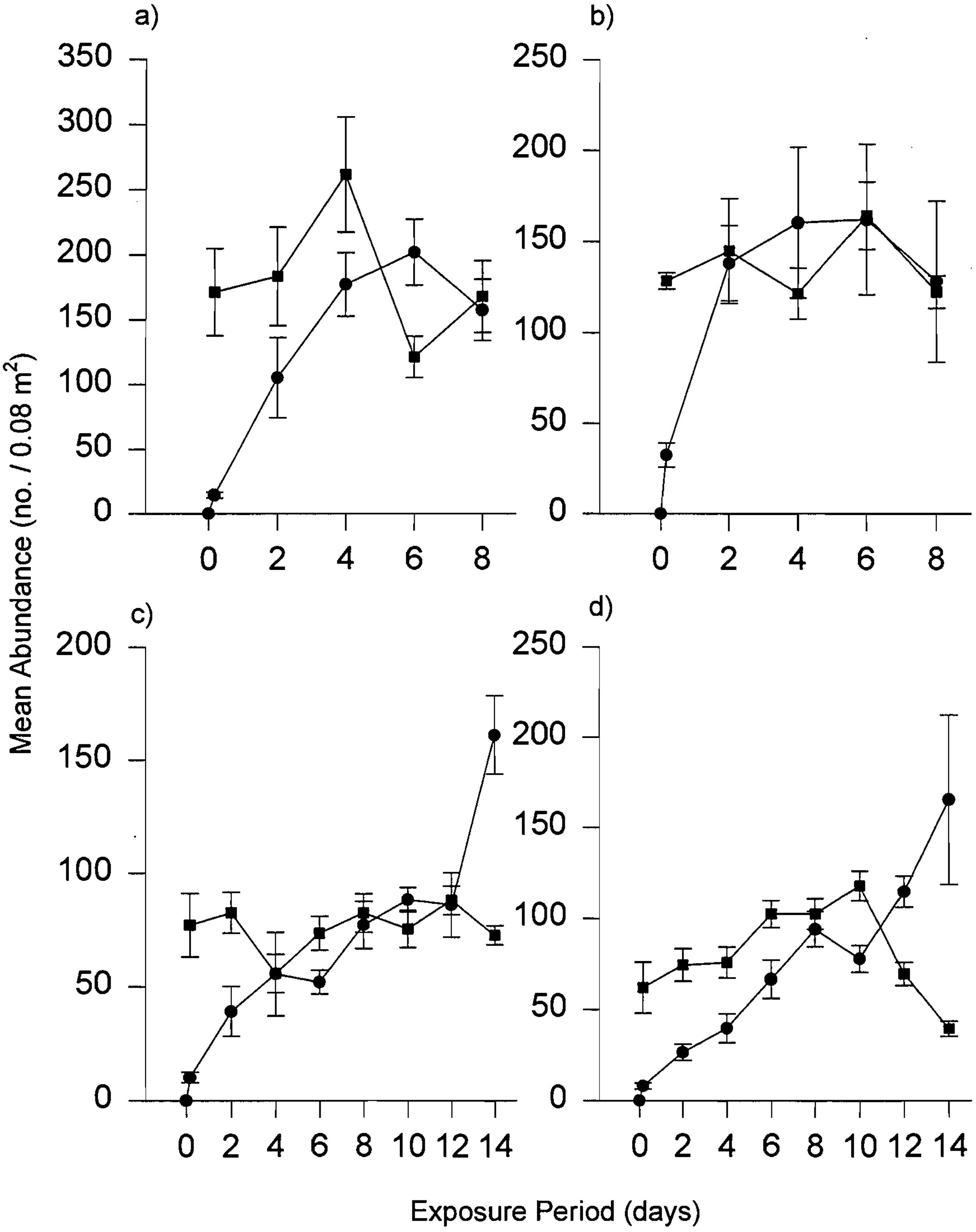
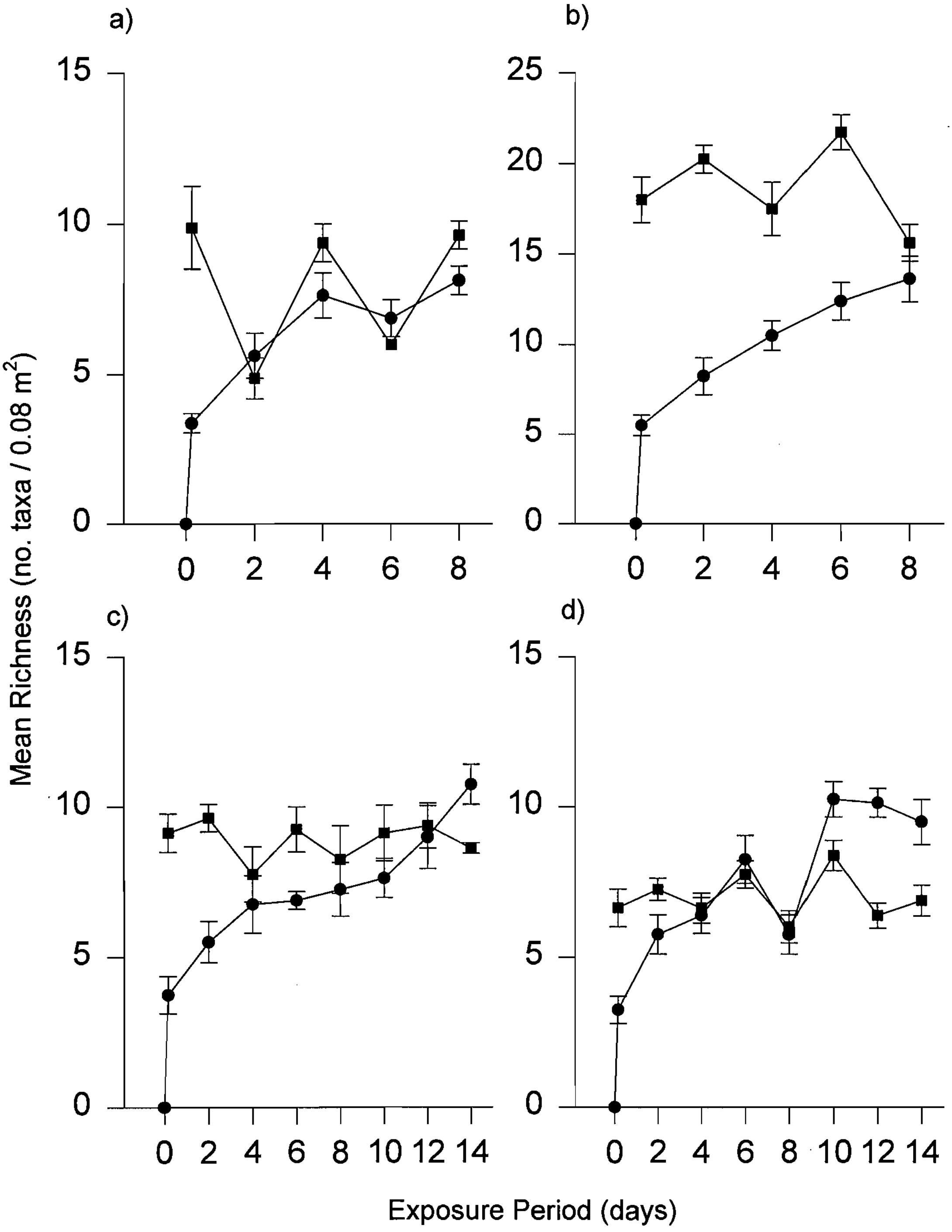

a)
b)
c)
d)
Mean Abundance (no. / 0.08 m2)
Exposure Period (days)
350
300
250
200
150
100
50
0
0
2
4
6
8
10
12
14

Figure 4.6 Mean richness (± 1 SE) of macroinvertebrates colonising bare stones (●) compared with controls (■) at a) Tam Creek, 1993; b) Birthday Creek, 1993; c) Tam Creek, 1994; and d) Creek 115.


a)
b)
c)
d)
0
5
10
15
20
25
0
2
4
6
8
10
12
14
Mean Richness (no. taxa / 0.08 m²)
Exposure Period (days)

At both Tam Creek and Creek 115, there was a significant increase in numbers relative to the controls at the end of the colonising period (day 14), coinciding with the spate (Figure 4.5c, 4.5d respectively; t-test, d.f. = 14, $p < 0.05$ in both cases). At Tam Creek, this increase was due to an almost doubling in numbers of many of the common taxa (e.g. Chironomidae, all Baetidae, *Cheumatopsyche* sp. 1), while at Creek 115 this increase was largely due to a rise in numbers of *Agapetus* sp. 1 following the spate. Richness was not significantly affected by the spate at either site.

Table 4.4 Time (days) to the attainment of comparable abundance, richness, and abundance of common taxa on colonisation and control stones for the common taxa at Tam Creek, Birthday Creek and Creek 115 (t-test, d.f. = 14, $p \geq 0.05$ in all cases). "-" indicates taxon rare or absent at this site.

Taxa	Tam Creek (1993)	Birthday Creek (1993)	Tam Creek (1994)	Creek 115 (1994)
Baetis sp.	-	4	-	-
Baetis sp. 1	-	-	2	4
Baetis sp. 2	4	-	2	-
Baetis sp. 3	2	-	2	4
Tasmanocoenis sp. 1	-	-	4	-
Chironomidae	2	2	4	4
Simulium sp.	2	6	-	2
Agapetus sp. 1	-	-	-	6
Cheumatopsyche sp. 1	4	-	2	2
Hydroptilidae sp. 1a	-	4	-	-
Nyctiophylax sp.	-	6	-	-
Oligochaeta	2	6	-	-
Total abundance	2	2	4	8
Total richness	2	8	4	2

Reflecting the overall trend, the common taxa had reached similar levels to the controls in the shortest time at Tam Creek with most, including the dominant taxa (*Baetis* sp. 3 and Chironomidae), reaching this level after only two days' exposure. The most abundant taxa at Creek 115 took slightly longer (range = 2-6 days), while six days was common at Birthday Creek.

At the time of comparable richness on the colonisation and control stones at the PNG sites (i.e. day 2 – Tam Creek, 1993; day 4 – Tam Creek, 1994; day 2 – Creek 115), similarity of community structure, in terms of composition and relative abundance, was high (PSI=0.76-0.85), suggesting that colonisation was essentially complete by this time (Figure 4.7). Although generally high throughout, proportional similarity decreased markedly at both these sites following the spate in 1994 (day 12-14).In contrast, although richness was similar on colonisation and control stones by day eight at Birthday Creek, the level of community similarity remained low (PSI=0.53). Low values at the end of the colonisation period (and throughout) suggests a relatively distinct suite of colonising taxa and that a longer period of time (> eight days) may be necessary for community structure to reach ambient levels at this site.

Ordination (Figure 4.8) shows that rate of change (indicated by the inter-centroid distance of consecutive samples on ordination plots) by the colonising fauna was always highest initially, between four hours and two days' exposure, after which the distances between consecutive dates were reduced. Following the spate, succession rate again increased on the colonisation stones (C12-C14) at Tam Creek (Figure 4.8c) and Creek 115 (Figure 4.8d), and samples were displaced (in ordination space) from the controls. These results, together with the decreased PSI, indicate that not only was community structure changed by the spate, but that the rate of change was increased following the spate. In contrast, rate of change on the controls was relatively unaffected by the spate.

The degree of change in the rankings of the common taxa over the colonising period varied between sites and years (Figure 4.9), with relatively little change at Tam Creek (in 1993) and Birthday Creek, and the greatest changes at Creek 115. The most abundant taxon, *Baetis* sp. 3 did not change in position through the colonising period at Tam Creek in 1993, while among other common taxa, *Baetis* sp. 2 dropped in ranking and Simuliidae increased with longer exposure.

Figure 4.7 Mean (± 1 SE) proportional similarity (Schoener 1968) of macroinvertebrate communities colonising bare stones compared with controls at a) Tam Creek, 1993; b) Birthday Creek, 1993; c) Tam Creek, 1994; and d) Creek 115, 1994.

Values ≥ 0.65 indicate high community similarity in terms of composition and relative abundance.

Arrows indicate the approximate timing of substratum-moving floods at Tam Creek and Creek 115 in 1994.

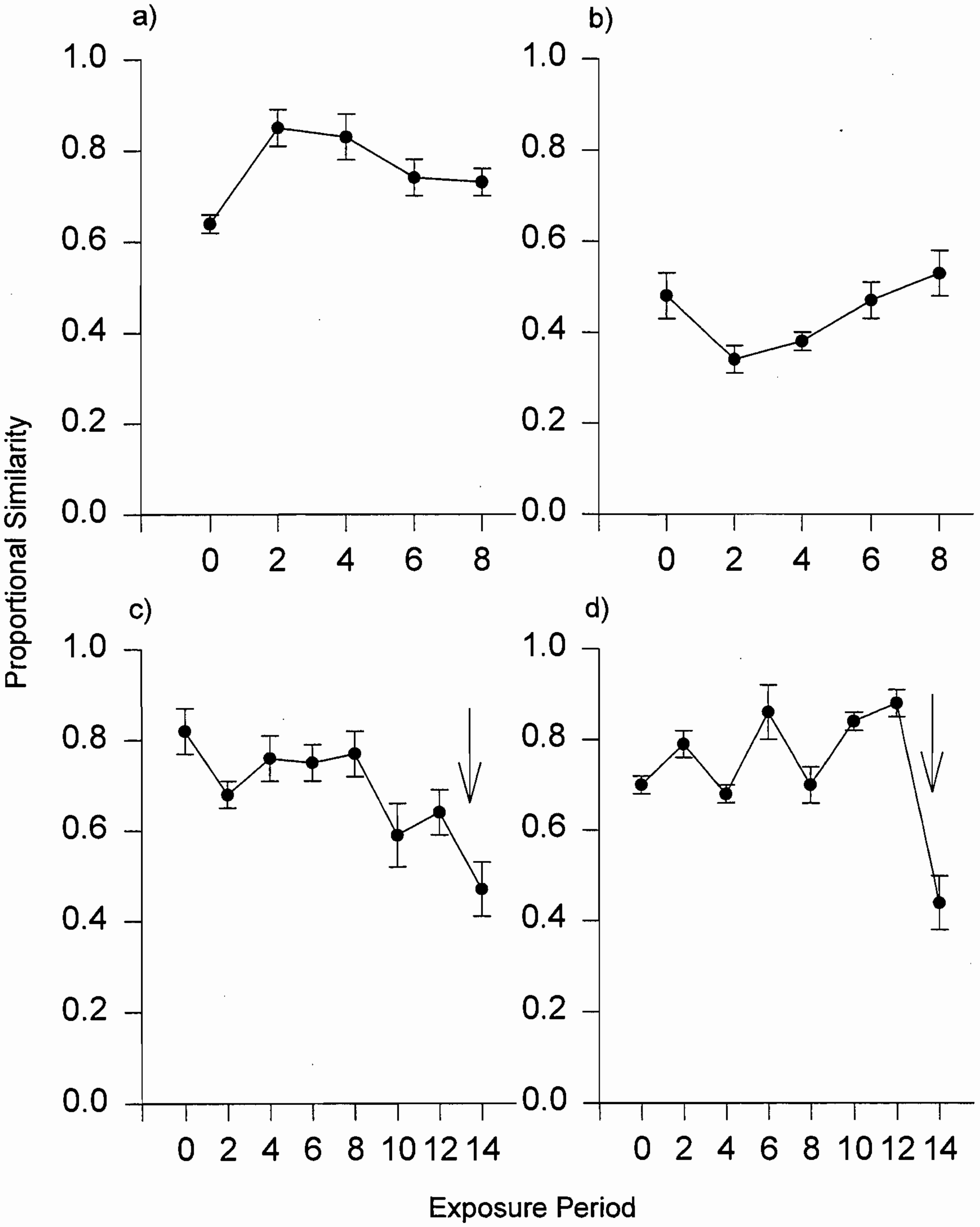

a)
b)
c)
d)
1.0
0.8
0.6
0.4
0.2
0.0
0 2 4 6 8
0 2 4 6 8
0 2 4 6 8 10 12 14
0 2 4 6 8 10 12 14
Proportional Similarity
Exposure Period

Figure 4.8 Plot of the first two dimensions of SSH ordinations (semi-strong hybrid multidimensional scaling) of macroinvertebrates colonising bare stones (●) compared with controls (■) at a) Tam Creek, 1993; b) Birthday Creek, 1993; c) Tam Creek, 1994; and d) Creek 115, 1994.

Arrows link consecutive times: 0 = 4 hr exposure and 2, 4, 6, 8 etc. represent the number of days exposure for colonisation stones; identical numbers indicate concurrently sampled controls.

Note that a substratum-moving flood occurred in 1994 at Tam Creek and Creek 115 between days 12–14, indicated by boldface arrows in colonisation and control samples.

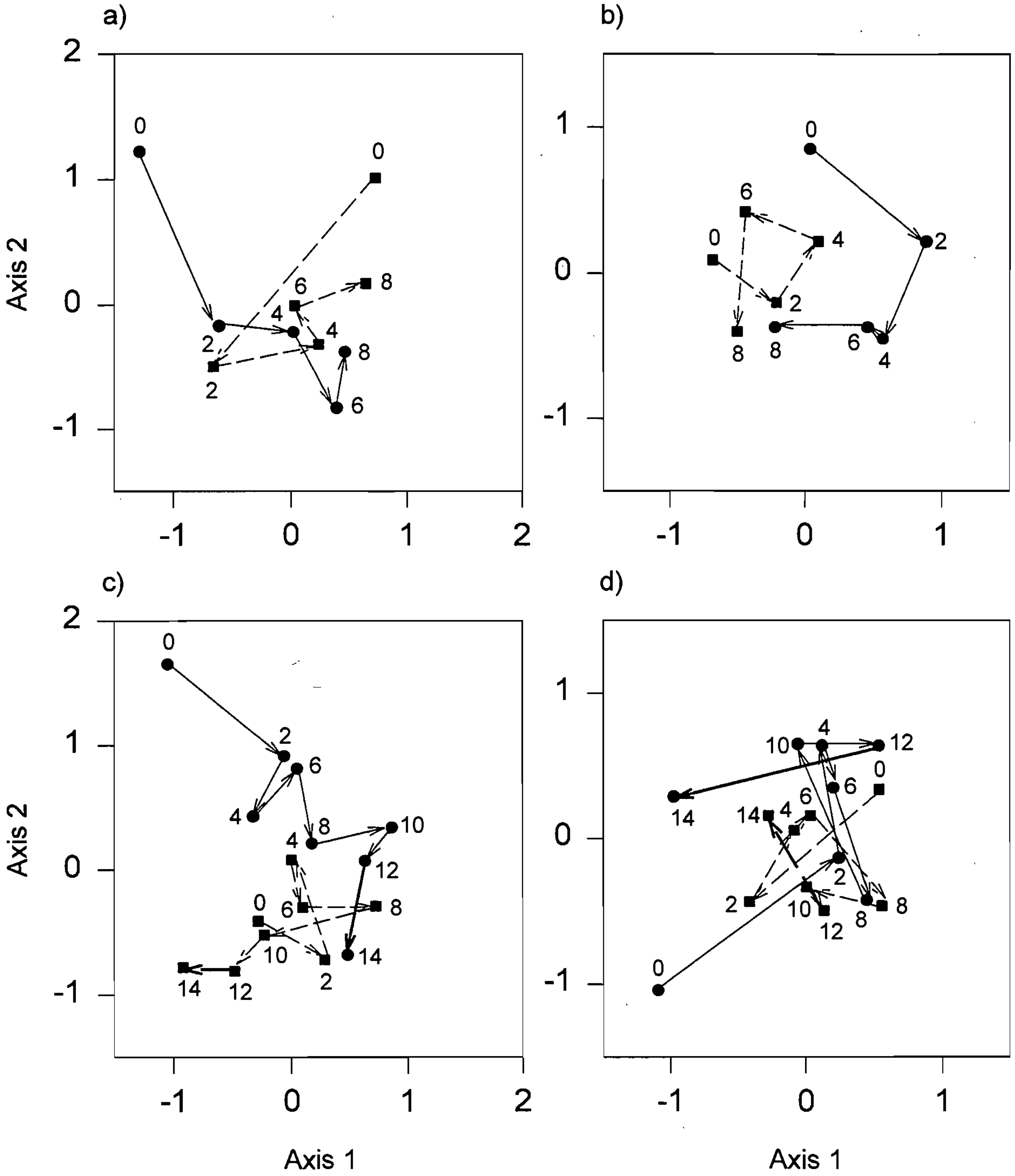
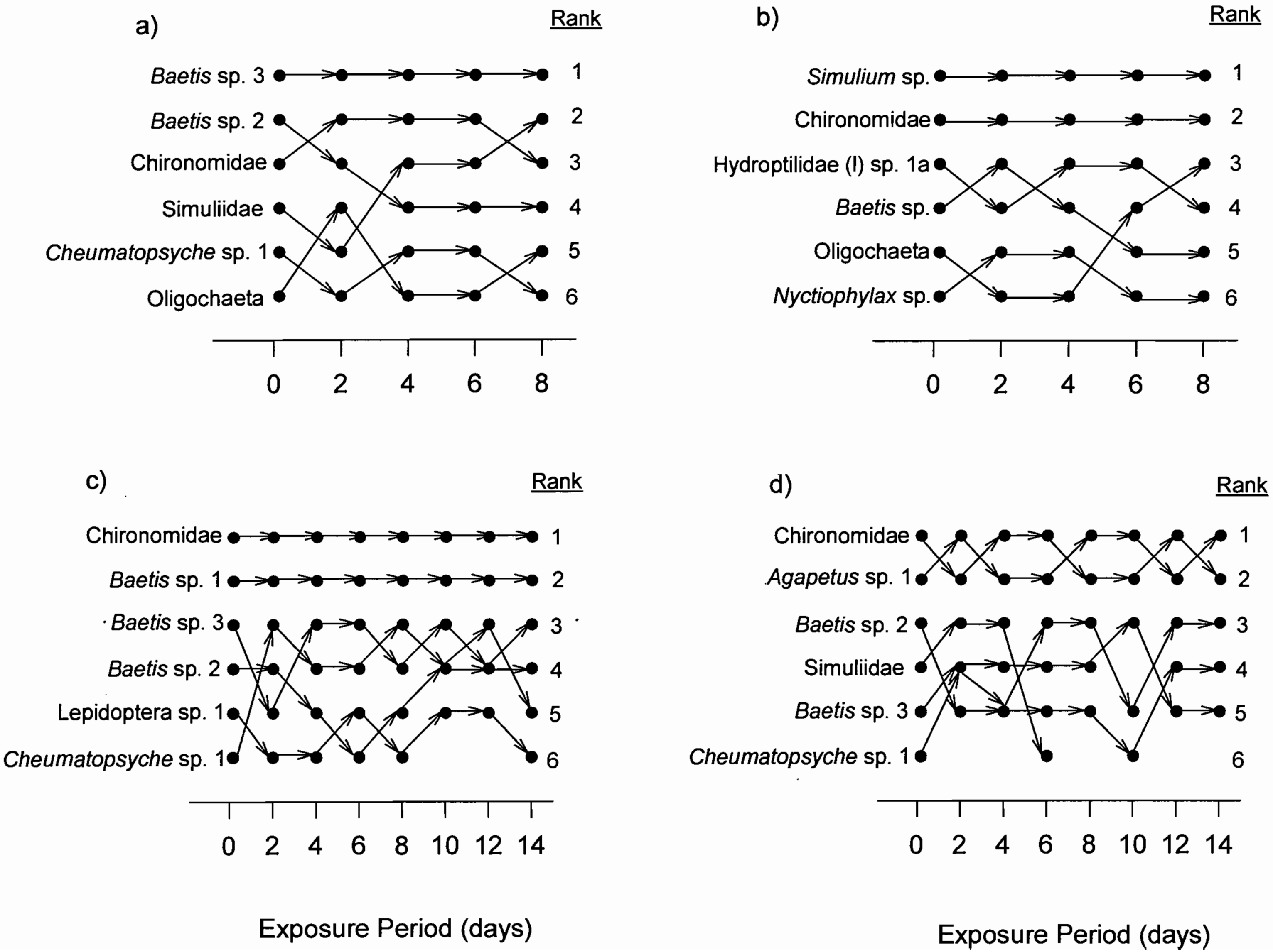

