The diversity of macroinvertebrate grazers in streams: relationships with the productivity and composition of benthic algae

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Thesis resubmitted for the degree of

Doctor of Philosophy

in the

Australian School of Environmental Studies

Griffith University

December 2003

Contents

Abstract

There has been much interest in the last decade concerning the factors that influence diversity, especially how diversity and ecosystem processes may be linked. This study was based in small, cobble streams in South East Queensland. Its aim was to determine how the diversity and composition of consumers (the grazer guild) is influenced by both the production and composition of benthic algae, at different spatial scales. It also aimed to ascertain whether this response differs among grazer sub guilds with different dispersal capabilities.

Ten sites in the Upper Brisbane and Mary catchments were sampled. The sites were selected to provide a range of productivity and composition. Grazers from these sites included snails and elmids, and larval mayflies, moths, and caddisflies. Grazer diversity and composition appeared to be structured by catchment scale influences, but environmental variables also affected which animals colonised patches and microhabitats (cobbles) within catchments. Primary productivity and algal composition could not be separated, with highly productive reaches also having a high cover of filamentous algal taxa. Grazer diversity displayed strongly positive, linear relationships with algal variables at the reach scale. It had a negative relationship with filamentous algae at the cobble scale, and a non-significant hump-shaped relationship with primary productivity. Survey data alone could not separate whether grazers were responding to habitat or food-related drivers, or to variations in productivity.

Experimental manipulation of algal variables at the patch scale, using light and nutrients, also could not clearly uncouple the relationship between primary productivity and filamentous algal cover. Once reach scale variation was removed, grazer diversity

displayed hump-shaped relationships with algal variables, including algal diversity. Much of this variation was due to patterns in mobile grazers, as sedentary grazers did not respond to algal variation at this scale. The density of the more mobile taxa showed similar patterns to those at the cobble scale (hump-shaped).

A second field experiment was carried out in order to further investigate the responses of invertebrates to algal community composition at the cobble scale. Data from all three chapters suggested that as sites shifted to a dominance of filamentous algae, often with an associated increase in GPP, there was also a shift in the grazer community towards more sedentary grazers and away from the more mobile taxa. This also occurred at the cobble scale in the second experiment.

The gut analysis and diet studies in the third chapter indicated that while many grazers consumed filamentous algae, it was not assimilated. This suggests that the preferences for sedentary taxa for cobbles and reaches dominated by filamentous algae are likely to be due to some other, possibly habitat-related, factor such as flow or predation refuge.

The study provides a rare examination of relationships between primary productivity and consumer diversity in freshwater streams, and finds support for the pattern found in other systems of monotonic relationships of these two variables at large scales and hump-shaped relationships at smaller scales. It emphasises the importance of understanding other, potentially confounding, aspects of communities of producers, and investigates the possible roles of the most important of these (community composition) in structuring consumer communities in the small cobble streams of South-East Queensland.

Declaration

This work has not previously been submitted for a degree or diploma in any university. To the best of my knowledge and belief, the thesis contains no material previously published or written by another person except where due reference is made in the thesis itself.

Claire McKenny

Acknowledgements

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1 – General introduction

The study of biological diversity has become a pressing issue in ecology (e.g. Singh 2002, Dayton 2003). The loss of species has been reported from many ecosystems worldwide (Ehrlich & Wilson 1991, Allan & Flecker 1993, Pimm *et al.* 1995, Dudgeon 2000, Singh 2002) and there is an urgent need to understand the causes of the decline, including how species interact with other components of the environment. In addition, there is a growing realisation that the maintenance of ecological processes is essential (e.g. Ehrlich & Mooney 1983, Edwards & Abivardi 1998).

In the past decade, these two imperatives for knowledge have led to ecological research becoming increasingly focussed on a key problem: understanding the ecosystem properties and processes that influence species richness (e.g. see reviews by Ricklefs & Schluter 1993, Huston 1994). In freshwater systems, patterns of species richness and abundance are often used as surrogate measures of these fundamental processes. Yet process and pattern are not necessarily linked (Barmuta 1987, Bunn 1995, Bunn & Davies 2000), and so it is not clear exactly what patterns are telling us about fundamental processes.

This thesis addresses one aspect of this knowledge gap for freshwater streams by examining the relationships of the productivity of benthic algae with the diversity of their macroinvertebrate consumers (grazers).

1.1 Defining diversity

Biological diversity is a term with many definitions, because it is a concept that is exceptionally broad. Fundamentally, it refers to the 'variety of life' (Gaston 1996a), or to 'the irreducible complexity of the totality of life' (Williams *et al.* 1994).

Diversity has a number of components, and is commonly divided into genetic diversity, species or taxonomic diversity, and ecosystem diversity (see review by Gaston 1996a). Species or taxonomic richness is the most frequently and widely applied measure (Gaston 1996b). Genetic diversity refers to morphological and phenotypic variation within and between populations and species (e.g. Baur & Schmid 1996, Mallet 1996). Ecosystem diversity is the variation between ecological systems, and has received little attention in the literature (Gaston 1996a). The diversity of functions within an ecosystem is increasingly studied as another aspect of diversity (e.g. Díaz & Cabido 2002, Petchey & Gaston 2002).

In this study, diversity is used primarily to refer to species richness. Not only does this provide a measure of the "variety of life" as represented by a count of species, but it also tends to capture a number of other facets of that variety (Gaston 1996b). In this, the study is in accord with the vast majority of investigations of diversity: productivity relationships (Abrams 1995, Rosenzweig 1995).

This study also uses three types of diversity measures proposed by Whittaker (1972, 1975). Alpha diversity (α) is the species richness of a particular habitat that is considered to be homogeneous; this is also called 'within-habitat' diversity (Huston 1994) or 'local' diversity. Beta diversity (β; between-habitat diversity, Huston 1994) refers to the degree of replacement of species among different habitats, and gamma

diversity (γ) is the species richness of the entire landscape, which is a result also of both

the α and ß diversities (Figure 1.1). The latter is often known as regional diversity.

This schema recognises the inter-relationship of regional and local diversity that may

occur in most or many environments (Ricklefs 1987, Cornell & Lawton 1992, Palmer *et al.* 1996, Caley & Schluter 1997, Vinson & Hawkins 1998). Regional diversity may in

fact ultimately constrain local diversity in most environments (Caley & Schluter 1997).

In stream and river ecosystems, invertebrate richness may be jointly structured by

historical events (at the regional scale) and by the physico-chemical conditions unique

to each location (Poff & Ward 1990, Vinson & Hawkins 1998, Lake 2000, Malmqvist

2002). The number of species in regional taxa pools may fluctuate over evolutionary

time and this should define the maximum number of taxa that can occur in smaller areas

(Heino *et al.* 2003).
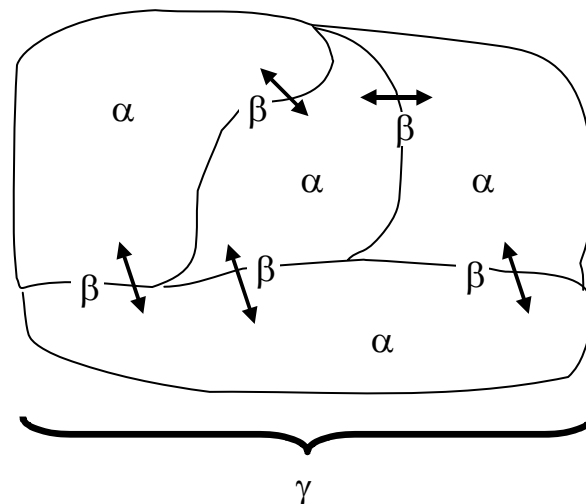
Figure 1.1 The components of landscape diversity proposed by Whittaker (1972): α (alpha) is local species richness, β (beta) is between-habitats turnover and γ (gamma) is total regional richness. After Moreno and Halffter *(*2001).

