

1 Associations of benthic invertebrates and flow alterations in the Nymboida River, NSW.

1.1 Pressure on water resources

Worldwide, human use of freshwater is rapidly rising and river regulation is having a major influence on the flow and ecology of many rivers. Humans use 54% of the world's available runoff, and water storages such as dams hold approximately 14% of the total annual runoff (Postel *et al.*, 1996). Increases in water demands as human population and consumption increases means more dams and diversion schemes will be built. Due to regulation, many rivers are now only a fraction of their original flow and this has intensified discussions concerning the development of rivers yet protecting their biodiversity value (Postel & Carpenter, 1997; World Commission on Dams (WCD) 2000). Undoubtedly, world rivers and their associated biodiversity are going to be under increasing pressure from continuing regulation, compromising their ability to perform important ecosystem services such as protecting water quality and sustaining fisheries (Postel & Carpenter, 1997; Dudgeon *et al.*, 2006).

Australia is the driest inhabited continent, averaging only 455mm of rainfall annually (Nix, 1981). Evapotranspiration losses are high and mean annual runoff is low, yielding the world's lowest percentage of rainfall as runoff (12%; Nix, 1981) while flow variability is the highest in the world (Puckridge *et al.*, 1998). Humans have responded to this low and variable runoff by building dams and weirs to ensure a reliable supply of water for towns, agriculture, power generation and other needs. However, such river regulation is now recognised as a major cause of worsening environmental conditions in many Australian rivers and wetlands (Lake, 1995; Walker *et al.*, 1995; Puckridge *et al.*, 1998; Kingsford, 2000; Bunn & Arthington, 2002). A stark example is the demise of the regulated Murray River. Australians have constructed 3600 weirs in the Murray–Darling Basin alone. More than 95% of the water being diverted from the Murray is used for irrigation which accounts for 78% of the mean annual flow (SEAC 1996; cited in Arthington & Pusey, 2003).

There has also been a long history of regulation in the Northern Rivers region which includes the Nymboida River, a tributary of the Clarence River, the largest coastal river in New South Wales. The Nymboida Weir was installed in the 1920s and continues to regulate flows downstream for the production of hydroelectricity and security of the regional water supply. Previous to August 1997, water was extracted from the Nymboida Weir pool over distinct periods (twice daily), representing a marked difference from the natural variation of river flows. Post August 1997, pulsing flows ceased and the extraction regime was amended to provide for an interim environmental flow of 225 ML/day (95%ile flows) downstream of the Nymboida Weir.

Major changes in instream habitat and the benthic invertebrate community result from river regulation. Effects of reduced flows on the physical environment include declines in habitat condition, decreased water velocity, depth and wetted perimeter, increased sedimentation, and changes in thermal regime and water chemistry (Gore, 1977; Cowx *et al.*, 1984; Malmqvist & Englund, 1996; Rader & Belish, 1999; Wright & Symes, 1999; McIntosh *et al.*, 2002). River regulation has been associated with declines in suitable habitat and food resources which influences individual behaviour and community interactions (Suren *et al.*, 2003b; Kinzie *et al.*, 2006). Furthermore, some aquatic invertebrate extinctions have been associated with river regulation (Sheldon & Walker, 1997). Although invertebrate densities may increase or decrease in response to reduced flows (Rader & Belish, 1999; Wright & Symes, 1999; Suren *et al.*, 2003a; Dewson *et al.*, 2007a), invertebrate taxa richness commonly decreases (Englund & Malmqvist, 1996; Cazaubon & Giudicelli, 1999; Wood & Armitage, 2004) and this has potential implications for ecosystem function, food web structure, and energy transfer in regulated streams and rivers.

1.1.1 Environmental flows

Environmental flows, in principle, are one solution to the problems caused by river regulation. Environmental flows are natural releases of water predicted to supply the environment's needs (Bunn *et al.*, 1999; Arthington & Pusey, 2003). Hydrological

variation is now recognised as a primary driving force within river ecosystems (Poff *et al.*, 1997; Richter *et al.*, 1997). A balance needs to be sought between compromising human management for a reliable water supply whilst maintaining particular features of ecological value.

Current management approaches aim to create environmental flow regimes that mimic the natural variability of flows, promoting more diverse habitats. An environmental flow may include water left in or allocated for a river in the interest of the maintenance or improvement of that system (King *et al.*, 2003). It is widely accepted in the literature that the natural integrity of flowing aquatic environments relies on natural variability within the system (Poff *et al.*, 1997; Richter *et al.*, 1997). Environmental flows can potentially be as variable as natural flows both in timing, magnitude and duration, from a single annual flow through to highly variable allocations piggy-backed on top of existing flows or seasonal low flow events (Tharme, 2003).

Development of methodologies for environmental flow assessment began at the end of the 1940s, in the western United States of America. In Australia, the process only gained significant ground in the early 1970s when wilderness areas of Tasmania were threatened by large dam schemes and hydropower generation. Then, management objectives were to provide 'maximum supplies with minimum wastage of water' (Water Conservation and Irrigation Commission, 1971). As recently as the early 1990s and in concert with growing environmental concerns and the need for economic restructuring of the water Industry, Australia adopted the National Strategy for Ecologically Sustainable Development. Federal, Commonwealth, State/Territory and local governments committed to the restructuring and development of a national water reform. The Council of Australian Governments (CoAG) expectation was that implementation of water pricing, trading and greater efficiency of use would bring about improvements in land and water management practices and in particular, promote the ecological integrity of river and floodplain ecosystems (Smith, 1998).

The Murray–Darling Basin is more affected by flow regulation and water diversions than any other Australian catchment (Kingsford, 2000). An early example of an environmental flow provision was in 1998 for watering the Barmah–Millewa Forest (65 000 ha) the largest stand of river red gum (*Eucalyptus camaldulensis*) in the world which is listed under the Ramsar Convention. Environmental flows have been tailored to satisfy the known water requirements of a range of terrestrial and aquatic biota, especially the breeding of waterbirds. Australian researchers progressed further in the early 1990s to advise on flows for maintenance of entire ecosystems with the establishment of a conceptual framework of the holistic approach (Arthington, 1998) and the Expert Panel Assessment Method (Swales and Harris, 1995). A progression from the combination of numerous holistic methodologies is the downstream response to imposed flow transformations (DRIFT) process. DRIFT’s basic philosophy is that all major abiotic and biotic components constitute the ecosystem to be managed; and within that, the full spectrum of flows, and their temporal and spatial variability, constitute the flows to be managed (King *et al.*, 2003).

1.1.2 The natural flow regime

The ‘habitat heterogeneity hypothesis’ is one of the cornerstones of ecology (e.g. Simpson, 1949; MacArthur & Wilson, 1967; Lack, 1969). It proposes that structurally complex habitats provide more niches and diverse ways of exploiting environmental resources and thus increase species diversity. In aquatic environments a multitude of environmental attributes (primarily the interaction of water velocity and depth with the substrate profile) have considerable influence on the distributions and interactions of aquatic invertebrates (Bunn & Arthington, 2002). Aquatic systems however, differ from the terrestrial environment in that they are naturally fragmented in both space and time (Coopers *et al.*, 1998) although river regulation can substantially increase this fragmentation. For example, decreased flows downstream from a point of abstraction such as a weir may increase fragmentation by isolating riffles and point bars from the main channel, reducing the wetted perimeter and limiting the area and degree of available habitats (Cowx *et al.*, 1984; Smakhtin, 2001; Brasher, 2003). Conversely, upstream of a weir, inundation may connect riffle run sequences therefore decreasing habitat

fragmentation culminating in a less diverse continuous single pool habitat (Smakhtin, 2001; Gordon *et al.*, 2005).

The natural flow paradigm, which is advocated by many scientists and river managers states: ‘the full range of natural intra- and interannual variation of hydrological regimes and associated characteristics of magnitude, frequency, timing, duration, and rate of change, are critical in sustaining the full native biodiversity and integrity of aquatic ecosystems’ (Richter *et al.*, 1997). To understand flow regime and its associated biodiversity, it is important to recognise that in a river, habitat is defined by the physical environment, especially the movement of water and sediment within and between the channel and floodplain.

Natural river flows vary temporally over many scales (hours to decades or longer). Natural flow regimes show regional patterns that are determined largely by river size and by geographic variation in climate, geology, topography, and vegetative cover. For example, rivers like the Nymboida in regions with high seasonality exhibit hydrographs where flows are elevated in the summer because of seasonally high summer rainfall and fluctuate rapidly due to intermittent sub-tropical storms (Fig 2.2). Components of the flow regime that regulate ecological processes in river ecosystems include: the magnitude, frequency, duration, timing, and rate of change of hydrologic conditions (Walker *et al.*, 1995; Poff *et al.*, 1997; Smakhtin, 2001). These components can be used to characterise the entire range of flows and specific hydrologic events including low flows (Fig 1.1).

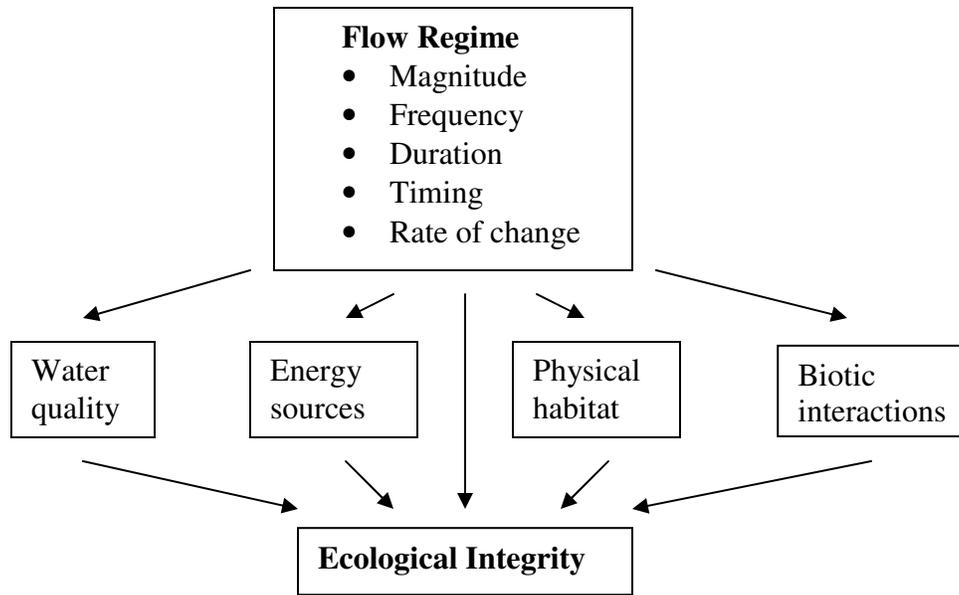


Figure 1.1 The five components of the natural flow regime including their effects on factors that regulate ecological integrity. Magnitude is the amount of water moving past a fixed location per unit time; frequency is how often a flow above a given magnitude recurs over some specified time interval; duration is the length of time associated with a specific flow condition; timing refers to the regularity with which a defined flow magnitude occurs; rate of change is how quickly flow changes from one magnitude to another (After Karr 1991, cited Poff *et al.*, 1997).

1.1.3 The effects of changing flow regimes

Disturbance in lotic systems is a concept long recognised and regarded as playing a pivotal role in community organisation (Resh *et al.*, 1988; Yount & Niemi, 1990; Lake, 2000). Disturbances impact on rivers at a range of temporal and spatial scales and can be characterised by their size, intensity, frequency, predictability, duration, mode of application and extent of physiochemical alteration to the affected system (Downes *et al.*, 1998; Lake, 2000; Downes *et al.*, 2002). Following Lake's (2000) review, a 'perturbation' to a population, community or ecosystem occurs when there is a distinct and abnormal change to properties of the system due to disturbance (Bender *et al.*, 1984). A perturbation consists of two events: the disturbance, which is the application of the

disturbing force such as a reduction of flow to the biota of the system and the response of the affected biota to the disturbance (Glasby & Underwood, 1996).

Generally a disturbance causing a reduction in flow is expected to decrease aquatic invertebrate density and diversity downstream from the point of the disturbance such as a weir (Poff *et al.*, 1997; Bunn & Arthington, 2002; Richter *et al.*, 2006). However benthic invertebrates can be highly resilient to the effects of reduced flows (Gunderson, 2000) because of their evolution within a highly variable and dynamic aquatic environment. This inherent capacity to recover from disturbance of many benthic invertebrates suggests when conditions are favourable recolonisation from the hyporheic zone (Fowler, 2004), refugia within the substrate (Lancaster & Hildrew, 1993) and by drifting from upstream (Anderson & Lehmkuhl, 1968; Svendsen *et al.*, 2004) could enable the recovery of invertebrates in response to environmental flows down a disturbed system.

River habitats are maintained by a wide range of flows. Ward and Stanford (1979) suggested the following ways in which regulation is likely to cause an ecological effect on habitats. Rivers with reduced flow will have decreased local current velocities, decreased overall stream habitat and increased siltation of the stream bed. Streams with seasonal flow constancy and uniform currents, may enhance riparian and aquatic vegetation through bed stability and limited disturbance. Increased flow in some regulated rivers leads to higher current velocities, which may in turn scour the bed, resulting in a shift to a coarser substratum. Short-term fluctuations in flow, for example those created during the generation of hydro-electricity can cause rapid current and depth fluctuations, turbidity, and substrate and bank instability (Poff *et al.*, 1997; Richter *et al.*, 1997).

The natural flow regime of a river operates over different temporal and spatial scales. Flood events physically characterise channel form and shape. Droughts and low flows generally decrease water velocity, depth and wetted perimeter (Gippel & Stewardson, 1998). Declining wetted perimeter is associated with declines in available aquatic habitat and habitat diversity (Stanley *et al.*, 1997). Decreases in velocity, depth and wetted

perimeter may gradually change with the duration of a particular low flow event (Englund & Malmqvist, 1996; Dewson *et al.*, 2007b). Therefore, if natural low flows and artificial low flow events are similar in their effect on instream habitat, natural low flow conditions may be compounded by the influence of artificially reduced low flows.

Physio-chemical changes under low flow conditions are primarily associated with changes in water temperature. Higher water temperatures occur in stream reaches with reduced flow (Cazaubon & Giudicelli, 1999; Rader & Belish, 1999). Dissolved oxygen, pH and electrical conductivity appear less predictable in response to low flows. Dewson *et al.* (2007a) found no evidence that low flows affected dissolved oxygen concentrations in a New Zealand stream, but during drying and drought, dissolved oxygen levels typically decline as streams dry to pools (Boulton, 2003). In an acidic stream, reduced runoff from the surrounding acidic landscape during a period of little rain was implicated as a cause of a rise in the pH (Woodward *et al.*, 2002). Solute-rich ground water inputs to surface water during periods of lower discharge can lead to increased electrical conductivity (Rader & Belish, 1999).

Increased sedimentation is often a consequence of low or reduced flow. Because slower velocities enable more sediment to settle out of suspension, sediment can accumulate and remain in the stream for longer time periods in the absence of high or flushing flows (Cazaubon & Giudicelli, 1999; Wood & Petts, 1999). The filling of gaps in the substratum with fine sediments especially in areas of the channel not usually subject to persistent sedimentation may reduce habitat diversity and dissolved oxygen in the lower substratum, isolating the hyporheic zone from the surface stream (Wood & Armitage, 1999). Furthermore in the absence of flushing flows, important resetting and reconnection of habitats and floodplains with the main river channel is lost (Reiser *et al.*, 1989; Richter *et al.*, 1997).

Flow regime is associated with changes in water velocity which is an important determinant of periphyton development. Water velocity can affect colonisation, production, and periphyton loss (Jowett & Biggs, 1997). Studies have found both positive

and negative relationships between velocity and periphyton (McIntire, 1966; Poff *et al.*, 1990; Jowett & Biggs, 1997). High flows generally scour periphyton whilst periphyton can also proliferate under low flow conditions (Gippel & Stewardson, 1998; Biggs *et al.*, 2005). Periphyton forms the base of food webs supporting grazers such as crustaceans, molluscs, some fish and benthic invertebrates (Rounick & Winterbourn, 1986; Stevenson, 1996 ; Suren *et al.*, 2003a; Suren *et al.*, 2003b).

1.1.4 Associations between flow regime and benthic invertebrates

Artificial low flows are predicted to have similar consequences for the invertebrate fauna as natural low flows. For example, reduced-flow sites on large regulated rivers had lower invertebrate densities than reduced-flow sites on unregulated rivers (Englund & Malmqvist, 1996; Malmqvist & Englund, 1996; Cazaubon & Giudicelli, 1999). Benthic invertebrates are vulnerable to sudden fluctuations in flow, and regulated river reaches below hydroelectric dams with erratic flow patterns are typically characterised by species-poor invertebrate communities (Munn & Brusven, 1991).

Benthic invertebrates play a central role within most lotic ecosystems as key processors of organic matter and as food for fish. Gore (1977) showed that many benthic invertebrates have a limited range of tolerances to extremes in discharge. Most benthic invertebrates lack the ability to return to the same habitat once vacated; instead they may drift or simply be forced to re-establish themselves downstream (Anderson & Lehmkuhl, 1968; Svendsen *et al.*, 2004; Downes *et al.*, 2005). Therefore, if invertebrate communities are more affected by further declines in already low flows, then this would imply that the potential to persist, recolonise and interact within the aquatic environment would be under increasing threat.

The inherent variability of the flow regime in many Australian rivers is thought to have driven the evolution of life history patterns of most aquatic invertebrates (Marchant *et al.*, 1984; Lake & Doeg, 1985). An example of the influence of flow regime on aquatic invertebrates is the “boom or bust” dynamics of invertebrates in rivers and wetlands in response to the unpredictable and episodic nature of flood events in the arid zones of

Australia (Walker *et al.*, 1995). Aquatic food webs in wetlands of arid Australia during dry spells are largely supported by algal production in the shallow edge zone, whereas during floods, inundated floodplains ‘boom’ as many invertebrates are cued to rising flood levels, emerging from resting stages and providing an immense food resource (Bunn *et al.*, 2006). Therefore the natural flow regime incorporating flood and flow pulses is now recognized as important in maintaining both habitat and biodiversity (Poff *et al.*, 1997; Boulton & Brock, 1999). Under the influence of fluctuating flows, habitats can support very different densities of benthic invertebrates and highly variable communities distributed as ‘patches’ in the ecosystem (Townsend, 1989; Downes, 1990; Lake, 2000). Declining densities and/or changes of community structure may limit important food supply for fish and restrict energy processing within the system.

Environmental variables contribute to the highly variable and patchy distribution of benthic invertebrates. Sheldon & Walker (1998) concluded that variation in the distribution of benthic fauna in the Murray–Darling river system of south-eastern Australia at the macrohabitat (river) level is primarily caused by hydrological and geomorphic factors while at the mesohabitat level (pool/riffle) variation has been related to longitudinal gradients in flow regime, particle size and environmental variables (Growth & Davis, 1994; Downes *et al.*, 2000a). Depth, velocity and substrate profile are three environmental variables of critical importance to the range of potential microhabitats (snags, vegetation, substrata) available to benthic invertebrates (Statzner *et al.*, 1988; Brooks *et al.*, 2005).

Diversity within rivers is influenced by the variety of pools and riffles, as pools and riffles are influenced by the variety of microhabitats and the diversity of substrates within them (Growth & Davis, 1994; Allen, 1995; Downes *et al.*, 2002). Modifications in flow regime that change these variables altering physical habitat, location and accessibility reduces the availability of adequate microhabitats to some invertebrate species whilst creating more suitable habitats for others. Loss of different types of available habitat and hence diversity is most often evident in riffles and edge environments where conditions change the most under the influence of low flows (Stanley *et al.*, 1997). As invertebrate

densities change with changes in the location and suitability of physical habitat, community structure under low flow events may be altered as some species will be favoured or alternatively locally eliminated from the system (Sheldon & Walker, 1997).

The dispersal, transport, settlement and community dynamics of invertebrates is specifically governed by the hydraulic character of water. Most stream benthic invertebrates use the current to assist respiration and feeding (Hynes, 1970; Statzner *et al.*, 1988). Predominantly benthic invertebrates live among hard substrates (Minshall & Robinson, 1998; Death, 2000). Filter-feeders, such as the black fly larvae (Simuliidae) or the net-spinning larvae of the predating caddisfly (Hydrobiosidae), need a stable platform for attachment and sufficient current to ensure the delivery of food into their net. If prey species can tolerate faster flows than their predators, then microhabitats with fast flows can serve as refuges from predation (Hansen *et al.*, 1991). Invertebrates such as larval black flies seem to exploit flow, decreasing their entry into the water column with increasing water velocity (Fonseca & Hart, 1996).

1.1.5 Indicator species and associations of benthic invertebrates with flow alterations

Water velocity is of particular importance to stream invertebrates as species traits including morphology (Statzner & Holm, 1989), feeding biology (Statzner *et al.*, 1988) mobility (Frutiger, 1998), and respiratory requirements (Ericksen *et al.*, 1996) contribute to an invertebrate's affinity to a preferred velocity environment. Associations between invertebrate density and water velocity have been observed in the laboratory (Hansen *et al.*, 1991) as well as in the field (Statzner *et al.*, 1987; Hart & Finelli, 1999). Worldwide, stream invertebrates often show distinct preferences for a particular water velocity or at least to regions of 'slow' and 'fast' flows (<0.1 m/s, 0.1 – 0.6 m/s, respectively) (Table 1.1). Community response downstream from a disturbance causing a decline in water velocity may also reflect a change in density and diversity as a result of the reduction in discharge. Considering their affinity to flow, specific rheophilic 'flow loving' species may prove especially useful in the detection of the effects of low flows on river ecosystems. Species flow preferences recorded in various field and laboratory studies of

which I found no suitable Australian examples have been allotted into velocity categories (Table 1.1). Hydrobiosids are one of the more common caddis flies and seem to prefer fast flows and of the studies included in this review (Table 1.1) hydrobiosids were not observed in flows slower than 0.1 m/s.

Table 1.1 Flow preferences for species recorded in various field and laboratory studies. Author details and the method used to record water velocity are included. * recorded within velocity category ** primarily recorded within velocity category

Order	Taxon	<0.1	0.1 - 0.6	>0.6	Comment	Author
Trichoptera	<i>Agapetus boulderensis</i>		*		0.4 stream depth	Wellnitz et al., 2001
Trichoptera	<i>Agapetus boulderensis</i>	*	*		directly above and perpendicular to rock surface	Poff, 1992
Trichoptera	<i>Costachorema</i> spp.			*	0.4 stream depth	Collier et al., 1995
Trichoptera	<i>H. parumbripennis</i>		*	*	0.4 stream depth	Collier et al., 1995
Trichoptera	<i>C. callistum</i>			*	0.4 stream depth	Collier et al., 1995
Trichoptera	<i>Pycnocentroides</i> spp., <i>Beraeoptera roria</i> <i>Olinga feredayi</i> , <i>Pycnocentria</i> spp.		*	*	0.6 stream depth	Jowett & Richardson, 1990
Trichoptera	<i>Pycnocentroides aeris</i>		*		flow tank, 2cm above substrate	Holomuzki et al., 2000
Trichoptera	<i>Hudsonema amabilis</i>		*		flow tank, 2cm above substrate	Holomuzki et al., 2000
Trichoptera	<i>Neureclipsis</i>	*			0.1 m in front of rock	Huncken & Mutz, 2007
Trichoptera	<i>Rhyacophila</i> sp.			*	stoppani propeller and floats	Ambuhl, 1959
Trichoptera	<i>Hydropsyche augustipennis</i>		*		stoppani propeller and floats	Ambuhl, 1959
Ephemeroptera	<i>Epeorus</i> sp.			*	0.4 stream depth	Wellnitz et al., 2001
Ephemeroptera	<i>Deleatidium</i> spp.			*	0.6 stream depth	Jowett & Richardson, 1990
Ephemeroptera	<i>Deleatidium</i> spp.	*	*		flow tank, 2cm above substrate	Holomuzki et al., 2000
Ephemeroptera	<i>Baetis</i>		*		stoppani propeller and floats	Ambuhl, 1959
Ephemeroptera	<i>Habroleptoides</i> sp.	*			stoppani propeller and floats	Ambuhl, 1959
Ephemeroptera	<i>Ephemerella ignita</i>	*	*		stoppani propeller and floats	Ambuhl, 1959
Diptera	<i>Chironomidae</i> , <i>Aphrophila neozelandica</i>		*	*	0.6 stream depth	Jowett & Richardson, 1990
Diptera	Simuliidae		*	*	experimental chamber	Hansen et al., 1991
Diptera	<i>Chirostilbia pertinax</i>		*	*	0.4 stream depth	Santos Junior et al., 2007
Diptera	Simuliidae			*	1-2 mm above hemicylinder	Fonseca & Hart, 1996
Diptera	<i>Simulium</i> sp.		*	*	stoppani propeller and floats	Ambuhl, 1959
Mollusca	<i>Potamopyrgus antipodarim</i>	*	*		flow tank, 2cm above substrate	Holomuzki et al., 2000
Mollusca	<i>Ancylus fluviatilis</i>		*	*	stoppani propeller and floats	Ambuhl, 1959

1.2 Aim of this study

The broad aim of this study was to describe the association of the assemblage structure of the aquatic benthic invertebrate community to flows in the Nymboida River, NSW, to help assess whether flow alterations may have affected aquatic invertebrate distribution in this river. The main objective was to determine whether a longitudinal gradient in benthic invertebrate community composition, diversity and abundance resembling that in a nearby unregulated reference river exists up and downstream of the Nymboida Weir. To assess this, a survey (Chapter 3) was conducted at three upstream and three downstream sites either side of a weir on the Nymboida River and six reference sites along a comparable longitudinal section of the unregulated Bellinger River.

A second aim was to ascertain how benthic invertebrates would respond to changes in flow in the Nymboida River. A manipulative experiment (Chapter 4) was conducted at two sites upstream and two sites downstream on the Nymboida River to compare assemblage structure when flows were increased or reduced across small sections of stream bed to assess the effect of velocity and whether the invertebrate assemblage response was consistent across different velocity habitats.

2 Regional setting and study context

2.1 Regional setting

2.1.1 Location

The effect of a weir on benthic invertebrate assemblages was examined in the Nymboida River in the Northern Rivers region of New South Wales, Australia. The Nymboida Weir is approximately 1.8km downstream from the town of Nymboida ($29^{\circ}56'32.06''\text{S}$, $152^{\circ}43'42.89''\text{E}$), 35km SW of Grafton. The 2006 study was conducted up- and downstream of this weir and along a comparable longitudinal section of the unregulated upper Bellinger River (Fig. 2.1). The Nymboida River study area occurs at approximately 180 m a.s.l., between the latitudes and longitudes of $29^{\circ}59'24.91''\text{S}$ and $152^{\circ}43'8.57''\text{E}$ (most upstream site) and $30^{\circ}17'9.63''\text{S}$ and $152^{\circ}37'20.23''\text{E}$ (most downstream site). The Bellinger River study area occurs at approximately 70 m a.s.l. and between latitudes of $30^{\circ}25'44.08''\text{S}$ and $152^{\circ}45'32.15''\text{E}$ (most upstream site) and $30^{\circ}27'40.00''\text{S}$ and $152^{\circ}38'7.50''\text{E}$ (most downstream site).