a)
b)
c)
d)
Axis 2
Axis 2
Axis 1
Axis 1
2
1
0
-1
-1
0
1
2
0
2
4
6
8
0
2
4
6
8
0
2
4
6
8
0
2
4
6
8
0
2
4
6
8
10
12
14
0
2
4
6
8
10
12
14
0
2
4
6
8
10
12
14
0
2
4
6
8
10
12
14

Figure 4.9 Changes in the rank abundance of the common macroinvertebrates colonising bare stones at a) Tam Creek, 1993; b) Birthday Creek, 1993; c) Tam Creek, 1994; and d) Creek 115, 1994.


a)
Rank
Baetis sp. 3
Baetis sp. 2
Chironomidae
Simuliidae
Cheumatopsyche sp. 1
Oligochaeta
1
2
3
4
5
6
0
2
4
6
8
b)
Rank
Simulium sp.
Chironomidae
Hydroptilidae (I) sp. 1a
Baetis sp.
Oligochaeta
Nyctiophylax sp.
1
2
3
4
5
6
0
2
4
6
8
c)
Rank
Chironomidae
Baetis sp. 1
Baetis sp. 3
Baetis sp. 2
Lepidoptera sp. 1
Cheumatopsyche sp. 1
1
2
3
4
5
6
0
2
4
6
8
10
12
14
Exposure Period (days)
d)
Rank
Chironomidae
Agapetus sp. 1
Baetis sp. 2
Simuliidae
Baetis sp. 3
Cheumatopsyche sp. 1
1
2
3
4
5
6
0
2
4
6
8
10
12
14
Exposure Period (days)

The rank order of colonising taxa at this site was slightly different the following year, with dominance by chironomids and a different species of mayfly (*Baetis* sp. 1). These two taxa did not change in their relative positions over the sampling period, and although slight fluctuations occurred in the remaining taxa, the initial configuration was almost unchanged at the end of the colonising period. Similarly, at Birthday Creek, the two dominant taxa, *Simulium* sp. and the chironomids, showed little change in their rank abundance over the eight days' exposure. In contrast, both the dominant taxa (the chironomids and *Agapetus* sp. 1) and the remaining common taxa fluctuated greatly over the colonising period at Creek 115. Simuliidae dropped markedly in ranking after day six, while *Baetis* sp. 3 and *Cheumatopsyche* sp. were elevated in rank abundance as exposure time increased. The highest level of fluctuation in species ranks occurred initially (days 0 – 2) and at the end of the sampling period (days 12 – 14) (Figure 4.9).

When the colonising fauna was examined in terms of functional feeding categories (for assignment to groups, see Appendix 2, Table A4.1), the stones were initially dominated by gatherers and scrapers in the New Guinea streams (Figure 4.10). Filterers were also common early on in the sequence (Tam Creek 1994), or increased over time (Tam Creek 1993). Predators were relatively more abundant in the second year at Tam Creek. Birthday Creek was clearly dominated by filterers (in particular *Simulium* sp.), with the other functional feeding groups relatively low in abundance. At Creek 115, scrapers (principally *Agapetus* sp. 1) dominated, increasing towards the end of the colonisation period, particularly following the spate.

Macroinvertebrate resistance to disturbance

Overall community-level resistance to disturbance was highest at Tam Creek, as samples taken immediately following the disturbance were not significantly different in terms of abundance (both years) and richness (1993) relative to the controls (day 0; Figures 4.11 and 4.12, Table 4.5). The following year, richness was significantly reduced at this site. Resistance to disturbance was relatively low at Birthday Creek, with significant reductions in both abundance and richness.

Figure 4.10 Mean abundance (± 1SE) of macroinvertebrate functional feeding groups colonising bare stones at a) Tam Creek, 1993; b) Birthday Creek, 1993; c) Tam Creek, 1994; and d) Creek 115, 1994.

Cg = collector-gatherers, Cscr = collector-scrapers, Cf = collector-filterers, Pred = predators. For allocation of macroinvertebrates to functional feeding groups, see Appendix 2, Table A4.1.

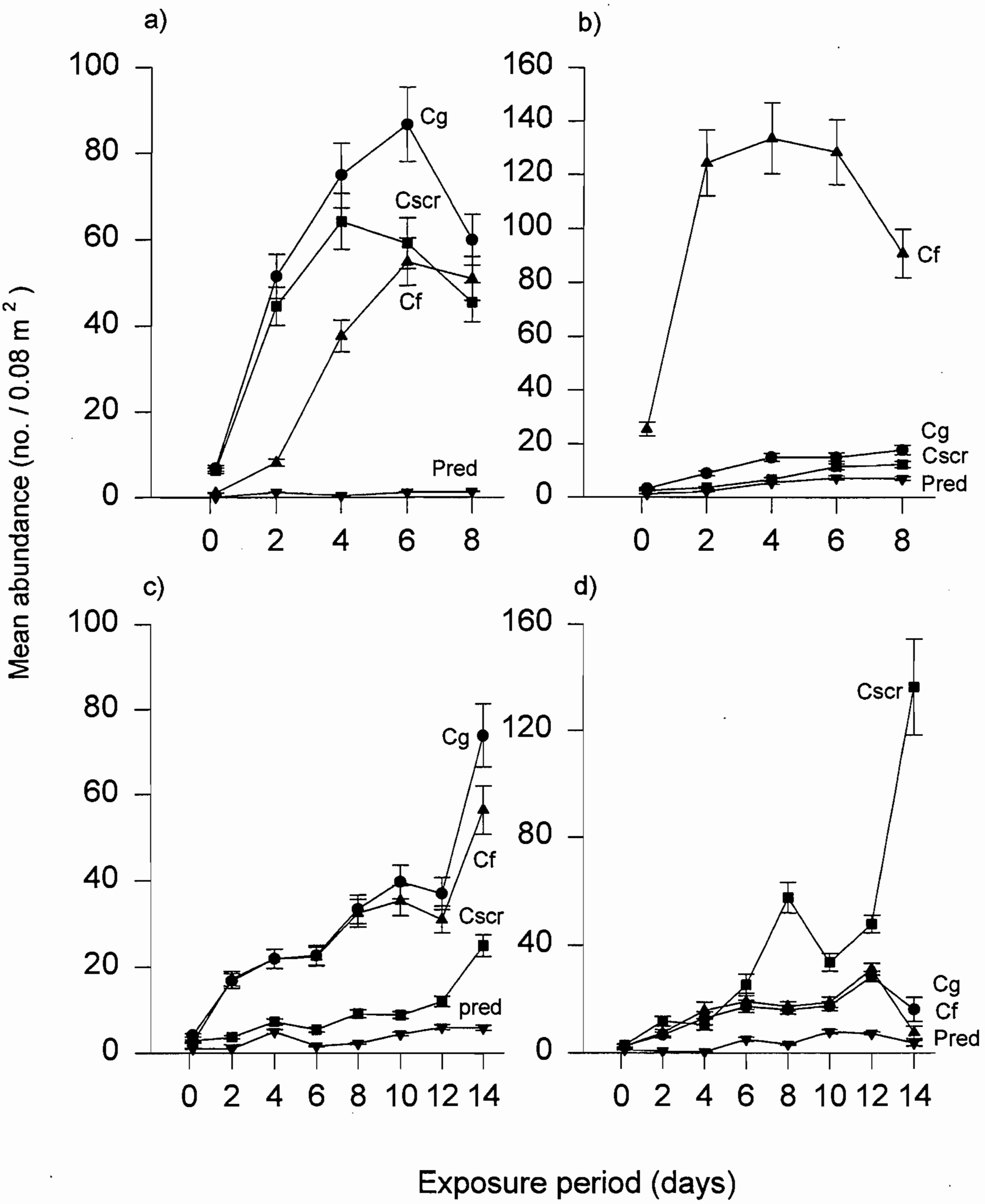

a)
b)
c)
d)
Mean abundance (no. / 0.08 m 2)
Exposure period (days)
100
80
60
40
20
0
160
140
120
100
80
60
40
20
0
0
2
4
6
8
10
12
14
Cg
Cscr
Cf
Pred
pred

Figure 4.11 Mean abundance (± 1 SE) of macroinvertebrates on stones following disturbance (●) compared with undisturbed controls (■) at a) Tam Creek, 1993; b) Birthday Creek, 1993; c) Tam Creek, 1994; and d) Creek 115.

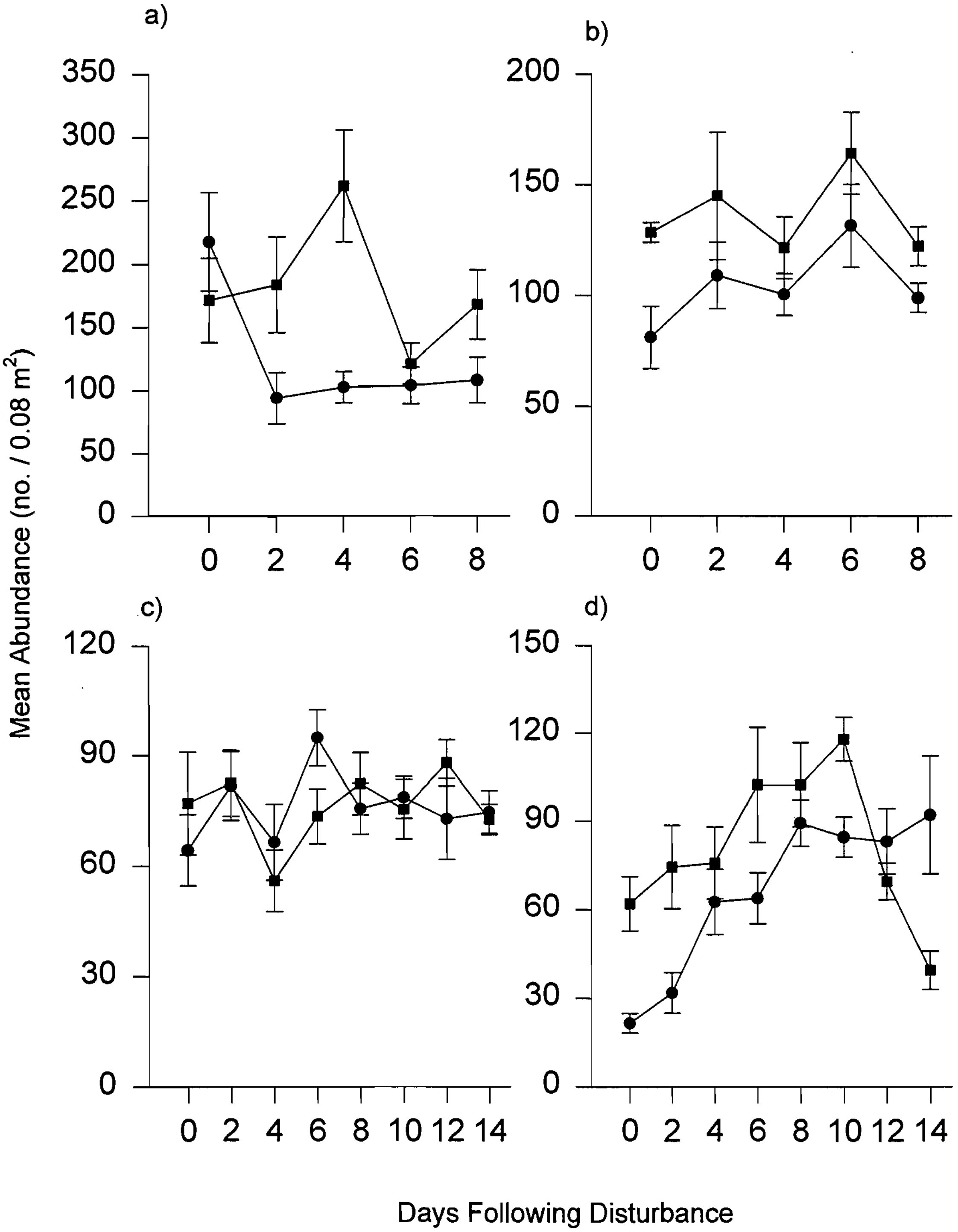

a)
350
300
250
200
150
100
50
0
0
2
4
6
8
b)
200
150
100
50
0
0
2
4
6
8
c)
120
90
60
30
0
0
2
4
6
8
10
12
14
d)
150
120
90
60
30
0
0
2
4
6
8
10
12
14
Mean Abundance (no. / 0.08 m²)
Days Following Disturbance

Figure 4.12 Mean richness (± 1 SE) of macroinvertebrates on stones following disturbance (●) compared with undisturbed controls (■) at a) Tam Creek, 1993; b) Birthday Creek, 1993; c) Tam Creek, 1994; and d) Creek 115.

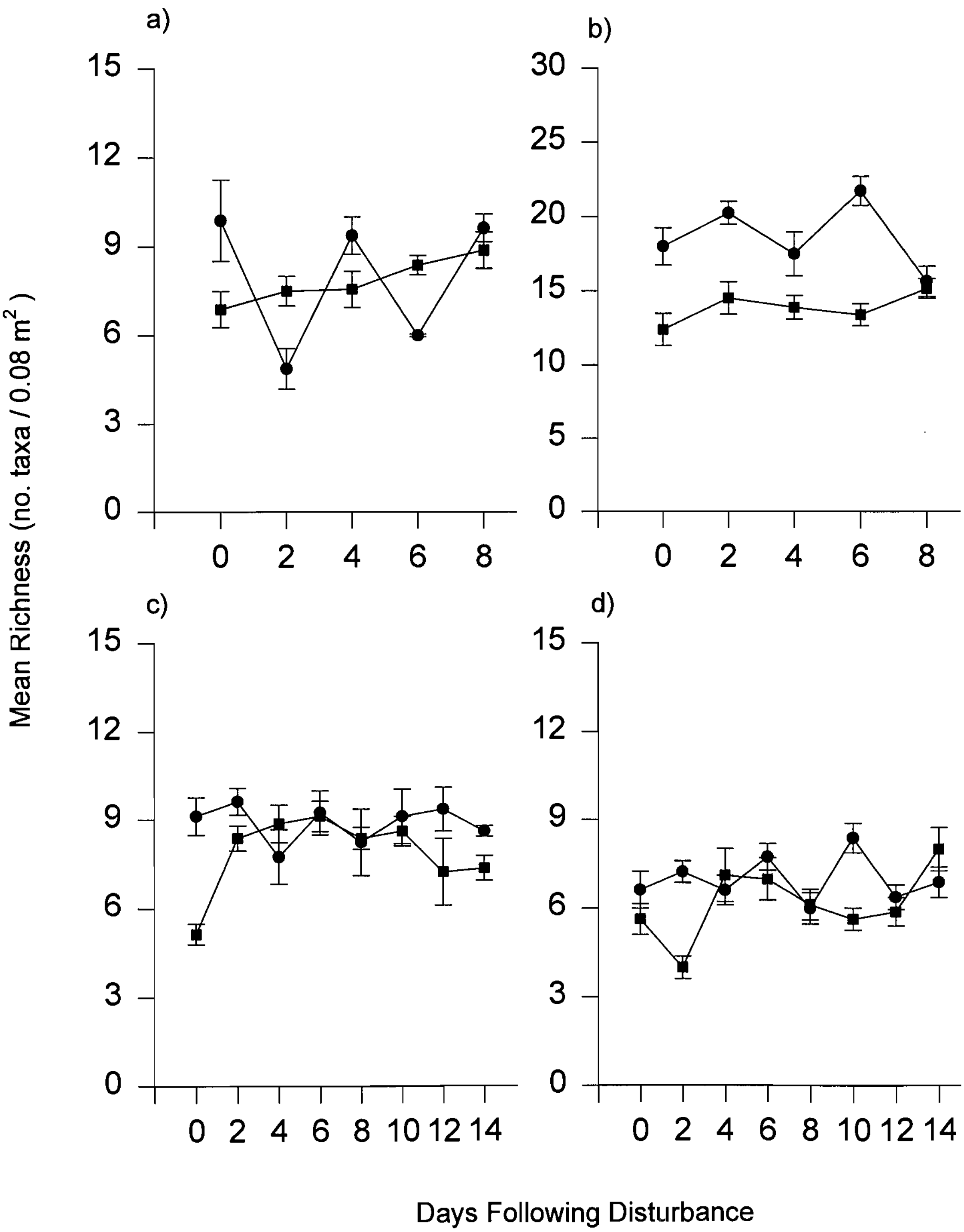

a)
b)
c)
d)
15
12
9
6
3
0
30
25
20
15
10
5
0
0
2
4
6
8
10
12
14
Mean Richness (no. taxa / 0.08 m^2)
Days Following Disturbance

Table 4.5 Macroinvertebrate resistance to disturbance, as measured by changes in abundance, richness and proportional similarity on stones sampled immediately following disturbance, relative to undisturbed controls (t-tests, d.f. = 14, $\alpha = 0.05$). Relative change (%) is given in parentheses. n.s. = non-significant ($p > 0.05$), *** = $p \leq 0.001$, ** = $p \leq 0.01$, * = $p \leq 0.05$.