Catchment scale | Reach scale | Patch | Microhabitat
10^4-10^5 m | 10^2-10^3 m | (pool and run) | (cobble) scale
 | | scale 10^0-10^1 m | 10^{-2} m
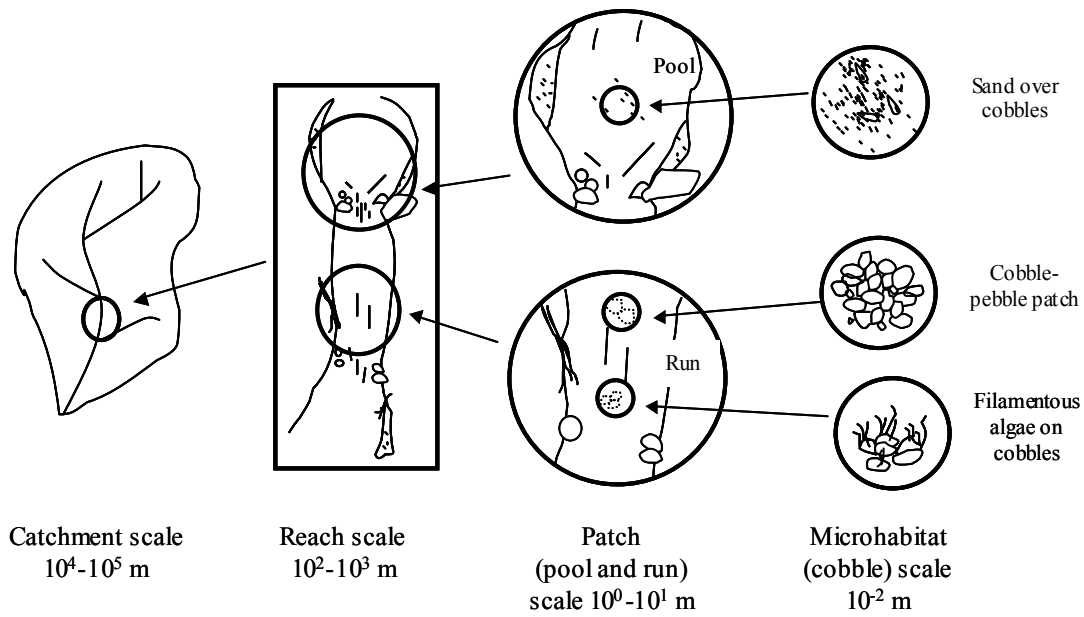
Figure 1.2 Hierarchical scales of a stream system. Approximate linear spatial scale, appropriate to a second or third order stream, is indicated. After Frissel *et al.* (1986).
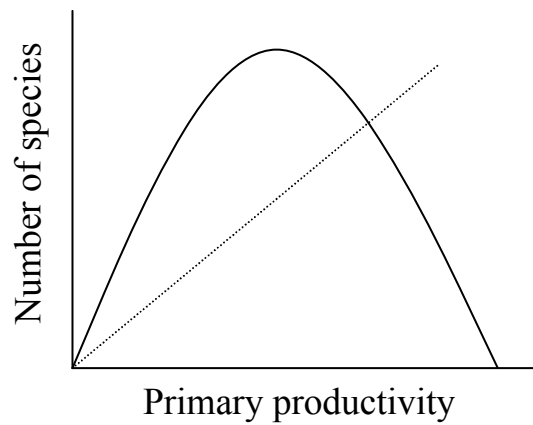
Figure 1.3 Hump-shaped and monotonic (positive) relationships of productivity and species richness. Monotonic relationship is dotted.

Aquatic macroinvertebrates, particularly insects, are typically viewed as highly dispersive and thus potentially able to colonise any local site (although see Bohonak & Jenkins 2003); however environmental conditions at finer spatial scales will often limit which specific taxa establish from these larger taxa pools (Poff & Ward 1990, Vinson & Hawkins 1998). Lotic systems can be viewed as operating at a nested hierarchy of spatial scales (Frissel *et al.* 1986), from catchment or watershed, through reaches, habitats or patches (e.g. pools or riffles) down to microhabitat systems at the level of the individual cobble (Figure 1.2). Catchment to reach scales are comparable with the 'across community' scale of Huston (1994) and Mittelbach *et al.* (2001), and the 'within-community' scale encompasses the habitat (individual pools, runs, riffles or discrete sections of these) to microhabitat scale (individual cobbles). This physical habitat hierarchy has implications for the distributions and abundances of organisms, since all lotic organisms are in intimate contact with the substratum for at least some stage of their life cycle (Poff & Ward 1990).

1.2 Diversity: productivity relationships

Evidence across a broad range of biomes suggests that a key determinant of diversity within an ecosystem is productivity; the rate at which energy flows through an ecosystem (see reviews by Rosenzweig & Abramsky 1993, Mittelbach *et al.* 2001). The relationship of species richness with productivity is often hypothesised to be hump-shaped or unimodal (e.g. Grime 1973, Huston 1979, Tilman 1982, Rosenzweig 1992; see Figure 1.3). This has been claimed by some authors to be the 'true' (Rosenzweig 1992) or 'ubiquitous' (Huston & DeAngelis 1994) relationship between productivity and species richness.

However, recent extensive reviews of literature report that the relationship occurs in this form only for some taxa and at some geographical and ecological scales, and that other patterns occur as well, most commonly monotonic increases (Waide *et al.* 1999, Mittelbach *et al.* 2001; see Figure 1.3). At the local scale there is considerable evidence across a range of systems that these relationships tend to be unimodal or 'hump-shaped' (Abramsky & Rosenzweig 1984, Tilman & Pacala 1993, Dodson *et al.* 2000). At the regional scale, however, species diversity often increases monotonically with increasing productivity (Wright *et al.* 1993, Waide *et al.* 1999, Gaston 2000).

Abrams (1995) suggests three possible mechanisms for a positive (monotonic) relationship:

1) Increased productivity raises the abundance of rare species, reducing their extinction rates.

2) Increased productivity increases intra-specific density dependence, allowing coexistence of species, some of which would be excluded at lower productivity.

3) Increased productivity increases the abundance of rare resources or combinations of resources and conditions that are required by specialist species.

However, there is no single hypothesis that successfully explains the pattern, nor that of the decrease phase of the hump-shaped relationship (Rosenzweig & Abramsky 1993, Abrams 1995). Many authors attribute the decreased diversity at high productivities to increased competitive exclusion under those conditions (e.g. Rosenzweig 1992, Rosenzweig & Abramsky 1993, Tilman & Pacala 1993, Huston & DeAngelis 1994; although see Abrams 1995). Other mechanisms for both relationships are summarised and reviewed by Rosenzweig and Abramsky (1993) and Abrams (1995).

There is a distinct lack of evidence concerning the productivity: species richness

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relationship in the benthos of freshwater lotic environments, particularly relating to macroinvertebrates (although see Abramsky 1978, Stout & Vandermeer 1975 and Bunn & Davies 1990 for discussion of macroinvertebrates and productivity at the global scale; see also Pearson & Connolly 2000). Studies that address the issue experimentally have related algal taxonomic richness to nutrient gradients (Carrick *et al.* 1988, McCormick & Stevenson 1991, Stevenson *et al.* 1991, Peterson & Grimm 1992, Rosemond 1993, Biggs & Smith 2002) but very few have measured productivity directly (although see Rosemond 1993) or examined higher trophic levels (but see Pearson & Connolly 2000).

1.3 Algae and grazers in streams

Algae are a major food source for lotic consumers, even in heterotrophic systems (Bunn *et al.* 1999, Finlay 2001, Thorp & DeLong 1994, 2002, Bunn *et al.* 2003). Indeed, there is growing evidence that epilithic algae plays a disproportionately important role in the food web of forested streams in the subtropics and tropics, including cobble streams in South-east Queensland such as those studied in this thesis (e.g. Bunn *et al.* 1999, March & Pringle 2003, Mantel *et al.* 2004). Authochthonous carbon is often easier to assimilate and contains more energy per unit mass than allochthonous carbon (Junk *et al.* 1989, Sedell *et al.* 1989, Thorp & Delong 1994, 2002), and it forms a major component of the diet of many species of lotic macroinvertebrates (see reviews by Cummins 1973, Cummins & Klug 1979, Gregory 1983, Lamberti & Moore 1984; also Chessman 1986 for Australian examples).

Key consumers of lotic algae are grazers: animals adapted to graze or scrape material (periphyton or attached algae) from mineral or organic substrates (Gregory 1983, Wallace & Webster 1996). They have a tightly coupled interaction with algae (Wallace & Webster 1996), and changes in algal community composition, productivity and

biomass can affect the abundance, distribution, growth and/or production of grazer species (Lamberti *et al.* 1989, Dudgeon & Chan 1992, Peterson *et al.* 1993, Hill *et al.* 1995, Wellnitz & Ward 1998, Rosemond *et al.* 2000).