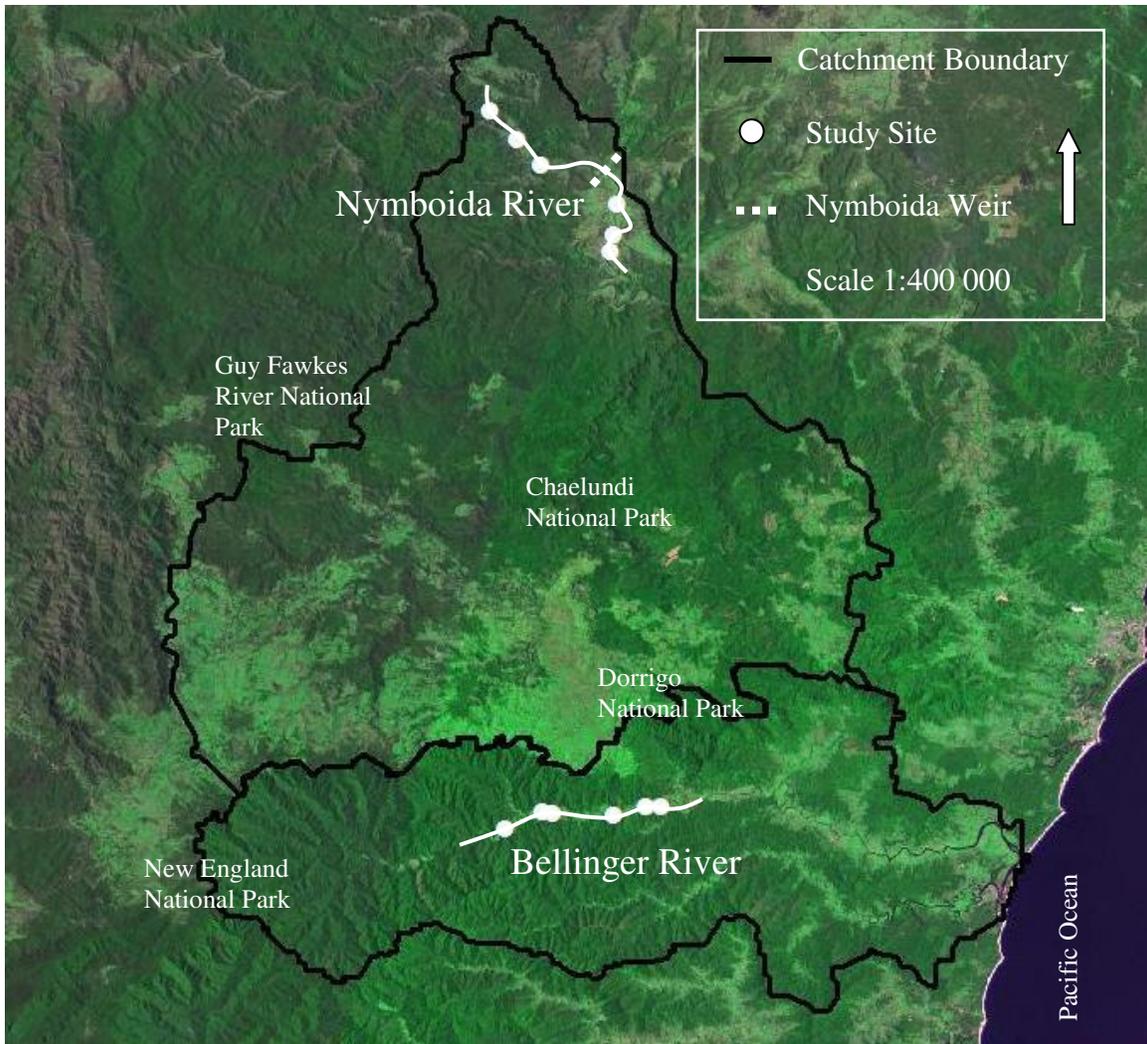


Figure 2.1 Map depicting Mann–Nymboida and Bellinger River Catchments. Circles represent study sites.

2.1.2 Climate

The Nymboida and Bellinger River catchments are primarily influenced by a summer dominant rainfall pattern generated within the Dorrigo Plateau, averaging 2030 millimetres annually (Fig. 2.2). The region is south of the cyclonic activity generated from December to April off the Queensland coast, however tropical depressions (degenerate cyclones) and summer storms resultant of orographic uplift in the local coastal ranges do deliver torrential rains in short time periods and are a major cause of flooding to both catchments (Speer & Leslie, 2000).

Summer mean maximum temperatures occur during January (Fig. 2.2). Summer maximums are typically higher in Grafton (30.8 °C) than Bellingen (29.8 °C). Bellingen (211.7mm) receives considerably more summer rains than Grafton (129.9mm). The heaviest falls in Bellingen occur in March (Fig. 2.2). Due to the Bellingen weather station's close proximity to the Dorrigo Plateau (source of rainfall for both catchments), Bellingen rainfall data is considered more representative of the flow regime characterising the Nymboida and Bellinger Rivers (Fig. 2.2). The Grafton weather station is approximately 30 kilometres away from the Nymboida River. Frosts do occur away from the coast and more heavily along the Nymboida than the Bellinger Rivers (Bureau of Meteorology, 2007).

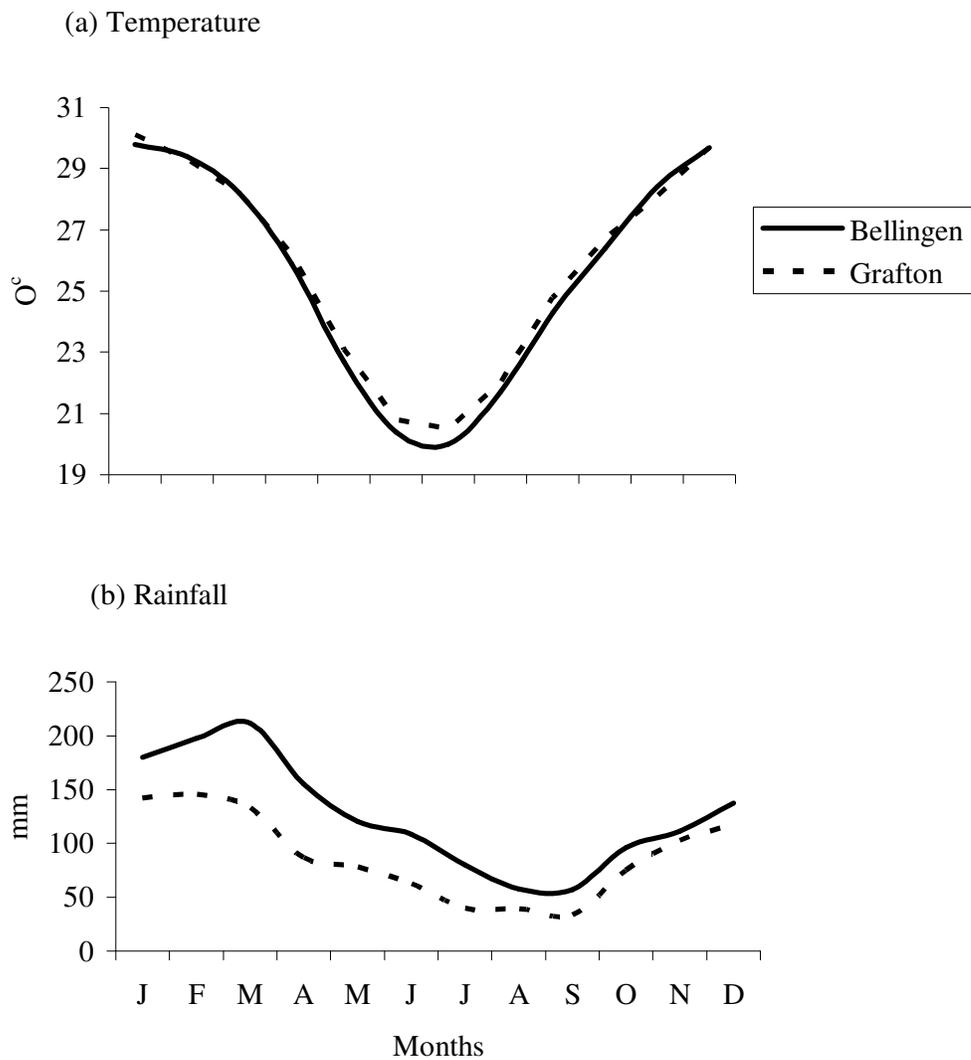


Figure 2.2. Average monthly climate statistics for (a) Temperature and (b) Rainfall for Bellinghen (station 059001) and Grafton (station 058130) (Bureau of Meteorology, 2007).

2.1.3 Flow regime

Minimum rainfall on the Dorrigo plateau occurs through August to September. This winter pattern coincides with typical low flows in both the Nymboida and Bellinger Rivers. Low flows extend from May till October (Fig. 2.3).

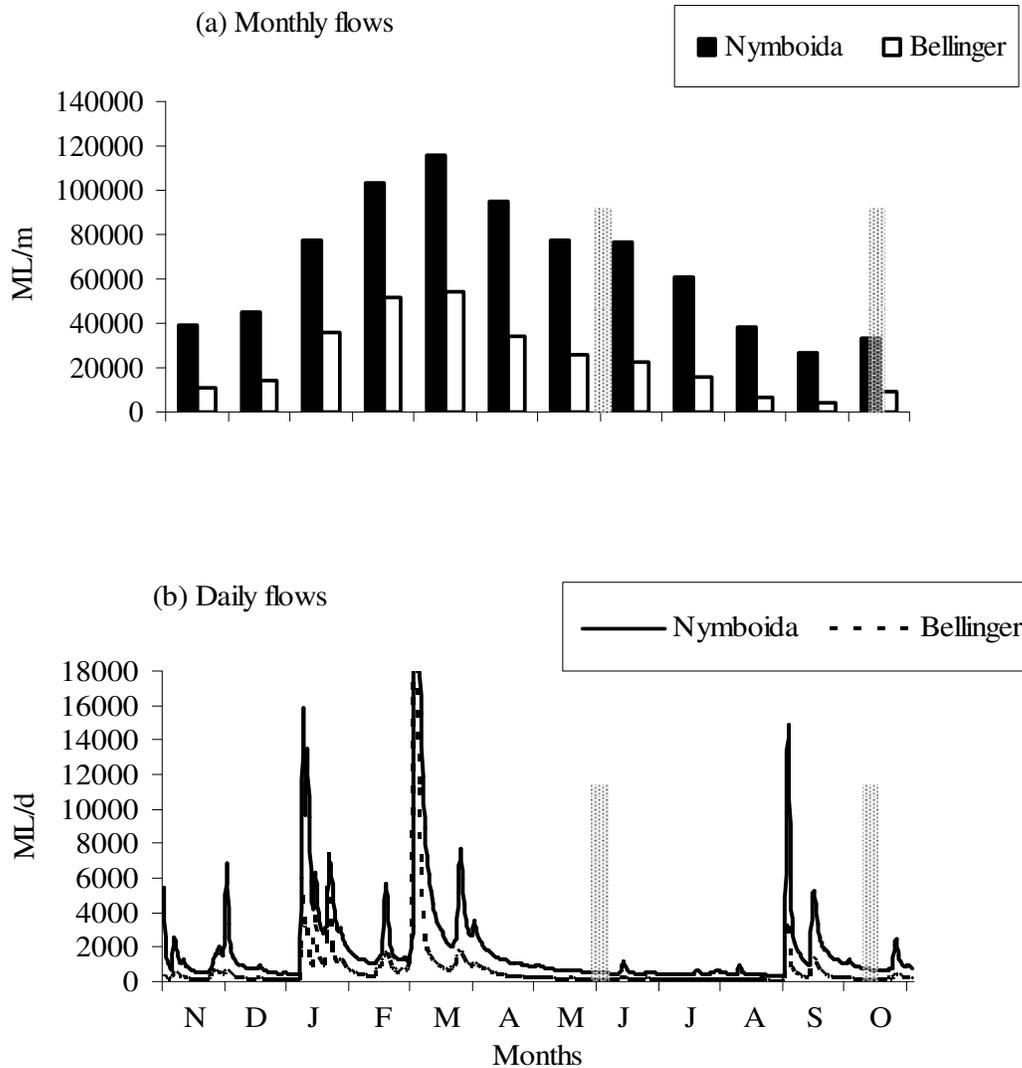


Figure 2.3 Hydrographs representing (a) Nymboida and Bellinger River average monthly flows, (b) Nymboida and Bellinger River study period. Shaded zones represent May/June survey and October experimental periods.

2.1.4 Topography and drainage

The Nymboida River flows NNW and is fed by several easterly flowing unnamed drainage lines generated in the Mann-Nymboida River catchment (1700 km²), a subcatchment of the much larger Clarence River Catchment. This southern portion of Clarence River Catchment characterises the flow regime of the Nymboida River and includes the conservation areas Chaelundi, Guy Fawkes and New England National Parks (Fig. 2.1). The Bellinger River is within the Bellinger River Catchment (1110 km²) and is fed by several unnamed drainage lines generated predominantly within the New England National Park and the world heritage listed Dorrigo National Park. Both rivers finally drain east and enter the Pacific Ocean (Fig. 2.1).

The Nymboida and Bellinger Rivers are set within confined valleys with a bedrock controlled discontinuous floodplain. The main channel substratum of the lowland study reaches are comprised of bedrock and boulders with extensive areas of cobble and gravel bars in the shallower pool, run, riffle sections (Ferguson & Brierley, 1998).

2.1.5 Nymboida and Bellinger River study reaches

Historically, the lowland portion of the Nymboida River prior to the installation of the weir in 1924 received uninterrupted flows. The Nymboida is a second order subtropical lowland river with long deep pools and fast flowing riffles linked by very long (100–500m) flowing runs. In the unregulated, upper reaches of the Nymboida (potential control sites) and the upper Bellinger similar pools, riffles and runs remain. Continuous flow upstream of the Nymboida Weir through the dry winter months never disconnects but simply reduces the extent of these habitats. Reduced discharge and the reduction of pool riffle run habitats in the regulated reaches downstream of the weir are further diminished during the winter low flow period. On average, the natural low-flow period below the Nymboida Weir appears to be extended into the late spring – early summer months by 6-8 weeks (Fig. 2.3). No major tributaries enter either the Nymboida or Bellinger Rivers between the most upstream and most downstream sites, ensuring a consistent and comparable flow regime throughout both study reaches (Fig. 2.1, 2.3).

2.1.6 Flow environments within riffle habitats

Along the edges of the river to up to a metre into the channel, there was a shallow (< 5 cm), 'slow flow' (current velocity < 0.1 m/s) habitat (Fig. 2.4). The slow flow habitat is present at all discharge levels but this habitat experiences change in areal extent and lateral position within the channel with changing discharge. Further into the channel was a habitat termed 'fast flow' where depth ranged from 5-15 cm and current velocity was between 0.2 – 0.6 m/s (Fig. 2.4). The fast flowing habitat experiences the greatest change in areal extent with changing discharge, being greatly reduced at low flows. These slow and fast habitats were also evident in riffles sampled in the Bellinger River.

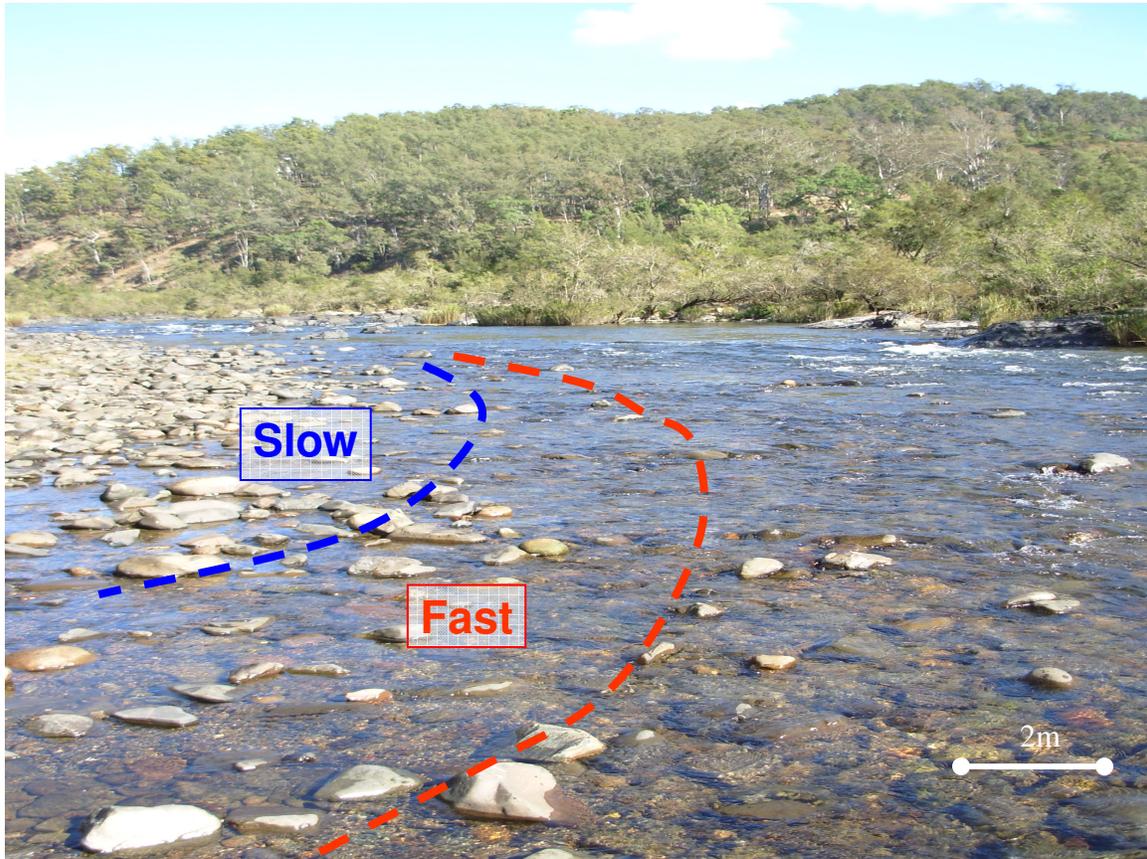


Figure 2.4 Slow and fast flow habitats within study riffles.

2.1.7 Geology

Catchment geology is classified as being of Paleozoic metamorphosed sediments of micaceous phyllites and slates with some siliceous argillites (DECC, 2007). These have weathered to pale yellow-brown clay loam on the steep slopes and brown loam elsewhere. The appearance of these soils and their associated rainforest vegetation however are indicative of a soil enriched by basic igneous rocks such as weathered basalt (Keith, 2004). Soils in the catchments are subject to moderate to high surface erosion hazard, with potential for mass movement, culminating in heavy silt loads being transported down the Nymboida and Bellinger systems after moderate to heavy rainfall (DECC, 2007).

2.1.8 Vegetation

Extensive tracts of tall lush eucalypt forest stretch along the north coast of New South Wales. Vegetation communities within the catchments include subtropical and dry rainforest, wet and dry sclerophyll forests and woodland (Keith, 2004). The North Coast Wet Sclerophyll Forests dominate the study catchments and indicative species include *Eucalyptus acmenioides* (white mahogany), *E. microcorys* (tallowood), *E. pilularis* (blackbutt), *E. saligna* (Sydney blue gum), *Lophostemon confertus* (brush box), *Syncarpia glomulifera* (Turpentine) (Keith, 2004). *Eucalyptus dunnii* predominates at mid elevations and in the foothills of the Dorrigo Plateau (Keith, 2004). Within the Nymboida and Bellinger River catchments the southerly aspects provide greater shading and have produced a moister subtropical rainforest vegetation type than that of the adjoining slopes of a northerly aspect. In addition east-facing slopes support the persistence of well-developed dry rainforest, whilst the drier west-facing slopes exposed to the strong dry westerly winds, exhibit wet sclerophyll forest (DECC, 2007).

Riparian vegetation ranges from continuously closed to open and grazed within the catchments. As mentioned above the North Coast Wet Sclerophyll Forests dominates however at high elevations (>900m) and especially in drainage lines where moisture laden air streams off the Pacific Ocean and is uplifted creating wet and misty conditions,

cool temperate rainforests are found. Cool temperate rainforests have a simple structure usually with a single dominate species (*Cryptocarya nova-anglica*, mountain laurel) and one or two subordinate ones (Keith, 2004). On the lower reaches of the Nymboida and Bellinger Rivers (study reaches), the riparian zone is heavily grazed wet sclerophyll forests with casuarinas (*Casuarina cunninghamii*) along the rivers' edge.

2.1.9 Landuse

Land use within both catchments includes State and private forestry operations, private freehold land for cattle grazing which is largely forested, traveling stock reserves, as well as low levels of rural residential development. Other differences between regulated and unregulated sections of the Nymboida lie in the nature of the catchment and land use intensity directly adjacent to the study reaches. Upstream and downstream reaches are both grazed by cattle however the upstream sections lie at the foothills of nearby ranges where grazing intensity is less than the more accessible downstream sections.

2.2 Study context

2.2.1 Proposed regional water supply scheme

Increased domestic pressure on the Clarence and Coffs coast regional water supply has put into action the upgrade of the existing bulk water supply system (Fig. 2.5). It was shown that the regional water needs to 2021 in the Headwork's Report (1997) could be met by a 30-GL off river-storage on Shannon Creek fed by surplus flows from the Nymboida River. This Regional Water Supply Scheme (RWSS) involves constructing a 30 GL storage at Shannon Creek, linking the Shannon Creek storage to Karangi Dam at Coffs Harbour with an 80 kilometer pipeline and via a second pipeline, linking the Nymboida Weir to the Shannon Creek/Karangi Dam pipeline (Fig. 2.5). The main aim of the scheme is to secure domestic water supply during drought periods in the Clarence and Coffs Harbour region, whilst enabling the maintenance of environmental flows especially during critical low flow periods in the Nymboida River. This is to be achieved by diverting water into the Shannon Creek storage during high flows, therefore limiting extraction from the Nymboida Weir and maximising downstream flows during seasonal low flow periods.

2.2.2 Historical flow regime

The Clarence River Catchment is the largest coastal river catchment in NSW at 22700 km². The southern portion of the catchment area feeds the Nymboida River and is approximately 1700 km². Flows have been gauged (station 204001) five kilometres upstream of the Nymboida Weir since 1909 (Table 2.1). Regulated downstream flows differ in magnitude and duration compared to unregulated upstream flows (Fig.2.6)

Table 2.1 Historical flows recorded above the Nymboida Weir (station 204001) (RWSS 1999)

Flow	ML
Mean Annual Flow	820 000
Minimum annual Flow	180 000
Mean Monthly Flow	68 300
Minimum Monthly Flow	2 670
Mean Daily flow	2 250
Minimum Daily Flow	62
Flow Exceeded 80% of Time	427
Flow Exceeded 95% of Time	213

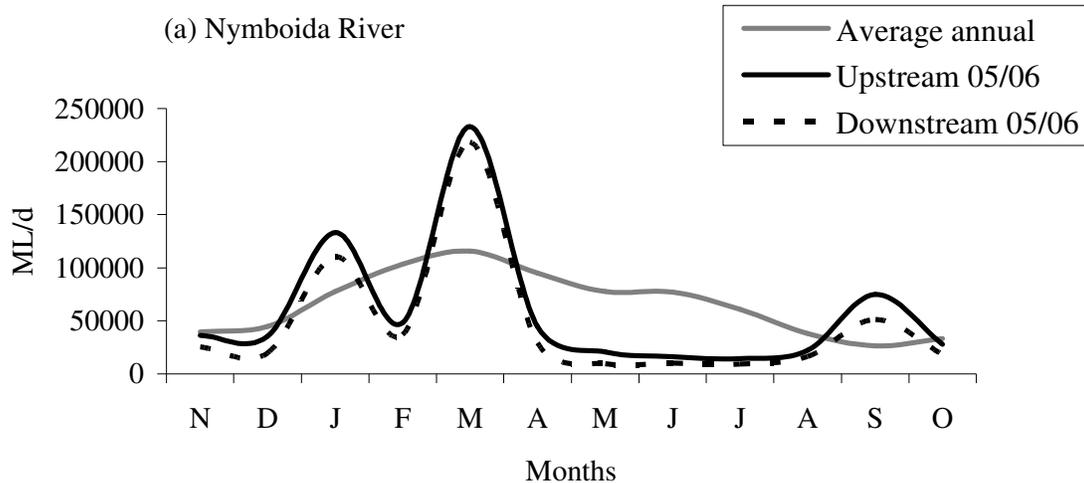


Figure 2.6 Hydrograph representing flow regime up –and downstream of the Nymboida Weir during 2006-07 study year.

2.2.3 Regulation

In 1936 the 3.25m Nymboida Weir which was first installed in 1924 along with the hydroelectricity plant was raised to 4.26m. From the Nymboida Weir, water is extracted for domestic water supply and generation of hydroelectricity for the Grafton and lower Clarence region. Domestic water supply extracts a maximum of 39.6ML/day from the power stations penstocks. For the generation of electricity, Country Energy removes up to 864 ML/day. Under the current flow rules, Country Energy can only extract water above a discharge of 400 ML/d and only town water supplies can be withdrawn below that discharge. Extraction for hydroelectricity currently and over recent years has run at half capacity due to damage to one of two intakes extracting from the Nymboida Weir pool.

Currently the Grafton and lower Clarence region has no major storage and relies on run of river flows in the Nymboida River to maintain water supply. The principal deficiency of the existing system is the absence of sufficient storage to maintain supplies during drought. Other deficiencies highlighted in the Grafton and lower Clarence scheme include the Nymboida River's ability to increase environmental flows downstream of the Nymboida Weir especially during natural low flow periods and peak hydroelectricity production, and poor water quality.

2.2.4 Past extraction regime

Previous to August 1997, water was extracted from the Nymboida Weir pool over distinct periods, generally at times of peak demand such as early morning and evening. The diversion of water for power generation was therefore pulsed and not drawn continuously from the Nymboida Weir pool. Minimum storage levels were set at the Nymboida Weir below which water for power generation was not permitted to draw below, however when river inflows exceeded 900 ML/day the power station was permitted to draw continuously.