Site	Abundance		Richness		Proportional Similarity (PSI)
	signif.	(%)	signif.	(%)	
Tam Creek (1993)	n.s.	(+21.63)	n.s.	(-30.8)	0.75
Birthday Creek (1993)	**	(-36.8)	**	(-31.2)	0.75
Tam Creek (1994)	n.s.	(-16.8)	***	(-43.8)	0.70
Creek 115 (1994)	**	(-65.3)	n.s.	(-15.08)	0.62

At Creek 115, abundance was reduced by disturbance, while richness was not significantly altered. Disturbance of the riffle had the greatest effect on community structure (as quantified by PSI) at Creek 115. Disturbance increased the variability within samples, as indicated by the coefficient of variation at Birthday Creek, while within-sample variability was generally reduced on the disturbed stones or remained unchanged relative to the controls at both PNG sites (Table 4.6).

Table 4.6 Within-sample variability as measured by the coefficient of variation on control and disturbed stones for macroinvertebrate abundance, richness, and common taxa at Tam Creek, Birthday Creek, and Creek 115. Higher CV values on disturbed stones relative to the controls are indicated in boldface.

	Tam Creek (1993)		Birthday Creek (1993)		Tam Creek (1994)		Creek 115 (1994)	
	Control	Disturbed	Control	Disturbed	Control	Disturbed	Control	Disturbed
Dinotoperla sp.			0.47	**0.86**				
Baetis sp. 1					0.92	0.59		
Baetis sp. 2							1.67	1.32
Baetis sp. 3	1.01	0.73			1.27	**1.73**	2.28	1.07
Chironomidae	0.5	**0.60**	0.34	**0.85**	0.68	0.55	0.66	0.62
Simulium sp.			0.44	**0.77**				
Tipulidae sp .3	0.65	**2.04**	0.56	**0.72**	1.88	0.82		
Agapetus sp. 1							0.58	0.57
?*Cheumatopsyche* sp.	2.82	0.87						
Cheumatopsyche sp. 1	1.91	1.46						
Oecetis sp.							2.20	0.93
Kingolus sp.			0.46	**0.67**				
Lepidoptera sp. 1					0.72	0.62		
Total abundance	0.55	050	0.29	**0.48**	0.51	0.42	0.42	0.42
Total richness	0.39	0.25	0.19	**0.25**	0.20	0.19	0.27	0.27

Resistance of individual taxa was variable between sites and between years (Table 4.7). Taxa were regarded as resistant if their abundance was not significantly reduced by disturbance (relative to the undisturbed controls), or they were significantly higher in abundance on the disturbed stones.

Table 4.7 Resistance of the common taxa to disturbance at Tam Creek (TC), Birthday Creek (BC), and Creek 115 (115) in 1993 (93) and 1994 (94). Significant differences between disturbed and control samples were determined using t-tests with $\alpha=0.05$. n.s. = non-significant (high resistance); * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$ (low resistance). "-" indicates rare or absent.

Taxa	High resistance (disturbed ≥ control)				Low resistance (control > disturbed)			
	TC(93)	BC(93)	TC (94)	115(94)	TC(93)	BC(93)	TC(94)	115(94)
Dinotoperla sp.	-	n.s.	-	-	-	-	-	-
Baetis sp. 1	-	-	n.s.	n.s.	-	-	-	-
Baetis sp. 2		-	***	-	*	-	-	-
Baetis sp. 3	n.s.	-	n.s.	n.s.	-	-	-	-
Atalophlebia sp.	-	-	-	n.s.	-	-	-	-
Austrophlebioides sp. 1	-	-	-	-	-	***	-	-
Austrophlebioides sp. 2	-	-	-	-	-	***	-	-
Tasmanocoenis sp. 1	n.s.	-	-	-	-	-	***	-
Chironomidae	-	-	n.s.	n.s.	*	*	-	-
Simulium sp.	-	-	-	-	-	*	-	-
Ceratopogonidae sp. 2	***	-	-	-	-	-	-	-
Tipulidae sp. 3	-	n.s.	n.s.	-	***	-	-	-
Agapetus sp. 1	-	-	-	-	-	-	-	***
?*Cheumatopsyche* sp.	***	-	-	-	-	-	-	-
Cheumatopsyche sp. 1	n.s.	-	-	n.s.	-	-	*	-
Helicopsyche sp.	-	-	-	-	-	***	-	-
Hydroptilidae sp. 1a	-	-	-	-	-	*	-	-
Nyctiophylax sp.	-	-	-	-	-	***	-	-
Oecetis sp. 1	-	-	-	n.s.	-	-	-	-
Kingolus sp. 1	-	n.s.	-	-	-	-	-	-
Simsonia sp.	-	-	-	-	-	*	-	-
Oligochaeta	***	n.s.	-	-	-	-	-	-
Lepidoptera sp. 1	-	-	*	-	-	-	-	-

Most of the common taxa at Tam Creek showed high resistance to the treatment, and some (e.g. Oligochaeta, Ceratopogonidae sp. 2) had positive resistance (greater numbers on disturbed stones).

One of the most common mayflies (*Baetis* sp. 3) showed consistently high resistance to disturbance across both years, while other taxa (e.g. Tipulidae sp. 3 and Chironomidae) displayed a variable response. At Birthday Creek, the majority of the common taxa, in particular the dominant Chironomidae and *Simulium* sp., were significantly reduced by disturbance. All common taxa at Creek 115, with the exception of *Agapetus* sp. 1, displayed high resistance to disturbance (Table 4.7).

Macroinvertebrate resilience to disturbance

Overall abundance was significantly reduced on the disturbed stones relative to the controls over the exposure period at Birthday Creek and Creek 115 (two-way ANOVAs, $p < 0.05$), while Tam Creek (both years) was not significantly affected (two-way ANOVA, $p > 0.05$) (Table 4.8, Figure 4.11). Similarly, richness was significantly lower on the disturbed stones at Birthday Creek and Creek 115 (two-way ANOVAs, $p < 0.05$), while no significant treatment effect was observed at Tam Creek (two-way ANOVA, $p > 0.05$) (Table 4.8, Figure 4.12). Of the common taxa, those significantly affected by the treatments included *Baetis* sp. 3, *Cheumatopsyche* sp. 2 (Tam Creek, 1993), *Baetis* sp. 1, *Helicopsyche* sp. (Birthday Creek, 1993), *Baetis* sp. 3, Tipulidae sp. 3 (Tam Creek 1994), and *Baetis* sp. 1, and Chironomidae (Creek 115). In many cases the interaction between disturbance intensity and time since disturbance was a significant factor.

Due to the sampling regime, the earliest possible time to measure recovery was two days following the disturbance as samples taken immediately after the disturbance (day 0 in all subsequent figures) provided a measure of resistance (see previous section). Recovery at the community level following disturbance was assessed in terms of recovery of total numbers, overall richness, and abundance of the common taxa to control levels (Table 4.9).

Table 4.8 Summary of two-way ANOVAs for Treatment (disturbed vs. control) by Time (day) for abundance, richness, and the most common taxa at each site. n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$, $\alpha = 0.05$. (refer to Appendix 2, Table A4.2 for ANOVA details).

Taxa	Main Effects		Interaction
	Treatment	Time	Treatment x Time
Tam Creek (1993)			
Baetis sp. 2	n.s.	*	**
Baetis sp. 3	**	**	***
Tasmanocoenis sp. 1	n.s.	*	n.s.
Chironomidae	n.s.	***	**
Simuliidae	n.s.	*	n.s.
Tipulidae sp. 3	n.s.	*	***
Cheumatopsyche sp. 1	n.s.	n.s.	n.s.
Cheumatopsyche sp. 2	***	***	***
Lepidoptera sp. 2	n.s.	***	n.s.
Oligochaeta	n.s.	***	***
Total abundance	n.s.	***	***
Total richness	n.s.	***	***
Birthday Creek (1993)			
Baetis sp. 1	***	n.s.	n.s.
Dinotoperla sp.	n.s.	n.s.	**
Chironomidae	n.s.	n.s.	n.s.
Simuliidae	n.s.	n.s.	n.s.
Tipulidae sp. 3	n.s.	*	n.s.
Helicopsyche sp.	***	n.s.	*
Hydroptilidae (l) sp. 1a	n.s.	n.s.	*
Kingolus sp.	n.s.	*	n.s.
Simsonia sp.	***	*	*
Oligochaeta	n.s.	*	*
Total abundance	***	n.s.	n.s.
Total richness	***	n.s.	**
Tam Creek (1994)			
Baetis sp. 1	n.s.	***	*
Baetis sp. 2	n.s.	**	***
Baetis sp. 3	**	***	***
Tasmanocoenis sp.	***	***	n.s.
Atalophlebia sp.	***	***	*
Chironomidae	n.s.	***	n.s.
Cheumatopsyche sp. 1	n.s.	***	n.s.
Tipulidae sp. 3	***	n.s.	n.s.
Lepidoptera sp. 1	n.s.	n.s.	***
Dugesia sp.	***	***	*
Total abundance	n.s.	n.s.	n.s.
Total richness	n.s.	n.s.	*
Creek 115 (1994)			
Baetis sp. 1	***	n.s.	***
Baetis sp. 2	*	*	**
Baetis sp. 3	n.s.	*	*
Atalophlebia sp. 1	n.s.	n.s.	n.s.
Chironomidae	***	***	n.s.
Chimarra sp.	n.s.	n.s.	n.s.
Oecetis sp.	*	n.s.	n.s.
Nyctiophylax sp.	n.s.	*	n.s.
Cheumatopsyche sp. 1	n.s.	***	**
Agapetus sp. 1	n.s.	**	***
Total abundance	**	***	***
Total richness	***	**	***

Table 4.9 Time (days) for abundance, richness, and abundance of common taxa on disturbed stones to recover to levels on undisturbed controls (t-test, $\alpha \geq 0.05$) at Tam Creek, Birthday Creek, and Creek 115.

Taxa	Tam Creek (1993)	Birthday Creek (1993)	Tam Creek (1994)	Creek 115 (1994)
Atalophlebia sp.	-	-	-	2
Baetis sp. 1	-	-	2	4
Baetis sp. 2	2	-	-	-
Baetis sp. 3	2	-	2	3
Tasmanocoenis sp. 1	2	-	-	-
Chironomidae	2	4	2	6
Simulium sp.	-	2	-	-
Tipulidae sp. 3	2	2	2	
				2
Agapetus sp. 1	-	-	-	2
Cheumatopsyche sp. 1	4	-	2	-
Hydroptilidae sp. 1a	-	2	-	
				-
Kingolus sp.	-	4	-	
				-
Oligochaeta	-	4	-	
		-		-
Lepidoptera sp. 1	-	-	2	
Total abundance	2	2	2	4
Total richness	4	4	2	4

Time to recovery of abundance and richness was similar at Tam Creek and Birthday Creek in 1993, with richness taking slightly longer to recover than total numbers (Table 4.9). The following year at Tam Creek, recovery was the most rapid of all sites, with both abundance and richness recovering to control levels after two days. Recovery of total numbers and richness was slowest at Creek 115, being complete four days after the disturbance. Although recovery of overall numbers and richness was similar at Tam Creek and Birthday Creek, most common taxa at Tam Creek recovered more rapidly following disturbance. All common taxa at this site had reached background levels after only two days, while at Birthday Creek four days was common. When these values for disturbed stones are compared with colonisation times on to bare stones (see Table 4.4), recovery (time taken to reach control levels) was generally faster on the disturbed stones.

By the time abundance and richness had recovered to control levels (see Table 4.9), community structure was similar on disturbed and control stones at all sites except Birthday Creek (Figure 4.13). Low values of the PSI on day four at this site (0.57) indicate that although abundance and richness had recovered, substantial differences in community structure still existed. The spate affected community structure differently at the two New Guinea sites. At Tam Creek, proportional similarity increased, while communities were less similar following the spate at Creek 115, indicating a greater impact on the community at this site (Figure 4.13b and 4.13d respectively).

Ordination of the data (Figure 4.14), shows strong overlap in community structure between disturbed and control samples at all sites in all three dimensions (for clarity, only the first two dimensions are presented), reflecting the rapid recovery times. Succession rate during the recovery period did not show a consistent pattern between sites. In some cases, succession rate was highest initially (Tam Creek, 1993; Creek 115), while in others the highest rate was during (Tam Creek, 1994) or at the end (Birthday Creek) of the recovery period.

Following disturbance of the riffle stones, there was substantial fluctuation in the rank abundance of the common taxa at each site (Figure 4.15). At Tam Creek in 1993, there was little change in the dominant taxa, *Baetis* sp. 3 and the Chironomidae, while others dropped from the top rankings following disturbance (e.g. Oligochaeta, Ceratopogonidae sp. 2). Chironomidae essentially remained the most abundant group at Birthday Creek throughout the eight day post-disturbance period, while other taxa tended to fluctuate in numbers over this time. *Simulium* sp, which was very high in abundance initially (day 0 – day 6), declined in numbers as other taxa increased between days six and eight. The following year at Tam Creek, Chironomidae and *Baetis* sp. 3 again dominated the community, with *Baetis* sp. 3 increasing rapidly in abundance following disturbance, being the most abundant taxon after 14 days. At nearby Creek 115, *Agapetus* sp. 1 dominated over much of the post-disturbance period, with Chironomidae the second most abundant taxon at the end of the sampling period.

Figure 4.13 Mean (± 1 SE) proportional similarity (Schoener 1968) of macroinvertebrate communities on disturbed stones compared with undisturbed controls at a) Tam Creek, 1993; b) Birthday Creek, 1993; c) Tam Creek, 1994; and d) Creek 115, 1994.

Values ≥ 0.65 indicate high community similarity in terms of composition and relative abundance.

Arrows indicate the approximate timing of substratum-moving floods at Tam Creek and Creek 115 in 1994.

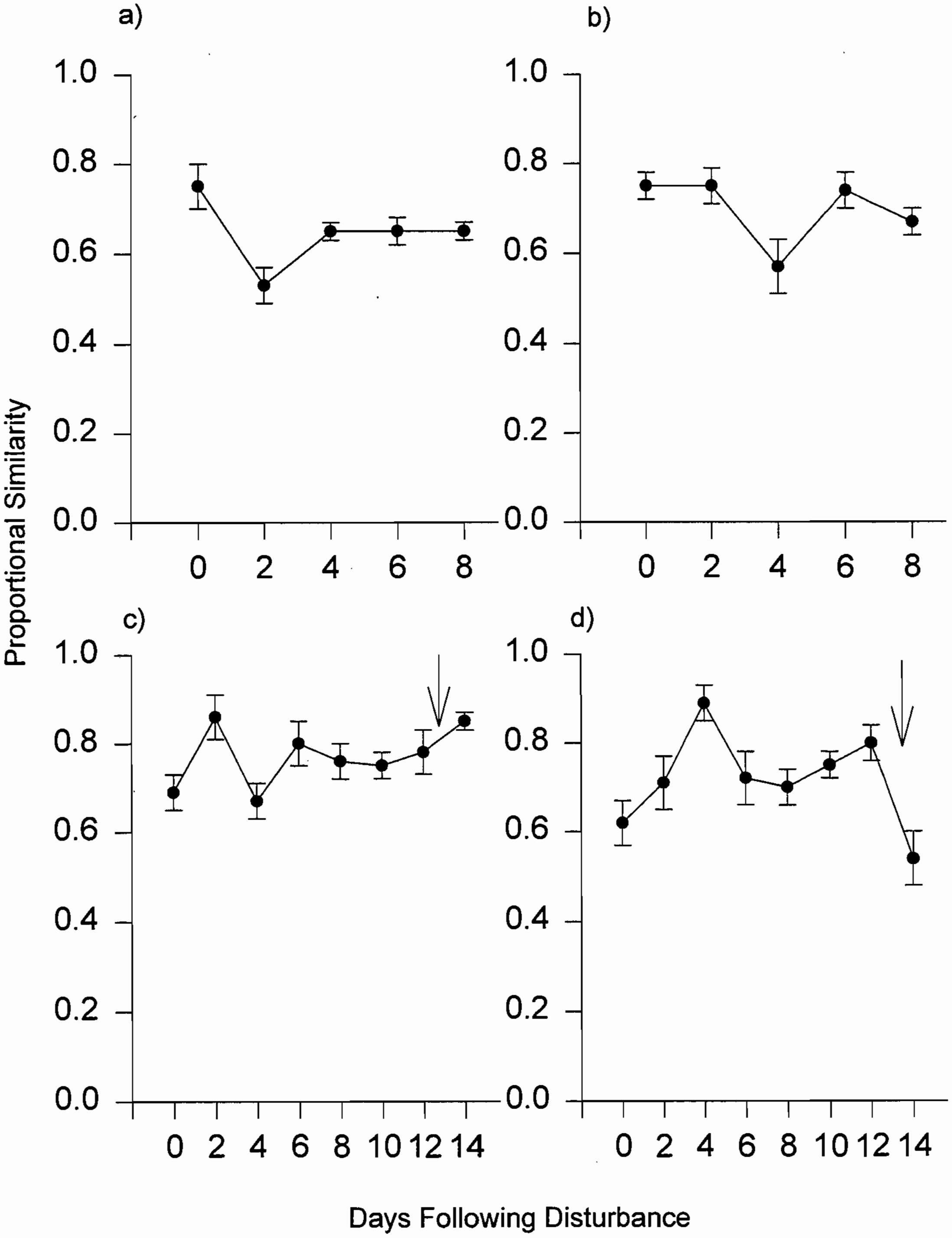
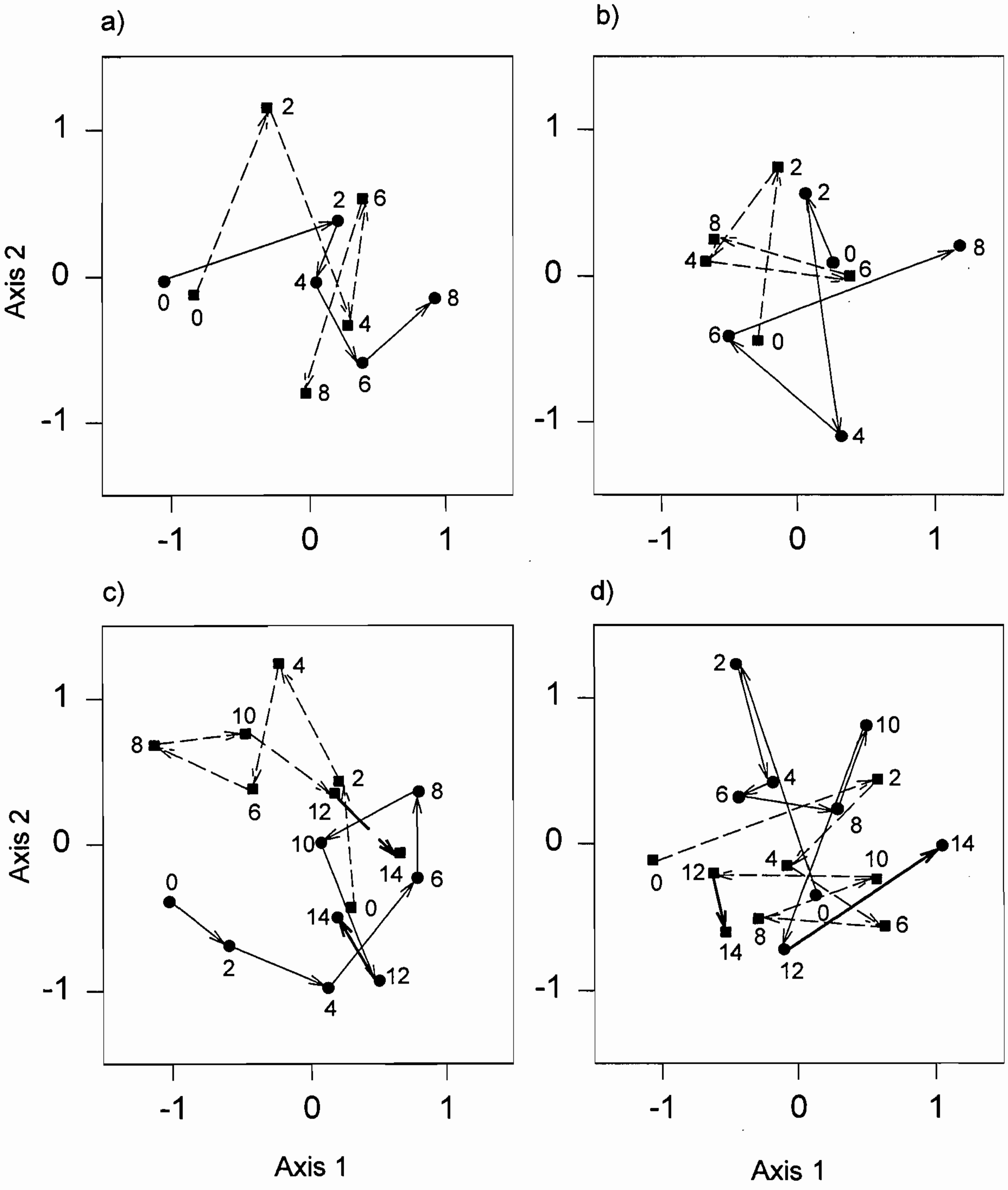

a)
b)
c)
d)
Proportional Similarity
1.0
0.8
0.6
0.4
0.2
0.0
0
2
4
6
8
10
12
14
Days Following Disturbance

Figure 4.14 Plot of the first two dimensions of SSH ordination (semi-strong hybrid multidimensional scaling) of macroinvertebrates on disturbed stones (●) compared with undisturbed controls (■) at a) Tam Creek, 1993; b) Birthday Creek, 1993; c) Tam Creek, 1994; and d) Creek 115.