Macroinvertebrate grazers of Australian streams typically include cased larvae of caddisflies (e.g. Helicopsychidae, Tasimiidae, and Glossosomatidae), aquatic Lepidopteran larvae, molluscs such as Hydrobiosidae and Ancylidae, larval mayflies (e.g. Baetidae, some Leptophlebiidae) and coleopterans such as Psephenidae larvae and larval and adult Elmidae. Note that this definition excludes Hydroptilidae larvae, which consume algae with piercing mouthparts. Some Chironomidae larvae are likely also to graze, but their feeding habitats and taxonomy are very poorly understood in these streams, and it was beyond the scope of this study to include them.

These grazers, as is typical of the guild worldwide, exhibit differences in modes of feeding, behavioural adaptations, consumptive abilities and mouthpart morphology (see Gregory 1983, Lamberti & Moore 1984). An intuitive functional separation into subgroups is provided by a combination of mobility and feeding behaviour (Bergey 1995).

Highly mobile grazers such as leptophlebiid and baetid mayflies are, in larval stages, strong swimmers and crawlers, and they are readily able to enter the drift of their own volition (Mackay 1992), and tend to focus their grazing on distinct patches of periphyton (Bergey 1995). In addition, these animals have 'brush' type mouthparts and may be able to feed on the epiphytes of filamentous algae (e.g. Dudley 1992).

On the other hand, more sedentary grazers including caddisfly larvae, snails and aquatic Lepidoptera, move more slowly while feeding, can crop periphyton closer to the substratum, and abandon food patches at a much lower density of food (see also Hart

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1981, Kohler 1984, Hill & Knight 1987, 1988a). These grazers generally have scraping and rasping mouthparts, and therefore are better suited to feed in zones where low profile, tightly attached algae grow (Steinman 1996). Most have cases, shells or build silk retreats onto the substrate, and all are less likely to enter the drift (Mackay 1992). Note that this definition can include, but is not limited to, 'sessile' species that are attached semi-permanently to the substrate.

All grazers are potentially impacted by the changes in algal communities caused by anthropogenic disturbances to streams. Catchment, and particularly riparian, clearing and the addition of nutrients through agricultural runoff have a significant influence on the production and composition of algal communities within streams (see review by Biggs 1996). For example, the removal of riparian shade augments primary production (Lowe *et al.* 1986, Hill & Knight 1988b, Hill & Harvey 1990) and causes a shift towards autotrophy (Bunn *et al.* 1999). Also, enrichment with limiting nutrients can cause large increases in primary production and algal biomass (Winterbourn 1990, Peterson *et al.* 1993, Rosemond 1994, Mosisch *et al.* 1999).

Such disturbances can also cause compositional changes. Increasing light levels tend to cause a shift away from communities dominated by rhodophytes, cyanobacteria and diatoms, towards communities consisting largely of chlorophytes (see review by Hill 1996). Extreme compositional shifts can involve the proliferation of nuisance species, including filamentous algae and large vascular plants such as *Urochloa mutica* (para grass; Graham *et al.* 1995, Bunn *et al.* 1997).

In addition to anthropogenic disturbance, natural disturbance can affect algal and macroinvertebrate communities, particularly in systems prone to periods of spates and 'flashy' floods such as the headwater streams of South-east Queensland (during the wet

season; see Chapter 2). Floods can cause significant reduction in the biomass and diversity of algae and macroinvertebrates (e.g. Fisher *et al.* 1982, Reice 1985, Boulton *et al.* 1988, Mosisch & Bunn 1997), and remove or reduce proliferations of filamentous algae (Dudley *et al.* 1986, Dudley & D'Antonio 1991, Feminella & Resh 1990).

The re-establishment of algal biomass and community structure can be rapid (see review by Peterson 1996). Anthropogenic factors such as enrichment and riparian clearing can affect the nature (species composition) and rate (productivity and biomass development) of algal re-establishment (see review by Peterson 1996, also Biggs & Smith 2002). Algal species composition, biomass and productivity may, in turn, significantly affect re-establishment of macroinvertebrate grazers (Mackay 1992, Boulton *et al.* 1998).

1.4 Algal community influences on grazers

As discussed, productivity may influence grazer diversity and composition in streams. In addition, other aspects of algal communities may be important to grazers, such as algal biomass, taxonomic composition, and diversity.

It is now well established that changes in algal community composition and biomass are important to grazers, as animals will move away from cobbles or patches with low food value by drifting or crawling (Hart 1981, Kohler 1984, Vaughn 1986, Poff & Ward 1992, Gresens & Lowe 1994).

Researchers have suggested that herbivores may be selective in their diets at the fine scale, i.e. that they are able to choose one algal cell over another (see Gregory 1983). In fact, true selectivity refers to a directed behaviour on the part of the herbivore, and this appears unlikely (Lamberti & Moore 1984, Steinman 1996). Rather, grazers are more likely to be able to graze some species and not others by virtue of their mouthpart

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morphology and feeding mode (e.g. Jacoby 1987, Peterson 1987, Hill & Knight 1988a, Blinn *et al.* 1989, McCormick & Stevenson 1989, Karouna & Fuller 1992).

Diatoms are a frequent food source for aquatic grazers, although some diatom taxa are often less numerous in herbivore diets than in the environment (see Gregory 1983 and also Hill & Knight 1987, 1988a, Peterson 1987, Blinn *et al.* 1989, McCormick & Stevenson 1989). In particular, large, erect diatom taxa (e.g. *Cymbella*, *Gomphonema*, *Rhoicosphenia*) may be more successfully ingested than small, adnate forms such as *Achnanthes* and *Cocconeis* (Jacoby 1987, Peterson 1987, McCormick & Stevenson 1989, Wellnitz & Ward 1998).

Some species of blue-green algae may be avoided by some grazers if they produce toxins or chemical deterrents (e.g. McCullough *et al.* 1979, Dudley & D'Antonio 1991), but this is not universal. For example, under certain conditions some species such as the caddisfly *Leucotrichia pictipes* are able to keep patches clear of a low quality, filamentous species of blue-green algae, by 'weeding' it out of the periphyton with their forelegs (Hart 1981).

Some grazers are able to graze filamentous macroalgae, particularly when it is in the early stages of establishment (e.g. Brown 1961, Feminella & Resh 1991, Hill *et al.* 1992, Dudley 1992, Karouna & Fuller 1992, Sarnelle *et al.* 1993). However, it is considered unpalatable to many grazers once it becomes established (Dudley *et al.* 1986). This unpalatability is generally attributed to its high cellulose and lignin content and a tough cell wall (Lamberti & Moore 1984, Wellnitz & Ward 1998), although *Cladophora* also produces chemicals toxic to grazers (Hutchinson 1981).

Filamentous algae may affect grazer density and richness in other physical ways. The long filaments increase the structural complexity and affect the architecture of cobble

surfaces; these aspects can significantly impact species richness on small scales (McKenny 1995, Robson & Barmuta 1998, Downes *et al.* 1998, 2000a & b). The algae may provide refuges from predation and flow, as for example current velocities below a mat of *Cladophora glomerata* can be reduced by up to 40% (Dudley *et al.* 1986) and may provide a greatly increased surface area for epiphytic diatoms and cyanobacteria which are grazed by animals such as *Agapetus* and *Baetis* (e.g. Dudley 1992). On larger scales, mats of filamentous algae are inherently patchy in structure and this may increase structural heterogeneity within reaches (e.g. Hart 1992). Filamentous algae may also compete for space with grazers and their preferred food species, and cause mechanical interference with invertebrate movement and feeding (Dudley *et al.* 1986).

It is also likely that changes in algal diversity will influence the diversity of the guild or subguilds of grazers. It has been considered for some decades that plant diversity could be important in determining herbivore diversity (e.g. Pimentel 1961, Southwood *et al.* 1979, Lawton 1983). This relationship is supported for plants and arthropod herbivores by theoretical models (e.g. MacArthur 1972, Whittaker 1975, Tilman 1986, Rosenzweig 1995) and by experimental and some correlative studies in terrestrial environments (Siemann *et al.* 1998, Knops *et al.* 1999, Haddad *et al.* 2001). Again, there is little empirical evidence of the nature of this relationship in freshwater lotic systems.