Downstream environmental flow criteria were not in place previous to 1997. A minimum riparian release was maintained downstream and the Lower Clarence County Council

(LCCC) are permitted to draw up to 53.5 ML/day for domestic water supply provided at least 12 ML/day passes downstream. Extraction for power generation would cease to allow the level of the weir pool to increase above the minimum storage level before extraction resumed. These pulsing flows occurred twice daily, representing a marked difference from the natural variation of river flows which fluctuate accordingly to changes in climatic and environmental factors.

2.2.5 Current extraction regime

Post August 1997, the extraction regime was amended to provide for an interim environmental flow of 225 ML/day (95%ile flows) downstream of the Nymboida Weir. This license required that the net amount passing downstream over a 24-hour period was a minimum of 225 ML/day. This environmental flow criterion at times allows for downstream flows to be drawn down to the riparian release, whilst still adhering to the new license arrangement over a given 24-hour period. During the reporting period of the 2005 State of the Environment Report flow in the Nymboida River was below 225 ML/d on 74 days.

2.3 Rationale for study

The development of a monitoring program was recommended by the Commission of Inquiry for the Regional Water Supply Project (RWSP) and is required by the project determination conditions of Lower Clarence County Council approval and license conditions issued for the Shannon Creek storage and Country Energy extraction from the Nymboida River.

A Technical Advisory Panel (TAP) formed in October 2001, comprising aquatic ecologists with expertise in benthic invertebrates, water plants, water quality, fish, and survey design was appointed to provide advice to the River Management Committee (RMC) to help with the development of an environmental monitoring program. The TAP's aim was to review recent studies (with a focus on The Ecology Lab report, 2000) and identify research gaps in the potential effects on river health of water extractions and

operations of Country Energy, Lower Clarence County Council and Coffs Harbour City Council on the Nymboida and Orara Rivers, and Blaxland and Shannon Creeks.

The TAP report highlighted key points such as the requirement for reference sites and the selection of a series of ecological indicators that are expected to be influenced by flows to be included in the environmental monitoring program. As there are no river locations that have a comparable history to the Nymboida River but alternatively there are rivers in the area that are relatively undisturbed (not pristine, but do not have a long history of human impacts on flow), TAP suggested that the best way for the RMC to answer the question: Is the condition of the Nymboida River improving? was to set a *'target'* condition or reference river to which the Nymboida River can be compared. By comparing the Nymboida River (impact) to the unregulated Bellinger River (reference), we can determine whether the Nymboida River is different to the reference river condition at the start of monitoring and whether it is beginning to move towards or away from that reference condition.

The RMC was established to oversee and have input into the development and implementation of the monitoring program. The Committee consists of a range of stakeholder interests including representatives from the community, University of New England, North Coast Water, Country Energy, recreational fishing and canoeing clubs and key government agencies such as DECC and DNR.

Benthic invertebrates are a critical component of aquatic ecosystem and the maintenance of biodiversity within river ecosystems probably rest heavily on the natural flow regime (section 1.1.2). TAP and the RMC outline several promising areas of research that would generate valuable information for refining the environmental monitoring program and help clarify the ecological responses by various biota and ecosystem processes to changes in flow regimes. This included outlining clear aims to address the general question, is the Nymboida improving towards the condition of the Bellinger River? Regulation is associated with declines in aquatic habitats and benthic invertebrates (section 1.1.4), and many benthic invertebrates do exhibit specific flow preferences (section 1.1.5; Table 1.1). Therefore determining the composition of benthic invertebrates within the Nymboida

(impact) and Bellinger (reference) Rivers as well as whether water velocity is causal of an invertebrate response is important for the ongoing development of this monitoring program and more broadly, maintenance of freshwater biodiversity in the Nymboida River.

3 Associations between invertebrate assemblages and flow regime upstream and downstream of a weir on the Nymbioda River, NSW.

3.1 Introduction

Regulation alters the natural flow of water which is a defining characteristic of rivers (Poff *et al.*, 1997; Boulton & Brock, 1999). Regulation threatens the maintenance of the natural biodiversity in rivers (Poff *et al.*, 1997; Bunn & Arthington, 2002). Projected anthropogenic demands of freshwater means more dams and weirs will be constructed increasing the threats associated with low flow events in downstream environments (Postel & Carpenter, 1997; Jackson *et al.*, 2001).

The natural flow regime of rivers varies spatially and temporally encompassing floods and low flow events (section 1.1.2). Natural low flows are often seasonal and coincide with periods of low rainfall. Artificially reduced low flows, for example those created downstream of small dams or weirs can alter the magnitude, duration and timing of specific natural low flow events (Poff *et al.*, 1997). Little is known on the associated response of benthic invertebrates to natural or artificially reduced low flows (sections 1.1.4, 1.1.5).

There are an infinite number of indicators (physio-chemical and biological) and ecological measures (e.g. species density, richness, community composition) from which to gain insight into the association between changes in flow regime and the invertebrate community (Downes *et al.*, 2002). Selection of a subset of variables that will respond to the predicted changes in flow regime and be as unambiguous as possible in their response is a common management and monitoring challenge. Reliable indicators (e.g. benthic invertebrates) therefore require an understanding of the ecosystem in which they are to be used (Growth & Davis, 1994; Fairweather, 1999).

The distribution and densities of benthic invertebrates is highly variable and patchy within stream habitats (Lake, 2000), and the literature describes many factors that influence the spatial distribution of stream invertebrates (Gore & Hamilton, 1996; Gore *et al.*, 2001; Hoffman *et al.*, 2006). Benthic invertebrate morphologies and life history patterns generally well suit them to a variety of natural flow regimes, however temporal changes in natural low flows and disturbance from river regulation may result in dramatic changes in invertebrate densities and diversities (Moog, 1993; Tiemann *et al.*, 2005). More specifically loss of invertebrate density and diversity is predicted downstream from weirs because reduced flows alter the timing and magnitude of specific flow events and limit the availability and number of different types of habitats important for the maintenance of species diversity (Bunn & Arthington, 2002; Downes *et al.*, 2002; Tiemann *et al.*, 2005).

Presses are long-term events such as flow reductions due to the barrier effects of weirs (Resh *et al.*, 1988; Lake, 2000). Press disturbances rise sharply before maintaining a constant level of disturbance (Bender *et al.*, 1984). Weirs causing press disturbances downstream potentially exacerbate periods of low flow and as described in the literature these prolonged low flows can reduce benthic invertebrate density and diversity (Cowx *et al.*, 1984; Englund & Malmqvist, 1996; Malmqvist & Englund, 1996; Cazaubon & Giudicelli, 1999; Rader & Belish, 1999; McIntosh *et al.*, 2002).

Decreased discharge usually causes decreased water velocity, water depth, and wetted perimeter (Gore, 1977; Malmqvist & Englund, 1996; McIntosh *et al.*, 2002), factors that are of critical importance to the range of potential microhabitats and therefore distribution of benthic invertebrates (Statzner *et al.*, 1988; Downes *et al.*, 2000b; Wellnitz *et al.*, 2001; Brooks *et al.*, 2005). Loss of different types of available habitat and hence diversity is most evident in riffles and edge environments where conditions change the most under the influence of low flows (Gippel & Stewardson, 1998; Gordon *et al.*, 2005). Invertebrate density may increase or decrease in response to a reduction of flow, whereas invertebrate diversity generally drops along with a decline in available habitat (Cazaubon & Giudicelli, 1999; Wright & Symes, 1999; Kinzie *et al.*, 2006). Interspecies

environmental tolerances and requirements are highly variable (Growth & Davis, 1994; Brooks *et al.*, 2005). Therefore loss of available habitat or shifts in potential food resources due to altered flows can affect invertebrate densities and community interactions (McIntosh *et al.*, 2002; Suren *et al.*, 2003a; Suren *et al.*, 2003b; Wood & Armitage, 2004). Thus rheophiles or 'flow loving' species which are defined as those species with an affinity for fast flowing habitats may be at most risk of decline as the availability of faster flowing habitats which these specific species exploit become more scarce under reduced flows.

Natural low flows and artificially reduced flows have similar effects on invertebrates, but the severity (duration and magnitude) of the flow decrease can influence invertebrate responses (Cox *et al.*, 1984; McIntosh *et al.*, 2002; Wood & Armitage, 2004). Thus, using key benthic invertebrate species that respond predictably to flow decreases from a range of habitats could be useful as response indicators for monitoring the ecological effects of low flows or indeed improvements under enhanced flow criteria.

This study tested two major hypotheses. First, if reduced flows downstream on the Nymboida River are having a statistically detectable effect on the benthic invertebrate fauna, then benthic invertebrates in regulated sites downstream of the Nymboida Weir are predicted to be depleted in density and diversity. Second, invertebrate density and diversity is predicted to be greater in the fast than the slow flow habitat.

Finally, I considered outcomes for the above hypotheses for total species richness and for a subset of rheophilic 'flow loving' species. Given the common management concern of detecting an improvement or adverse change with confidence and minimal sampling effort, it is important to know whether patterns deduced from a select number of rheophilic taxa in response to flow serves the same purpose as data that includes all rheophiles or indeed the entire invertebrate population.

3.2 Methods

3.2.1 Study site

The effect of a weir on benthic invertebrate assemblages was examined in the regulated, subtropical Nymboida River, New South Wales, Australia. Two rivers were surveyed for this study, the Nymboida River (impact) upstream and downstream of a weir and the Bellinger River with similar up - and downstream sections and no weir (Fig 3.1).

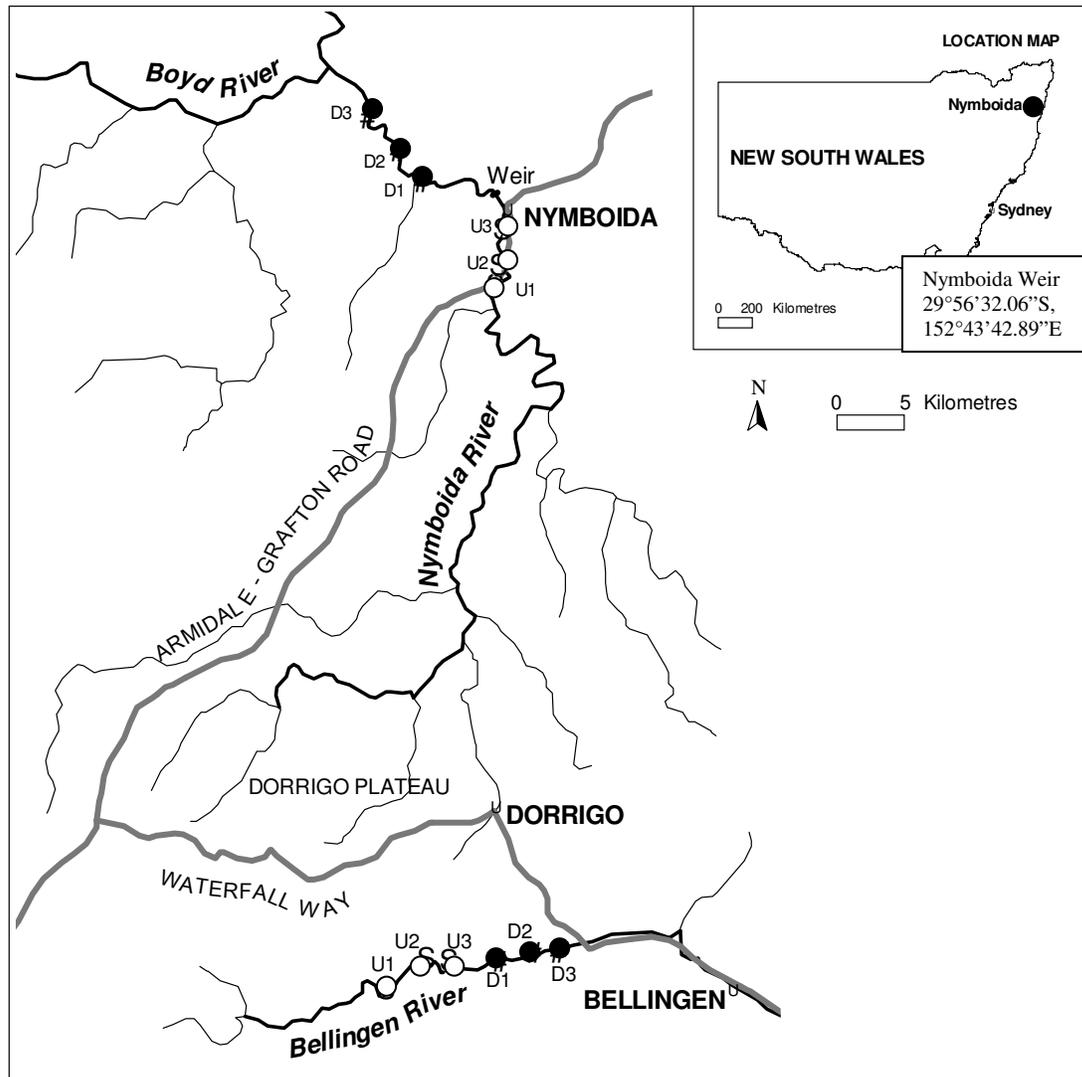


Figure 3.1 Map representing three riffles downstream (D1, D2 & D3), and three riffles upstream (U1, U2 & U3) on the Nymboida (Impact) and Bellinger (Reference) Rivers, NSW, Australia.

3.2.2 Sample timing

Sampling commenced end of May 2006 during the seasonal winter/spring low flow period following approximately three to four weeks of relatively stable discharge (c.a. 300ML/d) from the Nymboida Weir (Fig 2.3). During the same time period, the upstream discharge decreased gradually to below 500ML/d. A 125ML/d unregulated flow was recorded for the Bellinger River during the same period (Fig 2.3). At the time of this study water was continuously released from the Nymboida Weir at flows of approximately 225ML/d downstream from a background/upstream flow of 550ML/d.

3.2.3 Flow habitats

Before sampling, the extremities of both slow and fast flow habitats were established visually. Five random sampling points for benthic invertebrates were then determined within each of the flow habitats which were each located by means of a tape measure laid along the river's edge (Fig 2.4). Triplicate rocks were then sampled from each of these five random points within both flow habitats, resulting in the collection of 30 rocks per site (5 sets of triplicate rocks per flow environment). Sampling rocks as triplicates serves to improve the precision by providing improved estimates of the benthic invertebrate community within each flow environment and more broadly, locations up -and downstream. The first triplicate rocks were sampled by working upstream from the most downstream random sampling point within the slow flow habitat. This method ensured minimal disturbance within this and the neighbouring fast flow habitat. Rocks of a consistent size (e.g., large cobbles, 128 - 256 mm in diameter, $\phi = -7$, Table 6.2 in Boulton and Brock 1999) were sampled, and those that were more than half-buried avoided. The first rock of each triplicate was selected, removed and its location marked with a labelled wire pin. Subsequent rocks within each triplicate were then selected by taking the two stones approx. 0.5m upstream of the first, forming an equilateral triangle (after Downes *et al.* 1995).

3.2.4 Benthic invertebrates

Benthic invertebrates were collected by placing a hand net (25 cm diameter, 250- μ m-mesh) downstream of each rock. The rock was gently lifted into the net and both were then submerged into a bucket of filtered river water and scrubbed to dislodge fauna. The bucket contents were then filtered through a 250- μ m-mesh sieve and preserved in 70% ethanol. In the laboratory, invertebrates were counted and identified to the lowest practical level of taxonomic resolution (usually species).

3.2.5 Physical and hydraulic variables

Habitat variables for each rock measured prior to its removal included velocity and depth. Velocity was measured directly in front of each rock and at 0.4 of the total stream depth (Marsh- McBirney Flow-mate, Model 2000) above the rock. Depth (± 1 cm) was measured from the upper most point of each rock to the river surface. Stability as 1 (free of substrate) to 5 (embedded) was recorded during the removal of each rock. A further four habitat variables were measured post rock removal. Silt and detritus coverage were graded on a scale of 1 (nil) to 5 (complete coverage), pittedness 1 (smooth) to 5 (heavily pitted, > 60%), and substrate roughness 1 (gravel) to 5 (irregular large boulders) which was measured as the substrate within 0.25m² immediately upstream of the sample rock.

Rock surface area was determined by measuring three orthogonal axes (± 0.5 cm) and then following the lengths based equation of Graham *et al.* (1988). Density of benthic invertebrates was assessed by dividing the sample abundance by its respective rock surface area which was finally expressed as the number of benthic invertebrates per 0.1m²

Water quality sampling was undertaken at all sites at the same time that the benthic invertebrate samples were collected. Water temperature ($^{\circ}$ C), dissolved oxygen (DO, mg/L), pH and conductivity (EC, μ S/cm) were measured with a hand-held YSI 57 Oxygen meter and TPS WP81 pH-Conductivity-Salinity meter.

3.2.6 Data analysis

The mean number of invertebrates of the three rocks sampled from each random sample point was calculated to produce a new composite value expressed as invertebrate density / 0.1m². Compositing three rocks produced one value for each of the five sampling points within each velocity environment within each site. Therefore a total of 5 composite samples from each of two velocity habitats per site were analysed.

The experimental design is a three factor nested analysis of variance (Winer *et al.* 1991). Factors were River (2 levels, fixed), Location (2 levels, fixed), Sites (3 levels) randomly chosen from a subset of a number of riffles up and downstream of the weir, and Habitat (2 levels) being slow and fast flow habitats (Table 3.1). Habitats were fixed within a predetermined velocity range. Five sets of triplicate rocks were composited within each flow habitat within each site, as the level of interest lies in the different flow habitats and not among individual rocks within flow habitats. Sites were unique to one location only. Replicate sites were nested within a single regulated and unregulated location up- and downstream of a weir on the Nymboida River and within a comparable up –and downstream location on the unregulated Bellinger River.

Table 3.1. Three factor nested analysis of variance model with replication at both the site and sample levels. F, fixed factor; R, random factor; d.f., degrees of freedom.

Term	Description of test	F or R	d.f.	No. and description of levels
River = R	Effect of regulation in rivers	F	1	2, regulated and unregulated
Location = L	Effects of location along river	F	1	2, upstream and downstream
R x L	Interaction tests whether rivers vary in location effects		1	
Habitat = H	Effect of velocity	F	1	2, slow or fast
H x R	Interaction tests whether habitats vary in river effects		1	
H x L	Interaction tests whether habitats vary in location effects		1	
H x R x L	Interaction tests whether habitats vary in location and river effects		1	
Site(R x L) = S(R x L)	Estimates variance among sites, which are nested within Rivers and Locations	R	8	3 per location, i.e. 6 sites per river
H x S(R x L)	Estimates whether variability among sites differs between habitats		8	
Error	Replicate benthic samples within each habitat	R	96	5 samples per habitat per site, each a composite of 3 rocks

The interaction term R x L is the main term of interest in the ANOVA model. An interaction between the factors 'river and location' would indicate that differences between upstream and downstream locations vary among rivers. The influence of habitat is between sites within locations. Treatment effects are tested over the interaction term in the ANOVA model. The error term represents individual variability within habitats among sites within a location.

The final ANOVA model was run collectively on both the Nymboida and Bellinger Rivers. The advantage of this analysis is that it reveals the degree to which the slow and fast flow habitats differ within and between both locations and rivers. Species density and diversity measures included species density and taxa richness (total, rheophilic) as well as densities of select individual rheophiles. To meet the ANOVA assumption of normally distributed data and homogeneity of variances, dependent variables were $\log(x+1)$ transformed prior to analysis.

Similarities between assemblages of mean invertebrate densities were analysed using the multivariate analysis package PRIMER (PRIMER-5, Plymouth Marine Laboratory, Plymouth, U.K.)(Clark & Warwick, 1994). To test the null hypotheses that there were no differences between rivers and locations, average differences within groups to differences seen between groups were calculated using analysis of similarities (ANOSIM). Similarities among locations were calculated using the Bray-Curtis similarity on $\log(x+1)$ transformed data. Non-metric multi-dimensional scaling (nMDS) ordination plots were used to graphically represent the patterns of community similarity between flow habitats and locations. Pairwise comparisons were used to test specific differences between slow and fast flowing habitats within and between locations. Individual species contribution to the observed differences between communities between sites and up -and downstream locations were examined separately for each flow environment with the similarity percentage contribution function (SIMPER) in PRIMER.

3.3 Results

3.3.1 Hydraulic characteristics

Stream bed roughness was lower within riffles of the regulated Nymboida River than in the unregulated Bellinger River (Fig. 3.2; Table 3.2). For all remaining hydraulic measures there were no significant effects of river or overall differences between rivers (R term, effect of regulation in rivers, Table 3.2). Silt, detritus and stability were more variable than the terms velocity and depth among sites, which are nested within rivers and locations as well among sites between slow and fast velocity habitats (S(R x L) & H x S(R x L) terms; Table 3.2; Fig. 3.2).

Rock stability was significantly different between up- and downstream locations among rivers (RxL term, Table 3.2; Fig 3.2) and this term explained 41% of the variance. There was no significant River by Location interactions (RxL terms, Table 3.2) for all remaining hydraulic terms and furthermore these terms explained little variance between locations among rivers (refer to SA, Table 3.2). Overall means (\pm SE) in the fast flow habitat had higher water velocities (0.30 ± 0.0189 versus 0.05 ± 0.009 m/s) greater depth (11.1 ± 0.803 versus 2.0 ± 0.188 cm), less silt (1.0 ± 0.0 versus 1.7 ± 0.115) and more stable (2.70 ± 140 versus 2.9 ± 0.138) rocks compared to the slow flow habitat (Fig. 3.2).

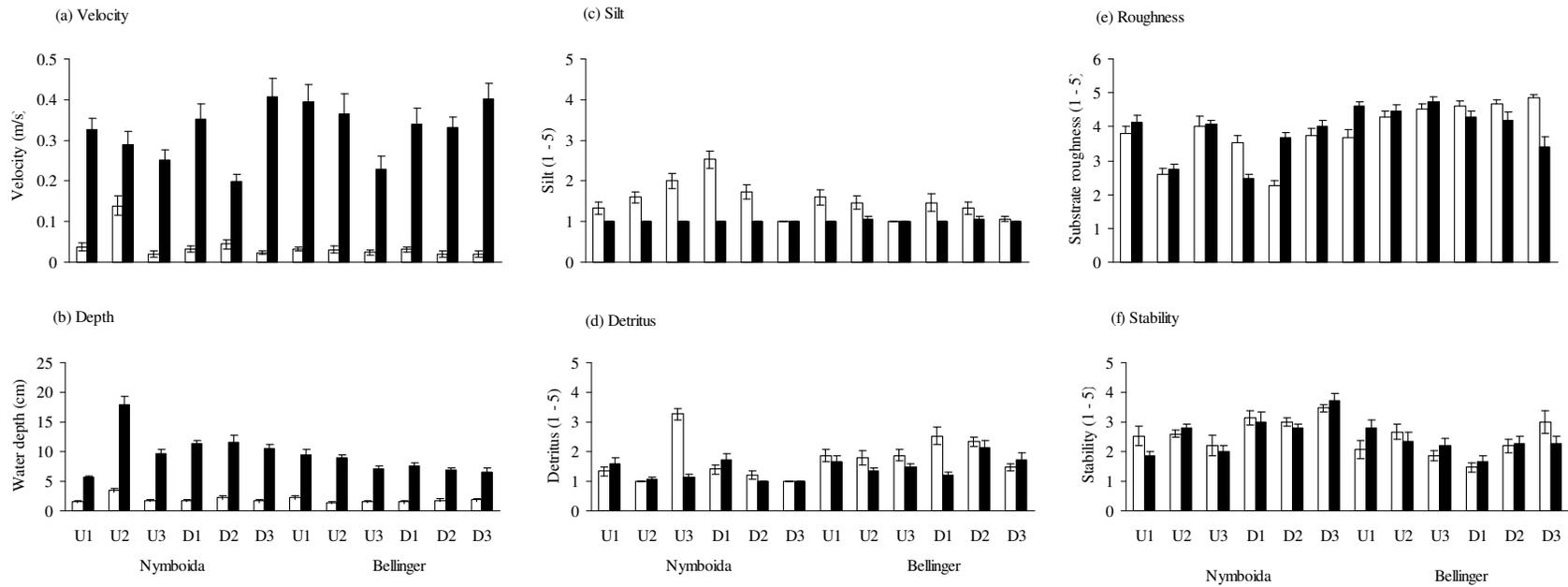


Figure 3.2 Mean (± 1 SE) for (a)velocity, (b)depth, (c)silt, (d)detritus, (e) roughness (f) stability for overall slow and fast flowing habitats within sites between up -and downstream locations on the Nymboida and Bellinger Rivers. Open bars represent slow flow and closed bars represent fast flow.

Table 3.2 Analysis of variance of overall (a) velocity, (b) depth, (c) roughness, (d) silt, (e) detritus, (f) pits, (g) stability;. d.f., degrees of freedom; F, F-ratio; P, significance level; SA, strength of association as percentage variation explained.

	d.f.	F-ratio	P	SA
(a) Velocity				
R	1	0.126	0.732	0.0
L	1	0.044	0.838	0.0
H	1	138.655	0.001	81.7
R x L	1	0.075	0.792	0.0
H x R	1	1.637	0.237	0.7
H x L	1	0.954	0.357	0.0
H x R x L	1	0.097	0.763	0.0
S (R x L)	8	3.305	0.002	2.2
H x S(R x L)	8	3.607	0.001	5.3
Error	96			10.1
(b) Depth				
R	1	2.825	0.131	2.7
L	1	0.161	0.699	0.0
H	1	91.643	0.001	70.2
R x L	1	0.072	0.795	0.0
H x R	1	3.644	0.093	4.1
H x L	1	0.110	0.749	0.0
H x R x L	1	0.326	0.584	0.0
S (R x L)	8	13.179	0.001	8.3
H x S(R x L)	8	6.849	0.001	7.9
Error	96			6.8
(c) Roughness				
R	1	11.174	0.010	32.1
L	1	0.329	0.582	0.0
H	1	0.006	0.939	0.0
R x L	1	0.173	0.689	0.0
H x R	1	0.676	0.435	0.0
H x L	1	1.975	0.198	3.4
H x R x L	1	2.127	0.183	7.9
S (R x L)	8	7.975	0.001	16.5
H x S(R x L)	8	4.437	0.001	16.3
Error	96			23.7
(d) Silt				
R	1	1.775	0.220	2.0
L	1	0.007	0.936	0.0
H	1	14.387	0.005	33.0
R x L	1	0.111	0.748	0.0
H x R	1	2.302	0.168	6.4
H x L	1	0.007	0.935	0.0
H x R x L	1	0.114	0.745	0.0
S (R x L)	8	7.642	0.001	13.2
H x S(R x L)	8	7.457	0.001	25.6
Error	96			19.9

Table 3.2 cont.

	d.f.	F-ratio	P	SA
(e) Detritus				
R	1	3.297	0.107	7.8
L	1	0.067	0.802	0.0
H	1	2.098	0.186	4.3
R x L	1	1.820	0.214	5.6
H x R	1	0.058	0.815	0.0
H x L	1	0.394	0.548	0.0
H x R x L	1	0.597	0.462	0.0
S (R x L)	8	10.007	0.001	18.4
H x S(R x L)	8	11.556	0.001	43.2
Error	96			20.6
(f) Pits				
R	1	3.777	0.088	3.1
L	1	0.201	0.666	0.0
H	1	31.858	0.001	21.4
R x L	1	1.430	0.266	0.9
H x R	1	0.035	0.855	0.0
H x L	1	0.035	0.855	0.0
H x R x L	1	0.000	1.000	0.0
S (R x L)	8	0.886	0.531	0.0
H x S(R x L)	8	0.559	0.809	0.0
Error	96			74.6
(g) Stability				
R	1	5.655	0.045	12.7
L	1	2.331	0.165	5.4
H	1	0.091	0.771	0.0
R x L	1	5.419	0.048	24.1
H x R	1	0.418	0.536	0.0
H x L	1	0.151	0.708	0.0
H x R x L	1	1.355	0.278	1.3
S (R x L)	8	3.960	0.001	12.3
H x S(R x L)	8	1.335	0.236	2.8
Error	96			41.4

3.3.2 Chemical characteristics

Water temperature was consistently elevated (1-2°C) downstream of the Nymboida Weir (Table 3.3). Overall, environmental measures including temperature, pH, dissolved oxygen and water conductivity were similar between the Nymboida and Bellinger Rivers (Table 3.3).