Arrows link consecutive times: 0 = 4 hr and 2, 4, 6, 8 etc. represent the number of days following disturbance, identical numbers indicate concurrently sampled controls.

Note that a substratum-moving flood occurred in 1994 at Tam Creek and Creek 115 between days 12–14, indicated by boldface arrows in disturbed and control samples.


a)
b)
c)
d)
Axis 2
Axis 2
Axis 1
Axis 1
1
0
-1
-1
0
1
2
2
6
0
0
4
4
6
8
8
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4
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8
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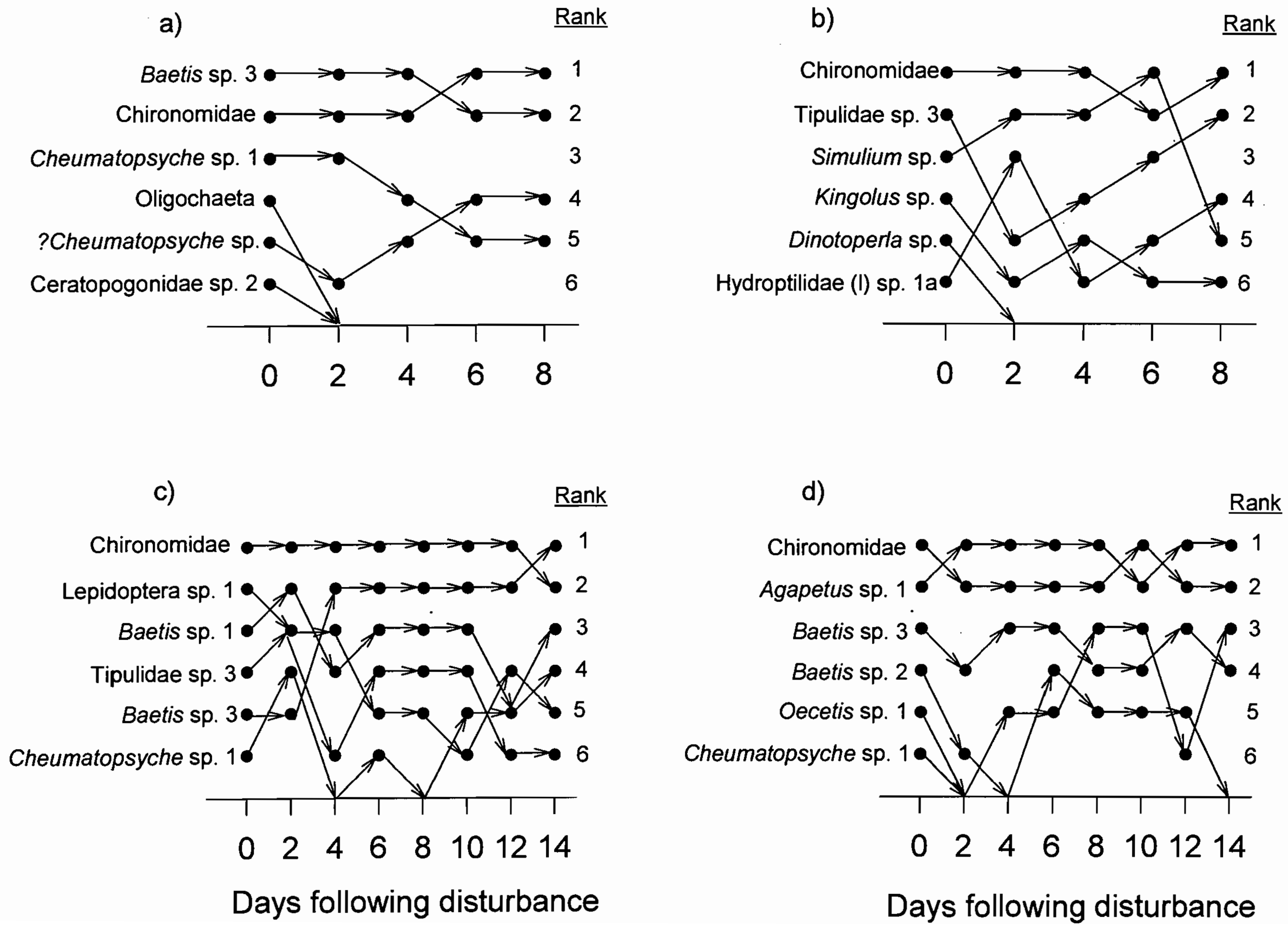
4
10
8
6
2
12
8
10
14
6
0
14
0
0
2
12
4
2
10
4
2
6
8
4
10
12
0
0
14
8
6
14
12

Figure 4.15 Changes in the rank abundance of the common macroinvertebrates on stones following disturbance at a) Tam Creek, 1993; b) Birthday Creek, 1993; c) Tam Creek, 1994; and d) Creek 115, 1994.


a)
Rank
Baetis sp. 3
Chironomidae
Cheumatopsyche sp. 1
Oligochaeta
?Cheumatopsyche sp.
Ceratopogonidae sp. 2
1
2
3
4
5
6
0
2
4
6
8
b)
Rank
Chironomidae
Tipulidae sp. 3
Simulium sp.
Kingolus sp.
Dinotoperla sp.
Hydroptilidae (l) sp. 1a
1
2
3
4
5
6
0
2
4
6
8
c)
Rank
Chironomidae
Lepidoptera sp. 1
Baetis sp. 1
Tipulidae sp. 3
Baetis sp. 3
Cheumatopsyche sp. 1
1
2
3
4
5
6
0
2
4
6
8
10
12
14
Days following disturbance
d)
Rank
Chironomidae
Agapetus sp. 1
Baetis sp. 3
Baetis sp. 2
Oecetis sp. 1
Cheumatopsyche sp. 1
1
2
3
4
5
6
0
2
4
6
8
10
12
14
Days following disturbance

Persistence, or constancy of community structure over time (Death and Winterbourn 1994), was compared at Tam Creek and Birthday Creek in samples taken twelve months apart (Table 4.10). Macroinvertebrate communities on undisturbed stones, in terms of composition and relative abundance (proportional similarity index) were similar at Birthday Creek. In contrast, there was a low degree of similarity between community structure on stones at Tam Creek in 1993 compared with the following year, suggesting that persistence of assemblage structure was higher at Birthday Creek.

Table 4.10 Persistence of macroinvertebrate assemblages on undisturbed stream stones as indicated by comparisons of species ranks and proportional similarity (PSI) in 1993 and 1994 at Tam Creek and Birthday Creek. Proportional Similarity Index values are given for comparisons between common (10) taxa, rare taxa (those remaining), and all taxa.

Tam Creek			Birthday Creek		
	Ranking			Ranking	
Taxa	1993	1994	Taxa	1993	1994
Baetis sp. 3	1	3	Chironomidae	1	1
Chironomidae	2	1	*Simulium* sp.	2	3
Cheumatopsyche sp. 1	3	7	Tipulidae sp. 3	3	4
Baetis sp. 2	4	2	Hydroptilidae sp. 1a	4	7
Lepidoptera sp. 2	5	-	*Dinotoperla* sp. 1	5	5
Cheumatopsyche sp. 2	6	-	*Kingolus* sp.	6	7
Oligochaeta	7	-	*Nyctiophylax* sp.	7	5
Tasmanocoenis sp. 1	8	8	Oligochaeta	8	2
Tipulidae sp. 3	9	6	*Simsonia* sp.	9	10
Simuliidae spp.	10	9	*Austrophlebioides* sp. 1	10	-
Proportional Similarity			Proportional Similarity		
common taxa		0.48	common taxa		0.40
rare taxa		0.91	rare taxa		0.90
all taxa		0.38	all taxa		0.65

Macroinvertebrate Drift

A total of 38 taxa were recorded in the drift at Tam Creek. Of these, 19 taxa were not recorded from the benthos during 1993. Almost double the number of taxa (70) were recorded in the drift samples taken at Birthday Creek. Twenty-seven of these taxa were not present in the benthic samples (Appendix 2, Table A4.3). Conversely, two taxa, (Empididae sp. and *Agapetus* sp. 2) common in benthic samples at Tam Creek, were not present in the drift. Similarly, a single taxon, *Helicopsyche* sp., not present in the drift at Birthday Creek, was common in the benthos.

Following the experimental disturbance of the riffle there were significant increases in total abundance, richness, and numbers of the majority of the common taxa in the drift at Tam Creek and Birthday Creek (Table 4.11). Of the taxa common in the drift, only Odontoceridae sp. (Birthday Creek) was significantly lower following disturbance (Tukey HSD, $p < 0.05$ in all cases).

Table 4.11 Comparison of total abundance, richness and abundance of the common taxa in the drift before and after experimental disturbance of the riffle at Tam Creek and Birthday Creek in 1993. Units given are drift rate (i.e. numbers per m^3 of water filtered over the four hour sampling interval). Significant differences (increase, ↑; or decrease, ↓) between pre- and post-disturbance samples were determined using Tukey HSD multiple comparison tests (following one-way ANOVAs testing for an overall effect of time, $\alpha = 0.05$, d.f. = 5).

Taxa	Disturbance		Post-Disturbance Change
	Pre-	Post-	
Tam Creek			
Baetis sp. 3	148.7 ± 24.9	1082 ± 92.3	↑
Baetis sp. 2	4.3 ± 0.7	173.1 ± 53.8	↑
Baetis sp. 1	18.5 ± 1.9	365.4 ± 51.9	↑
Chironomidae	7.9 ± 0.5	305.8 ± 48.1	↑
Cheumatopsyche sp. 1	4.7 ± 0.9	282.7 ± 42.3	↑
Helminthidae (l) sp. 14	8.4 ± 0.9	186.5 ± 26.9	↑
Total abundance	214.2 ± 16.4	3346.0 ± 387.3	↑
Total richness	8.9 ± 1.7	16.9 ± 1.2	↑
Birthday Creek			
Simulium sp.	152.2 ± 17.2	1259.2 ± 390.8	↑
Hydroptilidae sp. 1a	181.1 ± 17.7	701.3 ± 190.0	↑
Ulmerophlebia sp.	7.6 ± 0.6	30.3 ± 15.8	↑
Chironomidae	38.3 ± 8.9	417.1 ± 194.0	↑
Dixidae sp.	20.6 ± 5.5	61.8 ± 4.3	↑
Odontoceridae sp.	3.3 ± 0.5	0.7 ± 0.7	↓
Total abundance	537.0 ± 17.7	3898.0 ± 1064.0	↑
Total richness	18.0 ± 2.2	31.1 ± 1.8	↑

4.4 Discussion

There were differences in the response of the macroinvertebrate riffle fauna to disturbance between the aseasonal, Papua New Guinea streams and the seasonal, north Queensland stream (sampled during the dry season). When viewed in the context of hydrological variability, predictions of higher assemblage resistance and resilience at the more frequently disturbed site (Tam Creek) were supported.

Incorporation of hydrologic variability, particularly flood frequency and predictability, into conceptual models of stream environments (Poff and Ward 1989) has lead to predictions of species attributes which promote local persistence. To this end, many authors have favoured the approach of Southwood (1977, 1988), who suggested that the evolutionary selection of ecological strategies arose in response to spatial and temporal variation in habitat characteristics. Different disturbance regimes, which theoretically exert different selection pressures at the population level through effects on individual fitness (e.g. Levins 1965), may therefore constrain ecological response to and recovery from disturbance. Thus, the historical pattern of spatial and temporal variability within the environment may predetermine (within species' adaptive constraints) the response strategy (behavioural, physiological, life history characteristics) following natural and anthropogenic disturbance. In particular, the frequency of disturbance, relative to the generation time of the component species, imposes strong selective forces on species adaptation (Thiery 1982).

Following the premise that biological response to disturbance is a reflection of the experience of the fauna with historical, natural spatio-temporal variation (Poff and Ward 1990), the results of this study should be viewed within the framework of the natural disturbance regime. Fundamental differences in the disturbance regime exist between the aseasonal and seasonal streams; of particular relevance is the frequency at which natural disturbance events occur at these sites. The streams in PNG are subject to frequent spates of relatively low magnitude, while the North Queensland stream experiences low frequency, yet high magnitude, of flood disturbance (seasonally constrained). In line with theoretical expectations, the frequently disturbed site (Tam Creek) had relatively low richness (mean number of taxa per stone) when compared with Birthday Creek, which was sampled during a season of environmental stability (flow low and stable). The constraints imposed by disturbance frequency on species richness have been previously demonstrated in New Zealand streams by Death and Winterbourn (1995), and Death (1996) who found a direct relationship between hydrological stability and richness, with fewer species in frequently disturbed streams compared with more stable sites. Townsend *et al.* (1997a) found a typical bell-shaped response between species richness and disturbance levels, with maximum species richness at intermediate levels of disturbance of the stream bed by flooding, a finding consistent with the intermediate disturbance hypothesis (Connell 1978). It is likely that with increased temporal variability, in this case frequency of disturbance, there are fewer species within the regional pool capable of tolerating and persisting under these conditions (see Connell 1978). Dudgeon (1994) suggested that low richness in streams in Papua New Guinea, when compared with the Asian mainland and tropical Australia, reflected differences in the taxonomic resolution between studies and the absence of some of the major taxonomic groups such as the Plecoptera and Megaloptera in these streams. However, in the present study, taxonomic resolution was similar between sites and the absence of groups such as Plecoptera was compensated for by the increased diversity of other groups such as Gastropoda and Lepidoptera at the Papua New Guinea sites (Appendix 2, Table A4.1).

Resistance to disturbance

Although overall richness was relatively low at the frequently disturbed Tam Creek site, the ability to tolerate disturbance (i.e. resistance), was high for both the community and particular taxa. In this study, as with others (e.g. Boulton *et al.* 1992), it is difficult to comment on resistance at the level of the individual. There are practical reasons for this, as measurement of resistance at this scale would involve the direct marking of organisms to determine the degree to which individuals could withstand the effects of disturbance. Rather, samples taken immediately following the disturbance provide a relative measure of resistance of each taxon and overall community. Mechanisms promoting resistance to disturbance include: physiological tolerance, behavioural avoidance (e.g. use of refugia), and morphological characteristics (such as firm attachment structures, streamlined body form and dorso-ventral flattening) (Townsend and Hildrew 1994). It is difficult to determine which mechanism confers enhanced resistance to the fauna at Tam Creek, and is likely a combination of both resistance and resilience. Taxa with high resistance (e.g. *Baetis* sp. 3, *Cheumatopsyche* sp. 1) were not morphologically similar. Some taxa, however, such as the dominant Baetidae, were strongly dorso-ventrally flattened with a sprawling stance; whether this is an adaptive trait requires further investigation. Some groups displayed a consistent response (e.g. Oligochaeta had high resistance, Chironomidae low resistance) at both sites. Many of the taxa with low resistance at Birthday Creek (e.g. chironomids and *Helicopsyche* sp.), have been previously shown to be particularly susceptible to substratum tumbling at this site (Rosser and Pearson 1995). In addition, the tight coupling of ecological processes with season at Birthday Creek suggests that life history stages during the time of sampling (dry season) may be more susceptible to the effects of disturbance during this time than during the summer wet season, when flood disturbance occurs and resilience is high (Chapters 2 and 3, Rosser and Pearson, 1995).

Resilience following disturbance

Theory predicts that the fauna of more variable environments will not only show greater resistance to disturbance, but will also recover more rapidly (i.e. have high resilience) following disturbance, compared with the fauna of less variable systems. This is because the mechanisms influencing recovery, such as behavioural, physiological, life history and genetic characteristics, are all influenced to some degree by environmental variability (Poff and Ward 1990). The results of this study support the prediction, as recovery, relative to controls, was quicker at the more frequently disturbed site and was consistent across years at community and individual taxon levels. Similarly, in an aseasonal stream on Bouganville Island (PNG), Yule and Pearson (1996) found that the benthic fauna were very resilient to frequent disturbance by spates, which occurred unpredictably throughout the year.

In comparison to other studies, recovery following disturbance was particularly rapid, occurring within four days at Tam Creek. For example recovery of abundance and richness of raked substratum patches ($1m^2$) in a temperate Australian river took eight days during summer (Marchant *et al.* 1991). In a disturbance experiment conducted by Matthaei *et al.*

(1996), overall abundance in patches ($\approx 9m^2$) recovered to undisturbed levels within 30 days at one site and six days at another, being more rapid at the site with higher inferred disturbance frequency (implied from shear stress values).

Colonisation of bare stones (scrubbed and dried overnight) by macroinvertebrates was also very rapid at Tam Creek, being complete in only two days. In a review of lotic colonisation patterns, Mackay (1992) found that colonisation of bare substratum typically takes 10-30 days for total numbers, and 10-25 days for species richness. High resilience at Tam Creek may be a function of rapid species turnover (almost double the values for Birthday Creek) and characteristics promoting rapid dispersal of the fauna.

Mobility is one of the most commonly cited explanations for the high resilience observed in many stream environments. While most stream fauna are mobile, some taxa are particularly rapid colonisers, sharing similar ecological characteristics (Mackay 1992). The benthic assemblage at Tam Creek is dominated by *Baetis* spp. and Chironomidae. The benthic community at Tam Creek may share some parallels with frequently disturbed streams in New Zealand, dominated by the highly mobile mayfly *Deleatidium* sp., which becomes more prominent as environmental stability declines (Scarsbrook and Townsend 1993).

Both Baetidae and Chironomidae are repeatedly reported as abundant and early colonists of new or disturbed substratum, through high mobility (*Baetis* spp. only), ability to exploit newly developed organic layers on stone surfaces, and their propensity to enter the drift (Benson and Pearson 1987a). Drift is likely to be an important mechanism contributing to the rapid recovery in Tam Creek, as the dominant taxa in the benthos were also common in the drift, and all common taxa significantly increased in abundance in the drift following disturbance. Drift may be particularly important for dispersal of the relatively sedentary components of the fauna (e.g. those which do not possess strong swimming abilities) such as chironomids, Simuliidae and the net-spinning caddisflies. However, for some species drift is unlikely to be an important mechanism of recolonisation following disturbance, and instead these species may rely on benthic crawling and behavioural mechanisms of avoiding disturbance. This may be particularly true for species such as *Helicopsyche* sp. (Birthday Creek) and *Agapetus* sp. 1 (Creek 115), neither of which were present in the drift, presumably because of their heavy sand-grain cases. There was some evidence to suggest that the high resilience of *Agapetus* sp. 1 is due, in part, to behavioural avoidance mechanisms, as this species was observed to move to the downstream side of stones during the period of elevated flow in this study. The downstream face of stones is known to be a zone of relatively low flow (Davis 1986), and so may provide some protection from the forces of flow for this species. Behavioural mechanisms, involving movement into flow refugia, may be especially important for the less mobile components of the fauna, particularly those not prominent in the drift. At Birthday Creek, common benthic taxa were also well represented in the drift, although the relative importance of drift at this site may vary seasonally, peaking to coincide with summer wet season (Benson and Pearson 1987b). Therefore, reduced drift rates are likely to reduce the speed of recovery from disturbance in the dry season compared with during the summer months.

Some of the predictions suggested in models relating environmental variation to community structure are supported by the results of this study (Table 4.12). This table shows that macroinvertebrates from a stream with a high frequency of natural disturbance (Tam Creek, PNG) or during a time of seasonal disturbance (Birthday Creek, north Queensland – wet season), generally follow the predictions relating to environmental variation. Similarly, during the dry season at Birthday Creek, characterised by relatively stable hydrological conditions, the community conforms to many of the predictions related to a low frequency of disturbance. The only exceptions to this pattern is the high abundance and persistence during the wet season at Birthday Creek, due largely to increases in *Simulium* sp., and the relatively distinct community assemblage at this time.

In their variant of Southwood's (1977, 1988) habitat templet model, Scarsbrook and Townsend (1993) and Townsend and Hildrew (1994) suggested that in frequently disturbed environments, traits conferring resistance and/or resilience are predicted to increase in prominence. In contrast, temporally stable environments (i.e. with low frequency of disturbance) should be typified by more sedentary taxa. Certainly, there was a much higher proportion of taxa regarded as highly mobile (Mackay, 1992), such as *Baetis* spp., in the community at the frequently disturbed site, possibly a reflection of the temporal instability at this site.