1.5 Scale and dispersal

In conclusion, there is a number of ways in which the algal community may affect grazer diversity: algal biomass and taxonomic composition may be important, as well as algal productivity and diversity. Other factors will also influence grazer diversity, including variables such as disturbance, flow and physico-chemistry. However, not all of these factors will operate at every scale.

Typically, studies of freshwater benthic invertebrates are designed at one of a few discrete spatial scales: 1) comparisons among waterbodies (e.g. rivers or lakes); 2) comparisons within a waterbody but between stream segments or habitats (e.g. between riffles within one river, or between riffles and pools); and 3) comparisons at the microhabitat scale, within a particular habitat (cf. Crowl & Schnell 1990).

Some generalisations can be made about the factors that influence the density and richness of invertebrates at each scale (see reviews by Crowl & Schnell 1990, Vinson & Hawkins 1998). At the between-waterbody scale, physico-chemical attributes of the drainage basin or sub-catchment, such as water temperature (Townsend *et al.* 1983), pH and geomorphology (Heino *et al.* 2003), and flow and disturbance regime (Death & Winterbourn 1995, Nelson & Lieberman 2002), typically predominate, and it has been suggested that primary productivity is also important at this scale (e.g. Bunn & Davies 1990).

At the within-waterbody scale, a large number of variables are important such as flow and water chemistry (Rabeni & Minshall 1977, Barmuta 1990), food abundance (e.g. Lamberti & Resh 1983, Lodge 1986), habitat heterogeneity (e.g. Brown 2003) and biotic interactions (e.g. Hemphill & Cooper 1983, Hildrew & Townsend 1982). At the microhabitat scale, biotic interactions (e.g. McAuliffe 1984, Peckarsky 1984) and food abundance (e.g. Reice 1981, Richards & Minshall 1988), and substrate complexity and architecture (e.g. O'Connor 1991, Gawne & Lake 1995, Downes *et al.* 1998, 2000b) have been found to be influential.

A conceptual model can therefore be developed to illustrate the nested, scale-related factors that may influence, or be related to, grazer diversity (Figure 1.4). At the regional level, or in other words at the scale of ecoregions or catchments, grazer diversity may be
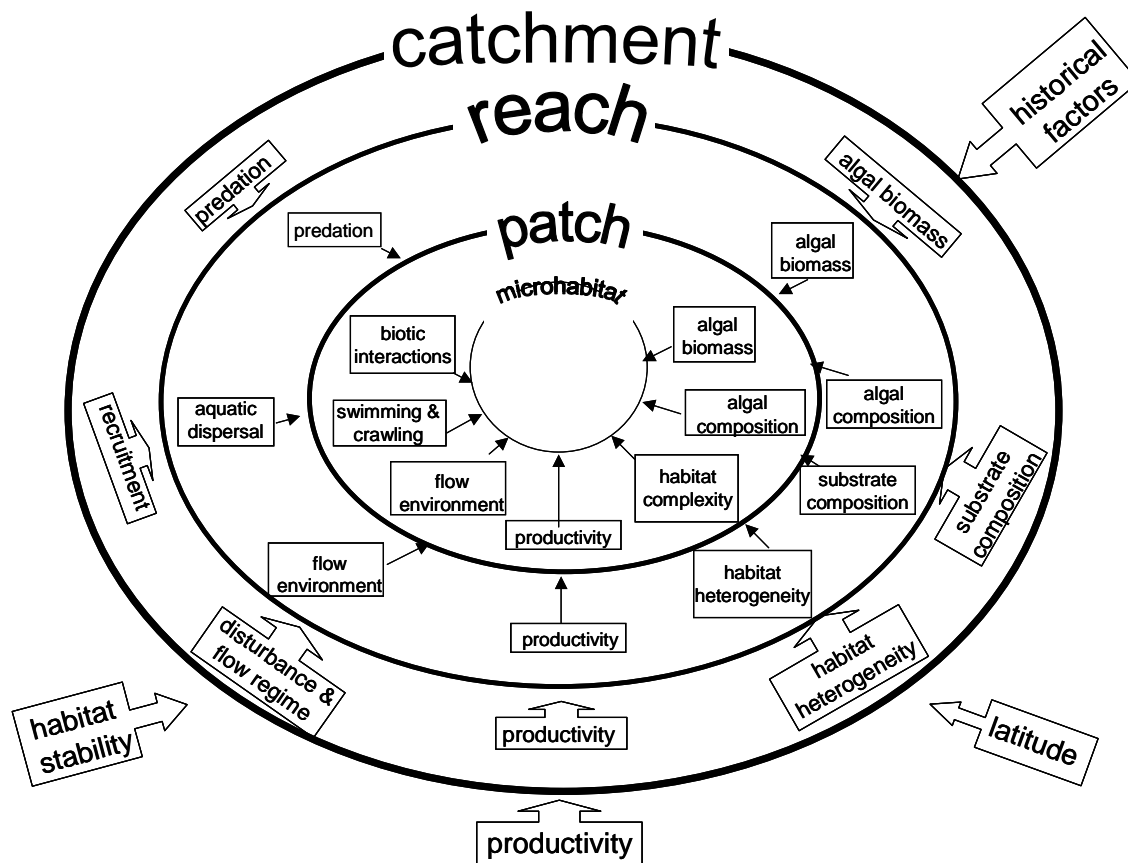
Figure 1.4 Conceptual model of the nested factors that may influence macro-invertebrate grazer diversity in streams at various scales. Each ring represents diversity at the nominated scale. Arrows indicate factors that influence diversity at this scale.

constrained by factors such as latitude and continentality (Boothroyd 2000), as well as those that operate over ecological time-scales. These include landscape habitat heterogeneity, landscape level productivity and habitat stability of the ecoregion (Shmida & Wilson 1985, Cornell & Lawton 1992), and those processes that operate on an ecological and/or evolutionary time scale to impact immigration (dispersal) and extinction. The latter include such factors as climate change, sea-level and other environmental changes (Milner *et al.* 2000, Petts 2000, Voelz & McArthur 2000, Sweeney *et al.* 1992).

Within a particular catchment, factors that will influence between-reach grazer diversity may include catchment scale productivity, flow and disturbance regime, substrate composition, algal biomass, habitat heterogeneity (relating to local geology and geomorphology), aerial and other long-distance aquatic dispersal, and recruitment. Similar factors might be expected to influence grazer diversity between patches (separate pools, riffles, runs) within a reach, although aquatic dispersal may begin to become more important at this scale and biotic interactions (particularly fish predation) may also be more important.

At the microhabitat scale, factors such as algal composition and biomass, microhabitat complexity, small-scale flow heterogeneity (hydraulics), predation, competition and aquatic dispersal, may influence species diversity between cobbles. There is a paucity of studies examining the relationship between algal productivity and macroinvertebrate diversity at this scale. However, it is possible that productivity might be related to grazer diversity at this scale. For instance, increased productivity of algal food species on a cobble may mean that a higher abundance of grazing invertebrates can feed on that cobble. The rise in abundance may be accompanied by a rise in species richness due to

an increase in sample size alone (Dean & Connell 1987a, b). In addition, increased productivity may be associated with an increase in the diversity of resources (algal taxa) on a cobble. This may allow in a diversification of niches, permitting resource partitioning and hence coexistence (e.g. Schoener 1974).

Moreover, while the role of competition in structuring stream communities is controversial (Reice 1981, Hart 1983, Peckarsky 1984, Hildrew *et al.* 1984), it is also possible that high productivity might increase the degree of intra-specific density-dependence so that more species can co-exist on one cobble (Abrams 1995, Siemann 1998).

Finally, the schema summarised by Figure 1.2 recognises that habitat is not the only determinant of the distributions of invertebrates: the process of dispersal links the various scales of microhabitats, patches, reaches and catchments. Aspects such as migratory behaviour, variation in mobility and movement distances contribute significantly to distribution patterns of invertebrate taxa (Malmqvist 2002). Grazers with differing dispersal behaviours and abilities, such as the sedentary and mobile groups suggested above, might therefore be expected to respond differently to processes that vary with scale.