Table 3.3 Chemical variables measured at each site in the Nymboida and Bellinger Rivers.

Site code	Water temperature (°C)	pH	Dissolved oxygen (mg L ⁻¹)	Conductivity(µs cm ⁻¹)
U1	11.2	8.07	13.4	39
U2	12.5	7.69	12.8	87
U3	11.2	8.81	12.2	39
D1	12.3	8.26	11.2	39
D2	12.3	7.51	10.6	missing
D3	12.3	7.89	10.2	37
U1	11	6.81	13.8	76
U2	13	8.01	10.6	70
U3	12	7.5	12.6	72
D1	12	7.32	10.8	63
D2	12	7.68	10	69
D3	13	7.37	10.1	61

3.3.3 Benthic invertebrate density and diversity

Nymboida River (regulated)

A total of 49 taxa were collected from the Nymboida River. Total mean invertebrate densities and total taxa richness per sample were $19.82 \pm 1.1 / 0.1\text{m}^2$ and $10.49 \pm 0.27 / 0.1\text{m}^2$ respectively. The single dipteran species (Simuliidae) had the highest densities on rocks sampled from within riffles, followed by the leptophlebiid mayfly *Austrophlebioides*, baetid mayfly Baetidae G.3 sp.2 and two net spinning caddis flies (*Cheumatopsyche*, *Chimarra*). Rheophiles dominated the total densities of invertebrates found on rocks (83.8%). The measures of rheophilic density and taxa richness were $16.65 \pm 1.01 / 0.1\text{m}^2$ and $6.32 \pm 0.14 / 0.1\text{m}^2$ respectively.

Bellinger River (unregulated)

Fifty-one taxa were collected from the Bellinger River. Overall mean invertebrate densities and the number of different taxa per sample were $15.24 \pm 0.69 / 0.1\text{m}^2$ and $11.23 \pm 0.31 / 0.1\text{m}^2$ respectively. The four most common species were the leptophlebiid mayfly *Austrophlebioides* (22.2%) which dominated followed by baetid mayfly nymphs species deemed to small to identify with confidence, (10.3%) the caddis fly *Cheumatopsyche* (9.8%) and the baetid mayfly, Baetidae G.3 sp.2 (8.8%). Rheophiles made up 81.6% of the samples. Mean rheophilic densities were $12.35 \pm 0.62 / 0.1\text{m}^2$ and

the mean number of different rheophilic taxa per sample were $6.04 \pm 0.15 / 0.1\text{m}^2$ over the same survey period.

3.3.4 Comparison of invertebrate densities between rivers

Total mean invertebrate and total mean rheophilic densities did not significantly differ between rivers (Fig 3.3; R term, Table 3.4). Mean total taxa and rheophilic taxa richness were not significantly different in both rivers (Fig 3.3; R term, Table 3.4). For all measures of mean invertebrate density and taxa richness (total and rheophilic) there was considerable variation among sites nested within rivers and locations as well among sites between slow and fast flow habitats (S(R x L) & H x S(R x L) terms respectively, Table 3.4). These site differences explained between 7.3% and 13.4% of the variance (Table 3.4).

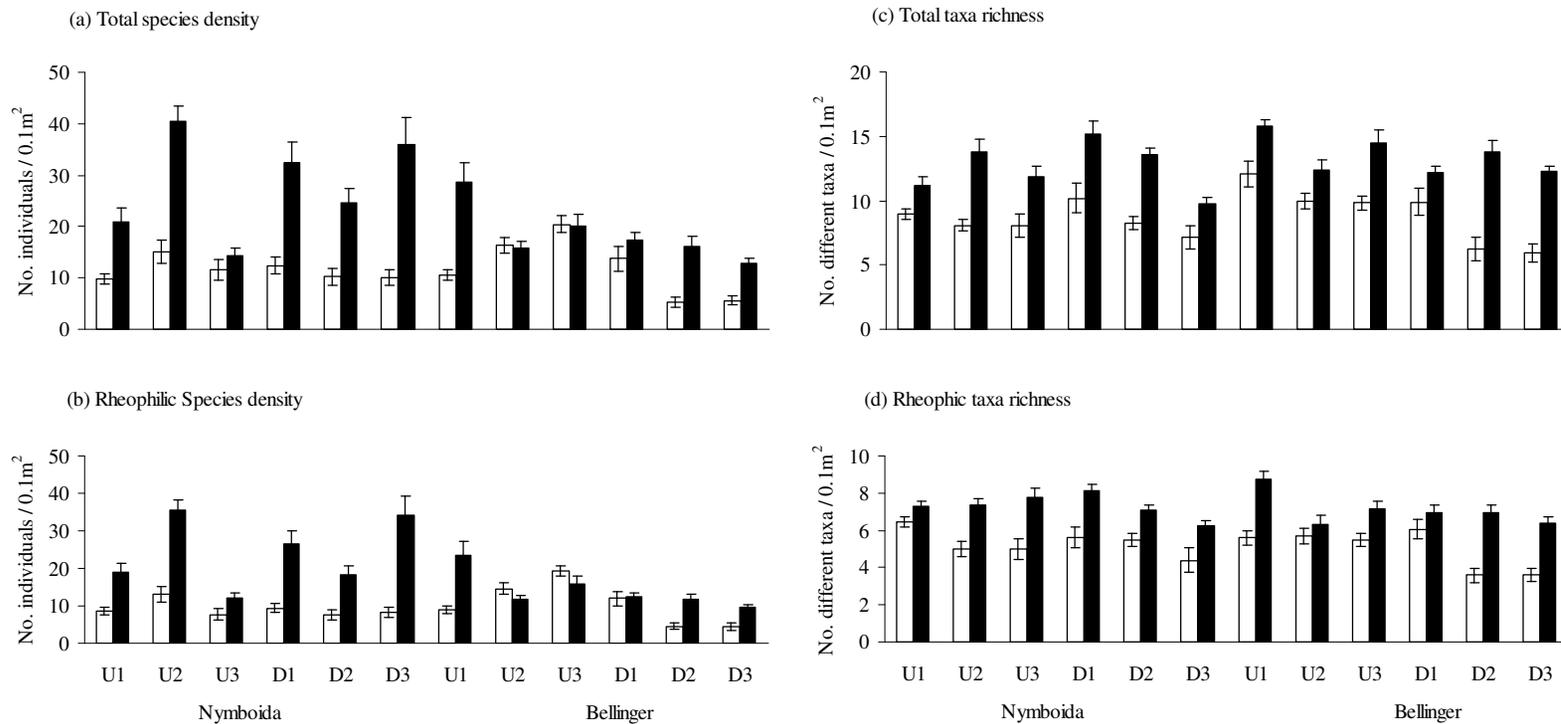


Figure 3.3 Mean ($\pm 1SE$) densities for (a) total species, (b) rheophilic species and the number of different taxa for (c) total species, (d) rheophilic species for overall slow and fast flowing environments within sites between up -and downstream locations on the Nymboida and Bellinger Rivers. Open bars represent slow flow and closed bars represent fast flow.

Table 3.4 Analysis of variance of (a) total species density (b) total taxa richness (c) rheophilic species density (d) rheophilic taxa richness per site as per model in table 3.1. d.f., degrees of freedom; MS, mean square; F, F-ratio; P, significance level; SA, strength of association as percentage variation explained.

Source	d.f.	F-ratio	P	SA
(a) Total species density per site				
R	1	2.346	0.164	2.3
L	1	2.220	0.175	2.6
H	1	32.835	0.001	38.8
R x L	1	4.362	0.070	11.5
H x R	1	2.315	0.167	3.2
H x L	1	2.954	0.124	4.8
H x R x L	1	0.019	0.893	0.0
S (R x L)	8	5.887	0.001	8.5
H x S(R x L)	8	4.210	0.001	11.1
Error	96			17.3
(b) Total taxa richness per site				
R	1	0.497	0.501	0.0
L	1	2.344	0.164	3.3
H	1	63.705	0.001	50.6
R x L	1	2.694	0.139	6.1
H x R	1	0.152	0.707	0.0
H x L	1	2.809	0.132	2.9
H x R x L	1	1.410	0.269	1.2
S (R x L)	8	4.723	0.001	8.6
H x S(R x L)	8	2.126	0.040	5.7
Error	96			21.5
(c) Rheophile species density per site				
R	1	1.931	0.202	1.8
L	1	2.526	0.151	3.8
H	1	26.442	0.001	31.1
R x L	1	3.413	0.102	9.6
H x R	1	5.128	0.053	10.1
H x L	1	2.465	0.155	3.6
H x R x L	1	0.017	0.899	0.0
S (R x L)	8	6.151	0.001	10.0
H x S(R x L)	8	3.778	0.001	10.8
Error	96			19.2

Table 3.4 cont.

Source	d.f.	F-ratio	P	SA
(d) Rheophile taxa richness per site				
R	1	0.618	0.454	0.0
L	1	2.968	0.123	4.3
H	1	41.713	0.001	47.0
R x L	1	0.576	0.470	0.0
H x R	1	0.043	0.841	0.0
H x L	1	0.968	0.354	0.0
H x R x L	1	0.387	0.551	0.0
S (R x L)	8	3.562	0.001	7.7
H x S(R x L)	8	2.225	0.032	7.7
Error	96			33.2

3.3.5 Associations with location on density and diversity

Between rivers

There were no overall differences in invertebrate densities between up -and downstream locations when compared across the regulated and unregulated rivers (non significant L terms, Table 3.4). Locations up -and downstream were not significantly different between rivers for measures of invertebrate density and taxa richness (Fig. 3.3; non significant R x L terms, Table 3.4). Nevertheless invertebrate density and taxa richness (total and rheophilic) varied significantly among sites within flow environments and locations (Fig 3.3; significant H x S(R x L) & S(R x L) terms, Table 3.4).

3.3.6 Associations with velocity on density and diversity

Between rivers (regulated versus unregulated)

Invertebrate densities and numbers of different taxa per sample each showed significant differences between slow and fast flow habitats (H terms, Table 3.4). This term explained 47% of the variance in rheophilic taxa richness (Table 3.4). Overall invertebrate density and diversity did not change significantly within flow habitats between locations. For example, among rivers the rheophilic dipteran Simuliidae was most dense in the fast, and the mayfly *Austrophlebioides* in the slow flow habitat irrespective of up –or downstream locations. *Austrophlebioides* was common to both slow and fast flow habitats (Fig.3.4; non significant H term; Table 3.5).

Nymboida (regulated)

Total mean invertebrate densities per sample in the slow flow habitat were $11.5 \pm 5.0 / 0.1\text{m}^2$ of which *Austrophlebioides* made up 30%. Total mean invertebrate densities in the fast flow habitat were significantly greater ($28.1 \pm 11.0 / 0.1\text{m}^2$) and dominated by a single rheophilic larval dipteran taxon (Simuliidae; 34.6%) and the mayfly *Austrophlebioides* (10.8%) compared to the slow flow habitat over the same survey period.

Bellinger (unregulated)

Total mean invertebrate densities in the slow flow habitat were $12 \pm 6.7 / 0.1\text{m}^2$ and although not as marked an increase as in the regulated Nymboida River, densities were greater by approximately 65% in the fast flow habitat of the Bellinger River ($18.5 \pm 7.3 / 0.1\text{m}^2$). Diptera (Simuliidae) were under-represented in the Bellinger River ($5.5 / 0.1\text{m}^2$) relative to the Nymboida River (Fig 3.5). Greater contribution of rheophiles in the fast flow habitat was attributed to high densities of the mayfly *Austrophlebioides*. Similarly in the slow flow habitat *Austrophlebioides* dominated (Table 3.7).

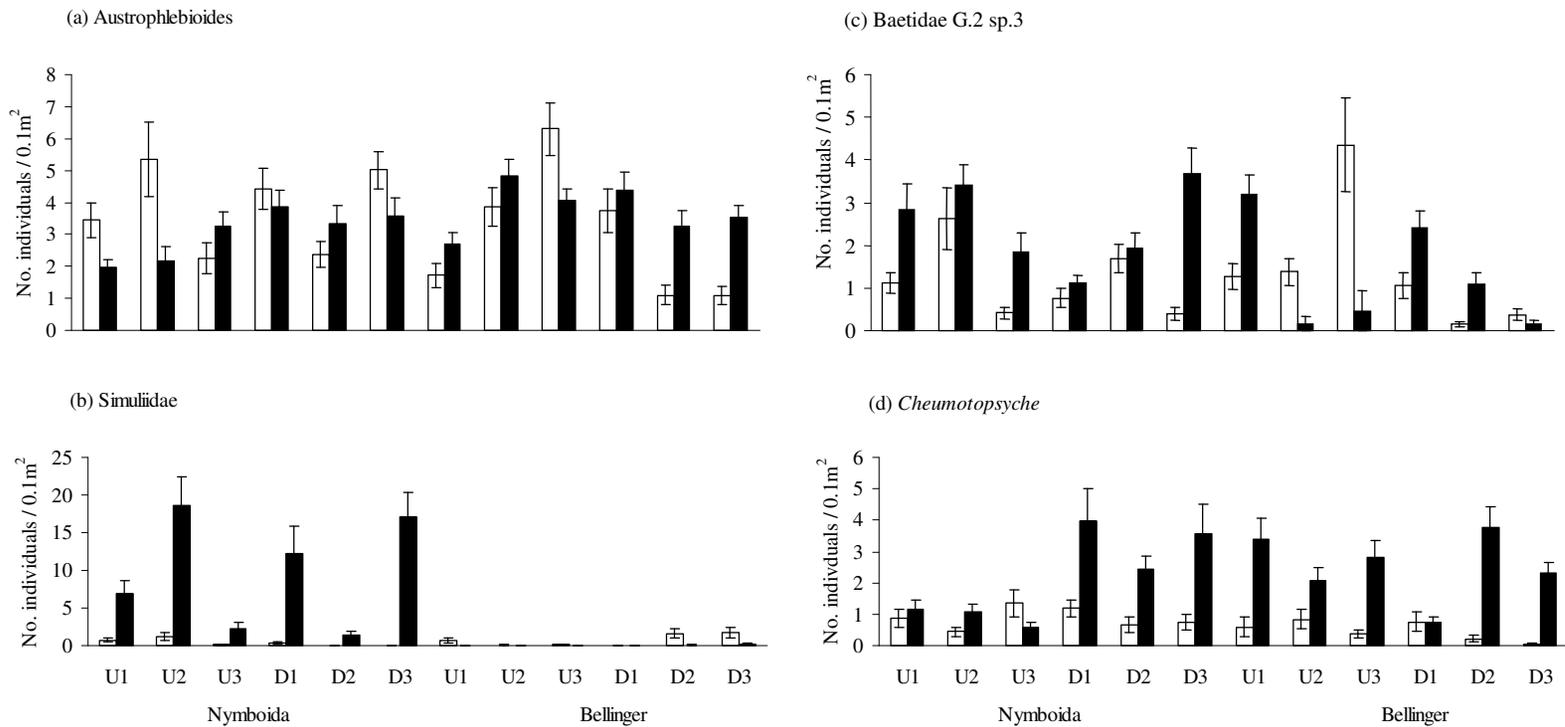


Figure 3.4 Mean (± 1 se) numbers of individuals of (a) *Austrophlebioides* (b) Simuliid (c) *Baetidae G.2 sp.3* (d) *Cheumatopsyche* for overall slow and fast flowing environments within sites between up - and downstream locations on the Nymboida and Bellinger Rivers. Open bars represent slow flow and closed bars represent fast flow.

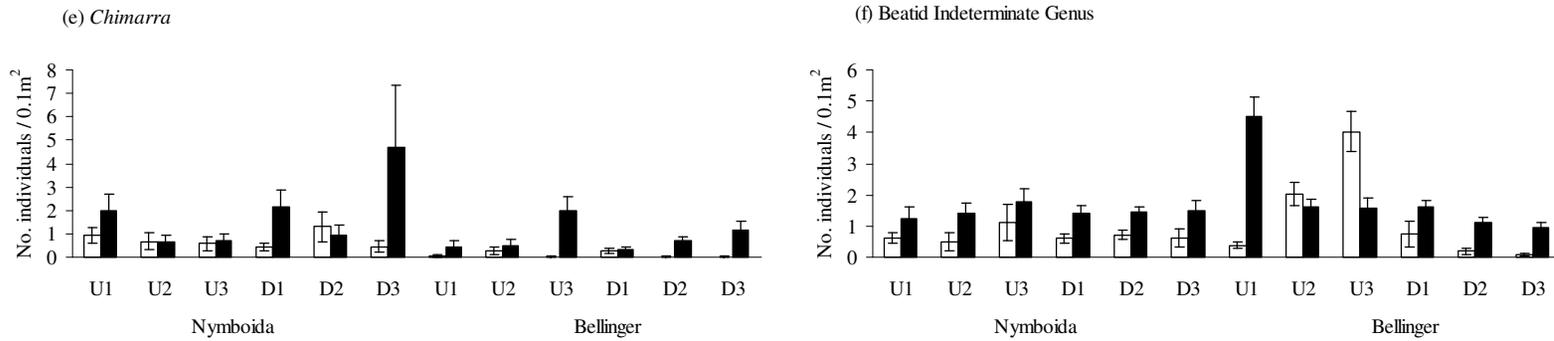


Figure 3.4 cont. Mean (± 1 se) numbers of individuals of (e) *Chimarra* (f) Baetid indeterminate genus for overall slow and fast flowing environments within sites between up -and downstream locations on the Nymboida and Bellinger Rivers. Open bars represent slow flow and closed bars represent fast flow.

Table 3.5 Analysis of variance of mean densities for total numbers of individuals for (a) *Austrophlebioides* (b) Simuliids (c) Baetidae G.2 sp.3 (d) *Cheumatopsyche* (e) *Chimarra* (f) Baetidae indeterminate genus per site as per model in table 3.1. d.f., degrees of freedom; F, F-ratio; P, significance level; SA, strength of association as percentage variation explained.

	d.f.	F-ratio	P	SA
(a) <i>Austrophlebioides</i>				
R	1	0.118	0.740	0.0
L	1	0.160	0.700	0.0
H	1	0.504	0.498	0.0
R x L	1	2.502	0.152	11.1
H x R	1	4.286	0.072	13.9
H x L	1	2.853	0.130	7.8
H x R x L	1	0.483	0.507	0.0
S (R x L)	8	7.910	0.001	19.4
H x S(R x L)	8	4.503	0.001	19.7
Error	96			28.0
(b) Simuliidae				
R	1	11.904	0.009	16.8
L	1	0.002	0.967	0.0
H	1	11.681	0.009	9.6
R x L	1	0.684	0.432	0.0
H x R	1	27.321	0.001	47.1
H x L	1	0.009	0.929	0.0
H x R x L	1	0.578	0.469	0.0
S (R x L)	8	9.876	0.001	8.3
H x S(R x L)	8	5.723	0.001	8.9
Error	96			9.4
(c) Baetidae G.2 sp.3				
R	1	1.915	0.204	3.1
L	1	1.568	0.246	1.8
H	1	1.346	0.279	1.2
R x L	1	0.233	0.642	0.0
H x R	1	2.802	0.133	12.6
H x L	1	1.060	0.333	0.4
H x R x L	1	1.254	0.295	3.6
S (R x L)	8	9.184	0.001	17.9
H x S(R x L)	8	9.556	0.001	37.5
Error	96			22.0

Table 3.5 cont.

	d.f.	F-ratio	P	SA
(d) <i>Cheumatopsyche</i>				
R	1	0.233	0.642	0.0
L	1	2.220	0.175	0.0
H	1	28.870	0.001	36.3
R x L	1	13.920	0.006	12.0
H x R	1	2.623	0.144	4.2
H x L	1	2.166	0.179	3.0
H x R x L	1	2.963	0.123	10.2
S (R x L)	8	1.233	0.288	0.5
H x S(R x L)	8	3.472	0.001	11.1
Error	96			22.5
(e) <i>Chimarra</i>				
R	1	16.132	0.004	14.8
L	1	0.574	0.470	0.0
H	1	11.342	0.010	20.0
R x L	1	1.065	0.332	0.1
H x R	1	0.098	0.763	0.0
H x L	1	0.610	0.457	0.0
H x R x L	1	0.839	0.386	0.0
S (R x L)	8	1.143	0.342	0.7
H x S(R x L)	8	2.265	0.029	13.0
Error	96			51.3
(f) Baetidae indeterminate genus				
R	1	2.564	0.148	1.1
L	1	13.142	0.007	6.6
H	1	6.785	0.031	16.3
R x L	1	14.053	0.006	18.6
H x R	1	0.001	0.982	0.0
H x L	1	0.516	0.493	0
H x R x L	1	0.228	0.646	0.0
S (R x L)	8	1.549	0.151	1.5
H x S(R x L)	8	6.110	0.001	28.2
Error	96			27.7

3.3.7 Association between regulation and community composition

Differences in community composition between the Nymboida and Bellinger Rivers were attributable to higher densities of mayfly nymphs (*Austrophlebioides*, Baetidae G.2 sp.3), dipteran larva (Simuliidae) and the filter feeding caddisfly *Chimarra* in the Nymboida River (Fig 3.5). The exception was the dipteran larva (Simuliidae) which was very rare and even absent from sites in the Bellinger River. Overall, locations up -and downstream and slow and fast flowing habitats differed ($p = 0.001$ and 0.001 respectively). Taxa

contribution is typically greater upstream and in the fast flowing habitats (Table 3.7). Significant differences between up -and downstream locations when rivers were analysed separately suggests a different community composition between locations up -and downstream on the regulated versus unregulated river (Table 3.6). There were also differences between rivers within locations and flow habitats – the slow flow habitat within both locations on the Nymboida River had higher numbers of the mayfly nymph *Austrophlebioides* and downstream lower numbers of Baetidae G.2 sp.3. Most taxa showed higher numbers within the fast flow habitat in the Nymboida River with the exception being the dipteran larva (Simuliidae) which was in much higher numbers compared to its' respective flow habitat within locations on the Bellinger River (Table 3.6).

3.3.8 Associations with location on community composition

Two-way ANOSIM indicated that locations up -and downstream were associated with shifts in community composition (Table 3.6). Within the slow flow habitat all tests between up -and downstream locations were significant (Table 3.6). Similarly, within the fast flow habitat all tests between up -and downstream locations were significant with the exception of the non-significant result for all rheophiles and common rheophiles (Bellinger upstream versus downstream, Table 3.6) - suggestive of no natural longitudinal change downstream in these two dependant variables in community composition within the fast flow habitats in the unregulated Bellinger River.

3.3.9 Effects of velocity on community composition

Community composition differed significantly between slow and fast flow habitats (Table 3.6). Two-way ANOSIM indicated that both slow and fast flowing habitats within locations and rivers were associated with shifts in community composition (Table 3.6). Species contribution in the slow flow habitat was associated with high densities of Ephemeroptera (*Austrophlebioides*, Baetidae G.2 sp.3), Hydropsychidae (*Cheumatopsyche*), *Thienemanniella* and also downstream on the Bellinger River high numbers of a single Psephenid species (*Schlerocyphon* F) (Table 3.7). Fast flow habitats were generally associated with more different types of taxa including Ephemeroptera

(*Austrophlebioides*, Baetidae G.2 sp.3.), Hydropsychidae (*Cheumatopsyche*, *Asmicridea* AV1) and Hydroptilidae (*Hydroptila*). Very high densities of dipteran larvae (Simuliidae) were associated with the fast flowing habitat both up -and downstream on the Nymboida River. SIMPER analysis showed that both slow and fast flowing habitats irrespective of location or river were associated with higher numbers of the nymphal mayfly *Austrophlebioides* (Table 3.7).

3.3.10 Taxonomic resolution

Measures of total density and diversity were similar between rivers and locations. Total densities and in particular densities of certain individuals showed clear patterns of an affinity towards a preferred flow environment. Separate ordinations (nMDS) of total invertebrates, rheophilic invertebrates and common rheophiles showed consistent patterns between and within rivers, locations and flow habitats (Fig 3.5). However, common rheophiles show tighter groupings within flow habitats and between locations and lower values of R from ANOSIM (fewer significant differences is reflective of increasingly less difference between groups for this term $p = 0.08$; Fig 3.5).

Table 3.6 Results of ANOSIM tests carried out on matrices of similarities among sites using All species, All rheophiles and Common rheophiles species level data for both rivers combined and for individual rivers.