Table 4.12 Characteristics of communities and individuals from streams with high and low temporal frequency of natural disturbance and the sites/times at which these characteristics were observed or predicted (?) from the results of this study. Riffle communities in Tam CreeK, PNG (TC – high frequency of disturbance), and Birthday Creek, north Queensland, sampled during the wet season (BC wet – high frequency of disturbance) and the dry season (BC dry – low frequency of disturbance) were included. The references indicate the proponents of the characteristics listed.

High frequency of disturbance (i.e. unstable)		Low frequency of disturbance (i.e. stable)		Reference
Traits	Site	Traits	Site	
species with good colonising abilities	TC, BC(wet)	competitively superior species	?BC(dry)	Connell (1978)
resource generalists	?TC	resource specialists		Poff and Allen (1995)
increased prominence of traits conferring i) resistance[a] and ii) resilience[b]	TC, BC(wet)	relatively low resistance and resilience	BC(dry)	Townsend and Hildrew (1994)
shorter life spans	?TC	longer life spans		Townsend and Hildrew (1994)
relatively low richness	TC, BC(wet)	high species richness	BC(dry)	Death and Winterbourn (1995)
relatively low abundance	TC, BC(dry)	high abundance	BC(wet)	Death and Winterbourn (1995)
low community persistence	TC	high persistence	BC(dry, wet)	Death and Winterbourn (1995)
stochastic control (e.g. disturbance)	TC, BC(wet)	deterministic control (e.g. competition)	BC(dry)	Death and Winterbourn (1995)

a = firm attachment, flexible body forms, streamlining or flattening
b = high mobility (promotes use of refugia and recolonisation), presence of invulnerable life stage
? = predicted

There were differences in macroinvertebrate community response to disturbance between the two Papua New Guinea streams, largely reflecting the response of the most abundant species. Instead of a benthic community dominated by highly mobile baetid mayflies, a stone-cased caddisfly, *Agapetus* sp. 1 was common, contributing to almost half the total numbers on the controls. In contrast to the other taxa at this site, this species showed low resistance to the tumbling disturbance. Although rapid relative to published values, recovery at assemblage and taxon levels at Creek 115 was slightly lower than at Tam Creek. While *Agapetus* sp. 1 recovered rapidly following disturbance (complete in two days), other taxa such as the chironomids were delayed, influencing overall recovery. The occurrence of a natural spate (of sufficient magnitude to move substratum particles) prior to the collection of the final samples at Tam Creek and Creek 115, permitted some comparisons between community response between natural and experimental disturbance. The spate had the greatest impact on the fauna colonising bare stones at both sites, altering community structure (PSI and ordination scores) and increasing the rate of species change (i.e. succession rate). This was due to the significant increase in numbers of many of the common taxa (e.g. *Baetis* spp., Chironomidae, and *Cheumatopsyche* sp. 1) at Tam Creek, and the dominant taxon, *Agapetus* sp. 1, at Creek 115. In contrast, the spate had little effect on the community on the disturbed stones at Tam Creek in terms of succession rate and community structure. Although rate of succession was not affected at Creek 115, *Agapetus* sp. 1 again increased significantly in abundance on the disturbed stones following the spate, which had the effect of altering community structure at this site. Interestingly, there was a significant reduction in *Agapetus* sp. 1 on the control stones during this time. The apparent disparity between the dramatic increase in numbers on the scrubbed colonisation stones or on the disturbed stones following the spate, while numbers were reduced on the controls, may be a response to periphyton levels. Lake and Doeg (1985) found that *Agapetus* sp. appeared to colonise stones with lower periphyton (and silt) levels in much higher numbers compared to the surrounding controls.

It is likely that frequent hydrological disturbance of the Papua New Guinea stream communities precludes strong biotic control of them. In contrast, the long inter-flood periods experienced by the fauna at the seasonal North Queensland stream, may allow the development of biotic interactions over time (Pearson *et al.* 1986, Hearnden and Pearson 1991). Thus, for example, in desert streams subject to frequent flash floods, where very rapid development times permit turnover of generations within the inter-flood period (Gray 1981), biotic interactions may intensify over time (Fisher and Grimm 1991). There is increasing evidence to suggest that rapid development times (involving multivoltine life histories) are common for tropical freshwater taxa (Marchant 1982, Nolen and Pearson 1992, Jackson and Sweeney 1995), compared with temperate insect assemblages which tend to show a higher proportion of univoltine and semivoltine species (Clifford 1982, Newbold *et al.* 1994). In a long-term study of a small stream on Bouganville Island, Yule and Pearson (1996) found that almost all species had multivoltine life histories, with continuous hatching and emergence throughout the year. The authors concluded that the occurrence of frequent, unpredictable spates during the year provided a sufficient selective mechanism to shape the aseasonal life cycles observed in this stream.

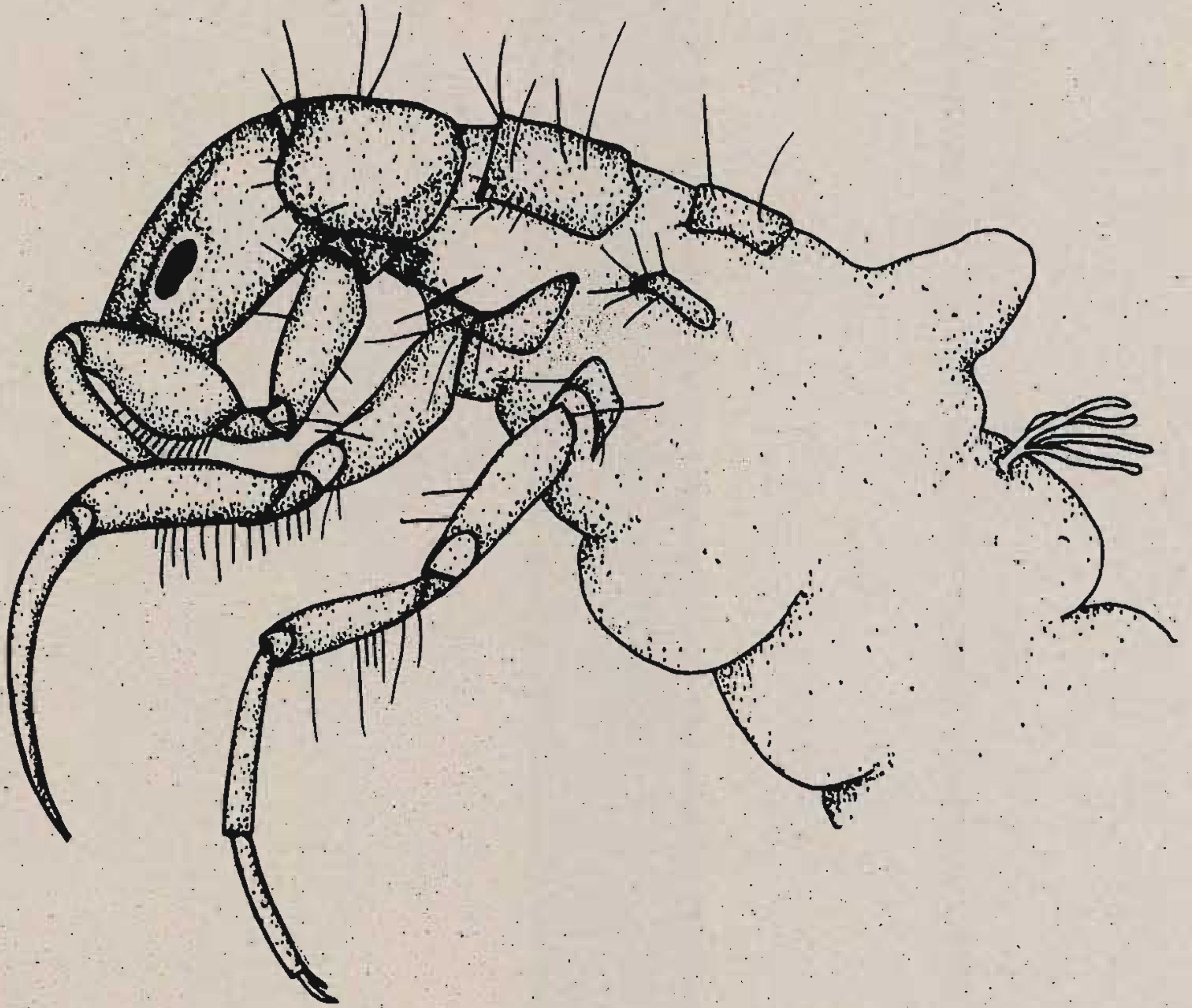
More rapid development times (i.e. time between oviposition and adult emergence) in tropical stream assemblages should increase the rate of recovery following disturbance as more individuals are produced which are also more effective in tracking and exploiting temporally variable resources compared with univoltine species (Mackay 1992). For example, baetid mayflies and many chironomids have particularly rapid development of egg and larval stages (Jackson and Sweeney 1995), suggesting that they may be prominent initially and recover rapidly following disturbance. Furthermore, presence of all life-history stages at any given time will enhance recovery ability of a species.

In summary, comparison of the responses of macroinvertebrates to disturbance in tropical streams with contrasting flow regimes has demonstrated that:

- Historical exposure to disturbance (i.e. the natural flow regime) influences macroinvertebrate response to physical disturbance of the substratum. In Papua New Guinea, frequent floods may provide an evolutionary basis for the selection of mechanisms for faunal response to substratum-moving disturbance events, resulting in a benthic assemblage characterised by high resistance and resilience to this form of disturbance. In these frequently disturbed streams, recovery following disturbance is likely to be enhanced by the very high mobility of many species, their propensity to enter the drift, high assemblage turnover, and active movement into low flow areas (refugia) during elevated flow conditions. The latter mechanism may be particularly important for the persistence of less mobile components of the fauna (e.g. those restricted by heavy cases such as *Agapetus* sp. 1) for which large-scale dispersal processes (e.g. drift) are less available.

- In streams which are highly seasonal (i.e. low within-year frequency of natural disturbance), macroinvertebrate resistance and resilience to substratum disturbance is relatively low during the time of low and stable flows, reflecting the seasonal shift to species which are less tolerant of disturbance (see Chapter 2). During the wet season, however, when the benthic community may be exposed to severe disturbance by high and variable flows, faunal characteristics and assemblage composition more closely resemble those observed in streams with a high frequency of disturbance (Table 4.12).

- Persistence of assemblage ranks and proportional similarity of the community was lowest at the site with a high frequency of disturbance (PNG), which agrees with the theoretical expectation that low persistence (i.e. less predictable asemblages) is associated with high levels of disturbance (Grossman 1982, Lake and Barmuta 1986). Higher persistence at the time of hydrological stability at the north Queensland site may indicate, as suggested by Death and Winterbourn (1994), greater deterministic control (e.g. competition and predation) of community structure, mediated by the relatively constant hydrological conditions during the dry season (see Chapter 2).



Trichoptera: Philorheithridae

Artist: Andi Cairns

CHAPTER 5: GENERAL DISCUSSION

The central theme of this study was to examine the response of the macroinvertebrate fauna of stones in tropical rainforest streams to physical disturbance. The approach combined long-term sampling encompassing natural floods, and smaller-scale experimental manipulations. The results are summarised in Table 5.1 with the relative positions of the macroinvertebrate communities, in terms of resilience, along axes of disturbance frequency and magnitude, defined in Figure 5.1. Much of the study focussed on seasonal streams of the Australian Wet Tropics and comparisons were made with aseasonal tropical streams in Papua New Guinea. Disturbance may be especially important in Australian streams, and in the tropics in particular, due to the high and variable flows, and may contribute to the creation and maintenance of the very high benthic diversities observed in these streams.

5.1 Review of major findings in relation to the proposed aims

a) How do macroinvertebrate communities on stream stones respond to temporal variations in flow, both severe substratum-moving floods and periods of low and stable flow? (Chapter 2)

Continuous, long-term sampling of the macroinvertebrate stone fauna within riffles and pools, the major habitats in the upland streams of the Australian Wet Tropics, revealed a fauna which was strongly influenced by the seasonal pattern of flow.

In riffles, during the very high and variable flows of the summer wet season, the stone fauna was dominated by an obligate lotic species, *Simulium* sp., capable of rapid recolonisation following floods of sufficient magnitude to physically rearrange the substratum. As flow declined in the transition to the dry season, there was a distinct shift in community structure, to dominance by a multi-species assemblage of chironomids.

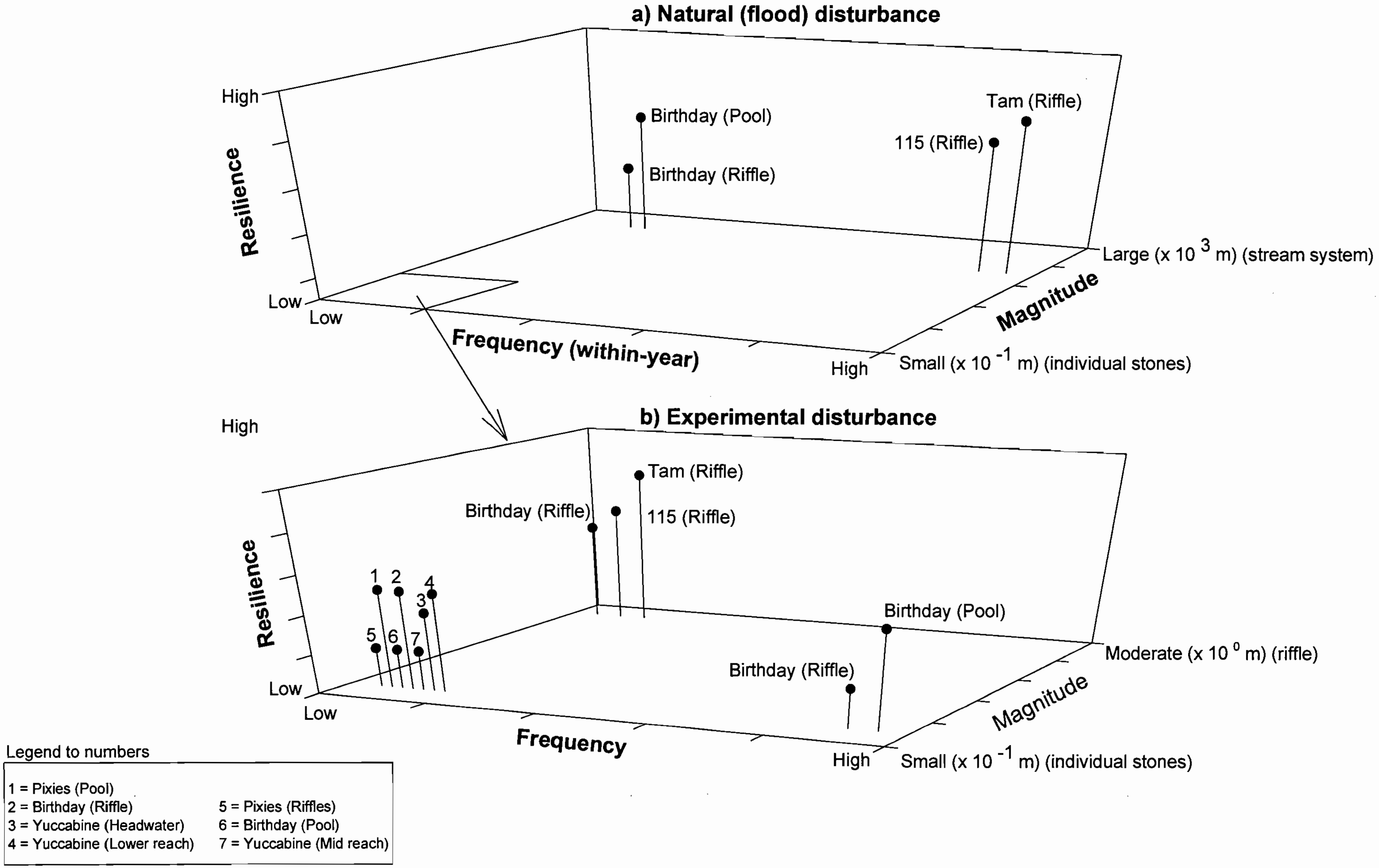
Table 5.1 Summary of the results of this study showing resistance and resilience characteristics following natural and experimental disturbance at different spatial scales and at sites with different frequencies of natural disturbance. Proposed mechanisms of recolonisation are given, listed in decreasing order of importance.

Disturbance	Spatial scale	Frequency of disturbance	Resistance	Resilience	Source of recolonisation
Wet Tropics		Low frequency			
Birthday Creek					
Riffle					
flood	large		low	moderate	drift > proximate refugia
experimental	moderate		low	high	proximate refugia > drift
experimental	small		low	high	proximate refugia > drift
Pool					
flood	large		moderate	high	drift > proximate refugia
experimental	small		moderate	moderate	proximate refugia > drift
Pixies Creek					
Riffle					
experimental	small		low	moderate	proximate refugia > drift
Pool					
experimental	small		low	high	proximate refugia > drift
Yuccabine Creek					
Headwater					
experimental	small		moderate	high	proximate refugia > drift
Mid reach					
experimental	small		low	low	proximate refugia > drift
Lower reach					
experimental	small		moderate	high	proximate refugia > drift
Papua New Guinea		High frequency			
Tam Creek					
Riffle					
flood	large		high	very high	drift > proximate refugia
experimental	moderate		high	very high	proximate refugia > drift
Creek 115					
Riffle					
flood	large		high	very high	drift > proximate refugia
experimental	moderate		moderate	high	proximate refugia > drift

Figure 5.1 Summary of benthic macroinvertebrate community response to disturbance at each site, in terms of relative resilience, placed within the spatial (magnitude) and temporal (frequency) scale of the disturbance:

a) Large scale (natural) disturbances and b) expansion of (a) to show small-scale (experimental) disturbances.

Refer to Table 5.1 for further details.


a) Natural (flood) disturbance
High
Resilience
Low
Low
Frequency (within-year)
High
Magnitude
Large (x 10 ^{3} m) (stream system)
Small (x 10 $^{-1}$ m) (individual stones)
Birthday (Pool)
Birthday (Riffle)
Tam (Riffle)
115 (Riffle)
b) Experimental disturbance
High
Resilience
Low
Low
Frequency
High
Magnitude
Moderate (x 10 ^{0} m) (riffle)
Small (x 10 $^{-1}$ m) (individual stones)
Tam (Riffle)
Birthday (Riffle)
115 (Riffle)
Birthday (Pool)
Birthday (Riffle)
1
2
3
4
5
6
7
Legend to numbers
1 = Pixies (Pool)
2 = Birthday (Riffle)
3 = Yuccabine (Headwater)
4 = Yuccabine (Lower reach)
5 = Pixies (Riffles)
6 = Birthday (Pool)
7 = Yuccabine (Mid reach)

Flooding, which in these streams may be severe, resulted in a reduction of individuals, while diversity was less affected. Flood disturbance was patchy in its impact on faunal abundances and therefore increased the variability (i.e. patchiness) on individual stones, possibly permitting the coexistence of rarer species. Variation in assemblage structure was high following flood disturbance, and may have reflected stochastic colonisation from drift and in-stream refugial sources.

In pools, the fauna appeared to be more resistant and resilient to the effects of flooding and these habitats may be less impacted (physically) by floods compared to riffles. Floods did not affect diversity, which was remarkably stable seasonally and, in contrast to riffles, tended not to increase the patchiness on individual stones (possibly a function of the high resilience). It is likely that pools act as important refugial areas during flooding as they tend to accumulate animals, some of which are displaced from nearby riffles. Monitoring of the movements of macroinvertebrates out of pools following floods would test this hypothesis.

Magnitude of flooding greatly influenced the seasonal pattern of variation in community structure. Where floods were small, probably below the threshold for substantial rearrangement of the substratum, the distinction between wet and dry season assemblages was much reduced.

Biotic interactions may be increased during the dry season in seasonal tropical streams, particularly when flood magnitude is reduced, resulting in longer periods of time over which biotic interactions may intensify, unconstrained by severe disturbance. Variation in community structure and diversity of macroinvertebrates on stones was highest during drier years (in the riffle habitat), suggesting intensifying biotic interactions in the absence of disturbance by large floods. The reduction of available habitat in riffles as the dry season progresses would increase the likelihood of biotic interactions as predators and prey are brought into closer contact and the organism-to-resource ratio rises (e.g. Pearson *et al.* 1986, Dudgeon 1993).

b) At the scale of individual stones, how do macroinvertebrates respond to physical disturbance, and are characteristics of resistance and resilience modified by habitat? (Chapter 3)

The experimental manipulations of individual substrata provided an insight into the effect of substratum movement as a source of disturbance to the macroinvertebrates living on their surface. The majority of fauna entered the water column when individual substrata were moved, and the degree to which total numbers and number of taxa were reduced was dependent on the number of times the substratum was tumbled (i.e. the intensity of the disturbance). Increased tumbling resulted in increased departure from stone surfaces, indicating that benthic macroinvertebrates responded to some measure of the stability of their habitat. Although some taxa showed a consistent response to the same levels of disturbance, others showed a variable response, indicating that a combination of factors influences the characteristics of resistance and resilience.