1.6 Aims and Outline of Thesis

The thesis investigates the relationship between algal composition and productivity and the diversity and taxonomic composition of macroinvertebrate grazers at various spatial scales, in small cobble streams of South-east Queensland, Australia. This was studied in the dry season (July-October) when physical disturbance through spates was minimal and macroinvertebrate abundance and diversity were at a maximum.

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The research aimed to answer the following key questions at the reach, patch and microhabitat (cobble) scales:

1. Is algal productivity related to grazer diversity and composition?

2. Are other aspects of the algal community, such as the cover of filamentous algae, taxonomic composition, biomass or diversity, related to grazer diversity and composition?

3. What role does diet play in the responses of grazers and their sub-guilds to algal community composition?

The first objective of the study was to establish the patterns of the richness, density and composition of larval grazers in association with varying productivity and composition of algae: particularly the cover of filamentous algae (Chapter 3). In addition, relationships of diversity with flow and water chemistry were examined. Patterns were investigated at both the reach (10^2 m) and cobble (10^{-2}m) scales. Grazers were separated into two groups on the basis of their larval mobility and feeding methods in order to understand compositional shifts.

A field experiment, manipulating shade and nutrients, was then undertaken in an attempt to separate the effects of productivity and algal community composition on larval grazers (Chapter 4). Relationships of grazers with these variables were investigated at the patch (10^0-10^1m) scale. The potential influence of algal diversity on grazer diversity was also examined.

A second field experiment, manipulating algal community composition (filamentous algae vs. biofilm) over time (10 days colonisation vs. 3 days colonisation) was carried out in order to further investigate grazer responses to filamentous algae and to further

understand the responses of grazers and subguilds at the cobble scale. Gut contents and stable isotope analysis were investigated in order to ascertain whether dietary preferences explained grazer responses to filamentous algal cover.

Final conclusions about diversity, composition and productivity relationships between benthic algae and macroinvertebrate grazers in streams are presented in Chapter 6.

2 - Study areas

2.1 Small streams of South-east Queensland

South-east Queensland lies at a latitude of about 25- 28 °S and at a longitude of about 152- 154 °E. The climate is sub-tropical, with warm, wet summers and mild, dry winters (Australian Bureau of Meteorology 1983). Average annual maximum temperatures vary between 20 and 29 °C (Australian Bureau of Meteorology 2003). Total annual rainfall ranges between 900 and 1800 mm and varies greatly between sub-catchments.

Temporal patterns of flow in streams of this region are variable and unpredictable, and the area can experience large volume floods and severe droughts (Mosisch & Bunn 1997). Most rainfall occurs during the wet season of December to March, with conditions of base flow prevailing in the streams during the dry season of July to October (Mosisch *et al.* 1999). During this dry period, stream flows can be markedly reduced, and many streams become a series of pools connected only by subsurface flow (e.g. Mosisch & Bunn 1997).

The research reported here was conducted within third- to fifth-order tributaries (100 – 400 m asl) of the Brisbane, Mary and Coomera rivers (see Figure 2.1 for location of catchments). These headwater streams have high slopes (approximately 1:10) in the study reaches, and are often characterised by an armoured bed of boulders, cobbles, gravel, and areas of exposed bedrock. During the wet season, intense rain events (at times greater than 400 mm.day^{-1}) can cause major disturbances to the stream bed, and tractive forces greater than 20 kg.m^{-3} have been recorded (Mosisch 1995).

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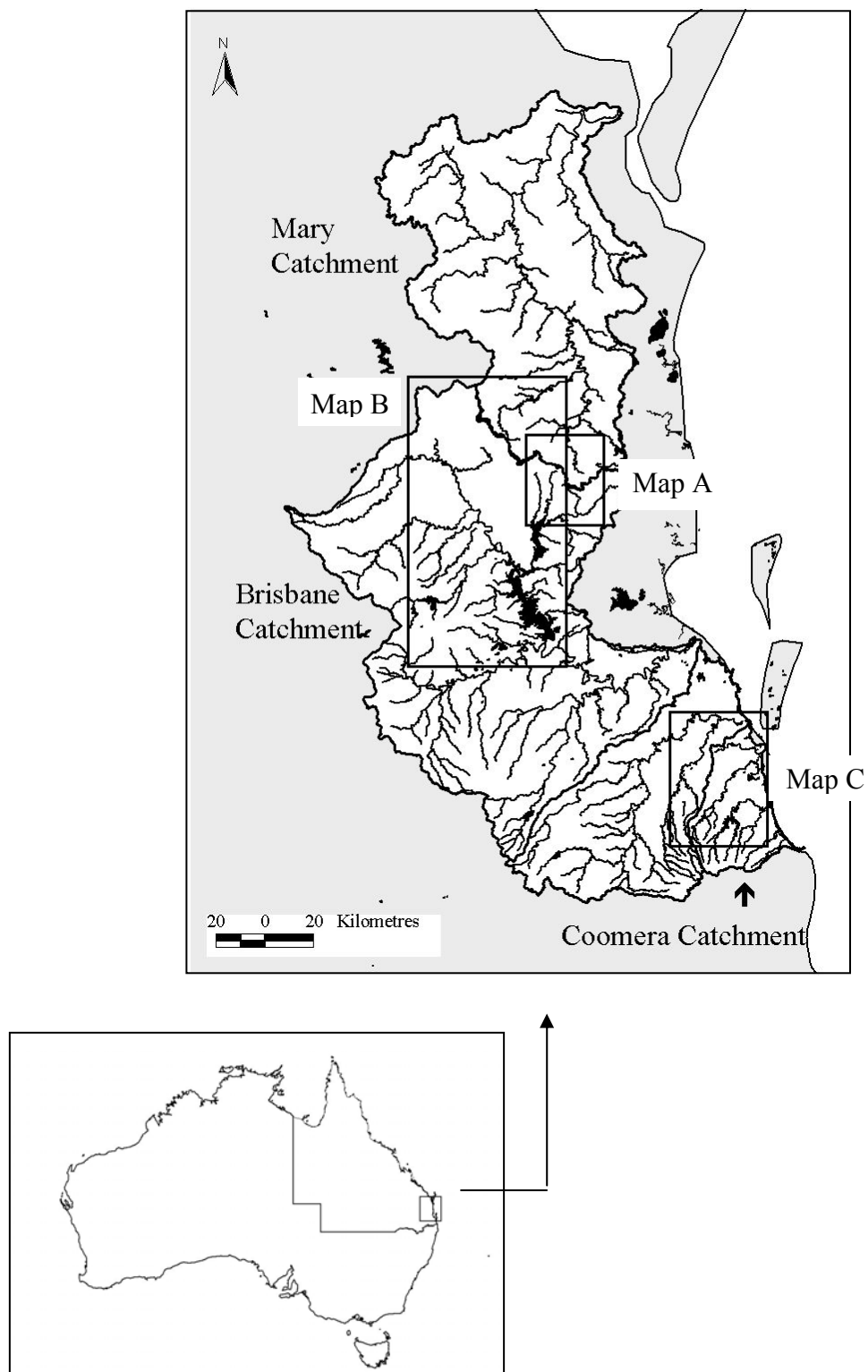
Figure 2.1 Location of maps presented in this thesis. Map A is of the upper Mary and Eastern Brisbane sites (Figure 2.2). Map B is of the upper Western Brisbane sites (Figure 2.3) and Map C is of the Coomera sites (Figure 2.4).

The remnant native vegetation of upland riparian zones in this area includes notophyll vine rainforests, dry eucalypt dominated forests, and fern thicket/hoop pine scrub (e.g. *Araucaria cunninghamii*). Endemic riparian vegetation of valley floors consists mainly of dry notophyll vine forest and semi-evergreen vine thickets/hoop pine scrub (e.g. black tea-tree (*Melaleuca bracteata*), river she-oak (*Casuarina cunninghamiana*), red bottlebrush (*Callistemon riminalis*), and lillipilly (*Syzygium, Eugenia*). Common weeds include lantana (*Lantana camara*), camphor laurel (*Cinnamomum camphora*) and para grass (*Urochloa mutica*) (Catterall *et al.* 1996, Young & MacDonald 1996).