Test comparison	All species		All rheophiles		Common rheophiles	
	R	P	R	P	R	P
Global tests						
Between rivers	0.224	0.001	0.1	0.001	0.064	0.001
Between up-and downstream locations	0.054	0.001	0.045	0.01	0.034	0.008
Between flow environments	0.319	0.001	0.276	0.001	0.261	0.001
Pairwise tests between up-and downstream locations						
Among rivers						
Upstream-Nymboida versus Bellinger	0.434	0.001	0.236	0.001	0.207	0.001
Downstream-Nymboida versus Bellinger	0.231	0.001	0.166	0.001	0.109	0.001
Within rivers						
Nymboida-upstream versus downstream	0.233	0.001	0.178	0.001	0.149	0.001
Bellinger-upstream versus downstream	0.11	0.001	0.11	0.001	0.105	0.001
Pairwise test between slow and fast flow environments						
Nymboida upstream versus downstream	0.473	0.001	0.178	0.001	0.149	0.001
Bellinger upstream versus downstream	0.482	0.001	0.11	0.001	0.105	0.001
Within upstream						
Nymboida	0.391	0.001	0.398	0.001	0.35	0.001
Bellinger	0.797	0.001	0.47	0.001	0.452	0.001
Within Downstream						
Nymboida	0.67	0.001	0.612	0.001	0.581	0.001
Bellinger	0.513	0.001	0.499	0.001	0.43	0.001
Pairwise test within slow and fast flow environments						
Slow flow						
Between rivers	0.328	0.001	0.181	0.001	0.097	0.001
Between up-and downstream locations	0.11	0.001	0.097	0.001	0.079	0.002
Within locations						
Upstream-Nymboida versus Bellinger	0.631	0.001	0.328	0.001	0.302	0.001
Downstream-Nymboida versus Bellinger	0.494	0.001	0.385	0	0.197	0.001
Between locations						
Nymboida upstream versus downstream	0.298	0.001	0.128	0.01	0.097	0.029
Bellinger upstream versus downstream	0.419	0.001	0.39	0.001	0.33	0.001
Fast flow						
Between rivers	0.616	0.001	0.427	0.001	0.378	0.001
Between up-and downstream locations	0.084	0.01	0.056	0.032	0.058	0.028
Within locations						
Upstream-Nymboida versus Bellinger	0.825	0.001	0.517	0.001	0.473	0.001
Downstream-Nymboida versus Bellinger	0.631	0.001	0.615	0.001	0.567	0.001
Between locations						
Nymboida upstream versus downstream	0.431	0.001	0.428	0.001	0.415	0.001
Bellinger upstream versus downstream	0.202	0.004	0.061	0.115	0.073	0.08

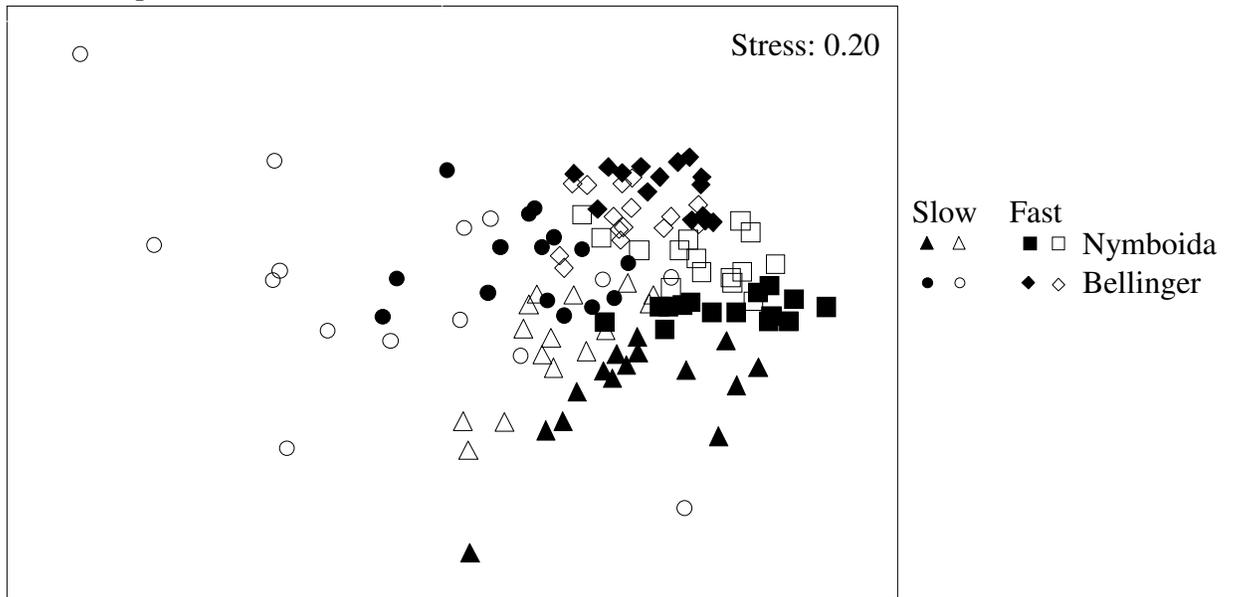
Table 3.7 Species contribution for slow and fast flow environments within the Nymboida and Bellinger Rivers.

Source	Species	Taxon	Mean density (number/ 0.1m ²)	Contribution %
Nymboida				
Slow upstream	<i>Austrophlebioides</i>	Ephemeroptera	3.68	37.65
	Baetidae G.2 sp.3	Ephemeroptera	1.38	10.49
	<i>Cheumatopsyche</i>	Hydropsychidae	0.89	9.37
	Baetidae IG	Ephemeroptera	0.74	7.4
	<i>Chimarra</i>	Philopotamidae	0.74	6.93
	<i>Tipulidae</i>	Chironomidae	0.84	5.82
Slow downstream				
Slow downstream	<i>Austrophlebioides</i>	Ephemeroptera	3.94	36.64
	<i>Thienemanniella</i>	Chironomidae	0.88	11.66
	Baetidae G2 sp.3	Ephemeroptera	0.95	10.13
	<i>Corynoneura</i>	Chironomidae	0.05	7.8
	<i>Cheumatopsyche</i>	Hydropsychidae	0.86	7.56
	Baetidae IG	Ephemeroptera	0.65	6.69
Fast upstream				
Fast upstream	Simuliidae	Diptera	9.28	18.8
	<i>Austrophlebioides</i>	Ephemeroptera	2.47	15.58
	Baetidae G.2 sp.3	Ephemeroptera	2.7	15.14
	<i>Asmicridea</i> AV1	Hydropsychidae	3.65	10.97
	Baetidae IG	Ephemeroptera	1.47	9.17
	<i>Cheumatopsyche</i>	Hydropsychidae	0.95	6.41
Fast downstream				
Fast downstream	<i>Austrophlebioides</i>	Ephemeroptera	3.58	17.84
	Simuliidae	Diptera	10.2	15.69
	<i>Cheumatopsyche</i>	Hydropsychidae	3.31	15.11
	Baetidae G.2 sp.3	Ephemeroptera	2.24	11.54
	Baetidae IG	Ephemeroptera	1.44	10.17
	<i>Chimarra</i>	Philopotamidae	2.6	7.35
Bellinger				
Slow upstream	<i>Austrophlebioides</i>	Ephemeroptera	3.9	29.96
	Baetidae G.2 sp.3	Ephemeroptera	2.01	15.49
	<i>Thienemanniella</i>	Chironomidae	1.71	14.17
	Baetidae IG	Ephemeroptera	1.8	9.37
	<i>Oecitis</i>	Leptoceridae	0.98	8.72
	<i>Thienemannimyia</i>	Chironomidae	0.85	7.81

Table 3.7 cont.

Source	Species	Taxon	Mean density (number/ 0.1m ²)	Contribution %
Slow downstream	<i>Austrophlebioides</i>	Ephemeroptera	1.97	29.6
	<i>Schlerocyphon F</i>	Psephenidae	1.13	17.39
	<i>Thienemannimyia</i>	Chironomidae	0.64	13.85
	Baetidae G.2 sp.3	Ephemeroptera	0.52	8.29
	<i>Austrolimnius</i> Larvae	Elmidae	0.35	6.04
Fast upstream	<i>Austrophlebioides</i>	Ephemeroptera	4	22
	<i>Hydroptila</i>	Hydroptilidae	3.33	18.24
	Baetidae IG	Ephemeroptera	2.32	13.04
	<i>Cheumatopsyche</i>	Hydropsychidae	2.26	11.97
	Baetidae G.2 sp.3	Ephemeroptera	1.56	5.08
	<i>Thienemannimyia</i>	Chironomidae	0.68	4.59
	<i>Thienemanniella</i>	Chironomidae	0.57	3.84
Fast downstream	<i>Austrophlebioides</i>	Ephemeroptera	3.73	25.29
	<i>Cheumatopsyche</i>	Hydropsychidae	2.27	14.4
	Baetidae IG	Ephemeroptera	1.23	12.55
	<i>Thienemannimyia</i>	Chironomidae	1.03	8.79
	Baetidae G.2 sp.3	Ephemeroptera	1.22	6.3
	<i>Chimarra</i>	Philopotamidae	0.72	5.89
	<i>Hydroptila</i>	Hydroptilidae	1.44	5.63

(a) Total species



(b) Total rheophiles

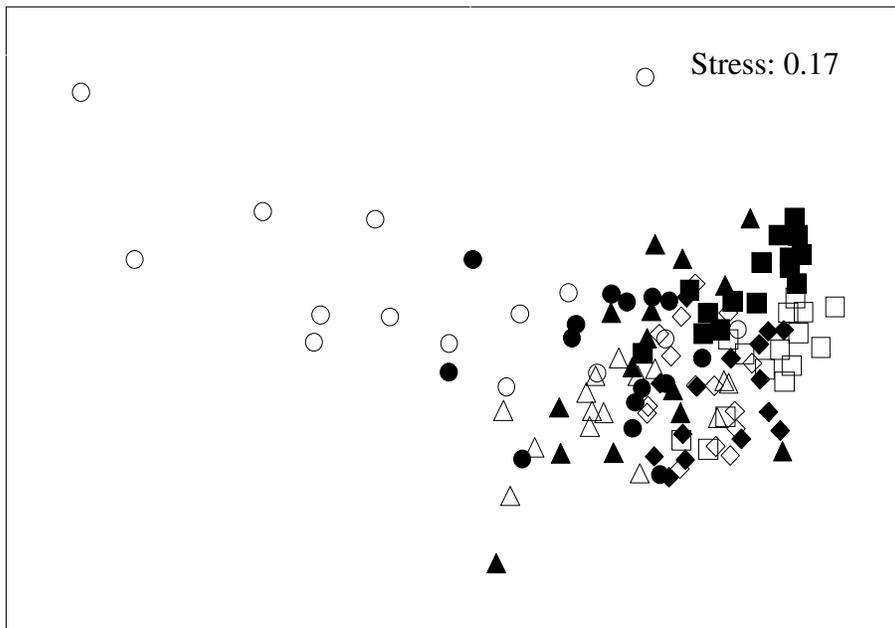


Figure 3.5 MDS plots of (a) Total invertebrates (b) Total rheophiles for slow and fast flow habitats within up - and downstream locations on the Nymboida and Bellinger Rivers. Closed symbols represent upstream sites and open symbols represent downstream sites.

(c) Common rheophiles

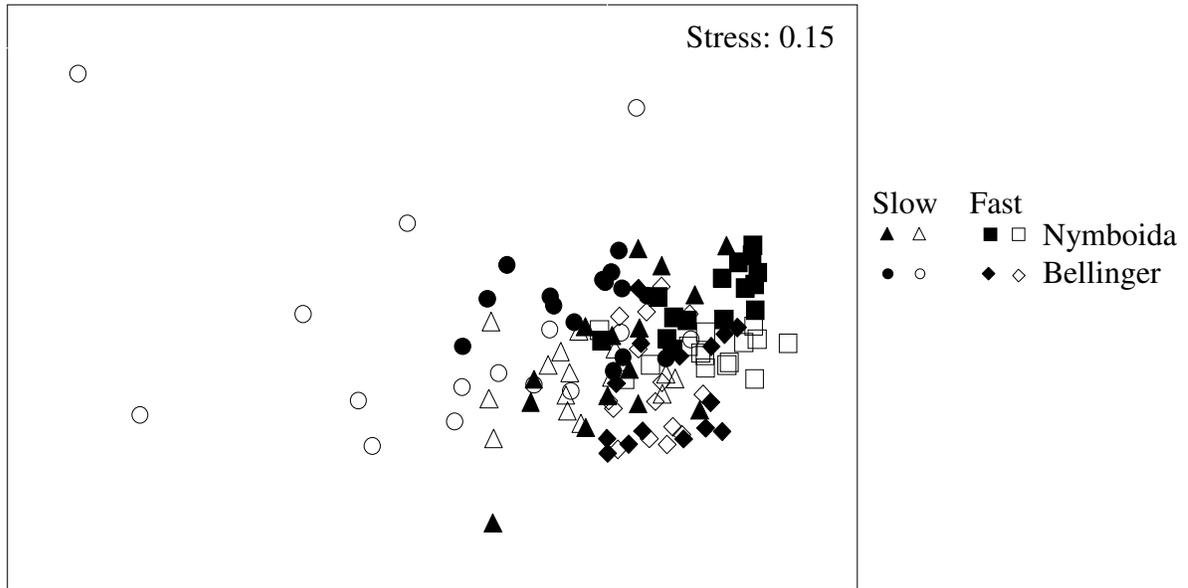


Figure 3.5 cont. MDS plots of (c) common rheophiles for slow and fast flow habitats within up - and downstream locations on the Nymboida and Bellinger Rivers. Closed symbols represent upstream sites and open symbols represent downstream sites.

3.4 Discussion

River reaches downstream from weirs were expected to experience press disturbances (Lake, 2000), extending periods of low flows and potentially exacerbating the reduction of invertebrate density and diversity (Cowx *et al.*, 1984; Englund & Malmqvist, 1996; Malmqvist & Englund, 1996; Rader & Belish, 1999; McIntosh *et al.*, 2002; Kinzie *et al.*, 2006). Alternatively on the unregulated Bellinger River that is absent from any influence of a weir, a natural longitudinal change in the invertebrate fauna from the upper reaches downstream and through the extent of the study reach is to be expected (Vannote *et al.*, 1980; Allen, 1995; Poff *et al.*, 1997). One aspect of this study relates specifically to the contrast of the difference between up -and downstream locations on the Nymboida River versus the average difference between locations on the Bellinger River. More specifically the hypothesis predicts the downstream sites on the Nymboida River to have lower

density and diversity relative to the unregulated sites and this difference to coincide with the location of the Nymboida Weir.

Regulated sites on the Nymboida River were not collectively poorer in either density or diversity of benthic invertebrates. Therefore the hypothesis predicting upstream versus downstream differences was rejected. Low flows on the Bellinger River were similar to uninterrupted low flows upstream of the Nymboida Weir, yet each location was seen to have a similar invertebrate assemblage. Benthic invertebrates are adaptable to the natural variability in river flows (Allen, 1995; Bunn & Arthington, 2002). High invertebrate resilience to disturbance is attributed to their evolved life history characteristics (Lake, 2000). Availability of suitable habitat and internal refugia in up -and downstream locations provide sources for invertebrates for recolonisation (Lancaster & Hildrew, 1993; Bunn & Arthington, 2002). Barriers such as dams and weirs may also hamper recolonisation of disturbed sections downstream by stream drift (Svendsen *et al.*, 2004; Tiemann *et al.*, 2005). Site to site variation was significant and this may have contributed to the lack of distinct up -and downstream patterns. However invertebrate persistence downstream of the Nymboida Weir implies that there remains within the benthic invertebrate community the capacity to recovery from the effects of regulated flows.

The effect of the flow habitat was sufficiently strong within sites to suggest that these two different flow categories provide distinctive habitats for invertebrate communities. Despite the degree to which slow and fast flow habitats explained variation in invertebrate composition, higher densities in the fast flowing habitat did not mean this habitat harboured a characteristic assemblages of invertebrates. MDS and SIMPER showed that there was considerable overlap in the composition of samples from the different flow habitats. This is not unexpected, given that very few taxa were found exclusively in either habitat and invertebrate composition is highly variable throughout different environments, as many benthic invertebrates are not only highly mobile, but different types of substrate naturally provide greater diversity of habitats (Rabeni & Gibbs, 1980; Barmuta, 1989).

Suren et al. (2003a) quantified changes to the invertebrate community in two New Zealand North Island Rivers during summer low flows with a particular interest in examining the degree to which nutrient enrichment influenced how the community altered over time. The invertebrate community during low flows changed least in the unenriched river and most in the enriched river, implying that the changes were due to the nutrient status of each river and associated productive capacity of the enriched river during low flows. Thus algal resources can regulate foraging activities of invertebrates (Poff, 1992; Poff & Ward, 1995) as can the degree of the response of algae as an invertebrate food source to low flow conditions (Hart & Finelli, 1999; Suren *et al.*, 2003b). My study showed similarities among the measured environmental variables and the dominance of rheophiles including detritivores, grazers and filter feeders even though flow was reduced downstream from the weir. This implies that sufficient slow and fast flowing habitats and a suitable supply of food resources remained downstream, enabling the persistence of similar benthic invertebrate densities in the regulated and unregulated section of the Nymboida River. My study did not sample periphyton communities at the time of sampling for benthic invertebrates and I suggest that this may help explain the similarities in macroinvertebrates at up –and downstream sites.

The response of invertebrates which have specific velocity requirements could be valuable in monitoring the effects of flow reductions or improvements with enhanced flows in the Nymboida River. This approach rather than monitoring the entire benthic community composition will improve our confidence that we can successfully measure the condition of the Nymboida River and its movement towards or away from the reference condition in response to changes in flow regime. The grouping by *Growns et al.* (1994) of benthic invertebrates with similar morphological or behavioural adaptations to flow into the flow exposure groups: obligate, facultative, and avoiders provides insight into the response of benthic invertebrates to local flow conditions. Their study showed that the obligate group was most abundant in turbulent habitats with high shear velocities and low amounts of organic matter and that the obligate group contained Simuliids and many filter feeders that rely on the continuing supply of suspended material within the water column on which to feed. In my study, rheophiles (obligates) such as dipteran

nymphs (Simuliidae), the mayflies (*Austrophlebioides*, Baetidae G.2 sp.3), and caddisflies Hydropsychidae (*Cheumatopsyche*) were also most dense in the fast flowing habitats and albeit in lower densities, rheophiles dominated the slow flow habitat. My results suggest that taxa specific habitat preferences exist in the Nymboida River which was to be expected and which is also reflected in the literature. Thus, as densities are generally higher with faster flows this is important when considering the implications of low flow periods, their effect on available riffle habitat and consequences for the invertebrate community.

Anderson and Howland (1998) estimated changes in discharge in the Nymboida River results in marked changes in wetted area. At the median flow of 898 ML/d there is 145,000 m² of riffle available downstream of the Nymboida Weir which declines by nearly two thirds (50,000 m²) at 211 ML/d. Natural low flows were indeed reduced downstream of the Nymboida Weir and declining flows are associated with declining habitat heterogeneity. Therefore within the Nymboida River, declines in fast flowing habitats will inevitably lead to declines in invertebrate densities and potentially declines of those taxa with a particular affinity for fast flowing conditions.

Over 50 invertebrate taxa were identified in this study and those conducted by the Technical Advisory Panel (2002) and Kneipp and Hunter (1999). Although the methods of Technical Advisory Panel (2002) and by Kneipp and Hunter (1999) differed to my study, the invertebrate composition found in riffles was similar. Kneipp and Hunter (1999) concluded that invertebrate abundance and richness was greater upstream of the Nymboida Weir and that taxa correlating with higher water velocity and coarser substrate included *Archichauliodes*, *Austrophlebioides*, Baetidae sp1, *Cheumatopsyche*, Elmidae, *Iliesperla* and Simuliidae whereas Chironomidae, *Caridina indistincta*, *Paratya australiensis*, *Micronecta* spp, and *Tasmanocoenis* and *Triplectides* appeared to prefer relatively lower flows. Based on these studies (Kneipp & Hunter, 1999; Boulton *et al.*, 2002) and my survey, the riffle habitats in the Nymboida River support high densities of benthic invertebrates from a broad range of taxa, many of which are key fish food or highly valuable for their role in the breakdown of organic matter. The heterogeneity of

habitats varying in flow and substrate size in riffles including those in the Nymboida River is certainly a key factor driving these high levels of diversity (Allen, 1995; Boulton & Brock, 1999).

Common rheophiles such as the mayflies (*Austrophlebioides*, Baetidae G.2 sp3), and caddisflies Hydropsychidae (*Cheumatopsyche*) were not negatively affected by the influence of reduced flows downstream of the Nymboida Weir. Most rheophilic taxa persisted albeit at lower densities in the slow flowing habitat. Simuliidae in this study as in others on the Nymboida River appeared specifically adapted to fast flowing habitats (Kneipp & Hunter, 1999). There was considerable overlap between the faunal composition of slow and fast flowing habitats, however rheophiles consistently occurred at greater densities within the faster flowing habitats. This association highlights the need to consider species density as opposed to presence absence data when selecting indicator species for monitoring changes in flow. The rheophilic component of the common taxa show promise as indicators for monitoring naturally low and artificially created low flows or indeed improvements under enhanced flows, as their densities appear to be reduced or augmented by decreases in flow.

In conclusion, my study showed the two flow habitats identified within the riffles on the Nymboida and Bellinger Rivers to have a characteristic invertebrate community. Invertebrates were most dense in the areas of riffles with faster flows, presumably where adequate food resources were presents. This study demonstrated that densities of common rheophiles were highest in fast flow habitats, implying their value as 'indicator taxa' to detect ecologically-relevant changes in flow in the Nymboida River. Finally I suggest it is important to consider variations in the duration and magnitude of flows and associated periphyton communities because naturally occurring low flows can alter the invertebrate response, and I predict similar effects on benthic invertebrates with artificially reduced low flows (Poff *et al.*, 1997; Suren *et al.*, 2003a). To test this prediction I conducted a manipulative experiment which is presented in the following chapter (Chapter 4).

4 Short term redistribution of benthic invertebrates in response to experimental manipulation of flow in a regulated subtropical river

4.1 Introduction

Small weirs and large dams have changed the natural flow regime of rivers (Boulton & Brock, 1999; Bunn & Arthington, 2002; Dewson *et al.*, 2007a). Hydraulic variables intrinsic to the physical and ecological processes in natural river systems have been altered by affecting flow magnitude, quality, timing, duration and rate of change of specific flow events (Bunn & Arthington, 2002). The interacting physical forces of flowing water govern individual aquatic invertebrate densities (Statzner *et al.*, 1988; Hart & Finelli, 1999; Lake, 2000). Water velocity has often been associated with the physical environment and the distribution and abundance of benthic invertebrates (Growth & Davis, 1994; Englund & Malmqvist, 1996; Malmqvist & Englund, 1996; Rader & Belish, 1999; Bunn & Arthington, 2002; Brooks *et al.*, 2005). However, mean water velocity is not a unique descriptor of the physical environment or of specific species - environment relationships, as flow in natural systems is complex varying in space and time. Flow is three dimensional (i.e., longitudinal, vertical, and lateral) and affected by environmental variables such as substrate roughness (Statzner *et al.*, 1988; Brooks *et al.*, 2005).

Water velocity is of particular importance to stream invertebrates and species traits contribute to an invertebrates preference of a particular flow velocity (Statzner *et al.*, 1988; Statzner & Holm, 1989; Ericksen *et al.*, 1996; Frutiger, 1998). Studies have associated invertebrate density with water velocity in the laboratory (Hansen *et al.*, 1991) and in the field (Statzner *et al.*, 1987; Hansen *et al.*, 1991; Hart & Finelli, 1999) and these studies reported stream invertebrates showing preference to a particular water velocity (Table 1.1). Invertebrates often rely on faster flows for delivery of food and fast flows can serve as refuges from predation (Hansen *et al.*, 1991). Some studies report variable invertebrate density and diversity associations with velocity (Rader & Belish, 1999; Suren *et al.*, 2003a), however in other situations density and diversity increases with

increased velocity as more faster flowing habitat areas and heterogeneity within these habitats is maintained with increased flows and their associated higher water velocities (Moog, 1993; Growns & Davis, 1994; Quinn & Hickey, 1994). Therefore if velocity is important in describing the distribution of invertebrates in different habitats within the Nymboida River it would suggest that changes in water velocity in response to changes in flow regime would affect invertebrate density and diversity.

Many studies have investigated the effects of altered flow regimes from instream structures such as weirs (review in Dewson *et al.*, 2007a). Perhaps the most pronounced effect on the benthic invertebrate community is the reduction in water discharge and consequent changes in flow velocity downstream from the diversion (Dewson *et al.*, 2007a). Generally, a disturbance producing a reduction in flow is expected to decrease aquatic invertebrate density and diversity downstream from the point of the disturbance (Poff *et al.*, 1997; Bunn & Arthington, 2002; Richter *et al.*, 2006). Hence, the community response downstream from a disturbance may also reflect the change in density and diversity as a result of the reduction in discharge (section 1.1.4).

Benthic invertebrates can be both resistant and resilient to the effects of reduced or increased flows (Gunderson, 2000). Because of their evolved morphologies and life history patterns, many benthic invertebrates are well adapted to withstanding the high water velocities associated with natural disturbances such as floods and freshes (Statzner & Holm, 1989). This inherent affinity for fast flows and resilience to disturbance of many benthic invertebrates suggests the capacity of invertebrates to recover in response to enhanced flows in an anthropogenically disturbed system where flows have been reduced is possible when suitable habitat for colonisation persists.

This experiment investigated changes in aquatic invertebrate distribution on stones in response to the experimental manipulation of flow velocity in a slow and a fast flowing habitat (section 2.1.6, Fig 2.4) at four riffles in a regulated river (2 riffles upstream - and downstream of a weir). Specifically, this experiment aimed to test two main hypotheses.

First, if velocity is the primary driver of an observed invertebrate response and assuming that an increase in flow leads to an increase in invertebrate densities, then I expect the effects of a local experimental increase of water velocity in the slow flow habitat to create more fast flow habitat and where a non-disturbed faunal response is to be expected upstream, increase species density and diversity (total and rheophilic). Secondly, I expect the effects of a local experimental decrease of water velocity in the fast flow habitat upstream to create more slow flow habitat and decrease species density and diversity (total and rheophilic). Downstream, where an altered response reflecting some long-term influence of the weir is expected, I hypothesise for the same density and diversity measures as above, no change in density or diversity (total and rheophilic) in the slow flow habitat and a similar positive response or increase in species density and diversity (total and rheophilic) in the fast flow habitat.

The idea of a target scenario for river flow management may be drawn from the outcomes of this experiment, whereby changes in the density and diversity of benthic invertebrates due to an experimental increase or decrease of water velocity within treatments may result in the manipulated treatments moving away from their pre-manipulated state and towards their respective control or 'target' flow habitats. These hypotheses address our capacity to detect the effect of velocity and how consistent the invertebrate response is across different flow habitats both within each site, and between sites and locations. Additionally, these hypotheses test whether the invertebrate community downstream potentially retains the capacity to recover from approximately 80 years of regulated flows.