In most cases, recovery following overturning of individual stones was complete within twenty-four hours, indicative of the capacity of stream invertebrates for high resilience through very rapid redistribution. Recovery at the scale of individual stones is strongly influenced by the proximity of colonists in the surrounding undisturbed stream bed. It is likely that this colonising pathway assumes greater importance for recovery of small patches, while longer recovery times following stream-wide disturbance by floods probably reflects greater isolation of the colonising fauna, which relies more on drift and movement from refugial areas.

c) Do streams with contrasting hydrological regimes (i.e. low versus high frequency of natural disturbance), respond in the same way to physical disturbance? (Chapter 4)

Experimental disturbance within streams of very different hydrological regimes, indicated that sites with short inter-flood periods (i.e. a high frequency of natural disturbance) supported a fauna that was much more resistant and resilient to disturbance, but less persistent, compared with streams with a low frequency of disturbance (sampled during a time of hydrological stability). This indicates that historical pattern of disturbance may be a factor providing a strong selective force for the fauna inhabiting frequently disturbed streams.

5.2 Results in the context of general disturbance theory

The following discussion places the results in the context of theoretical expectations outlined in the general introduction (Chapter 1).

a) Disturbance, at all scales, creates patchiness in the environment; in addition, spatial heterogeneity modifies the effects of disturbance. Disturbance is the major mechanism of density-independent population reductions, through direct mortality or displacement. The removal of individuals creates opportunities for new species to colonise through the creation of new physical and niche space. This is the mechanism for generating high diversity (e.g. Reice 1994).

The present study has demonstrated that disturbance at three spatial scales – the whole stream, a stream section (riffle), and individual stones – tended to increase the patchiness of macroinvertebrates on stone surfaces. The role of disturbance in generating patchiness was reduced where resistance/resilience of the fauna was highest, in pool habitats (relative to riffles) and in streams with a high frequency of natural disturbance (PNG sites). Therefore the role of disturbance in generating patchiness and (potentially) enhancing diversity may be more pronounced where resistance and resilience are relatively low, for example in riffles (vs. pools). Although site-specific variations in factors such as light, temperature, and habitat complexity unquestionably influence local diversity, there is no doubt that the streams in the Australian Wet Tropics support particularly high richness, both when considering individual stones (this study) and more inclusive benthic habitats (Pearson *et al.* 1986).

b) Stream faunas typically show low resistance to and high resilience following disturbance (e.g. Fisher and Grimm 1991).

In agreement with other stream studies from temperate regions and limited data from the tropics (Table 5.2), the macroinvertebrate stone fauna of tropical streams appears to be remarkably resilient to physical disturbance. Resilience, when assessed in terms of restoration to pre-disturbance community parameters, was high compared with published values following substratum-moving floods. Recovery following disturbance was particularly rapid in pool habitats where the impact of disturbance may be reduced (i.e., resulting in lower mortality) and flow refugia may be more widespread (increasing local sources of colonists).

The flux between dispersal processes, such as drift, which operate over large spatial scales, and local, small-scale movements may be crucial in influencing post-disturbance recovery in these and other streams (Palmer *et al.* 1996). The results of the present study indicate that mobility of the component fauna, and their propensity to enter the drift are primary factors influencing recovery following disturbance over different spatial scales, with large-scale dispersal processes increasing in importance as the spatial scale of the disturbed area increases.

Measures of persistence, or the constancy of community structure through time, are a function of resistance and resilience, and provide an insight into how similar communities remain (i.e. are stable) in the face of environmental fluctuations and disturbance, a question of fundamental ecological interest. Absolute persistence (species composition and relative abundance), assessed over ~3.5 years at Birthday Creek, was high despite severe flood disturbance during the wet season, supporting the conclusion of Hildrew and Giller (1994) that in the medium term (2 – 10 years) at least, stream communities appear to be highly persistent. Relative persistence (i.e. among streams) however, appears to be influenced by the degree of environmental variation, with the increased temporal variability in flow (i.e. high disturbance frequency) reducing community persistence when compared with fauna subject to a low frequency of disturbance which had relatively high persistence.

Table 5.2 Macroinvertebrate responses to disturbance: a global comparison. Resistance is given as the percentage remaining of overall macroinvertebrate abundance/density following disturbance. Resilience is measured as the time taken to pre-disturbance characteristics (given in the corresponding reference). Where specific values for resistance and resilience are not available, the descriptors "low, moderate, or high" are used.

Location	Stream type	Disturbance	Spatial scale	Resistance (low/high or % remaining)	Resilience (low/high or time in days)	Reference
Temperate						
New Zealand	lowland, braided	Flood	stream	low	132	Scrimgeour *et al.* 1988
USA	headwater	Flood	stream	28 – 34	42	Angradi 1997
USA	desert	Flood	stream	2	7–14	Grimm and Fisher 1989
USA	prairie	Flood	stream	< 10	67–94	Miller and Golladay 1996
Mexico	upland	Flood	stream	6	365	Molles 1985
Australia	intermittent	Flood	stream	low	14	Boulton and Lake 1992b
Switzerland	prealpine	experimental	≈ 9 m^2	13 – 17	3–30	Matthaei *et al.* 1996
Australia	upland, rocky	experimental	1 m^2	low	8–71	Doeg *et al.* 1989b
Australia	upland, rocky	experimental	2–4 m^2	low	7–21+	Marchant *et al.* 1991
Tropics						
Venezuela	upland, piedmont	Flood	stream	low	high	Flecker and Feifarek 1994
Australia	upland, rocky	experimental	0.08 m^2	low	high	Rosser and Pearson 1995
Australia (Birthday Creek)	upland, rocky					This study
riffle		Flood	stream	low[a]	≤ 40-45	
pool		Flood	stream	moderate[a]	≤ 6-21	
Australia (Birthday Creek)	upland rocky					This study
riffle		experimental	56 m^2	63.2 – 68.8	2–4	
PNG (Tam Creek)	lowland, rocky					This study
riffle		experimental	68 m^2	56 – 122	2–4	
PNG (Creek 115)	lowland, rocky					This study
riffle		experimental	60 m^2	35 – 85	4	

a = predicted resistance, as fauna could not be sampled immediately post-flood.

Similarly, increased temporal variability in stream flow (Meffe and Minckley 1987) and decreased habitat stability (Wallace *et al.* 1988, Weatherly and Ormerod 1990) have previously been shown to reduce macroinvertebrate community persistence.

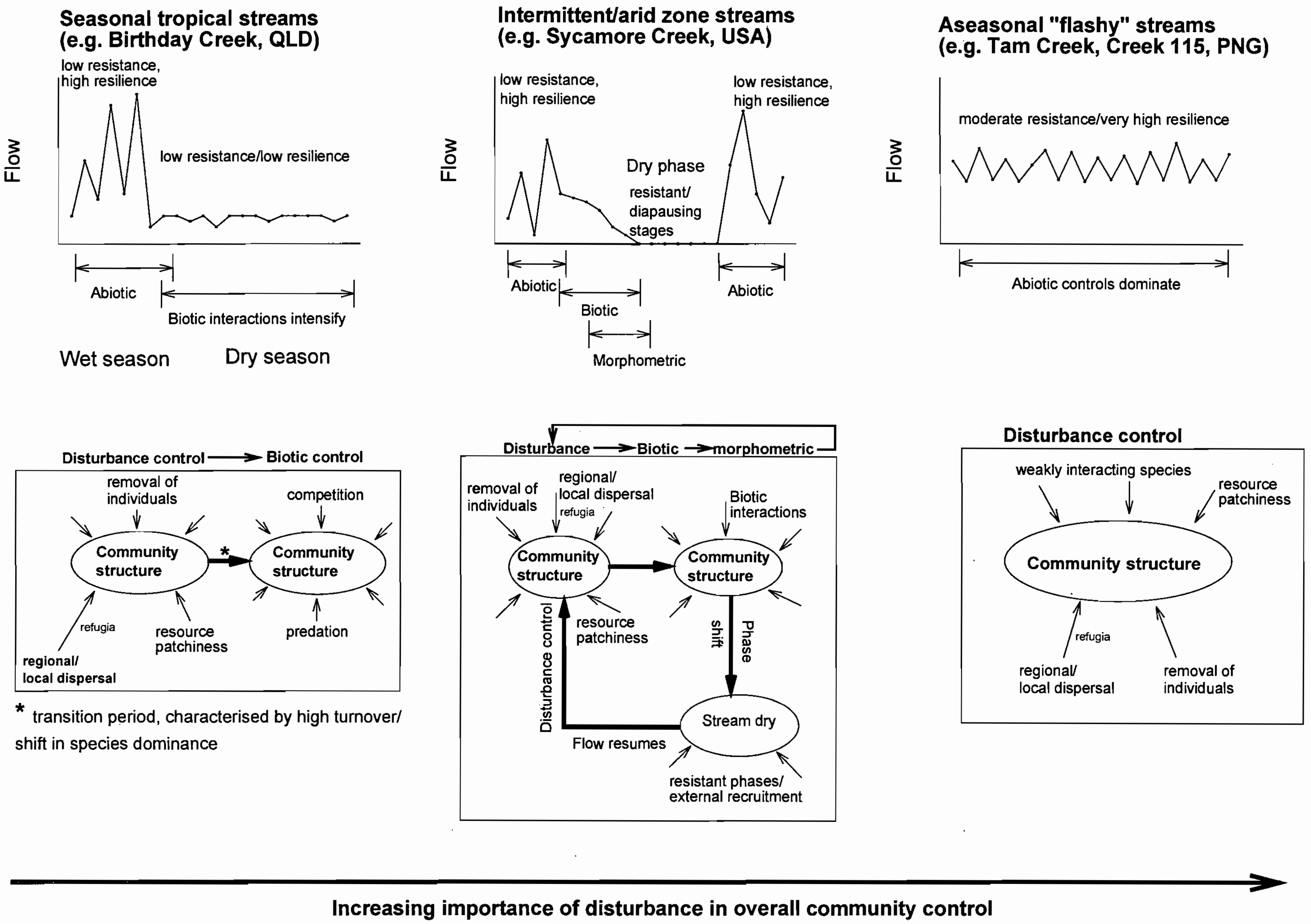
c) Disturbance maintains systems in non-equilibrial states, with the normal state of communities and ecosystems to be recovering from disturbance (e.g. Lake 1995). *Where the interval between disturbance is long relative to the generation time of the component fauna, biotic interactions may become more important* (e.g. Flecker and Fiefarek 1994).

No evidence was found to support the contention that colonisation of bare stones, or those patchily affected by disturbance, follow the predictions of equilibrial models. The underlying assumption of asymptotic densities did not appear for any length of time on stream stones: instead, the number of individuals fluctuated considerably over short temporal scales and seasonally. This pattern has also been found for stream stones in temperate Australia (Lake *et al.* 1985a). Stream stones are characterised by highly dynamic communities, with high rates of turnover, and fluctuating diversity and structure, and this underscores the inappropriateness of equilibrial models to streams at this scale.

However, stream communities may show different patterns of temporal shifts between abiotic and biotic controls depending on their disturbance (flow) regime (Figure 5.2). This figure suggests placement of stream "types" in the present study (i.e. seasonal streams of the Australian Wet Tropics, and aseasonal PNG streams), as well as intermittent streams (e.g. desert streams in the U.S.A., Boulton *et al.* 1992) in the context of increasing importance of disturbance.

It is suggested that disturbance will be the overriding factor influencing communities in Papua New Guinea, as frequent disturbance by floods (i.e. multi-annual) will limit interactions between species. Time since last disturbance is probably the best predictor of current state community variables in these streams, which may be the case for many streams where the frequency of natural disturbance is high (see model proposed by Fisher and Grimm 1991), for example in New Zealand (Scarsbrook and Townsend 1993) or on Bouganville Island (Yule and Pearson 1996).

Figure 5.2 Conceptual model placing the streams in the present study along a gradient where disturbance controls of community structure and function become increasingly important.


Seasonal tropical streams
(e.g. Birthday Creek, QLD)
low resistance,
high resilience
low resistance/low resilience
Flow
Abiotic
Biotic interactions intensify
Wet season
Dry season
Intermittent/arid zone streams
(e.g. Sycamore Creek, USA)
low resistance,
high resilience
Dry phase
resistant/
diapausing
stages
low resistance,
high resilience
Flow
Abiotic
Biotic
Morphometric
Abiotic
Aseasonal "flashy" streams
(e.g. Tam Creek, Creek 115, PNG)
moderate resistance/very high resilience
Flow
Abiotic controls dominate
Disturbance control ⟶ Biotic control
removal of
individuals
competition
Community
structure
*
Community
structure
refugia
resource
patchiness
predation
regional/
local dispersal
* transition period, characterised by high turnover/
shift in species dominance
Disturbance ⟶ Biotic ⟶ morphometric
removal of
individuals
regional/
local dispersal
refugia
Biotic
interactions
Community
structure
Community
structure
resource
patchiness
Disturbance control
shift
Phase
Stream dry
Flow resumes
resistant phases/
external recruitment
Disturbance control
weakly interacting species
resource
patchiness
Community structure
refugia
regional/
local dispersal
removal of
individuals
Increasing importance of disturbance in overall community control

Intermittent streams, such as those in arid zones in Australia and the USA, undergo complex shifts between disturbance, biotic and morphometric controls of community structure (e.g. Fisher and Grimm 1991). Biotic interactions and physical constraints intensify as habitat area is reduced, with dramatic changes in community structure as the stream dries (Boulton *et al.* 1992, Miller and Golladay 1996). In these streams, those species with resistant stages (e.g. diapausing eggs) or effective mechanisms of external recruitment (e.g. adult flight) are most likely to persist (Gray 1981).

In seasonal streams which are perennial (e.g. many of those of the Australian Wet Tropics), there is a similar shift in control by abiotic and biotic factors. In Birthday Creek, community structure is clearly dominated by the severe and unpredictable flow disturbances during the summer wet season and these disturbances are likely to preclude strong interspecific interactions. Instead, the community is composed of weakly interactive species, most common of which is the poor competitor, *Simulium* sp., a species which only reaches very high densities on stones when flow disturbance has reduced the densities of other species, creating favourable filtering sites. Dispersal mechanisms (with large-scale processes increasing in importance as the magnitude of disturbance increases) and recolonisation from refugia are important determinants of community structure during the high and variable flows of the summer wet season.

Many of the macroinvertebrates in Birthday Creek (and in the tropics in general) have short generation times, and given that interflood periods are relatively long in seasonal streams (approximately annual), there is ample opportunity for the development of biotic interactions during the dry season. In the absence of very large substratum-moving floods (e.g. during the 1992 failed wet season in the present study) interspecific interactions may intensify – suggested by the particularly high variability in species diversity and community structure in drier compared with wetter years.

In summary then, it is suggested that stochastic controls of the benthic community predominate in Birthday Creek during the wet season when floods prevent strong biotic interactions, while deterministic controls are likely to become more prevalent during the dry season when physical disturbance is rare/absent. This is likely to be the pattern common to seasonal tropical streams in Australia (Pearson *et al.* 1986, Outridge 1988, Hearnden and

Pearson 1991) and the combination of abiotic controls in the wet season, coupled with the long evolutionary history of Wet Tropics streams (Pusey and Pearson, *in press*) may provide the basis for the observed high diversity. In contrast, the disturbance regime in aseasonal Papua New Guinea streams, where frequent disturbance by floods occurs, likely precludes the macroinvertebrate communities from strong deterministic controls and stochastic models seem most applicable.

5.3 Relevance to applied research

Streams reflect catchment processes through responses by the fauna and therefore can represent a useful tool for rapid catchment assessment and monitoring (Norris and Norris 1995, Wright 1995). Quantifying the response of stream fauna to natural disturbance is a necessary prerequisite to the detection of anthropogenic impacts. This study of tropical rainforest streams identifies those taxa which are indicative of disturbed conditions and when the benthic community is most able to recover rapidly following disturbance. However, it also provides a caution to the indiscriminate use of macroinvertebrates as a monitoring tool. Clearly, the fauna and its response to disturbance is closely linked to the characteristics of each stream, so models for monitoring purposes need to accommodate hydrological and other (e.g. habitat-related) site-specific variables.

5.4 Future research

Although this study clearly demonstrates that substratum movement is an important agent of disturbance and plays a major role in community dynamics, further work is required to fully elucidate the mechanisms by which benthic macroinvertebrates persist in these tropical streams.

It is suggested that as a priority, future research investigating the role of disturbance in these streams should be directed towards the following areas:

a) Comprehensive measurement of the forces required and the conditions under which substratum particles (covering the naturally occurring size range) are mobilised by high discharge events. This is currently receiving some attention in these streams (A. Pomeroy, unpublished data). This will not only provide a more detailed picture of the natural disturbance regime (e.g. frequency), but will also assist in the identification of habitat areas which may function as flow refugia (e.g. higher stability) under particular flow conditions.

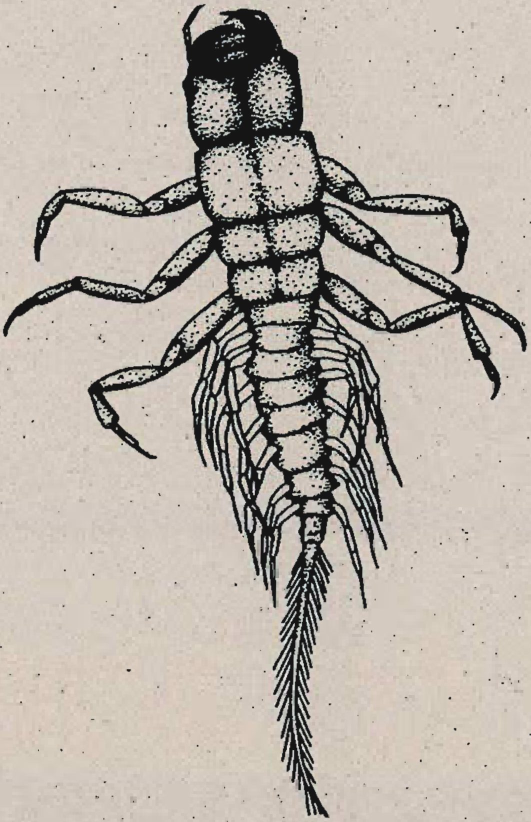
b) Expanding on this, the identification of areas (in addition to stable substrata) where the impacts of disturbance are reduced (refugia), the conditions under which they operate, their use by macroinvertebrates, and the importance of these areas in the subsequent recovery process is required.

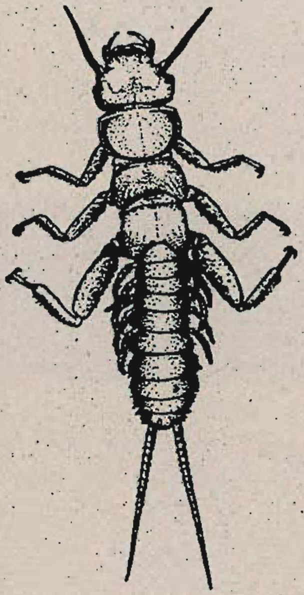
c) While it is clear that, during the dry season at Birthday Creek, resistance and resilience of macroinvertebrates was relatively low compared with the faunal response to disturbance in frequently disturbed streams (PNG), these results must be viewed in a seasonal context. Further work, comparing response during the north Queensland wet season to both natural and experimental disturbance is necessary, as the results of this study have shown that although resistance is low (reflecting the severity of the flood disturbance) resilience is very high. Therefore the distinction between the response to disturbance is likely to be less pronounced at this time of year. As well as examining streams during different seasons, incorporating more streams, across a range of types, would broaden the context of the results.

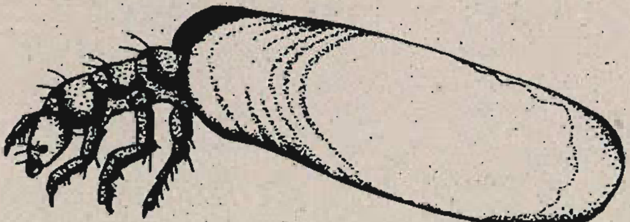
d) Finally, the relative importance of biotic interactions as a determinant of community structure and the interaction with disturbance requires further attention, as the results of this study and others suggest that: i) factors such as predation and competition may at times be important (Hearnden and Pearson 1991, Cheshire 1997), and ii) abiotic and biotic controls may change seasonally and within different habitats (e.g. Pearson *et al* 1986, Hearnden and Pearson 1991).