Since European settlement in 1820, more than half of South-east Queensland has been cleared of native vegetation. Currently, about 60% of the cleared land is used for stock grazing, 10% for cropping, 10% has been urbanised and the remainder is used for plantations and forestry (SLATS 1997). The heavy disturbance to riparian zone caused by such land-clearing (Telfer *et al.* 1998) has led to problems such as nutrient enrichment, habitat loss, increased sedimentation and erosion, and increased primary production have been reported in many rivers and streams (Arthington *et al.* 1996, 2000, Bunn *et al.* 1999).

2.2 Biota of study area streams

Characteristic vertebrates of upland streams in the study area include the platypus (*Ornithorhynchus anatinus*), eels (*Anguilla* spp.), and teleost fish such as southern blue-eye (*Pseudomugil signifer*), Australian smelt (*Retropinna semoni*), hardyhead (*Craterocephalus* sp.) and gudgeons such as *Mogurnda adspersa and Hypseleotris klunzingeri* (Udy *et al.* 2002, Marshall 2001, Koster 2004). Non-insect benthic macroinvertebrates typically include hydrozoans, worms (Gordiidae, Oligochaeta, Turbellaria), snails (Ancylidae, Hydrobiidae, Planorbidae, Thiaridae), crustaceans

(Atyidae, Palaemonidae and Parastacidae), and various mites (Witting 1999, Appendix B, Marshall 2001).

Of the fauna that inhabit the stony benthos of these streams, a number of Ephemeropteran families are common, including Baetidae, Caenidae and Leptophlebiidae, while stoneflies (Eustheniidae and Gripopterygidae) are not common (Witting 1999, Appendix B, Marshall 2001). Damselflies are most often represented by Synlestidae and Diphlebiidae, while Gomphidae are the most common of at least six dragonfly families (Appendix B, Witting 1999, Marshall 2001). Cased caddisflies include Calamoceratidae, Calocidae, Glossosomatidae, Hydroptilidae, Helicopsychidae, Leptoceridae and Tasimiidae, while the most abundant free-living caddis include Ecnomidae, Philopotamidae, Polycentropodidae, and Hydropsychidae (Appendix B, Negus 1995, Witting 1999). Pyralid Lepidopterans are abundant but not highly speciose. There are a number of beetle families, with the most common in the benthos being Elmidae, Hydrophilidae, Psphenidae and Scirtidae, and the only common benthic hemipterans are Corixidae. Most abundant benthic dipterans include Athericidae, Ceratopogonidae, (most commonly Chironominae, Orthocladinae and Tanypodinae), Empididae, Simuliidae and Tipulidae (Appendix B, Witting 1999, Marshall 2001).

Floods and spates can quickly and dramatically reduce algal biomass and grazer abundances in streams of South-east Queensland, but these communities appear to recover rapidly (Mosisch 1995, Mosisch & Bunn 1997, also cf. Rosser & Pearson 1995). Long periods of stable flow often occur in the dry season, and under these conditions, there is re-establishment of communities of algae and grazers (including mature stands of filamentous algae, C. McKenny personal observations). During extended periods of low physical disturbance, the relationship between grazer numbers

and algal biomass may become more tightly coupled (Mosisch 1995, Biggs 1996, also cf. Northern Hemisphere systems that experience summer low flow e.g. Lamberti & Resh 1983, Feminella *et al.* 1989, Feminella & Resh 1990).

Typical abundances of benthic macroinvertebrates in upland and rainforest streams of South-East Queensland are low. Marshall, in his study of the cobble fauna in pools of two rainforest streams in the Conondale Ranges (2001), found mean abundances to range between 34 individuals per m^{-2} (*Hellyethira simplex*) and 200 individuals per m^{-2} (*Atalophlebia*), with *Bungona sp.* the only exception at around 3600 per m^2. Mosisch, in his four-year study of the cobble fauna of two rainforest streams in the Upper Brisbane and Mary catchments, found typical abundances of around 10 grazers per 500 cm^2 (40 per m^2), and maxima of only 40 grazers per 500 cm^2 (600 per m^2) during the dry season in 1992.

Genetic evidence suggests that some species have limited dispersal of larvae between pools in rainforest streams in such conditions (Hughes *et al.* 2003). This may particularly be the case for species with more sedentary larvae such as the caddisfly *Tasiagma ciliata,* where populations within stream pools may be the product of only a few matings (Bunn & Hughes 1997). This limited aquatic dispersal also appears to be the case for animals without a winged adult phase, such as atyid shrimps *Paratya* and *Caradina* which have very limited instream movement (Hughes *et al.* 1995, Hancock 1996, Woolschot *et al.* 1999).

Grazer abundances within rainforest streams of the Conondale region (shown in Figure 2.2.) show similar temporal patterns among streams, but the taxonomic composition of the guild varies considerably in space and time, and can depend on factors such as the time since the last spate (e.g. Bunn *et al.* submitted).
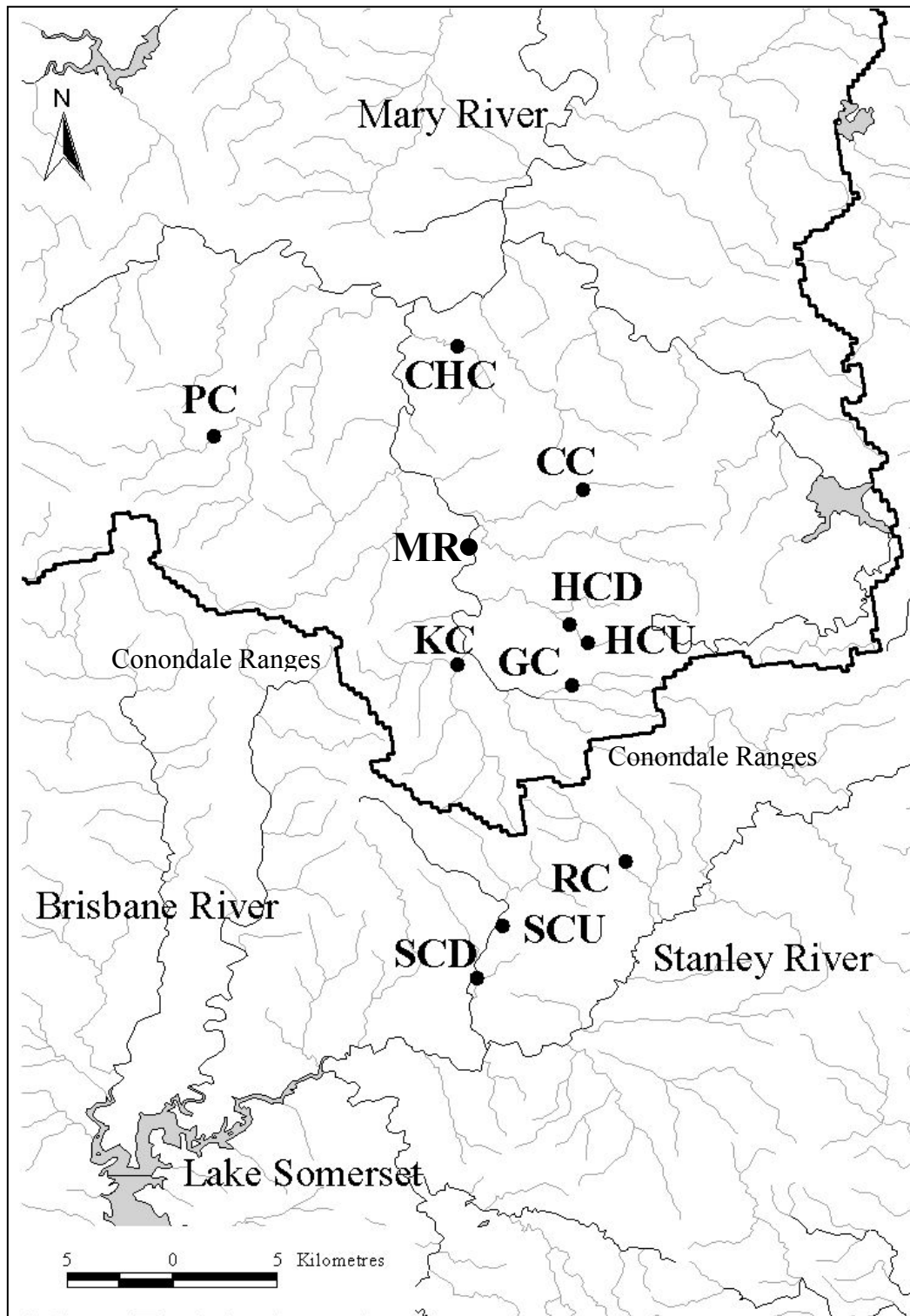
Figure 2.2 Survey sites in the Upper Mary catchment (CC= Cedar Creek, CHC= Chinaman Creek, GC= Geraghty's Creek, HCD= Harper Creek Downstream, HCU= Harper Creek Upstream, KC= Kilcoy Creek, PC= Peters Creek) and the Upper (Eastern) Brisbane (RC= Running Creek, SCD= Stony Creek Downstream, SCU= Stony Creek Upstream). Site from habitat and diet experiment, Mary River at Conondale (MR) also shown. The Conondale Ranges traverse the boundary between Mary River (to North) and Brisbane River (to South).