4.2 Methods

4.2.1 Study site

This flow redistribution experiment was conducted upstream and downstream of a weir on the Nymboida River, NSW (Fig. 4.1, section 2.1). The objective of this experiment was to test whether changes in velocity up -and downstream of a weir would elicit a short-term response in the spatial distribution of aquatic invertebrate diversity, density

and benthic invertebrate community composition within two different flow habitats. To test this hypothesis a flow redistribution experiment was conducted at two upstream and two downstream sites either side of a weir on the Nymboida River under low flow conditions in mid October 2006.

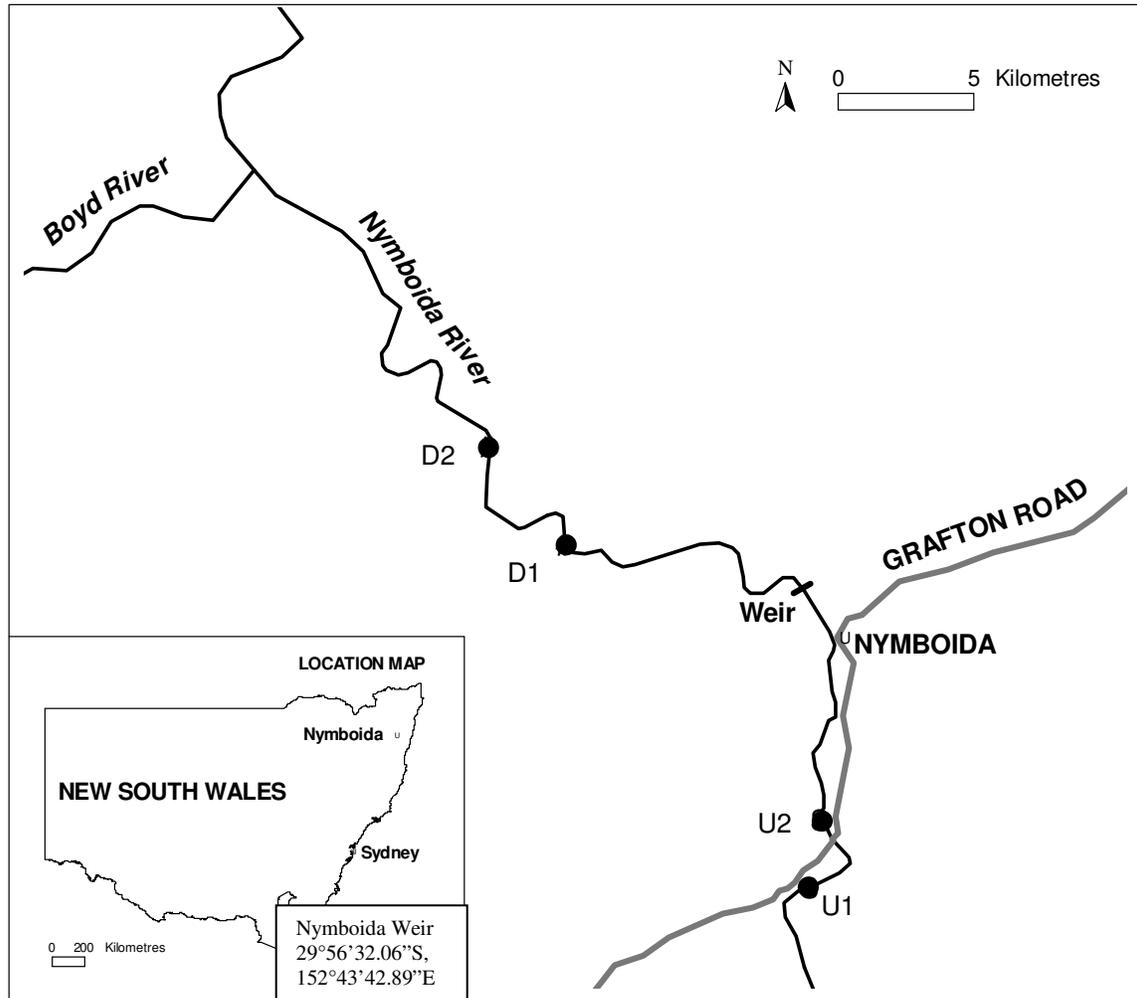


Figure 4.1 Map representing two riffles upstream (U1 & U2) and two riffles downstream (D1 & D2), of the Nymboida Weir, Nymboida River, NSW, Australia.

Slow and fast flow treatments were derived from field surveys of predominant velocity and depth characteristics along the Nymboida River (Fig. 2.4). Along the edges of the river to up to 1m into the channel, there was a shallow (< 5 cm), slow flowing (< 0.1 m/s)

habitat. Further into the channel was a habitat termed ‘fast flow’ where depth ranged from 5-15 cm and current speeds were 0.2 – 0.6 m/s (section 2.1.6, Fig 2.4). At the four sites in this study, the slow and fast flowing treatments covered a larger fraction of the wetted bed (Table 4.1).

Table 4.1. Flow treatment area (m²) and total area of entire riffle (%) represented by slow and fast flow treatments at each site. U = upstream, D = downstream.

Site	Area (m ²)		Area of Riffle (%)	
	Slow	Fast	Slow	Fast
U1	25	84	3	12
U2	25	45	5	9
D1	13	28	5	11
D2	15	36	4	10

The October 2006 flow redistribution experiment was conducted at four sites (two upstream and two downstream of a weir spanning the Nymboida River (Fig. 4.1) where there was sufficient room to install three sets of flow diversion barriers (FDBs) within each site (Fig. 4.2). These FDBs diverted flow to create a ‘slow flow’ treatment behind the barrier in a formerly ‘fast flow’ habitat. Simultaneously, flow was diverted into a formerly ‘slow flow’ habitat to create a ‘fast flow’ treatment.

FDBs were constructed of thick clear plastic sheets (Solarfilm 7.5m/m, Absolute Trade Supplies Yatala, Queensland) supported with wire-mesh (105 x 4 x 1.4mm, White Wires, Arndell, Park, New South Wales). FDBs were fixed in position with four metal star pickets (Heavy Star Post Black 165cm, White Wires Arndell Park NSW Australia) (Fig.4.2). Before installation of the FDBs, current velocity was mapped at each site at 0.5 meter intervals down the channel in both slow and fast flow habitats. After the first FDB was installed at the head of the riffle, current velocity was re-measured downstream and the next FDB was installed at least 1m downstream of where flows had returned to ambient conditions. In this way, the structures were considered not to interfere with each other’s flow paths. Three FDBs at each of four sites diverted flow for seven days to allow sufficient time for invertebrate redistribution.

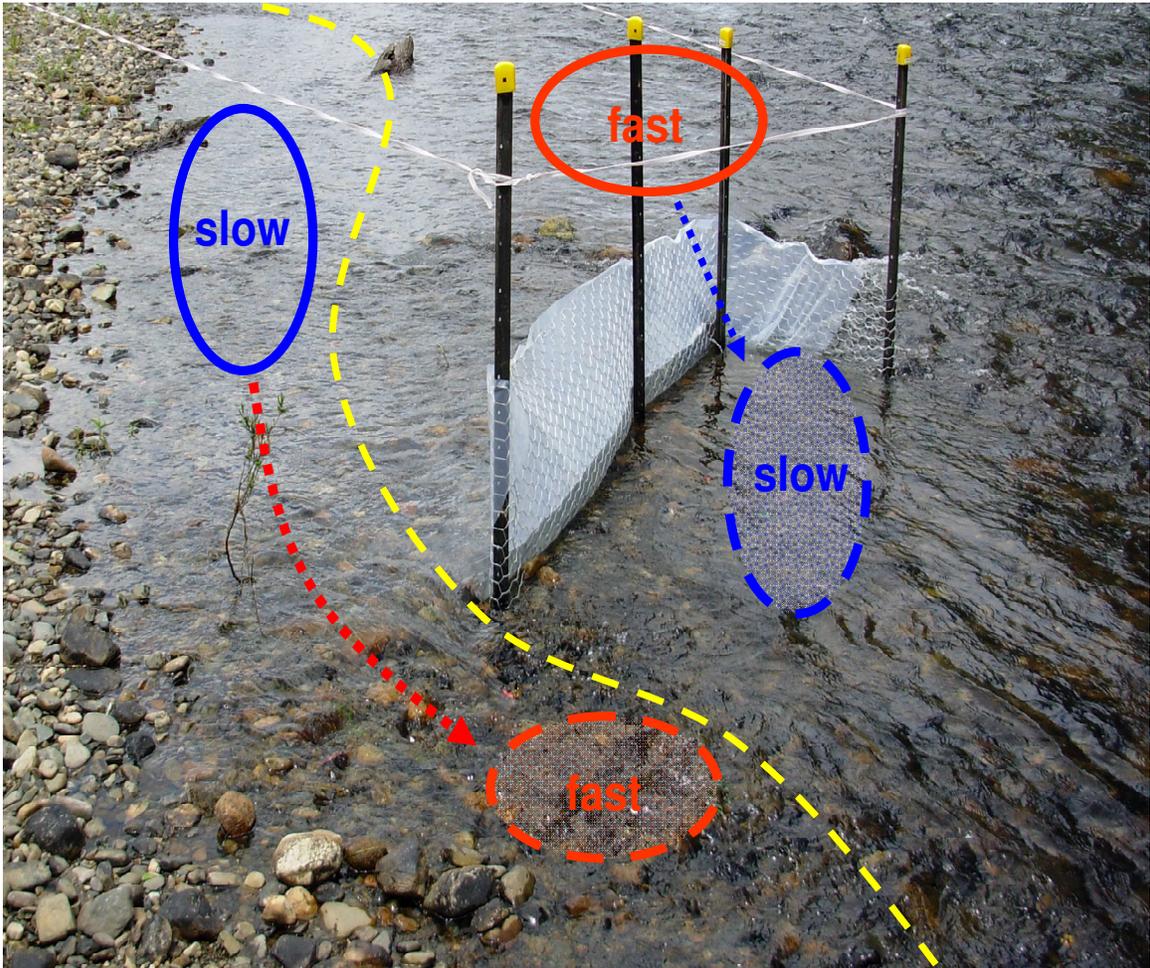


Figure 4.2 Photo depicting slow and fast flow treatments at one of three replicate FDBs installed per site. Slow and fast control (blue and red open), slow and fast manipulated (blue and red shaded).

At each FDB, invertebrates were collected from six sets of three rocks before and after the experimental change of velocity (Fig. 4.3). The first two sets of triplicate rocks were sampled from both the slow and fast flowing treatments before FDB installation ('controls' - SC₀ and FC₀). After seven days, triplicate rocks were sampled from each treatment where slow and fast flows had been manipulated (SM₇ and FM₇) and their respective control rocks where flows remained unchanged (SC₇ and FC₇). Thus, a total of 54 rocks per site were sampled, enabling comparisons of community composition of

rock-dwelling benthic invertebrates within each flow treatment before and after flow diversion.

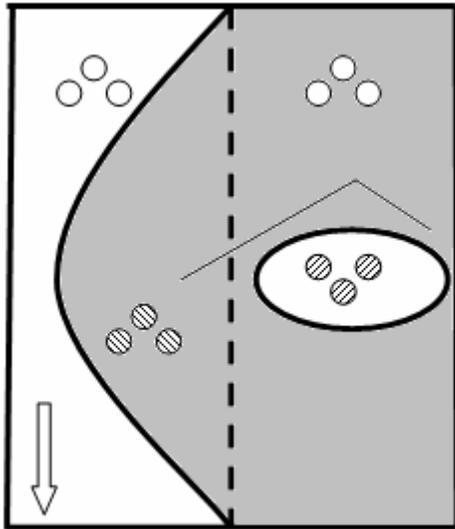


Figure 4.3 Schematic representation of triplicate rocks sampled from both slow (open portion) and fast (shaded portion) flow treatments on day zero before manipulation ('controls' - SC₀ & FC₀, open circles) and day seven after manipulation ('controls' - SC₇ & FC₇, open circles; 'manipulated' - SM₇ & FM₇, cross-hatched circles).

Benthic invertebrates were collected by placing a hand net (25 cm diameter, 250- μ m-mesh) downstream of each rock. The rock was gently lifted into the net and both were then submerged into a bucket and scrubbed to dislodge fauna. The bucket contents were then filtered through a 250- μ m-mesh sieve and preserved in 70% ethanol. In the laboratory, invertebrates were counted and identified to the lowest practical level of resolution (usually species).

Physical and hydraulic variables for each rock and site were measured before and after the flow diversions (section 3.2.5). Rock surface area was determined following the equation (surface area = $1.15(LW + LH + WH)$ where L = length, W = width, H = height) of Graham et al. (1988) (section 3.2). Invertebrate density was assessed by

dividing the abundance of each taxon on each rock by its respective rock surface area which was finally expressed as the number of benthic invertebrates per 0.1m^2 .

4.2.2 Data analysis

Invertebrate abundance of triplicate rocks sampled from each treatment was calculated to produce a new composite value expressed as invertebrate density / 0.1m^2 . Compositing three rocks produced one value for each of the four treatments (slow control, slow manipulated, fast control, fast manipulated) within the three replicate (FDBs) within each site before the manipulation (day zero: SC_0, FC_0) and after the manipulation (day seven: SC_7, SM_7, FC_7, FM_7). For all analyses, data were checked for normality and whether variances were heterogeneous between treatments, and to detect outliers. As composite values for treatments were not normally distributed they were log transformed prior to the calculation of the difference between treatments. Temporal differences between control treatments were calculated as the difference between controls on day seven and their respective controls before the experimental manipulation on day zero, to see if any change occurred in the control flow treatments over 7 days without any manipulation of water velocity (slow treatment $SC_7 - SC_0 = SC$; fast treatment $FC_7 - FC_0 = FC$). The effect of the manipulations were calculated as the difference between manipulated and control values on day seven.

The experimental design fits a three factor nested analysis of variance with planned comparisons between treatments (Winer *et al.*, 1991). Factors were location (2 levels, fixed) up and downstream of the weir, sites (2 levels) randomly chosen from a subset of a number of riffles up and downstream of the weir, and treatments (4 levels) being controls slow and fast (SC and FC) and treatments slow and fast (SM and FM). Treatments were fixed because a predetermined velocity range was set for each treatment (Table 4.2).

Table 4.2 Three factor nested analysis of variance model with replication at both the dam and treatment levels. F, fixed factor; R, random factor; d.f., degrees of freedom.

Term	Description of test	F or R	d.f.	No. and description of levels	F-ratio denominator
Location = L	Effects of location along river	F	1	2, upstream and downstream	S(L)
Site = S(L)	Estimates variance among sites nested within locations	R	2	2 per location	e
Treatment = T	Effect of flow velocity	R	3	4,2 manipulated and 2 unmanipulated	S(L) x T
L x T	Interaction tests whether treatments vary in location effects		3		S(L) x T
S(L) x T	Estimates whether variability among treatments differs between sites within locations		6		e
Error	Replicate benthic samples at each FDB	R	32		

Replication of experimental treatment units demonstrates that statistically significant differences among experimental treatments are due to the experimental treatments and not simply a result of chance variation among the units measured (Underwood, 1997). Triplicate rocks were composited within each treatment at three replicated FDBs within each site, as the research objective was to compare between the different treatments and not among individual rocks within treatments. Replicate sites were nested within locations up -and downstream of a weir as sites were unique to one location only. The interaction term S(L) x T is the main term of interest in the ANOVA model. When tested over the error term (e) we can distinguish whether the effect of treatment (velocity) was consistent among sites within locations. Treatment effects are tested over the interaction term in the ANOVA model. The error term represents individual variability within treatments among FDBs within a site.

The ANOVA model was run on all four treatments (slow control and slow manipulated in the slow flow habitat and fast control and fast manipulated in the fast flow habitat). By combining all four treatments in the one analysis, the degrees to which the treatments differ within and between both slow and fast flow habitats can be determined. Dependent variables included species richness and taxa density (total and all rheophiles) as well as densities of four abundant and dominant rheophiles, Diptera (Simuliidae), Philopotamidae (*Chimarra*) Hydropsychidae (*Cheumatopsyche*), and Ephemeroptera (*Austrophlebioides*).

Comparisons between treatments were planned as part of the analysis strategy before the data were examined. The various treatments were set up orthogonally to each other and the two specific comparisons of interest were SC v SM and FC v FM. These comparisons reveal the directions of predicted differences in variables such as species richness and taxa density when, for instance, extraction is reduced and more water is let downstream beyond the weir, velocity increases in the slow flow treatment. Alternatively, when extraction increases less water passes beyond the weir, therefore velocity decreases in the fast flow treatment.

4.2.3 Multivariate analysis (Primer)

Differences in community composition among the four treatments within and between sites were analysed using non-metric multidimensional scaling (nMDS) computed with PRIMER (Clark & Warwick, 1994). Similarities among samples were calculated using the Bray-Curtis similarity on $\log(x+1)$ transformed data. To test the null hypotheses that there were no differences between treatments (SC_0 , SC_7 , SM_7 , FC_0 , FC_7 , FM_7) at each site, differences in community composition between groups were calculated using analysis of similarities (ANOSIM). Pairwise comparisons were used to test specific differences between controls and manipulated treatments within the slow and fast velocity habitats. Individual species contribution to the observed differences between communities between sites and up -and downstream locations were examined separately for each treatment with the similarity percentage contribution function SIMPER in PRIMER (Clark & Warwick, 1994).

4.3 Results

4.3.1 Flow related and physiochemical characteristics

Mean flow above the Nymboida Weir in the months prior to the seven day experimental period in October 2006 was 1033 ML/d. This winter and early spring low flow regime is typical of other subtropical east coast lowland rivers draining the coastal and dividing ranges eastward into the Pacific Ocean. For the duration of the experiment, natural flows above the Nymboida Weir averaged 646 ML/d, whereas average downstream flows were reduced due to the influence of the weir to 380 ML/d (Department of Water and Energy 2007). Minimal flow variation within locations (upstream and downstream) and among the four sampling times during the experimental period meant the redistribution of water at each FDB within each site was consistent through time.

Average river discharge downstream (378 ± 117 ML/d) of the weir was 58% lower than upstream base flows for the seven day experimental period. River discharge downstream steadily declined by 35% from its original baseflow, whereas flows upstream were more variable and deviated by 35% from the mean upstream flows (650 ± 86 ML/day) with a net

change in river discharge for the experimental period of just 3%. Control and manipulated slow and fast flow treatments remained within their prescribed velocity range for the entire seven days (Fig. 4.4)

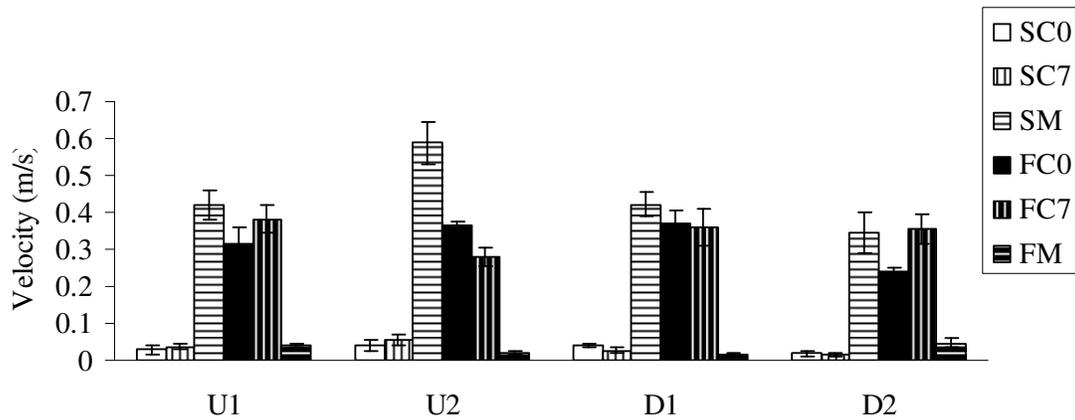


Figure 4.4 Average velocity (\pm SE) for control treatments before (SC0, FC0) and control and manipulated treatments after (SC7, FC7, SM, FM) for each site.

Flow velocity was consistently increased in the slow and decreased in the fast flow treatments by the manipulation (Fig 4.4). The Tukey post hoc test for velocity showed that the effect of the manipulation was to make the slow and fast manipulated treatments less like their respective control treatments and more similar to the other slow and fast control treatments (Table 4.4).

Table 4.4 Analysis of variance of hydraulic variables with unplanned comparisons (Tukeys) among treatment levels, for experimental results for (a) velocity, (b) depth, (c) detritus, (d) stability, (e) pittedness and (f) roughness. d.f., degrees of freedom; MS, mean square; F, F-ratio ; P, level of significance; Homogenous groups , Tukeys. SC, slow control; FC, fast control; SM, slow manipulated; FM, fast manipulated.

(a) Velocity		d.f.	F	P	Homogenous Groups
	Treatment (T)	3	54.876	0.001	
	SC				FM
	FC				SM
(b) Depth					
	Treatment (T)	3	11.9	0.001	
	SC				SM, FM
	FC				
(c) Detritus					
	Treatment (T)	3	3.069	0.022	
	SC				SM, FM
	FC				SC, FM
(d) Stability					
	Treatment (T)	3	0.65	0.589	
(e) Pittedness					
	Treatment (T)	3	0.84	0.478	
(f) Roughness					
	Treatment (T)	3	0.16	0.924	

Decreased velocity significantly decreased water depth in the fast flow treatment (Fig 4.5). No effect of treatment on water depth was observed in the slow flow treatment, such that the experimental increase of velocity in the slow flow treatment failed to significantly increase water depth across the shallow river edge characteristic of the slow velocity treatment (Table 4.4). There was a significant effect of treatment on velocity (Table 4.4). Variance in the dependant variable silt was very low and therefore not explained in Table 4.4. Detritus levels were low and neither differed among locations or treatments (Table 4.4). Mean rock stability, pittedness and roughness did not differ among treatments (Table 4.4).

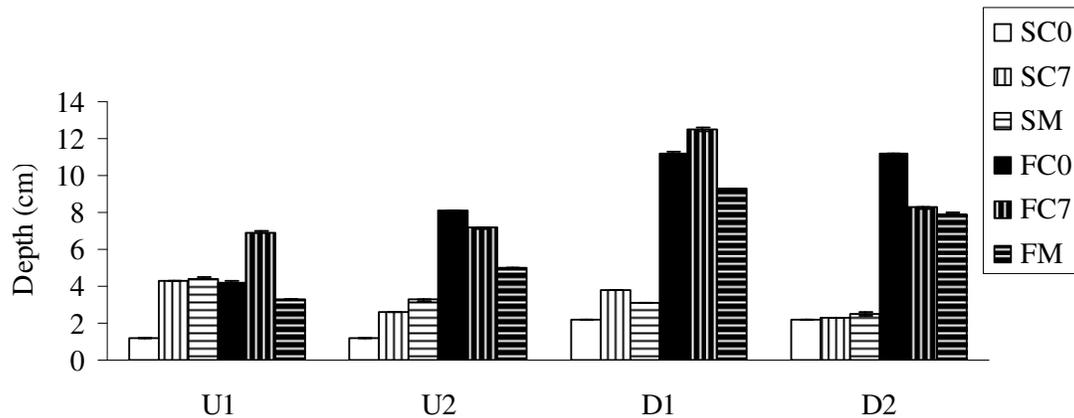


Figure 4.5 Average depth (\pm SE) for control treatments before (SC0, FC0) and control and manipulated treatments after (SC7, FC7, SM, FM) for each site.

Water temperature was consistently elevated (1-2°C) at both downstream sites (Table 4.3). Environmental measures including temperature, pH, dissolved oxygen and water conductivity resembled earlier June survey results obtained within the same winter low flow period in 2006 (Table 3.3).

Table 4.3 Mean (\pm SE) chemical variables (n = 3) measured at each site in the Nymboida River on days 0, 3 and 7.

Site code	Water temperature(°C)	pH	Dissolved oxygen (mg L ⁻¹)	Conductivity (µs cm ⁻¹)
U1	22±4	7.18±0.64	8.65±1.3	50.1±1.4
U2	21.5±3	7.15±0.6	8±1.6	50.6±1.8
D1	22.5±5.1	7.28±0.14	9.35±1.7	48.8±4.8
D2	23.5±3	7.1±0.1	7.7±1.4	51.3±0.2

4.3.2 Treatment effects on density and diversity of benthic invertebrates

A total of 64 taxa were collected during the experiment. Eleven taxa occurred in greater than 50% of the samples and comprised 95% of the total invertebrate densities. Nine taxa dominated both locations. Of the dominant taxa, seven were rheophilic (Table 4.5).

Table 4.5 Mean invertebrate density (\pm SE) and percent of total density of dominant species for up and downstream locations in the Nymboida River. *rheophile

Taxon	Order	mean density (number per 0.1m ²)		Percent of overall total densities (%)
		upstream	downstream	
Simuliidae*	Diptera	54.58	13.79	59.27
<i>Austrophlebioides</i> *	Ephemeroptera	5.18	4.32	8.24
Baetidae G.2 sp.3*	Ephemeroptera	3.69	2.44	5.31
<i>Cheumatopsyche</i> *	Hydropsychidae	1.84	3.99	5.05
<i>Thienemanniella</i>	Chironomidae	2.74	2.52	4.56
<i>Chimarra</i> *	Philopotamidae	1.54	3.25	4.15
<i>Sclerocyphon F</i> *	Psephenidae	3.13	0.97	3.55
<i>Nilotanypus</i>	Chironomidae	1.62	1.89	3.04
Baetidae IG*	Ephemeroptera	3.05	2.99	5.24
<i>Corynoneura</i>	Chironomidae	N/A	1.83	1.59

4.3.3 Treatment effects on species density

Total densities (species and rheophilic) showed a significant relative increase irrespective of location when velocity was increased in the SM treatment. Total species density decreased in the FM treatment relative to the FC treatment with a reduction in velocity (Fig. 4.5). This term explained 54% of the total variance (significant interaction terms S(L) X T, Table 4.6). Total species and rheophilic species densities showed no response in the SM treatment where an increase in density was expected with increased velocity, and either no response or an increase in the FM treatment when a relative decrease in density was expected with a reduction in velocity (Fig. 4.6).

4.3.4 Treatment effects on taxa richness

Taxa richness (total and rheophilic) increased with increased velocity in the slow flow treatment (SM) upstream of the weir (U1 and U2). Total taxa richness increased in the SM treatment at a single upstream site (D1). Rheophilic taxa richness in the SM treatment increased upstream and decreased downstream (L x T p=0.023; Table 4.6). Total taxa richness and rheophilic taxa richness decreased across all sites in the FM treatment relative to their controls except at the single upstream site U1 (Fig. 4.5).