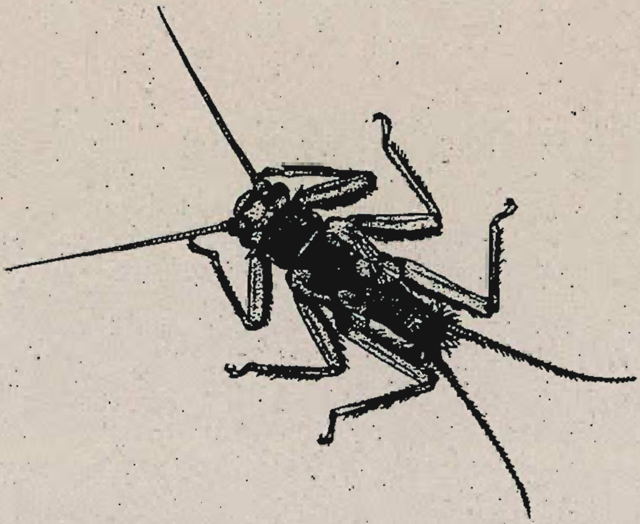
5.5 Concluding remarks

Physical disturbance of the substratum is clearly an important factor influencing benthic community structure in tropical rainforest streams. However, the faunal response to disturbance is influenced by the magnitude and frequency (i.e. spatial and temporal axes) of the disturbance itself and by intrinsic features of the habitat. Further studies within streams at different positions along the continuum of disturbance (defined by the magnitude and frequency), as well as *incorporating* rather than *controlling for* site specific variability (heterogeneity) are required before comprehensive predictive models relating disturbance and stream ecosystem dynamics can be developed.









Macroinvertebrates of the Wet Tropics

Artists: Andi Cairns & Linda Davis

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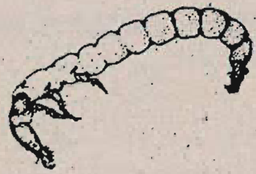

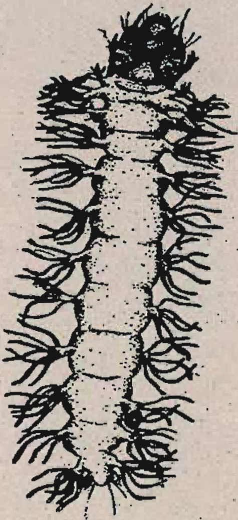

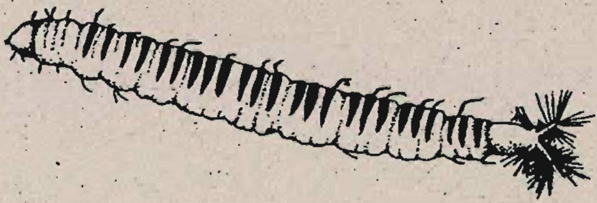

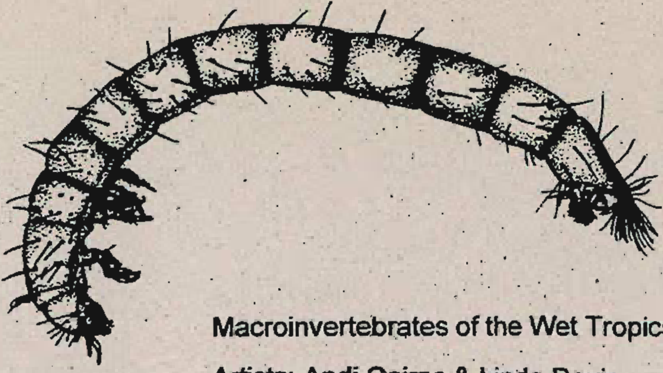

Macroinvertebrates of the Wet Tropics

Artists: Andi Cairns & Linda Davis

APPENDIX 1

The following ANOVA tables are the output from the SPSS™ statistical package. Tables numbers reflect the chapter they correspond to.

Table A3.1 (Corresponds to Chapter 3, Figure 3.10)

The effect of disturbance frequency on macroinvertebrate riffle fauna

a) Within times (i.e. D1 – D5)

D1: Results of one-way ANOVA for **abundance** (dependent variable) by disturbance treatment (grouping variable). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
Between groups	3	10475.2	3491.75	22.13	0.0000 (***)
Within groups	28	4418.25	157.794		
Total	31	14893.5			

D2: Results of one-way ANOVA for **abundance** (dependent variable) by disturbance treatment (grouping variable). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
Between groups	3	27282.6	9094.2	10.54	0.0001 (***)
Within groups	28	24151.2	862.544		
Total	31	51433.8			

D3: Results of one-way ANOVA for **abundance** (dependent variable) by disturbance treatment (grouping variable). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
Between groups	3	16382.5	5460.86	22.08	0.0000 (***)
Within groups	28	6924.62	247.308		
Total	31	23307.2			

D4: Results of one-way ANOVA for **abundance** (dependent variable) by disturbance treatment (grouping variable). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
Between groups	3	8123.59	2707.86	8.42	0.0004 (***)
Within groups	28	9002.37	321.513		
Total	31	17125.9			

D5: Results of one-way ANOVA for **abundance** (dependent variable) by disturbance treatment (grouping variable). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
Between groups	3	76591.0	25530.3	9.71	0.0001 (***)
Within groups	28	73622.3	2629.37		
Total	31	150200.0			

D1: Results of one-way ANOVA for **richness** (dependent variable) by disturbance treatment (grouping variable). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
Between groups	3	111.25	37.08	7.71	0.0007 (***)
Within groups	28	134.75	4.81		
Total	31	246.0			

D2: Results of one-way ANOVA for **richness** (dependent variable) by disturbance treatment (grouping variable). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
Between groups	3	351.63	117.21	25.79	0.0000 (***)
Within groups	28	127.25	4.54		
Total	31	478.88			

D3: Results of one-way ANOVA for **richness** (dependent variable) by disturbance treatment (grouping variable). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
Between groups	3	265.09	88.36	17.78	0.0000 (***)
Within groups	28	139.13	4.97		
Total	31	404.22			

D4: Results of one-way ANOVA for **richness** (dependent variable) by disturbance treatment (grouping variable). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
Between groups	3	156.84	52.28	10.04	0.0001 (***)
Within groups	28	145.88	5.21		
Total	31	302.72			

D5: Results of one-way ANOVA for **richness** (dependent variable) by disturbance treatment (grouping variable). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
Between groups	3	338.25	112.75	20.53	0.0000 (***)
Within groups	28	153.75	5.49		
Total	31	492.00			

The effect of disturbance frequency on macroinvertebrate pool fauna

D3: Results of one-way ANOVA for **abundance** (dependent variable) by disturbance treatment (grouping variable). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
Between groups	3	1502.50	500.833	16.70	0.0000 (***)
Within groups	28	839.50	29.98		
Total	31	2342.00			

D5: Results of one-way ANOVA for **abundance** (dependent variable) by disturbance treatment (grouping variable). α = 0.05 (n.s. = non-significant, * = p ≤ 0.05, ** = p ≤ 0.01, *** = p ≤ 0.001).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
Between groups	3	295.75	98.58	5.08	0.0062 (**)
Within groups	28	543.75	19.42		
Total	31	839.50			

D3: Results of one-way ANOVA for **richness** (dependent variable) by disturbance treatment (grouping variable). α = 0.05 (n.s. = non-significant, * = p ≤ 0.05, ** = p ≤ 0.01, *** = p ≤ 0.001).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
Between groups	3	65.38	21.79	10.80	0.0001 (***)
Within groups	28	56.50	2.02		
Total	31	121.88			

D5: Results of one-way ANOVA for **richness** (dependent variable) by disturbance treatment (grouping variable). α = 0.05 (n.s. = non-significant, * = p ≤ 0.05, ** = p ≤ 0.01, *** = p ≤ 0.001).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
Between groups	3	6.09	2.03	0.62	0.61 (n.s.)
Within groups	28	92.38	3.30		
Total	31	98.47			

<u>**Table A3.2**</u> (Corresponds to Chapter 3, Table 3.8)

The effect of disturbance frequency on macroinvertebrate riffle fauna

b) Treatment x Time

1) Results of two-way ANOVA for **total abundance** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = p ≤ 0.05, ** = p ≤ 0.01, *** = p ≤ 0.001).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	1.073	0.268	11.388	0.000 (***)
TREATMENT	3	7.678	2.559	108.697	0.000 (***)
TIME X TREAT.	12	0.744	0.062	2.635	0.003 (**)
Residual	140	3.296	0.024		
Total	159	12.792	0.080		

2) Results of two-way ANOVA for **total richness** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = p ≤ 0.05, ** = p ≤ 0.01, *** = p ≤ 0.001).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	0.508	0.127	14.779	0.000 (***)
TREATMENT	3	0.697	0.232	27.028	0.00 (**)
TIME X TREAT.	12	0.933	0.078	9.040	0.00 (**)
Residual	140	1.204	0.009		
Total	159	3.342	0.021		

3) Results of two-way ANOVA for ***Baetis* sp. 1** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = p ≤ 0.05, ** = p ≤ 0.01, *** = p ≤ 0.001).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	1.167	0.292	5.168	0.001 (***)
TREATMENT	3	0.668	0.223	3.946	0.010 (**)
TIME X TREAT.	12	1.081	0.090	1.596	0.099 (n.s.)
Residual	140	7.901	0.056		
Total	159	10.816	0.068		

4) Results of two-way ANOVA for ***Austrophlebioides* sp. 1** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = p ≤ 0.05, ** = p ≤ 0.01, *** = p ≤ 0.001).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	4.409	1.102	14.067	0.000 (***)
TREATMENT	3	5.547	1.849	23.597	0.00 (**)
TIME X TREAT.	12	1.231	0.103	1.309	0.220 (n.s.)
Residual	140	10.970	0.078		
Total	159	22.157	0.139		

5) Results of two-way ANOVA for ***Simulium* sp.** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = p ≤ 0.05, ** = p ≤ 0.01, *** = p ≤ 0.001).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	11.694	2.923	17.644	0.00 (**)
TREATMENT	3	1.252	0.417	2.519	0.061 (n.s.)
TIME X TREAT.	12	2.252	0.188	1.133	0.339 (n.s.)
Residual	140	23.197	0.166		
Total	159	38.395	0.241		

6) Results of two-way ANOVA for **Hydroptilidae sp. 1a** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \le 0.05$, ** = $p \le 0.01$, *** = $p \le 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	6.379	1.595	18.440	0.00 (**)
TREATMENT	3	6.239	2.080	24.050	0.00 (**)
TIME X TREAT.	12	1.208	0.101	1.164	0.315 (n.s.)
Residual	140	12.107	0.086		
Total	159	25.933	0.163		

7) Results of two-way ANOVA for **Chironomidae** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \le 0.05$, ** = $p \le 0.01$, *** = $p \le 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	4.788	1.197	24.765	0.00 (**)
TREATMENT	3	9.276	3.092	63.964	0.000 (***)
TIME X TREAT.	12	1.253	0.104	2.160	0.017 (*)
Residual	140	6.767	0.806		
Total	159	22.084	0.139		

8) Results of two-way ANOVA for ***Helicopsyche* sp.** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \le 0.05$, ** = $p \le 0.01$, *** = $p \le 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	2.773	0.693	9.900	0.000 (***)
TREATMENT	3	5.603	1.868	26.667	0.00 (**)
TIME X TREAT.	12	1.912	0.159	2.275	0.011 (*)
Residual	140	9.805	0.070		
Total	159	20.093	0.126		

9) Results of two-way ANOVA for ***Oecetis* sp. 1** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \le 0.05$, ** = $p \le 0.01$, *** = $p \le 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	3.612	0.903	14.188	0.000 (***)
TREATMENT	3	3.565	1.188	18.671	0.000 (***)
TIME X TREAT.	12	2.373	0.198	3.107	0.001 (***)
Residual	140	8.910	0.503		
Total	159	18.459	0.116		

10) Results of two-way ANOVA for ***Nyctiophylax* sp.** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	1.518	0.380	6.838	0.000 (***)
TREATMENT	3	3.063	1.021	18.394	0.000 (***)
TIME X TREAT.	12	1.785	0.149	2.679	0.003 (**)
Residual	140	7.771	0.056		
Total	159	14.136	0.089		

The effect of disturbance frequency on macroinvertebrate pool fauna

1) Results of two-way ANOVA for **total abundance** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	1	0.852	0.852	24.250	0.000 (***)
TREATMENT	3	1.773	0.591	16.824	0.000 (***)
TIME X TREAT.	3	0.140	0.047	1.324	0.276 (n.s.)
Residual	56	1.967	0.035		
Total	63	4.731	0.075		

2) Results of two-way ANOVA for **total richness** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	1	0.060	0.060	2.940	0.092 (n.s.)
TREATMENT	3	0.294	0.098	4.766	0.005 (**)
TIME X TREAT.	3	0.200	0.067	3.244	0.029 (*)
Residual	56	1.152	0.021		
Total	63	1.707	0.027		

3) Results of two-way ANOVA for ***Austrophlebioides* sp. 1** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	1	0.726	0.726	16.197	0.000 (***)
TREATMENT	3	0.186	0.062	1.383	1.383 (n.s.)
TIME X TREAT.	3	0.056	0.019	0.419	0.740 (n.s.)
Residual	56	2.510	0.045		
Total	63	3.479	0.055		

4) Results of two-way ANOVA for **Chironomidae** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	1	1.777	0.060	2.940	0.092 (n.s.)
TREATMENT	3	2.491	0.098	4.766	0.005 (**)
TIME X TREAT.	3	0.200	0.067	3.244	0.029 (*)
Residual	56	1.152	0.021		
Total	63	1.707	0.027		

APPENDIX 2

Table A4.1

Macroinvertebrate taxa recorded from stone samples at Tam Creek (TC), Birthday Creek (BC), and Creek 115 (115), and their allocation to functional feeding groups. Samples collected in 1993 and 1994 from Tam Creek are pooled. Cscr = collector-scraper, Cg = collector-gatherer, Cf = collector-filterer, Pred = predator, n.f. = non-feeding stage; (a) = adult, (l) = larva.

Taxa	Sites Recorded			Functional Feeding Group
	TC	BC	115	
Insect orders:				
Ephemeroptera				
Atalomicria sp.		X		Cg
Atalophlebia sp. 1		X		Cg
Atalophlebia sp. 2	X		X	Cg
Austrophlebioides sp. 1		X		Cg
Austrophlebioides sp. 2		X		Cg
Baetis sp.		X		Cscr
Baetis sp. 1	X		X	Cscr
Baetis sp. 2	X		X	Cscr
Baetis sp. 3	X		X	Cscr
Tasmanocoenis sp. 1	X	X	X	Cg
Tasmanocoenis sp. 2	X		X	Cg
Nousia sp. 1		X		Cscr
Nousia sp. 2		X		Cscr
Plecoptera				
Dinotoperla sp.		X		Cscr
Illiesoperla sp.		X		Cg
Odonata				
Diphlebia sp.		X		Pred
Nannophlebia sp.	X		X	Pred
Gomphidae sp.		X		Pred
Trichoptera				
Oecetis sp. 1		X	X	Pred
Oecetis sp. 2		X		Pred
Oecetis sp. 3	X			Pred
Nyctiophylax sp. 1		X		Pred
Nyctiophylax sp. 3	X		X	Pred
Agapetus sp.		X		Cscr
Agapetus sp. 1			X	Cscr
Agapetus sp. 2			X	Cscr
?*Cheumatopsyche* sp.	X			Cf
Cheumatopsyche sp. 1		X		Cf
Cheumatopsyche sp. 2	X		X	Cf
Cheumatopsyche sp. 3			X	Cf
Chimarra sp. 1		X		Pred
Chimarra sp. 2			X	Pred
Hydroptilidae (early instars)	X	X	X	Cscr
Hydroptilidae sp. 1	X	X	X	Cscr
Hydroptilidae sp. 1a		X		Cscr
Hydroptilidae sp. 1d			X	Cscr
Hydroptilidae sp. 1e			X	Cscr
Hydroptilidae sp. 3	X		X	Cscr
Hydroptilidae sp.5			X	Cscr
Hydroptilidae sp.6	X			Cscr

Table A4.1 continued.

Taxa	Sites Recorded			Functional Feeding Group
	TC	BC	115	
Hydroptilidae sp.7	X			Cscr
Hydroptilidae sp.8	X			Cscr
Diptera				
Chironomidae spp.	X	X	X	Cg / Cf / Pred
Simuliidae spp.	X		X	Cf
Simulium sp.		X		Cf
Empididae sp.	X	X	X	Cg
Culicoides sp.		X		Pred
Atrichopogon sp.	X			Cscr
Sciomyzidae sp. 1		X		Pred
Tipuliidae sp. 3	X	X		Pred
Coleoptera				
Simsonia sp.		X		Cscr
Austrolimnius (a) sp. 1	X	X		Cscr
Austrolimnius (a) sp.4		X		Cscr
Coleoptera (a) sp. 1	X			Cscr
Coleoptera (a) sp. 2	X		X	Cscr
Coleoptera (a) sp. 3	X			Cscr
Coleoptera (a) sp.4	X			Cscr
Coleoptera (a) sp.5	X		X	Cscr
Helminthidae (l) sp. 1		X		Cscr
Helminthidae (l) sp. 2	X	X	X	Cscr
Kingolus sp.		X		Cscr
Kingolus sp.c			X	Cscr
Helminthidae (l) sp. 14	X		X	Cscr
Psephenidae sp. 1		X		Cscr
Psephenidae sp. 2	X		X	Cscr
Psephenidae sp. 3	X		X	Cscr
Hemiptera				
Hemiptera sp. 1	X		X	Pred
Hemiptera sp. 2	X		X	Pred
Gerridae sp. 1		X		Pred
Lepidoptera				
Lepidoptera sp. 1	X	X	X	Cscr
Lepidoptera sp. 2	X			Cscr
Lepidoptera sp. 3	X		X	Cscr
Lepidoptera sp.4	X			Cscr
Lepidoptera sp.5	X			Cscr
Non-insect orders:				
Hydracarina	X	X	X	Pred
Oligochaeta	X	X		Cg
Turbellaria				
Dugesia sp. 1	X	X		Pred
Nematomorpha				
Nematomorpha sp. 1	X		X	n.f.
Nematomorpha sp. 2	X		X	n.f.
Gastropoda				
Gastropoda sp. 1	X		X	Cscr
Gastropoda sp. 2	X			Cscr
Gastropoda sp. 3	X			Cscr
Gastropoda sp.4	X		X	Cscr
Gastropoda sp.5			X	Cscr

Table A4.2

Effect of experimental disturbance

1) **Tam Creek** **(1993)** Results of two-way ANOVA for **total abundance** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = p ≤ 0.05, ** = p ≤ 0.01, *** = p ≤ 0.001).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	6.808	1.702	5.270	0.001 (***)
TREATMENT	1	0.819	0.819	2.535	0.116 (n.s.)
TIME X TREAT.	4	10.560	2.640	8.174	0.000 (***)
Residual	70	22.606	0.323		
Total	79	40.792	0.516		

2) **Tam Creek** **(1993)** Results of two-way ANOVA for **total richness** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = p ≤ 0.05, ** = p ≤ 0.01, *** = p ≤ 0.001).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	1.945	0.486	7.393	0.000 (***)
TREATMENT	1	0.005	0.005	0.083	0.774 (n.s.)
TIME X TREAT.	4	1.720	0.430	6.535	0.000 (***)
Residual	70	4.604	0.066		
Total	79	8.275	0.105		

3) **Tam Creek** **(1993)** Results of two-way ANOVA for ***Baetis* sp. 2** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = p ≤ 0.05, ** = p ≤ 0.01, *** = p ≤ 0.001).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	1.773	0.443	3.142	0.020 (*)
TREATMENT	1	0.343	0.343	2.435	0.123 (n.s.)
TIME X TREAT.	4	2.625	0.656	4.652	0.002 (**)
Residual	70	9.875	0.141		
Total	79	14.616	0.185		

4) **Tam Creek** **(1993)** Results of two-way ANOVA for ***Baetis* sp. 3** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = p ≤ 0.05, ** = p ≤ 0.01, *** = p ≤ 0.001).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	6.681	1.670	4.360	0.003 (**)
TREATMENT	1	4.013	4.013	10.475	0.002 (**)
TIME X TREAT.	4	9.083	2.271	5.927	0.000 (***)
Residual	70	26.82	0.383		
Total	79	46.597	0.590		