2.3 Site descriptions

2.3.1 Survey sites

Ten survey sites were located in small stony streams within the upper catchments of the Mary and Brisbane rivers, where they meet in the Conondale Ranges in South-east Queensland (Figure 2.2). Vegetation in this region is a mixture of complex notophyll vine forest, wet sclerophyll forest and dry sclerophyll forest (Czechura 1991; see plate 1), with valley floors largely cleared but with patches of remnant forest. Forestry is the major land use, with a major part of the range included within State Forests. There are also some 7100 ha protected within a National Park. Most agriculture involves grazing for beef cattle and occurs on the lower slopes and in the surrounding lowland areas.

Sites were selected to provide a range of benthic primary productivity and algal species composition. In the Brisbane River catchment, these included two on Stony Creek and one on Running Creek (Table 2.1; see plate 2). These streams flow south and east into the Stanley River and then into the Brisbane River system. Sites in the Mary River catchment included one site on each of Kilcoy Creek, Geraghty's Creek, Cedar Creek, Chinaman Creek, Peters Creek and two sites on Harper Creek (see plates 3 and 4). These streams flow generally north or west into the Mary River, apart from Peters Creek, which joins Bouloumba Creek before it reaches the Mary, and Kilcoy Creek, which flows east into the Mary.

Streams were all third- or fourth-order at the site sampled, with the exception of the downstream Stony Creek site, which is on a fifth-order reach (Table 2.1). Sample reaches or "sites" each comprised one run habitat with slow flow (0.1- 0.4 m.s^{-1}) and unbroken surface, and with a substrate dominated by cobbles (60– 260 mm diameter).

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Table 2.1 **Physical characteristics of survey sites (Chapter 3). Gradient has no units (calculated as rise/run, both in metres). Altitude is given as metres above sea-level. % Fines refers to % substrate less than 8 mm diameter. Other diameters used for substrate estimation include: Boulder (> 260 mm), Cobble (60 – 260 mm), and Pebble (8 – 60 mm). Mean ± 1 S.E provided for relevant variables, n = 10 for each measurement of cobble surface area.**

Site	Site Code	Stream order	Gradient	Altitude	Flow Direction	Wetted width (m)	Depth (m)	% Boulder	% Cobble	% Pebble	% Fines	Cobble S.A. (m^2)
Cedar Ck at Cookes Rd	CC	4	0.006	126	W	3.2 ± 0.2	0.12 ± 0.04	10	40	20	30	0.056 ± 0.003
Chinaman Ck upstream of highest ford	CHC	4	0.017	124	NW	3.5 ± 0.3	0.20 ± 0.06	30	30	40	0	0.060 ± 0.004
Geraghty's Ck, Policeman's Spur Rd	GC	3	0.013	193	W	2.5 ± 0.1	0.20 ± 0.06	40	30	20	10	0.054 ± 0.009
Harper Ck downstream	HCD	3	0.023	200	NW	4.2 ± 0.2	0.10 ± 0.02	0	30	30	40	0.038 ± 0.010
Harper Ck upstream	HCU	3	0.023	215	NW	3.0 ± 0.2	0.07 ± 0.04	5	50	45	0	0.045 ± 0.007
Kilcoy Ck at Crystal Waters Rd	KC	4	0.010	204	NE	5.0 ± 0.1	0.40 ± 0.08	15	35	10	40	0.052 ± 0.005
Peters Ck	PC	4	0.013	454	NE	2.5 ± 0.4	0.25 ± 0.08	10	40	40	10	0.056 ± 0.012
Running Ck at Bellthorpe Rd	RC	4	0.013	145	SE	3.0 ± 0.1	0.25 ± 0.06	0	45	40	15	0.054 ± 0.005
Stony Ck downstream	SCD	5	0.007	122	SW	4.0 ± 0.1	0.30 ± 0.11	5	40	40	15	0.061 ± 0.007
Stony Ck upstream at picnic area	SCU	4	0.024	125	SW	4.1 ± 0.3	0.30 ± 0.13	30	50	20	0	0.050 ± 0.006

Table 2.2 Habitat characteristics of survey sites. Temperature was averaged over a 24hr period of production measurement (at least 150 data points), mean ± 1 S.E. provided. No data was available for Running Creek Total Nitrogen or Phosphorus.

Site	Canopy cover (%)	N (ammonia) (mg.L^{-1})	N (oxides) (mg.L^{-1})	Reactive P (mg.L^{-1})	Total P (mg.L^{-1})	Total N (mg.L^{-1})	Min. T (°C)	Max. T (°C)	T (°C)
Cedar Ck at Cookes Rd	21.1	0.007	0.003	0.010	0.039	0.16	10.9	17.7	13.76 ± 0.14
Chinaman Ck upstream of highest ford	60.9	0.013	0.006	0.002	0.012	0.11	13.7	17.3	15.29 ± 0.07
Geraghty's Ck, Policeman's Spur Rd	70.1	0.010	0.067	0.014	0.025	0.17	12.0	15.3	13.17 ± 0.09
Harper Ck downstream	89.6	0.007	0.011	0.012	0.041	0.11	13.6	17.0	14.90 ± 0.07
Harper Ck upstream	11.4	0.008	0.004	0.013	0.040	0.11	15.6	20.5	17.40 ± 0.07
Kilcoy Ck at Crystal Waters Rd	83.6	0.008	0.081	0.004	0.021	0.22	12.1	14.6	13.07 ± 0.05
Peters Ck	54.0	0.019	0.068	0.003	0.003	0.15	9.1	11.2	9.93 ± 0.04
Running Ck at Bellthorpe Rd	1.5	0.012	0.028	0.004	.	.	13.7	19.2	15.77 ± 0.11
Stony Ck downstream	0.0	0.006	0.002	0.002	0.021	0.14	16.4	24.1	19.32 ± 0.10
Stony Ck upstream at picnic area	29.8	0.011	0.032	0.003	0.015	0.14	14.4	16.1	15.15 ± 0.04

In order to characterise each site, measurements of physical habitat variables were taken. Width was measured at each site at three points, generally at the widest and the narrowest points of the reach and at one other point. Water depth was taken in a similar manner. Photographs of the riparian canopy were taken mid-stream at 50– 100 cm above the water surface at each of the study sites, using a 35 mm camera (Nikonus V) and fish-eye lens. The camera was mounted horizontally on a surveyor's tripod with an adjustable base and oriented with the top edge of the film facing magnetic north, and the lens facing vertically. Negatives of the resultant hemispherical photographs (ASA25 black and white document copy film) were digitised and enhanced to maximise the distinction between canopy and sky. Images were then analysed for percentage cover (ter Steege 1993).

Water samples for nutrient analysis were collected from each of the stream sites in 500 mL acid-washed polyethylene bottles, at the time of benthic metabolism measurements and grazer sampling (see Chapter 3). Two samples were taken per stream on one occasion; one sample was stored in a detergent-washed bottle and immediately placed on ice and the other was first filtered through a Sartorius 0.45μm filter into an acid-washed bottle, and then frozen for transport.