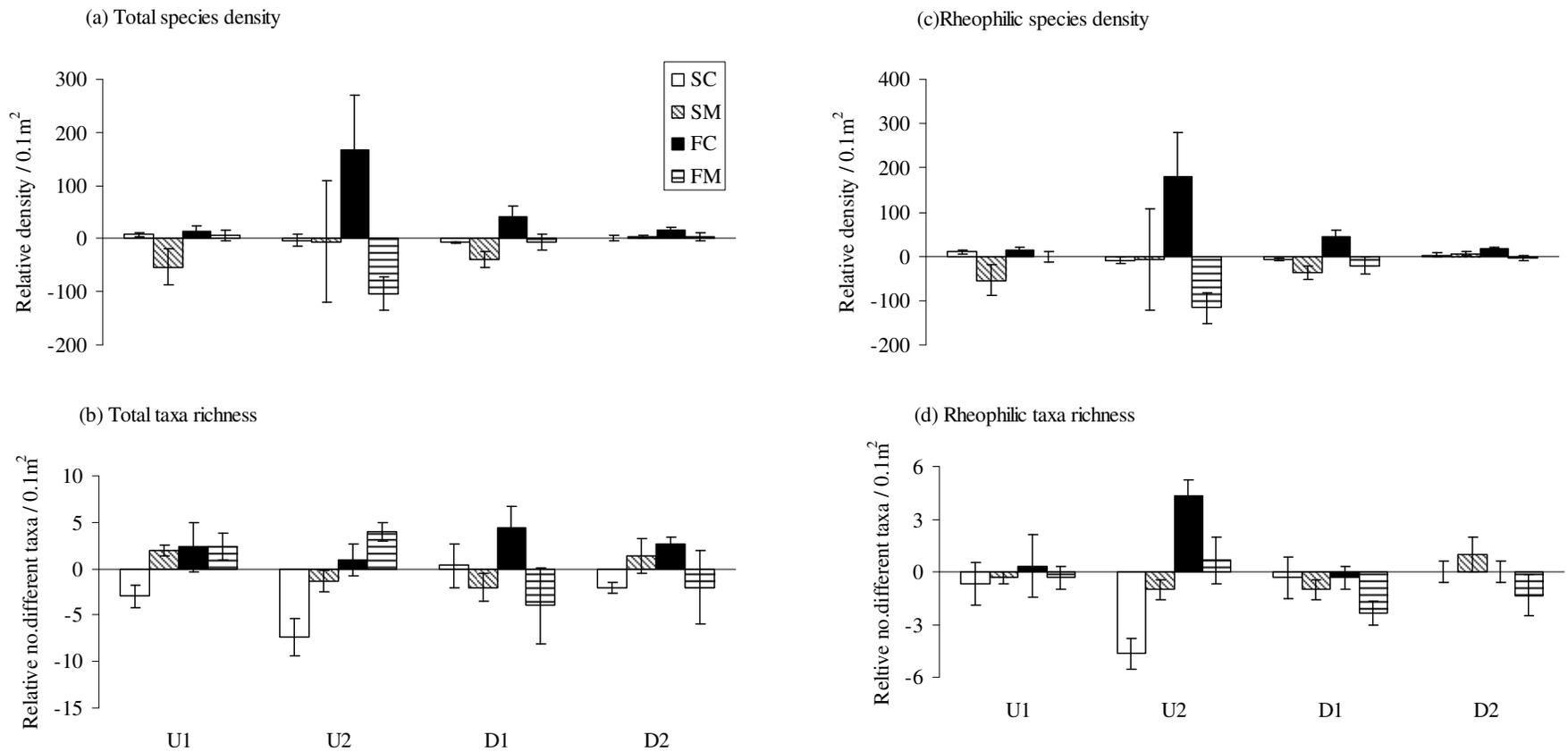


Figure 4.5 Relative average (\pm SE) difference between invertebrate densities before and after the flow manipulation per 0.1m² for (a) Total Species density (b) Total taxa richness (c) Rheophilic species density (d) Rheophilic taxa richness. A negative result indicates more species were recorded within that particular flow treatment after the manipulation whilst a positive result means less species were observed. A zero result indicates no change in invertebrate densities before and after the flow manipulation.

Table 4.6 Three-factor, factorial analysis of variance with planned comparisons among treatment levels for (a) Total species density, (b) Rheophilic species density, (c) Total taxa richness and (d) Rheophilic taxa richness. d.f., degrees of freedom; MS, mean square; F, F-ratio ; P, level of significance; SA, strength of association as percentage variation explained. Analyses were performed on log (x + 1) transformed data because of heterogeneous variances and outliers.

Source	d.f.	MS	F	P	SA
(a) Total species density					
LOC	1	0.01	0.196	0.701	0.0
SIT(LOC)	2	0.049	0.659	0.524	0.0
TREATMENT	3	1.940	8.873	0.013	53.8
SC V SM	1	1.347	18.013	0.001	0.0
FC V FM	1	1.082	14.468	0.001	0.0
LOC*TREATMENT	3	0.037	0.169	0.914	0.0
SIT(LOC(TREATMENT))	6	0.219	2.923	0.022	18.0
Error	32	0.075			28.2
(b) Total taxa richness					
LOC	1	0.004	1.276	0.376	0.0
SIT(LOC)	2	0.003	0.530	0.594	0.0
TREATMENT	3	0.030	3.379	0.095	20.0
SC V SM	1	0.066	11.292	0.002	0.0
FC V FM	1	0.019	3.287	0.079	0.0
LOC*TREATMENT	3	0.009	1.051	0.436	0.0
SIT(LOC(TREATMENT))	6	0.009	1.492	0.212	11.4
Error	32	0.006			68.6
(c) Rheophilic species density					
LOC	1	0.001	0.006	0.943	0.0
SIT(LOC)	2	0.134	1.827	0.177	1.9
TREATMENT	3	1.325	3.205	0.105	28.4
SC V SM	1	2.07	28.21	0.001	0.0
FC V FM	1	0.027	0.373	0.546	0.0
LOC*TREATMENT	3	0.018	0.043	0.987	0.0
SIT(LOC(TREATMENT))	6	0.413	5.635	0.001	42.4
Error	32	0.073			27.3
(d) Rheophilic taxa richness					
LOC	1	0.009	10.069	0.087	0.0
SIT(LOC)	2	0.001	0.112	0.894	0.0
TREATMENT	3	0.012	2.110	0.200	4.2
SC V SM	1	0.017	2.187	0.149	0.0
FC V FM	1	0.015	1.875	0.180	0.0
LOC*TREATMENT	3	0.037	6.835	0.023	38.3
SIT(LOC(TREATMENT))	6	0.005	0.686	0.662	0.0
Error	32	0.008			57.5

4.3.5 Taxon specific response to experimental treatments

Treatment effects explained 80% of the overall variance in the relative change of densities of the Philopotamid caddisfly *Chimarra* (Table 4.7). *Chimarra* densities increased significantly in the SM treatment upstream relative to their controls ($p=0.001$). A similar increase occurred downstream where no relative change was hypothesised. As predicted *Chimarra* densities decreased in the FM treatment with a decrease in velocity relative to their controls at all sites (Fig. 4.6).

The relative change in densities of *Cheumatopsyche* and Simuliidae mimicked trends displayed by *Chimarra*. However the treatment term explained 70% (*Cheumatopsyche*) and 52% (Simuliidae) of the overall variability, with both measures having a significant treatment effect between sites within locations (significant interaction terms S(L) X T, Table 4.7; Fig. 4.6). *Cheumatopsyche* densities increased at all sites in the SM treatment relative to their controls. This increase in the SM treatment also occurred downstream (D1 and D2) where no response was hypothesised. The significant interaction between S(L) x T may be explained by the different response among the SC treatments between up- and downstream locations, whereby the relative change in densities of *Cheumatopsyche* on control rocks within sites and locations both remained unchanged (U1 & D2) as well as reduced (U2 & D1) (Fig 4.6). The source of the difference in Simuliidae densities (significant interaction terms S(L) X T, Table 4.7) is because downstream where densities increased at D1 and decreased at D2 in the slow flow treatment where no response was hypothesised.

Treatment effects explained 40% of the overall variance in the relative change in densities of the chironomid *Nilotanypus*. *Nilotanypus* densities increased with an increase in velocity in the slow flow treatment at a single site upstream (U2) (Fig. 4.6). A relative negative change in density although non significant was observed at sites U1, D1 and D2 (non significant planned comparison SC V SM, Table 4.7; Fig. 4.6). In the fast treatment where velocity was decreased *Nilotanypus* densities increased downstream relative to their controls, whilst upstream densities remained unchanged (non significant planned comparison FC V FM, Table 4.7; Fig. 4.6).

The response of the mayfly *Austrophlebioides* to changes in velocity varied within treatments among sites within locations (significant interaction term S(L) X T, Table 4.7). This term explained 60% of the variance in the relative change in densities of *Austrophlebioides*. Densities increased in the SM treatment with an increase in velocity at a single upstream site (U2) relative to its control (SC) whilst elsewhere in the slow manipulated treatment no relative change in density was observed (Fig. 4.6). Densities decreased with decreased flow in the FM treatment relative to their controls (FC) at two sites downstream and a single upstream site (U1) (Fig. 4.6).

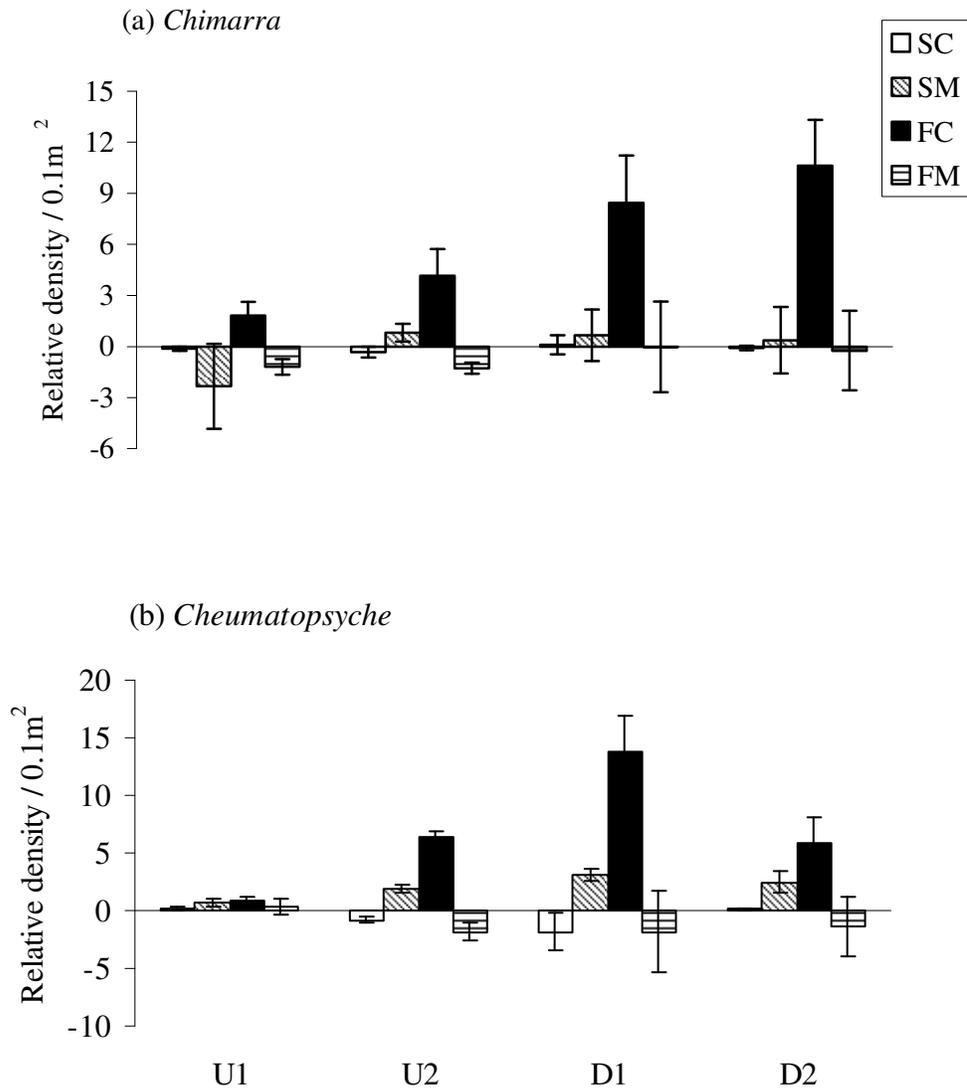


Figure 4.6 Individual species densities per 0.1m^2 for (a) *Chimarra* (b) *Cheumatopsyche*, (c) Simuliidae, (d) *Nilotanypus*, (e) *Austrophlebioides*

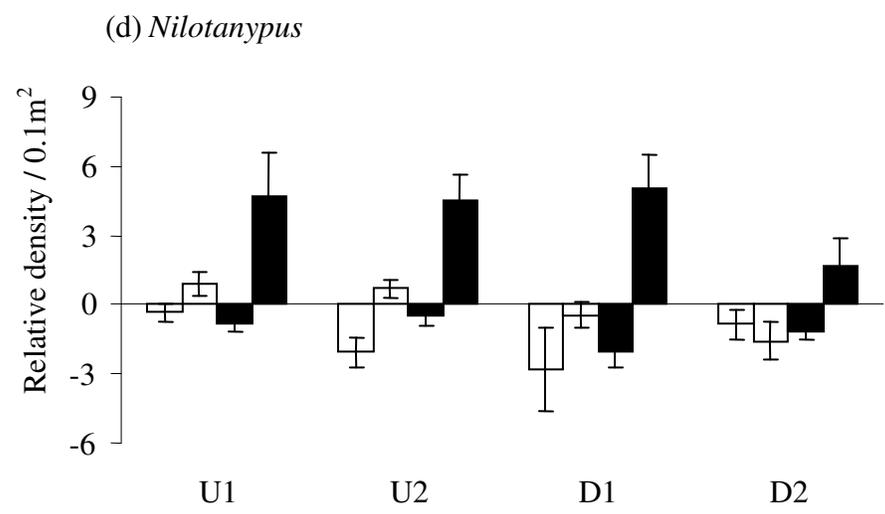
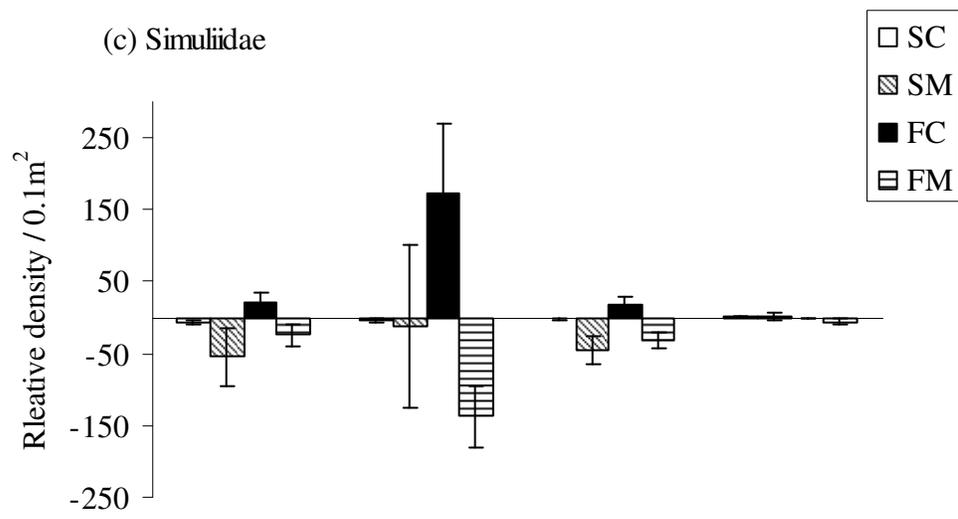


Figure 4.6 cont. Individual species densities per 0.1m² for (c) Simuliidae, (d) *Nilotanypus*.

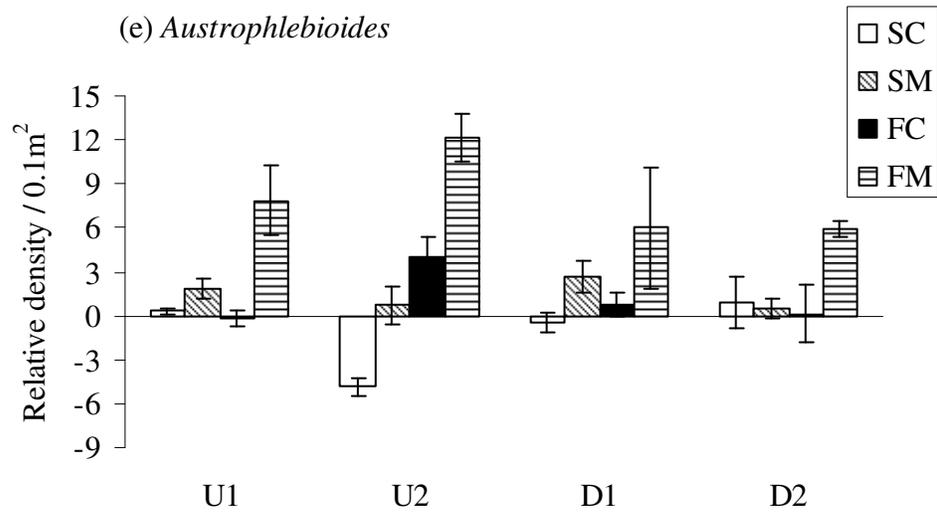


Figure 4.6 cont. Individual species densities per 0.1m² for (e) *Austrophlebioides*

Table 4.7. Three-factor, factorial analysis of variance with planned comparisons among treatment levels, for experimental results for (a) *Chimarra* (b) *Cheumatopsyche*, (c) Simuliidae, (d) *Nilotanypus*, (e) *Austrophlebioides*. d.f., degrees of freedom; F, F-ratio ; P, level of significance; SA, strength of association as percentage variation explained.

Source	d.f.	F	P	SA
(a) <i>Chimarra</i>				
LOC	1	3.729	0.193	0.0
SIT(LOC)	2	0.78	0.467	0.0
TREATMENT	3	48.04	0.001	80.5
SC V SM	1	44.646	0.001	
FC V FM	1	13.493	0.001	
LOC*TREATMENT	3	0.769	0.552	0.0
SIT(LOC(TREATMENT))	6	0.686	0.662	0.0
Error	32			19.5
(b) <i>Cheumatopsyche</i>				
LOC	1	1.634	0.329	0.0
SIT(LOC)	2	0.275	0.761	0.0
TREATMENT	3	15.168	0.003	70.2
SC V SM	1	82.793	0.001	
FC V FM	1	56.922	0.001	
LOC*TREATMENT	3	0.641	0.616	0.0
SIT(LOC(TREATMENT))	6	3.917	0.005	14.8
Error	32			15.0
(c) Simuliidae				
LOC	1	0.044	0.853	0.0
SIT(LOC)	2	1.589	0.220	0.8
TREATMENT	3	9.792	0.010	52.1
SC V SM	1	51.67	0.001	
FC V FM	1	19.125	0.001	
LOC*TREATMENT	3	2.02	0.213	12.1
SIT(LOC(TREATMENT))	6	4.193	0.003	18.0
Error	32			17.0

Table 4.7 cont.

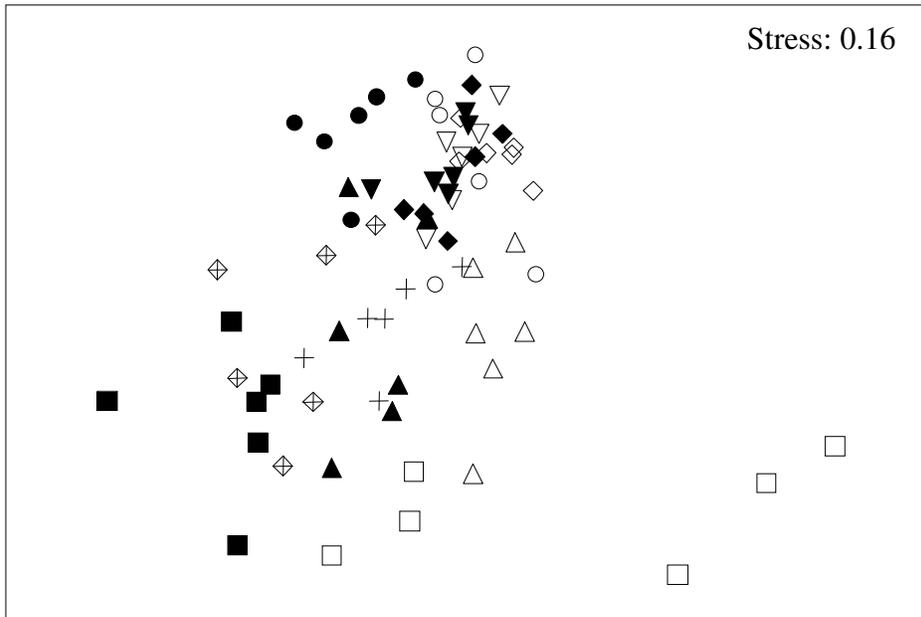
Source	d.f.	F	P	SA
<i>(d) Nilotanypus</i>				
LOC	1	14.092	0.064	0.0
SIT(LOC)	2	0.385	0.683	0.0
TREATMENT	3	10.042	0.009	40.0
SC V SM	1	0.689	0.413	
FC V FM	1	3.026	0.092	
LOC*TREATMENT	3	2.176	0.192	10.3
SIT(LOC(TREATMENT))	6	1.101	0.383	1.8
Error	32			47.9
<i>(e) Austrophlebioides</i>				
LOC	1	0.005	0.949	0.0
SIT(LOC)	2	0.56	0.577	0.0
TREATMENT	3	1.36	0.341	6.4
SC V SM	1	19.601	0.001	
FC V FM	1	5.223	0.029	
LOC*TREATMENT	3	0.662	0.605	0.0
SIT(LOC(TREATMENT))	6	6.46	0.001	60.2
Error	32			33.4

4.3.6 Community response to location

Analysis of overall community composition between sites showed a number of patterns on the Nymboida River. First, there were no significant site differences, and similarly no significant differences were observed among sites between up -and downstream locations (Table 4.8a). Second, there were significant differences in the invertebrate community structure between slow and fast flow treatments (Table 4.8a; Fig. 4.7). Overall differences in community composition were attributed to the higher contribution of the leptophlebiid mayfly *Austrophlebioides* in the slow, and simuliids in the fast flowing treatments (Table 4.9; Fig. 4.7).

Table 4.8 Results of ANOSIM tests carried out on matrices of similarities among locations using species level data for (a) all sites together and (b) between treatments within sites

Test comparison	R	P
(a) All sites		
Global tests		
Between sites	0.083	0.099
Between up-downstream locations	0.046	0.154
Pairwise tests between sites within locations		
U1 versus U2	-0.033	0.659
D1 versus D2	-0.042	0.707
(b) All treatments		
Between treatments	0.538	0.001
Within slow treatment	0.871	0.001
SC0 versus SC7	0.271	0.086
Within fast treatment	0.668	0.001
FC0 versus FC7	0.010	0.371
Pairwise tests among treatments		
Within slow treatment		
SC0 versus SM7	0.958	0.029
SC7 versus SM7	0.521	0.057
Within fast treatment		
FC0 versus FM7	1.000	0.029
FC7 versus FM7	0.896	0.029
Between slow and fast treatment (Target)		
SC0 versus FM7	0.167	0.143
SC7 versus FM7	0.313	0.029
FC0 versus SM7	0.667	0.029
FC7 versus SM7	0.542	0.029



Up	Down	
△	▲	SC0
□	■	SC7
○	●	SM7
◇	◆	FC7
▽	▼	FC7
+	⊕	FM7

Figure 4.7 MDS plot of benthic invertebrate community data for slow and fast flow treatments within sites up and downstream in the Nymboida River, NSW.

Table 4.9 Overall taxa contribution (%) for all sites for control (SC and FC) and manipulated (SM and FM) treatments.

Order	Family	Taxon	SC	SM	FC	FM
Ephemeroptera	Leptophlebiidae	<i>Austrophlebioides</i>	30.08	15.73	14.94	34.03
Ephemeroptera	Baetidae	Baetidae IG	18.82	12.41	15.62	16.19
Ephemeroptera	Baetidae	Baetidae G.2 sp.3	18.71	11.64	13.83	15.67
Coleoptera	Psephenidae	<i>Sclerocyphon type F</i>	11.10	4.81	n/a	n/a
Diptera	Simuliidae		7.00	15.54	26.75	10.41
Tricoptera	Hydropsychidae	<i>Cheumatopsyche</i>	5.33	15.68	11.83	9.41
Tricoptera	Philopotamidae	<i>Chimarra</i>	n/a	15.66	11.83	5.67

4.3.7 Community response to flow treatments

No significant changes in community composition were observed between controls in either the slow or fast treatments for the duration of the seven day experimental manipulation of velocity (SC0 V SC7, FC0 V FC7; Table 4.8).

The community response following an increase of velocity in the slow flow treatment could be attributed to differences in filter feeding Simuliids, *Chimarra*, *Cheumatopsyche* and the leptophlebiid mayfly, *Austrophlebioides*. *Austrophlebioides* clearly dominated the slower flowing treatments (SC). *Cheumatopsyche*, *Chimarra* and simuliid contribution increased in response to increased water velocity in the slow flowing treatment (Table 4.9).

Overall community composition in the FM treatment relative to their respective controls across all sites and between up -and downstream locations was significantly different (within fast treatment, Table 4.8). Following the experimental decrease of velocity in the fast flow treatment, simuliids that dominated the fast flow treatment (FC0 29% & FC7 21%) contributed only 7 % to the overall faunal composition in the slower flows of the FM treatment. The Leptophlebid mayfly, *Austrophlebioides* contribution to overall community composition increased two fold due to the influence of decreased velocity in the FM treatment (SC0 & SC7 V SM, Table 4.9).

4.3.8 Comparisons between control and manipulated treatments

Manipulated velocity treatments (SM0, SM7 and FM0 FM7; Fig 4.7) resembled their respective 'target' velocity treatments (FC0, FC7 and SC0, SC7; Fig. 4.7), however overall community composition representative of a 'target' velocity treatment was achieved just once in the FM treatment (FM7 V SC0; Table 4.8). *Austrophlebioides*, Baetidae G2 sp.3 and Baetidae IG dominated the slow velocity habitat; these same species were representative of the FM treatment where velocities were reduced (Table 4.9). Simullid, *Chimarra*, and *Cheumatopsyche* densities were highest in the fast flowing treatments. These same species were underrepresented in the slow flow treatments however they responded quickly to increased water velocity in the slow flowing treatments, rapidly resembling contributions observed in the FC treatments within seven days (Table 4.9).