5) Tam Creek (1993) Results of two-way ANOVA for ***Tasmanocoenis* sp. 1** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	0.567	0.142	2.544	0.047 (*)
TREATMENT	1	0.066	0.066	1.185	0.280 (n.s.)
TIME X TREAT.	4	0.466	0.117	2.091	0.091 (n.s.)
Residual	70	3.902	0.056		
Total	79	5.002	0.063		

6) Tam Creek (1993) Results of two-way ANOVA for **Chironomidae** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	7.597	1.899	8.486	0.000 (***)
TREATMENT	1	0.074	0.074	0.330	0.567 (n.s.)
TIME X TREAT.	4	4.331	1.083	4.838	0.002 (**)
Residual	70	15.665	0.224		
Total	79	27.667	0.350		

7) Tam Creek (1993) Results of two-way ANOVA for **Simuliidae** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	1.368	0.342	3.141	0.020 (*)
TREATMENT	1	0.009	0.0.009	0.087	0.769 (n.s.)
TIME X TREAT.	4	0.703	0.176	1.614	0.180 (n.s.)
Residual	70	7.621	0.109		
Total	79	9.701	0.123		

8) Tam Creek (1993) Results of two-way ANOVA for **Tipulidae sp. 3** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	1.350	0.338	3.124	0.020 (*)
TREATMENT	1	0.215	0.215	1.987	0.163 (n.s.)
TIME X TREAT.	4	2.242	0.561	5.188	0.001 (***)
Residual	70	7.564	0.108		
Total	79	11.371	0.144		

9) <u>Tam Creek</u> (1993) Results of two-way ANOVA for ***Cheumatopsyche* sp. 1** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	**d.f.**	**Sum of squares**	**Mean squares**	**F-ratio**	**P**
TIME	4	1.128	0.282	1.385	0.248 (n.s.)
TREATMENT	1	0.319	0.319	1.565	0.215 (n.s.)
TIME X TREAT.	4	1.910	0.478	2.345	0.063 (n.s.)
Residual	70	14.253	0.204		
Total	79	17.610	0.223		

10) <u>Tam Creek</u> (1993) Results of two-way ANOVA for ***Cheumatopsyche* sp. 2** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	**d.f.**	**Sum of squares**	**Mean squares**	**F-ratio**	**P**
TIME	4	0.942	0.236	7.395	0.000 (***)
TREATMENT	1	0.714	0.714	22.414	0.000 (***)
TIME X TREAT.	4	0.942	0.236	7.395	0.000 (***)
Residual	70	2.230	0.032		
Total	79	4.828	0.061		

11) <u>Tam Creek</u> (1993) Results of two-way ANOVA for **Lepidoptera sp. 2** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	**d.f.**	**Sum of squares**	**Mean squares**	**F-ratio**	**P**
TIME	4	2.415	0.604	13.695	0.000 (***)
TREATMENT	1	0.026	0.026	0.597	0.442 (n.s.)
TIME X TREAT.	4	0.245	0.061	1.390	0.246 (n.s.)
Residual	70	3.086	0.044		
Total	79	5.773	0.073		

12) <u>Tam Creek</u> (1993) Results of two-way ANOVA for **Oligochaeta** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	**d.f.**	**Sum of squares**	**Mean squares**	**F-ratio**	**P**
TIME	4	1.534	0.383	5.635	0.001 (***)
TREATMENT	1	0.082	0.082	1.211	0.275 (n.s.)
TIME X TREAT.	4	2.384	0.596	8.758	0.000 (***)
Residual	70	4.764	0.068		
Total	79	8.765	0.111		

13) Birthday Creek (1993) Results of two-way ANOVA for **total abundance** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	**d.f.**	**Sum of squares**	**Mean squares**	**F-ratio**	**P**
TIME	5	0.222	0.056	2.429	0.056 (n.s.)
TREATMENT	4	0.258	0.258	0.258	0.001 (***)
TIME X TREAT.	4	0.081	0.020	0.884	0.478 (n.s.)
Residual	70	1.601	0.023		
Total	79	2.162	0.027		

14) Birthday Creek (1993) Results of two-way ANOVA for **total richness** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	**d.f.**	**Sum of squares**	**Mean squares**	**F-ratio**	**P**
TIME	4	0.048	0.021	2.106	0.089 (n.s.)
TREATMENT	1	0.287	0.287	50.191	0.000 (***)
TIME X TREAT.	4	0.086	0.022	3.770	0.008 (**)
Residual	70	0.400	0.006		
Total	79	0.821	0.010		

15) Birthday Creek (1993) Results of two-way ANOVA for ***Baetis* sp.** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	**d.f.**	**Sum of squares**	**Mean squares**	**F-ratio**	**P**
TIME	4	0.839	0.210	2.046	0.097 (n.s.)
TREATMENT	1	2.147	2.147	20.946	0.000 (***)
TIME X TREAT.	4	0.247	0.062	0.602	0.662 (n.s.)
Residual	70	7.175	0.102		
Total	79	10.408	0.132		

16) Birthday Creek (1993) Results of two-way ANOVA for ***Dinotoperla* sp.** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	**d.f.**	**Sum of squares**	**Mean squares**	**F-ratio**	**P**
TIME	4	0.513	0.128	1.094	0.366 (n.s.)
TREATMENT	1	0.211	0.211	1.800	0.184 (n.s.)
TIME X TREAT.	4	2.152	0.538	4.584	0.002 (**)
Residual	70	8.213	0.117		
Total	79	11.090	0.140		

17) **Birthday Creek** **(1993)** Results of two-way ANOVA for **Chironomidae** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	0.324	0.081	0.703	0.593 (n.s.)
TREATMENT	1	0.023	0.023	0.199	0.657 (n.s.)
TIME X TREAT.	4	0.520	0.130	1.128	0.351 (n.s.)
Residual	70	8.077	0.115		
Total	79	8.945	0.113		

18) **Birthday Creek** **(1993)** Results of two-way ANOVA for ***Simulium*** **sp.** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	1.333	0.333	1.556	0.196 (n.s.)
TREATMENT	1	0.052	0.052	0.241	0.625 (n.s.)
TIME X TREAT.	4	1.238	0.310	1.446	0.228 (n.s.)
Residual	70	14.992	0.214		
Total	79	17.615	0.223		

19) **Birthday Creek** **(1993)** Results of two-way ANOVA for **Tipulidae sp. 3** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	1.637	0.409	3.007	0.024 (*)
TREATMENT	1	0.499	0.499	3.668	0.060 (n.s.)
TIME X TREAT.	4	0.792	0.198	1.454	0.225 (n.s.)
Residual	70	9.529	0.136		
Total	79	12.457	0.158		

20) **Birthday Creek** **(1993)** Results of two-way ANOVA for ***Helicopsyche*** **sp.** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	0.545	0.136	1.970	0.109 (n.s.)
TREATMENT	1	5.179	5.179	74.947	0.000 (***)
TIME X TREAT.	4	0.840	0.210	3.037	0.023 (*)
Residual	70	4.837	0.069		
Total	79	11.401	0.144		

21) **Birthday Creek (1993)** Results of two-way ANOVA for **Hydroptilidae sp. 1a** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	0.919	0.230	1.644	0.173 (n.s.)
TREATMENT	1	0.093	0.093	0.668	0.416 (n.s.)
TIME X TREAT.	4	0.408	0.408	2.917	0.027 (*)
Residual	70	0.140	0.140		
Total	79	0.157	0.157		

22) **Birthday Creek (1993)** Results of two-way ANOVA for ***Kingolus* sp.** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	1.150	0.287	3.107	0.021 (*)
TREATMENT	1	0.007	0.007	0.077	0.782 (n.s.)
TIME X TREAT.	4	0.020	0.005	0.053	0.995 (n.s.)
Residual	70	6.475	0.093		
Total	79	7.652	0.097		

23) **Birthday Creek (1993)** Results of two-way ANOVA for ***Simsonia* sp.** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	0.960	0.240	3.193	0.018 (*)
TREATMENT	1	2.006	2.006	26.687	0.000 (***)
TIME X TREAT.	4	0.855	0.214	2.843	0.030 (*)
Residual	70	5.261	0.075		
Total	79	9.082	0.115		

24) **Birthday Creek (1993)** Results of two-way ANOVA for **Oligochaeta** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	4	1.513	0.378	2.592	0.044 (*)
TREATMENT	1	0.396	0.396	2.715	0.104 (n.s.)
TIME X TREAT.	4	1.922	0.481	3.294	0.016 (*)
Residual	70	10.212	0.146		
Total	79	14.044	0.178		

25) Tam Creek (1994) Results of two-way ANOVA for **total abundance** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	**d.f.**	**Sum of squares**	**Mean squares**	**F-ratio**	**P**
TIME	7	0.350	0.050	1.021	0.420 (n.s.)
TREATMENT	1	0.031	0.031	0.641	0.425 (n.s.)
TIME X TREAT.	7	0.599	0.086	1.749	0.105 (n.s.)
Residual	112	5.480	0.049		
Total	127	6.460	0.051		

26) Tam Creek (1994) Results of two-way ANOVA for ***Baetis* sp. 1** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	**d.f.**	**Sum of squares**	**Mean squares**	**F-ratio**	**P**
TIME	7	3.003	0.429	4.071	0.001 (***)
TREATMENT	1	0.261	0.261	2.480	0.118 (n.s.)
TIME X TREAT.	7	1.972	0.282	2.674	0.013 (*)
Residual	112	11.803	0.105		
Total	127	17.041	0.134		

27) Tam Creek (1994) Results of two-way ANOVA for ***Baetis* sp. 2** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	**d.f.**	**Sum of squares**	**Mean squares**	**F-ratio**	**P**
TIME	7	2.355	0.336	3.123	0.005 (**)
TREATMENT	1	0.411	0.411	3.812	0.053 (n.s.)
TIME X TREAT.	7	3.948	0.564	5.235	0.000 (***)
Residual	112	12.068	0.108		
Total	127	18.782	0.148		

28) Tam Creek (1994) Results of two-way ANOVA for ***Baetis* sp. 3** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	**d.f.**	**Sum of squares**	**Mean squares**	**F-ratio**	**P**
TIME	7	14.176	2.025	12.033	0.000 (***)
TREATMENT	1	1.406	1.406	8.357	0.005 (**)
TIME X TREAT.	7	7.409	1.058	6.289	0.000 (***)
Residual	112	18.850	0.168		
Total	127	41.840	0.329		

29) Tam Creek (1994) Results of two-way ANOVA for ***Tasmanocoenis* sp.** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = p ≤ 0.05, ** = p ≤ 0.01, *** = p ≤ 0.001).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	7	3.119	0.446	4.999	0.000 (***)
TREATMENT	1	1.409	1.409	15.805	0.000 (***)
TIME X TREAT.	7	0.559	0.080	0.895	0.513 (n.s.)
Residual	112	9.984	0.089		
Total	127	15.071	0.119		

30) Tam Creek (1994) Results of two-way ANOVA for ***Atalophlebia* sp.** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = p ≤ 0.05, ** = p ≤ 0.01, *** = p ≤ 0.001).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	7	2.211	0.316	4.758	0.000 (***)
TREATMENT	1	1.747	1.747	26.319	0.000 (***)
TIME X TREAT.	7	0.984	0.141	2.117	0.047 (*)
Residual	112	7.435	0.066		
Total	127	12.376	0.097		

31) Tam Creek (1994) Results of two-way ANOVA for **Chironomidae** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = p ≤ 0.05, ** = p ≤ 0.01, *** = p ≤ 0.001).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	7	2.960	0.423	5.034	0.000 (***)
TREATMENT	1	0.063	0.063	0.747	0.389 (n.s.)
TIME X TREAT.	7	1.226	0.175	2.086	0.051 (n.s.)
Residual	112	9.408	0.084		
Total	127	13.656	0.108		

32) Tam Creek (1994) Results of two-way ANOVA for ***Cheumatopsyche* sp. 1** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = p ≤ 0.05, ** = p ≤ 0.01, *** = p ≤ 0.001).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	7	2.748	0.393	3.709	0.001 (***)
TREATMENT	1	0.022	0.022	0.207	0.650 (n.s.)
TIME X TREAT.	7	1.261	0.180	1.702	0.116 (n.s.)
Residual	112	11.855	0.106		
Total	127	15.877	0.125		

33) **<u>Tam Creek</u> (1994)** Results of two-way ANOVA for **Tipulidae sp.3** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	7	1.100	0.157	1.239	0.288 (n.s.)
TREATMENT	1	1.928	1.928	15.194	0.000 (***)
TIME X TREAT.	7	0.904	0.129	1.018	0.422 (n.s.)
Residual	112	14.212	0.127		
Total	127	18.145	0.143		

34) **<u>Tam Creek</u> (1994)** Results of two-way ANOVA for **Lepidoptera sp. 1** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	7	1.007	0.144	1.551	0.157 (n.s.)
TREATMENT	1	0.149	0.149	1.608	0.207 (n.s.)
TIME X TREAT.	7	2.532	0.362	3.901	0.001 (***)
Residual	112	10.385	0.093		
Total	127	14.073	0.111		

35) **<u>Tam Creek</u> (1994)** Results of two-way ANOVA for ***Dugesia* sp.** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	7	1.165	0.166	3.901	0.001 (***)
TREATMENT	1	0.768	0.768	17.995	0.000 (***)
TIME X TREAT.	7	0.748	0.107	2.504	0.020 (*)
Residual	112	4.778	0.043		
Total	127	7.459	0.059		

36) **<u>Creek 115</u> (1994)** Results of two-way ANOVA for **total abundance** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	7	2.844	0.406	9.721	0.000 (***)
TREATMENT	1	0.411	0.411	9.830	0.002 (**)
TIME X TREAT.	7	1.700	0.243	5.811	0.000 (***)
Residual	112	4.682	0.042		
Total	127	9.637	0.076		

37) Creek 115 (1994) Results of two-way ANOVA for **total richness** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = p ≤ 0.05, ** = p ≤ 0.01, *** = p ≤ 0.001).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	7	0.189	0.027	3.175	0.004 (**)
TREATMENT	1	0.093	0.093	11.015	0.001 (***)
TIME X TREAT.	7	0.238	0.034	4.000	0.001 (***)
Residual	112	0.950	0.008		
Total	127	1.470	0.012		

38) Creek 115 (1994) Results of two-way ANOVA for ***Baetis* sp. 1** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = p ≤ 0.05, ** = p ≤ 0.01, *** = p ≤ 0.001).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	7	1.184	0.169	1.615	0.138 (n.s.)
TREATMENT	1	2.939	2.939	28.069	0.000 (***)
TIME X TREAT.	7	2.757	0.394	3.761	0.001 (***)
Residual	112	11.726	0.105		
Total	127	18.605	0.146		

39) Creek 115 (1994) Results of two-way ANOVA for ***Baetis* sp. 2** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = p ≤ 0.05, ** = p ≤ 0.01, *** = p ≤ 0.001).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	7	1.259	0.180	2.521	0.019 (*)
TREATMENT	1	0.341	0.341	4.774	0.031 (*)
TIME X TREAT.	7	1.445	0.206	2.893	0.008 (**)
Residual	112	7.988	0.071		
Total	127	11.032	0.087		

40) Creek 115 (1994) Results of two-way ANOVA for ***Baetis* sp. 3** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = p ≤ 0.05, ** = p ≤ 0.01, *** = p ≤ 0.001).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	7	2.656	0.379	2.669	0.014 (*)
TREATMENT	1	0.037	0.037	0.261	0.610 (n.s.)
TIME X TREAT.	7	2.667	0.381	2.680	0.013 (*)
Residual	112	15.923	0.142		
Total	127	21.283	0.168		

41) **Creek 115** **(1994)** Results of two-way ANOVA for ***Atalophlebia*** **sp.** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	7	1.210	0.173	1.985	0.063 (n.s.)
TREATMENT	1	0.118	0.118	1.354	0.247 (n.s.)
TIME X TREAT.	7	0.910	0.130	1.492	0.177 (n.s.)
Residual	112	9.757	0.087		
Total	127	11.995	0.094		

42) **Creek 115** **(1994)** Results of two-way ANOVA for **Chironomidae** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	7	4.260	0.609	5.276	0.000 (***)
TREATMENT	1	1.526	1.526	13.229	0.000 (***)
TIME X TREAT.	7	0.594	0.085	0.736	0.642 (n.s.)
Residual	112	12.921	0.115		
Total	127	19.302	0.152		

43) **Creek 115** **(1994)** Results of two-way ANOVA for ***Chimarra*** **sp.** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	7	0.232	0.033	0.701	0.671 (n.s.)
TREATMENT	1	0.034	0.034	0.721	0.398 (n.s.)
TIME X TREAT.	7	0.669	0.096	2.025	0.058 (n.s.)
Residual	112	5.289	0.047		
Total	127	6.224	0.049		

44) **Creek 115** **(1994)** Results of two-way ANOVA for ***Oecetis*** **sp.** (dependent variable) by disturbance treatment and time (grouping variables). $\alpha = 0.05$ (n.s. = non-significant, * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$).

Source of variation	d.f.	Sum of squares	Mean squares	F-ratio	P
TIME	7	0.237	0.034	0.516	0.821 (n.s.)
TREATMENT	1	0.323	0.323	4.909	0.029 (*)
TIME X TREAT.	7	0.693	0.099	1.507	0.172 (n.s.)
Residual	112	7.360	0.066		
Total	127	8.614	0.068		

45) **<u>Creek 115</u> (1994)** Results of two-way ANOVA for ***Nyctiophylax* sp.** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = p ≤ 0.05, ** = p ≤ 0.01, *** = p ≤ 0.001).

Source of variation	**d.f.**	**Sum of squares**	**Mean squares**	**F-ratio**	**P**
TIME	7	0.709	0.101	2.513	0.019 (*)
TREATMENT	1	0.025	0.025	0.625	0.431 (n.s.)
TIME X TREAT.	7	0.363	0.052	1.286	0.264 (n.s.)
Residual	112	4.513	0.040		
Total	127	5.610	0.044		

46) **<u>Creek 115</u> (1994)** Results of two-way ANOVA for ***Cheumatopsyche* sp. 1** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = p ≤ 0.05, ** = p ≤ 0.01, *** = p ≤ 0.001).

Source of variation	**d.f.**	**Sum of squares**	**Mean squares**	**F-ratio**	**P**
TIME	7	3.196	0.457	4.659	0.000 (***)
TREATMENT	1	0.155	0.155	1.584	0.211 (n.s.)
TIME X TREAT.	7	2.155	0.302	3.083	0.005 (**)
Residual	112	10.974	0.098		
Total	127	16.440	0.129		

47) **<u>Creek 115</u> (1994)** Results of two-way ANOVA for ***Agapetus* sp.** (dependent variable) by disturbance treatment and time (grouping variables). α = 0.05 (n.s. = non-significant, * = p ≤ 0.05, ** = p ≤ 0.01, *** = p ≤ 0.001).

Source of variation	**d.f.**	**Sum of squares**	**Mean squares**	**F-ratio**	**P**
TIME	7	3.427	0.490	3.009	0.006 (**)
TREATMENT	1	0.094	0.094	0.576	0.449 (n.s.)
TIME X TREAT.	7	5.243	0.749	4.603	0.000 (***)
Residual	112	18.225	0.163		
Total	127	26.989	0.213		

Table A4.3

Taxa which were recorded from drift samples only (not recorded from stone samples) at Tam Creek and Birthday Creek. Taxa are presented in decreasing order of abundance. (a) = adult, (l) = larvae.

Tam Creek	**Birthday Creek**
Coleoptera (a) sp. 5	*Ulmerophlebia* sp.
Hydroptilidae (l) sp. 1	Odontoceridae sp.
Tasmanocoenis sp. 3	Odonata (early instars)
Nyctiophylax sp.	Hydroptilidae (l) sp. 5a
Sciomyzidae sp.	Helminthidae (l) sp. c
Gastropoda sp. 1	Hydroptilidae (l) sp. 1c
Nannophlebia sp.	*Chorismagrion risi*
Chimarra sp.	Philorheithridae sp. 1
Cheumatopsyche sp. 3	Corduliidae sp.
Coleoptera (a) sp.4	Ecnomidae sp.
Philodactylidae sp.	Coleoptera (l) sp. 2
Lepidoptera sp.4	Coleoptera (a) sp.4
Coleoptera (a) sp. 6	*Tasmanocoenis* sp. 2
Decapoda sp.	*Jappa* sp.
Anisocentropis sp.	*Synlestes tropicus*
Hydracarina sp.	Hydroptilidae (l) sp. 7
Gordiidae sp. 2	*Neosticta* sp.
Psychodidae sp.	Helminthidae (l) sp. 14
Helodidae	*Oecetis* sp. 2
	Megaloptera sp.
	Ptilodactylidae sp.
	Gordiidae sp.
	Leptoceridae sp. 3
	Psychodidae sp.
	Lepidoptera sp. 5
	Corduliidae sp. 2
	Odontoceridae sp. 2