4.4 Discussion

4.4.1 Influence of velocity on benthic invertebrates in the Nymboida River

My first hypothesis predicted that regulated sites downstream of a weir would exhibit a different faunal response to changes in water velocity relative to unregulated sites located upstream. Instream structures such as weirs are expected to decrease invertebrate density and diversity downstream due to the press disturbance decreasing discharge magnitude, frequency, duration and timing of flow events (Poff *et al.*, 1997; Bunn & Arthington, 2002; Richter *et al.*, 2006). In contradiction to our first hypothesis, there was no altered faunal response at the regulated downstream sites associated with the expected effect of decreased river flow. Rate and variability of flow were reduced at the regulated compared to the unregulated sites and therefore potentially able to lead to a depauperate invertebrate community. Nevertheless, regulated sites downstream were not collectively lower in either density or diversity of benthic invertebrates, nor were the invertebrate responses to short term changes in slow and fast water velocity markedly different to those of the two upstream sites.

Authors have reported conflicting responses in density and taxonomic richness due to the effects of reduced stream flow. In headwater streams of the central Rocky Mountains USA, Radar and Belish (1999) reported that mean invertebrate densities increased downstream of mild diversions and decreased downstream of severe diversions. McIntosh *et al.* (2002) compared benthic invertebrate populations above and below a diversion in a Hawaiian stream and found that the relative abundance of the most dominant taxa (*Chironomidae*, *Hydroptila arctia*, *Cheumatopsyche pettit*) remained consistent above and below the diversion. However the mean total benthic invertebrate density above the diversion was 46% greater than below the diversion. McIntosh *et al.* (2002) explained that shifts in food quality and quantity as suitable habitat declined due to decreased discharge were affecting the benthic invertebrate communities downstream of the diversion. On the Nymboida River temperatures downstream were slightly warmer and may have influenced the invertebrate community. Authors have correlated elevated temperatures with reduced flows in both small streams and large rivers (Cazaubon & Giudicelli, 1999; Rader & Belish, 1999) and during natural low flows and droughts water temperature usually increases as discharge decreases (e.g. Cowx *et al.*, 1984). Radar and Belish (1999) reported that in headwater streams of the Rocky Mountains USA, where diversions had also been reducing discharge for many years, increased densities may be the result of increased temperatures characteristic of regulated stream sections increasing productivity and food availability. Therefore, it may be a plausible that increased productivity and food availability downstream of the diversion on the Nymboida River may have been more important in sustaining invertebrate densities (e.g. *Austrophlebioides*) than flow conditions and the extent of suitable habitats.

4.4.2 Species response to short-term changes of water velocity

Change in the invertebrate community due to short term flow reductions can be caused by a reduction in water velocity and depth resulting in the concentration of invertebrates into a reduced wetted area (Englund & Malmqvist, 1996; Suren *et al.*, 2003a). Coupled with declining wetted area is a general contraction of available habitat (Brasher, 2003), habitat diversity (Cazaubon & Giudicelli, 1999) and habitat suitability (Cowx *et al.*, 1984). This explanation may hold true following short-term reductions of flow which this experiment

aimed to reproduce. However in this experimental manipulation, local changes of flow velocity at each FDB did not change the extent of wetted area (personal observations). Examples where wetted area was not coupled with reduced discharge are typically found in headwater streams with lower width to depth ratios (Wright & Symes, 1999), of which this study showed a decrease in species diversity and density.

The Nymboida Weir has been consistently reducing flows downstream for approximately 80 years, yet the benthic invertebrate response to water velocity in the regulated portion of the river was similar to the unregulated river environment upstream. For example, despite 80 years of regulation the known rheophile *Chimarra* responded rapidly within seven days to increased water velocity by colonising the newly available fast habitat irrespective of up -and downstream locations.

4.4.3 Habitat suitability downstream

I anticipated that lower taxonomic richness and invertebrate densities downstream as habitat suitability declined with flow reduction would change the invertebrate response within the slow and fast flow treatments compared to the faunal response expected of the unregulated upstream environment. For example, when flow velocity was increased in the slow flow treatment at a regulated downstream site which due to the long-term influence of reduced discharge had a depauperate invertebrate community there would not be the invertebrate community available to exhibit a marked and rapid response as observed upstream to the newly created fast flow treatment. However, when water velocity within the slow flow treatment downstream was increased, the species response suggests that there were enough suitable habitats for potential colonists. The newly created faster flow treatment downstream was colonised as rapidly as at the unregulated upstream sites within the seven day experimental period. This suggests that suitable refugia were available in the regulated downstream sections or in addition colonisers were able to drift downstream and beyond the weir from unregulated refugia upstream. Secondly, 80 years of flow regulation have not detectably reduced the capacity of that community to respond to increased flows.

4.4.4 Water velocity and the community/density environment relationship

Differences in dominant taxa and shifts in species contribution between slow and fast flowing habitats on the Nymboida River suggest that water velocity is potentially a driver of the observed density environment relationship. More rheophiles (e.g. Simuliidae, *Chimarra* and *Cheumatopsyche*) were found in the faster flowing habitats and filter feeding caddisflies are known to show distinct preference for fast flow (e.g. Nelson & Lieberman, 2002; Table 1.1). The response, shift and contribution of the above mentioned rheophiles to increased water velocity in the slow flowing habitat resembled that of the fast flowing habitat. The feeding biology of these species relies on a stable substrate for net attachment and fast flow for the uptake and delivery of detritus and algae into their nets (Gooderham & Tsyrlin, 2005). This affiliation for fast flowing habitats highlights the dependence species exhibit towards particular water velocities and the importance of traits unique to each species that contribute to the selection of a preferred velocity habitat as in this case, one with suitable fast flowing water for filter feeding.

Rheophiles colonised experimentally created fast flowing habitats as effectively within regulated and unregulated riffles. As recolonisation of invertebrates is established from external sources or internal refugia (Lancaster & Hildrew, 1993; Fowler, 2004), such an outcome suggests that invertebrates are able to drift over the weir from upstream refuges into downstream sections and/or adequate and suitable fast flowing refugia remains within the regulated downstream river section studied on the Nymboida River. However mean water velocity is not the only descriptor of the physical environment or of a specific species environment relationship, yet considering the observed response of some rheophiles (e.g. Simuliidae, *Chimarra* and *Cheumatopsyche*) to short-term changes in water velocity, these species show promise as potential indicators for the detection of increased flows.

4.4.5 Capacity to recover from the potential effects of the weir

The invertebrate response to the experimental flow manipulation raises the question; does the invertebrate community maintain the capacity to recover from the potential effects of 80 years of regulation? The *Chimarra* showed a very strong positive relationship for fast

over slow flowing water in both up -and downstream locations. Furthermore, *Chimarra* responded rapidly to increased water velocity in that very habitat where it was considered rare (slow flow) by colonising the newly available, experimentally created fast flowing treatments. There seems to be some capacity of this species within the Nymboida River to increase in density despite the potential effects of the weir. Secondly, whilst the weir has been effective in reducing flows on the Nymboida River for approximately 80 years, a species response such as this highlights that there is still an inherent ability in the invertebrate fauna to respond positively to enhanced flows downstream beyond the weir. I think it is important however to acknowledge that one must take a population-level perspective with regards to these observations, because if species live above the weir as well as below it, then obviously they can always recruit downstream from upstream. The Nymboida is fortunate to have a largely intact section upstream and reference rivers in the vicinity. If that were not the case, perhaps one would see very different results.

In conclusion this study identified two velocity habitats with unique invertebrate communities. The majority of the Nymboida River's invertebrate community preferred the fast flowing habitat, presumably where food resources were available and morphological traits specific to each individual enabled some persistence within that environment. Of the directly measured variables, velocity had the most influence on the distribution of invertebrates among treatments within the study riffles (SA, Table 4.6). This experiment demonstrated that within the invertebrate community there remains the capacity to recover downstream of the weir following the potential effects of approximately 80 years of reduced flows, and furthermore, the invertebrate community is likely to respond positively and in the direction of the upstream unregulated riffles to increased flows downstream of the weir.

4.4.6 Management implications

Benthic invertebrates play an important role within lotic ecosystems as processors of organic material and food for fish. Gore (1977) showed that many benthic invertebrates have a limited range of tolerances to changes in discharge. Therefore, it is important to quantifying the short-term redistribution of benthic invertebrates in response to

experimental manipulation of flow on Nymboida River for number of reasons. First, because the ability to detect a change in the invertebrate community in regulated sections downstream will help elicit an improvement or otherwise in river condition, and second declining invertebrate densities and or changes of community structure may limit important food supply for fish and restrict energy processing within the system.

Invertebrate density and diversity are thought to initially increase downstream as flows decrease, and then decrease as the magnitude and duration of the low flow period downstream increases (Englund & Malmqvist, 1996; Bunn & Arthington, 2002; Dewson *et al.*, 2007b). For the Nymboida River, reduced discharge downstream did not inhibit responses because local changes to water velocity did result in both increases and decreases in invertebrate densities. My results showed that individual rheophilic species had a particularly strong affinity for fast and artificially created fast flow treatments. Therefore I suggest that rheophiles (e.g. *Chimarra*, *Austrophlebioides*) should be considered as potential indicator taxa when monitoring for an ecological improvement with an increase in flows in the Nymboida River.

Setting minimum environmental flows should also consider the duration of the low flow period as the effect of a longer low flow period on the invertebrate community is likely to be greater than natural low flow events potentially of a shorter duration. The results of my short-term flow manipulation which followed a low flow period support the assertion that within the invertebrate community downstream there remains the capacity to recover from the potential effects of the weir. However the inherent variability of the natural flow regime and that the natural flow regime is so important in maintaining both habitat and biodiversity (Poff *et al.*, 1997; Boulton & Brock, 1999), suggests that the invertebrate community may behave differently depending on the duration of the low flow period. Therefore setting absolute levels for minimal flows with the expectation that the invertebrate community will respond in the same way throughout different low flow periods may conclude a missed change in response to what was to be an improvement due to increased flow conditions.

5 Synthesis and recommendations

5.1 Introduction

This study was undertaken to investigate the association between benthic invertebrates, flow regime and water velocity upstream and downstream of a weir on the Nymboida River NSW. The benthic fauna of the regulated location downstream of the Nymboida Weir (impact) was not significantly different to the unregulated upstream location (control sites) or to up -and downstream locations on the unregulated Bellinger River (reference). Similar associations between regulated and unregulated locations on rivers have been observed in Europe and New Zealand (Cortes *et al.*, 2002; Suren *et al.*, 2003a), however many studies show significant declines in invertebrate densities in regulated river sections (Englund & Malmqvist, 1996; Malmqvist & Englund, 1996; Cazaubon & Giudicelli, 1999; McIntosh *et al.*, 2002; Wood & Armitage, 2004; Kinzie *et al.*, 2006). I concluded that whilst the weir has been effective in reducing flows on the Nymboida River for approximately 80 years there appears to be some capacity to recover of the invertebrate fauna downstream from the potential effects of the weir within the Nymboida River.

Different benthic invertebrates showed different preferences for a range of habitats associated with slow and fast flows. The 'habitat heterogeneity hypothesis' proposes that diversity of habitats provide more niches and diverse ways for biota to exploit resources and thus increase species diversity (Simpson, 1949; MacArthur & Wilson, 1967; Lack, 1969). Different habitats within a river are defined by the physical environment (sections 1.1.3, 1.1.4). The slow and fast flow habitats studied on the Nymboida River harboured some species showing strong preference for one habitat; however most were linked to environmental features characteristic of both flow habitats. This implies that species maintenance in the Nymboida River will require a diversity of flows to increase the number of different habitats and heterogeneity within habitats.

The Nymboida River Management Committee recognised the hydrological effects associated with regulation and extraction especially during low flow periods, the need for

baseline monitoring and the use of biotic indicators for detecting improvements towards a reference condition in response to changes in flow. The use of surrogates for biomonitoring has been widely advocated (Fairweather, 1999; Downes *et al.*, 2002). Compromises in design are inevitable and the main trade-offs involve balancing the level of spending on monitoring against the willingness to accept risks of making incorrect inferences about impacts of regulation on the Nymboida River. Focusing on particular rheophiles as 'key indicators' of changes in flow condition may help optimise the monitoring program given the objectives for which the monitoring is being done (section 2.2.1). However, it is important to understand that species contribution is not solely driven by a unique flow environment but the interaction of multiple environmental factors (e.g. temperature, dissolved oxygen, substrate, periphyton). Therefore in addition to monitoring for a species specific responses to changes in flow the inclusion of a collective community response may also help provide strong signals for the monitoring program.

5.2 Effects of low flows

Rivers and their associated biodiversity are going to be under increasing pressure from continuing regulation. Natural variability in river flows and the associated characteristics of magnitude, frequency, timing, duration, and rate of change are critical in sustaining the full native biodiversity of aquatic ecosystems (Walker *et al.*, 1995; Poff *et al.*, 1997; Richter *et al.*, 1997; Smakhtin, 2001). Components of the Nymboida River's flow regime that regulate ecological processes and characterise the entire range of flows and specific hydrologic events including low flows have been altered for 80 years. The flow regime of the Nymboida River is altered downstream and I am unaware of any similarly detailed macroinvertebrate studies on the Nymboida River or rivers in a similar sub-tropical region.

Low flows generally decrease water velocity; depth and wetted perimeter (Gippel & Stewardson, 1998). Decreases in velocity, depth, and wetted perimeter may gradually change with the duration of a particular low flow event. Declining wetted perimeter is associated with declines in available aquatic habitat and habitat diversity (Stanley *et al.*,

1997; Brasher, 2003). Natural low flow conditions may be compounded under the influence of artificially reduced low flows. Sites studied in the regulated location below the Nymboida Weir had reduced flows and slightly elevated temperatures during both survey and experimental periods. Although this study failed to associate wetted perimeter with changes in flow regime, Anderson and Howland (1998) concluded that reduced discharge below the Nymboida Weir corresponded with marked declines in wetted area.

5.3 Benthic invertebrate response

Instream barriers such as weirs cause a reduction in flow and generally declines in aquatic invertebrate density and diversity (Poff *et al.*, 1997; Bunn & Arthington, 2002; Richter *et al.*, 2006) Disturbances impact on rivers at a range of temporal and spatial scales and include natural periods of low flows (Lake, 2000). Benthic invertebrates are inherently resilient to the effects of lows flows (Gunderson, 2000) because of their evolution within a highly variable aquatic environment. However disturbance potentially compounds the magnitude and duration of an existing low flow event which may be catastrophic for the invertebrate community. Low flows downstream of the Nymboida Weir were certainly disturbed, being further reduced relative to unregulated natural low flows upstream.

Natural low flows and artificially reduced flows have similar effects on invertebrates, but the severity (duration and magnitude) of the flow decrease can influence invertebrate responses. Generally invertebrate density varies in response to decreased flow, whereas invertebrate richness commonly decreases with declines in the number and different types of habitats (Englund & Malmqvist, 1996; Malmqvist & Englund, 1996; Cazaubon & Giudicelli, 1999; McIntosh *et al.*, 2002; Wood & Armitage, 2004; Kinzie *et al.*, 2006). Declines in available habitat or shifting food resources from changes in flow regime can benefit particular individuals whilst disadvantaging others.

The survey data (Ch. 3) and the more specific effects of changes in flow velocity (a critical component of the natural flow regime) from the manipulative experiment (Ch. 4) associate the invertebrate community to different habitats in the Nymboida River.

Inferences made from this study are applicable to other regulated rivers, these include - community response to artificially reduced low flows, information on what river managers should consider when applying environmental flows specifically aimed at improving habitat and species diversity; and how to measure improvements in river condition due to a particular flow strategy with the use of indicator species.

The effects low flows on aquatic invertebrates is an important issue, but few studies on the impacts of artificially reduced low flows on rivers have been undertaken. It is important to remember that this is a preliminary study specifically relevant to other regulated systems and particularly so to sub-tropical rivers experiencing winter low flows. The low flow survey (Ch. 3) aimed to contrast the differences between regulated and unregulated locations by sampling benthic invertebrates from rocks from two different flow habitats within riffles. Riffles were chosen because these zones are at greatest risk of declines in areal extent during low flow conditions. Preferences for particular flow habitats cannot be inferred from the survey data because the survey reflects the interacting effects of multiple environmental and hydraulic variables which characterise each flow habitat (Downes *et al.*, 2002). Manipulative experiments are needed to establish benthic invertebrate preferences for a particular flow environment if flow is the mechanism driving change (Ch. 4). Nevertheless the survey data can be used to predict the optimal habitat for invertebrates under changed conditions such as artificially reduced flows caused by water extraction (Downes *et al.*, 2002).

Similar benthic invertebrate densities were found in the regulated and unregulated reaches of the Nymboida River. This implies that sufficient slow and fast flowing habitats and a suitable supply of food resources enabled the persistence of similar invertebrate densities up -and downstream. The inherent capacity to recover from disturbance of many benthic invertebrates, suggests when habitat conditions are favourable potential recovery of invertebrates in the direction of the reference condition is also possible in response to increased flows down the Nymboida River. In addition, the condition of the Nymboida River's unregulated upstream environment continues to retain enough suitable habitat for the harbouring of colonisers potentially available to the regulated downstream reaches.

A fortunate attribute of the Nymboida River system is the apparent availability of suitable refugia in the relatively intact environment upstream. The natural flow regime upstream appears to have maintained the natural variability of flood and flow pulses recognised as important in maintaining both habitat and biodiversity (Poff *et al.*, 1997; Boulton & Brock, 1999) Therefore the uninterrupted natural variability in flow regime upstream has continued to provide a variety of habitats influenced by these fluctuating flows, importantly these habitats support different densities of benthic invertebrates and highly variable communities distributed as 'patches' in the environment as is advocated by many authors (e.g. Townsend, 1989; Downes, 1990; Lake, 2000; Bunn & Arthington, 2002). If the upstream sections of the Nymboida River and the availability of reference rivers in the vicinity were not in as good a condition, different or possibly declining densities and/or changes of community structure may have been observed in the downstream sections of the Nymboida River, potentially limiting important food supply for fish and restricting energy processing within the system.

There was considerable overlap between the faunal composition of slow and fast flowing habitats, however rheophiles consistently occurred at greater densities within the faster flowing habitats (Table 5.1). Stream invertebrates often show distinct preferences for a particular water velocity and associations between invertebrate density and water velocity have been observed in the field and the laboratory (Statzner *et al.*, 1987; Hansen *et al.*, 1991). It was concluded that rheophiles show promise as indicators for monitoring ecological changes resulting from naturally low and artificially created low flows or indeed improvements under enhanced flows, as their densities were greater in faster than slower flowing water. These findings concur with general ecological theories on aquatic invertebrate density and diversity within rivers, whereby invertebrates are dependant on the natural variability in river flows and the heterogeneity of flow velocities and habitats characteristic of the natural flow regime.

Changes in flow alter invertebrate densities. Changes in habitat suitability affect each taxon differently and certain invertebrate taxa (especially sensitive to flow changes) might be useful when monitoring for an improvement with enhanced flows. For instance,

filter feeding larvae tend to prefer faster flowing water where feeding rates may be better than in slow flowing water, whilst the Black fly larvae (Simuliidae) has been observed in a laboratory experiment selecting higher flows where risk from predation by stoneflies is less (Georgian & Thorp, 1992). Decreased flows might cause larvae to move into declining zones of faster flow (Edington, 1965), increasing competition for resources. More manipulative experiments are needed to further understand the ecological consequences of increases and decreases in flow, and the persistence of the change.

The flow manipulation experiment (Ch. 4) aimed to associate the response of the invertebrate fauna in the Nymboida River with the short-term effects of changes in water velocity. The experimental manipulation increased water velocity in the slow flow habitat and decreased water velocity in the fast flow habitat, aiming to reflect increased releases from the Nymboida Weir. The experiment manipulated flow as well as other hydraulic and environmental variables that may regulate invertebrate density and diversity – therefore demonstrating velocity as the mechanism regulating change.

The common filter-feeding rheophile *Chimarra* showed a very strong positive association with fast over slow flowing water. The *Chimarra* responded rapidly to increased water velocity in the very habitat where it was considered rare (slow habitat) by colonising the newly available, experimentally created fast flow habitat. Whilst the weir has been effective in reducing flows on the Nymboida River for approximately 80 years, a species response such as this highlights that there is still inherent ability in the invertebrate fauna to respond positively to enhanced flows and that upstream reaches continue to provide sufficient habitat for colonisers potentially available to the downstream sections. The larval mayfly *Austrophlebioides* dominated the slow habitat whilst continuing to exhibit a preference for the different habitats associated with fast flows. This implies that declines in either slow or fast flowing habitats may correspond with decreases in densities of *Austrophlebioides*, a common species predated by fish.

5.4 Data considerations

The flow regime is regarded as being a key driver of river ecosystems (Karr, 1991; Poff *et al.*, 1997). Flow is a major determinant of the different types of physical habitat within a river and in turn a major determinant of invertebrate composition. Weirs and water extraction can disrupt the maintenance of a rivers' natural longitudinal and lateral connectivity essential to the viability of many riverine species. My study implies that the Nymboida Weir is not having a significant effect on the invertebrate fauna and individual species are responding to changes in flow in an expected way. Nevertheless caution in the interpretation of data from this study is strongly advised. If the natural spatial and temporal variation is not accounted for in monitoring, there is a great risk of incorrectly interpreting an impact or, conversely that a real impact might be masked by underlying natural variation, especially where already extensive human modification affects the river. This study was conducted over one season only due to the limitations of a two year Masters research. For rivers with strong seasonality such as the Nymboida River, studies should include more than one instance of each low flow period and cover multiple years so as to improve precision and lower the uncertainty of inferences made from the data.

Long-term quantitative studies of benthic invertebrates are surprisingly few (Resh *et al.*, 1988). Species richness and density or biotic compositions are being used to detect a variety of impacts. Species richness is simplistic in that it does not account for the relative abundance of different species whilst abundance does not capture changes in community structure. It is becoming more common to use measures of community or assemblage similarity to measure the response to disturbance or changes over time. The advantage is that huge sample by species matrices can be simplified and subject to ordination techniques to summarise the data. A drawback is that many ordination techniques do not provide for formal hypothesis testing. The univariate models formally tested the association between benthic invertebrate, flow regime and flow velocity. However through the course of the Nymboida study, multivariate techniques were highly valuable in helping clarify patterns in the data and therefore helping to generate hypotheses about species to be included in future monitoring of the Nymboida River.

Flow is a critical factor in river ecosystems and many river studies do not provide species and flow velocity data to help explain the relationship between benthic invertebrates and flow. Some studies report species names without including the higher taxonomic groups and therefore I was not certain of the kinds of species being discussed. I conducted a review of the literature that reported species names including their higher taxonomic levels and the water velocities from which they were collected. Studies including this basic information were few (Table 1.1). Some papers measured velocity then used the measurement to calculate more complex hydraulic variables to identify the different environments; these papers were important for the interpretation of my results as they characterised different flow habitats, albeit in a much more complex way without presenting the original velocity data. If the original velocity data was provided from these studies they would have been included in the review. Water velocity has been established as a major determinant of the distribution of benthic invertebrates in rivers, and limited studies are reporting velocity species data even though it has often been collected with enormous effort in the field. Table 5.1 lists two distinct water velocity categories preferred by species sampled in the Nymboida and Bellinger Rivers and provides information on the preference of each species in the comments column when a species was observed in both flow categories.

Table 5.1 Velocity preferences exhibited by species sampled in the Nymboida and Bellinger Rivers, NSW. * recorded within velocity category ** primarily recorded within velocity category. Caution of interpretation advised where (low densities) were observed.

Order	Family	Taxon	<0.1m/s	0.1 - 0.6m/s	Comment
Tricoptera	Hydropsychidae	<i>Cheumatopsyche</i>	*	**	positive response to enhanced flows
Tricoptera	Philopotamidae	<i>Chimarra</i>	*	**	large positive response to enhanced flows
Tricoptera	Leptoceridae	<i>Oecetis</i>	**	*	negative response to enhance flows
Tricoptera	Hydropsychidae	<i>Asmicridea</i>	*	**	positive response to enhanced flows (low densities)
Tricoptera	Hydroptilidae	<i>Hydroptila</i>		**	positive response to enhanced flows
Tricoptera	Hydroptilidae	<i>Orthotrichia</i>	*	**	(low densities)
Ephemeroptera	Leptophlebiidae	<i>Austrophlebioides</i>	*	*	common irrespective of flow
Ephemeroptera	Baetidae	Baetidae G.2 sp.3	*	*	common irrespective of flow
Ephemeroptera	Baetidae	Baetidae IG	*	*	common irrespective of flow
Diptera	Chironomidae	<i>Thienemanniella</i>	**	*	negative response to enhance flows
Diptera	Simuliidae		*	**	dominates fast flows
Diptera	Chironomidae	<i>Thienemannimia</i>	*	*	common irrespective of flow
Diptera	Chironomidae	<i>Corynoneura</i>	**	*	(low densities)
Diptera	Chironomidae	<i>Cricotopus</i>	**	*	(low densities)
Diptera	Tipulidae		*	*	(low densities)
Diptera	Chironomidae	<i>Rheotanytarsus</i>	*	**	positive response to enhanced flows
Diptera	Chironomidae	<i>Cardiocladius</i>	*	**	(low densities)
Coleoptera	Psephenidae	<i>Sclerocyphon type F</i>	**	*	negative response to enhance flows
Coleoptera	Elmidae	<i>Austrolimnius Larvae</i>	**	*	negative response to enhance flows

5.5 Future work

River managers need to be convinced that providing additional environmental flows (e.g., by reducing extraction during low flows) is producing some demonstrable improvement. Interrelated environmental and hydraulic variables operating over different temporal and spatial scales complicate the determination of which attributes of the altered flow regime are directly responsible for the observed impacts. More studies associating benthic invertebrates with different flow-reduction regimes from multiple rivers and experimental manipulations of flow within rivers are needed to gain a better understanding of these questions.

The effects of the duration and timing of flow reductions were not accounted for in this study. For example, do short periods of reduced flow during an existing low flow period have more impact on benthic invertebrates than long periods of reduced flow? Many recent Australian studies have been preceded by a long drought period resulting in potentially longer than average seasonal low flow periods. I recommend continuing comparative studies between rivers with comparable flow regimes over years whilst considering the nature of the hydrological lead time marking the years prior to the study. As the lead time varies I would expect differences to arise in the invertebrate community, and therefore caution and flexibility is recommended in the continued monitoring of the Nymboida River and the nature of the recommended environmental flows.

Finally, I found that after approximately 80 years of regulation, including years where flows were pulsed daily for hydroelectricity production and the modification of natural low flows downstream which continues today, that the invertebrate community not only retains the potential capacity to recover but also to respond to enhanced flows in a similar way to the benthic invertebrates colonising the unregulated upstream river sections. In addition the unregulated upstream environment on the Nymboida River appears to be providing adequate habitat suitable for the development and continuing supply of colonisers to the regulated river sections downstream of the Nymboida Weir.

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