Analyses for FRP, NO_x, NO_3, and NH_3 were performed simultaneously using an automated LACHAT 8000QC flow injection system using methodology based on (a) ascorbic acid reduction of phosphomolybdate for FRP (Standard Methods 1998); (b) cadmium reduction of nitrate to nitrite by diazotizing the nitrite with sulfanilamide and coupling with N-(1-naphthyl)ethylenediamine dihydrochloride for NO_x (Standard Methods 1998) and (c) production of the indophenol blue colour complex for NH_3 (Standard Methods 1998). Samples for TN and TP were digested using a simultaneous persulfate procedure based on that described by Hosomi and Sudo (1986; with

modifications to allow analysis for freshwaters). After digestion, analyses for TN and TP were performed using instruments and chemistries described for NO_x and FRP. All analyses were undertaken by Queensland Health Scientific Services, Nathan, Queensland.

Water temperature averages, maxima and minima were calculated from 24 hours of data taken on the day of invertebrate sampling, recorded using submersible electronic data loggers associated with metabolism measurement (see 3.3.1.2 for details).

Sites ranged in canopy cover from 0% (Stony Creek downstream) to 90% (Harper Creek downstream) (Table 2.2). Total nitrogen varied from $0.11-0.22$ mg.L^{-1} and total phosphorus from $0.003 - 0.041$ mg.L^{-1}. Note that the downstream site on Harper's Creek had the most canopy cover yet also has the highest total phosphorus reading; this may have been due to the site itself being relatively undisturbed yet located immediately downstream of heavy grazing by cattle. Peters Creek was at a considerably higher altitude than other streams (Table 2.1); this is reflected in the range and mean of temperatures (Table 2.2).

2.3.2 Sites for enrichment and shading experiment

Four sites were used for the enrichment and shading experiment (Table 2.3, see Figure 2.3). The sites were not the same as the sites chosen for the survey, because the experiment was part of a larger project that had not been established at the beginning of the study, and that had broader aims. These sites were chosen to be similar in substrate composition and fauna to those of the survey, but also they were more suited to experimental manipulation, as they were larger, and thus contained more cobbles (allowing greater replication).

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Table 2.3 Physical characteristics of sites used in enrichment and shading experiment (Chapter 4). Gradient has no units (calculated as rise/run, both in metres). Altitude is given as metres above sea-level. % Fines refers to % substrate less than 8 mm diameter. Other diameters used for substrate estimation include: Boulder (> 260 mm), Cobble (60– 260 mm), and Pebble (8- 60mm). Mean ± 1 S.E. provided for relevant variables, n= 10 for each measurement of cobble surface area.

Site	Site Code	Stream order	Gradient	Altitude	Flow direction	Wetted width (m)	Depth (m)	% Boulder	% Cobble	% Pebble	% Fines	Cobble S.A. (m^2)
Upper Brisbane	UB	7	0.005	169.3	E	5 ± 0.2	0.16 ± 0.03	0	50	35	15	0.058 ± 0.004
Lower Brisbane	LB	7	0.005	158.0	E	4 ± 1.0	0.21 ± 0.10	0	30	50	20	0.059 ± 0.004
Upper Coomera	UC	4	0.050	265	N	6 ± 0.6	0.19 ± 0.10	25	20	25	30	0.067 ± 0.006
Lower Coomera	LC	5	0.008	69.2	N	50 ± 6	0.41 ± 0.10	50	45	5	0	0.074 ± 0.006

Table 2.4 Physical characteristics of site used in diet and habitat experiment. Gradient has no units (calculated as rise/run, both in metres). Altitude is given as metres above sea-level. % Fines refers to % substrate less than 8 mm diameter. Other diameters used for substrate estimation include: Boulder (> 260 mm), Cobble (60 – 260 mm), and Pebble (8 – 60 mm). Mean ± 1 S.E provided for relevant variables (for these variables n= 3).

Site	Site Code	Stream order	Gradient	Altitude	Flow Direction	Wetted width (m)	Depth (m)	% Boulder	% Cobble	% Pebble	% Fines	% Filamentous algal cover
Mary River at Conondale	SCU	5	0.002	128	S	10 ± 0.9	0.25 ± 0.13	20	70	10	0	90

Plate 1 Peter's Creek site (PC). Note intact, remnant, notophyll vine forest.

Plate 2 Running Creek site (RC) with domes in place for measuring cobble scale (between-rock) production.

Plate 3 Upstream site on Harper's Creek (HCU).

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Plate 4 Downstream site on Harper's Creek (HCD).

Plate 5 Lower Brisbane (LB) experimental site with shadecloth in place.

Plate 6 Mary River at Conondale site used for diet and habitat experiment
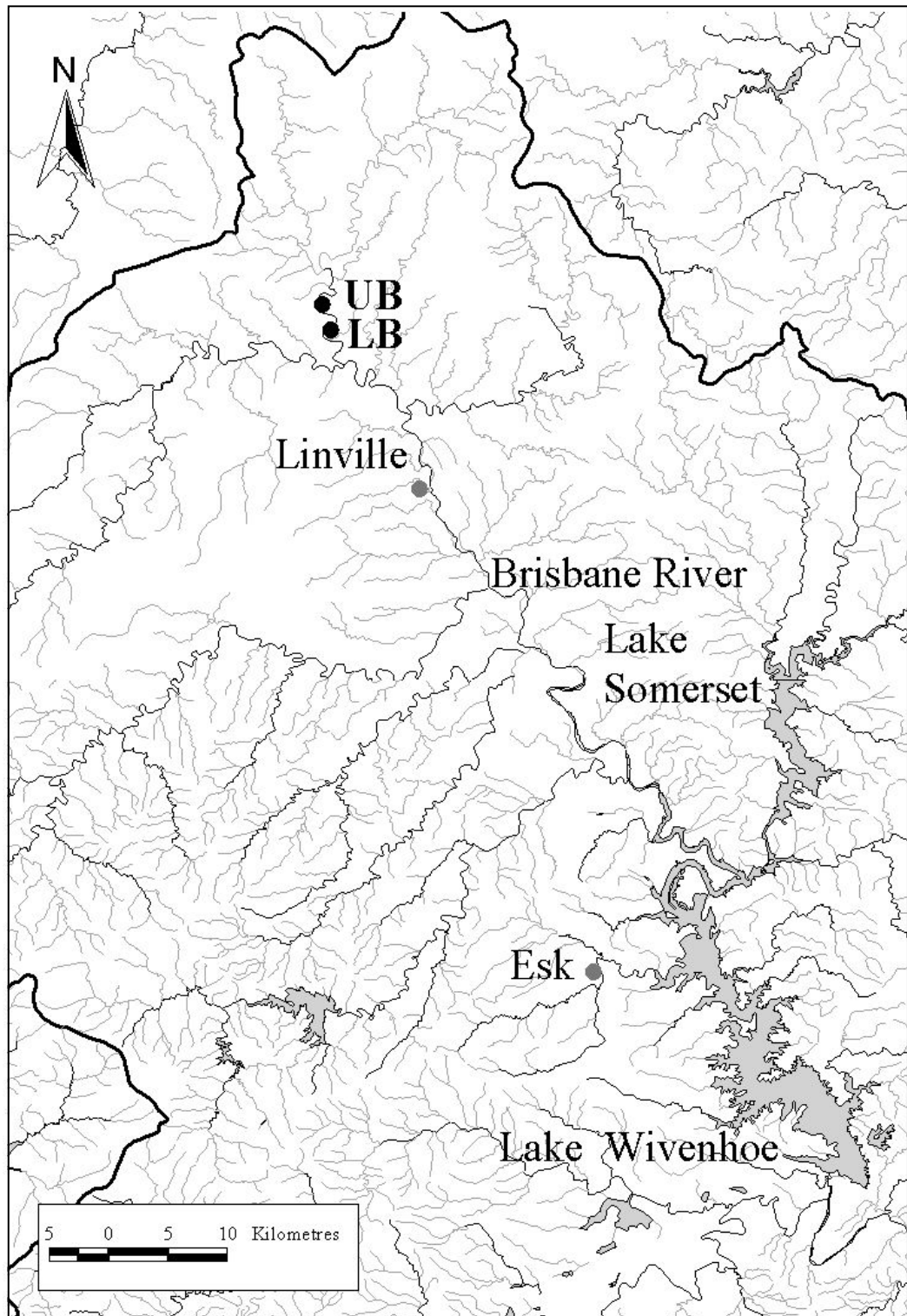
Figure 2.3 Experimental sites in the western catchment of the Brisbane River: UB= Upper Brisbane, LB= Lower Brisbane.

Two sites were in the upper Brisbane catchment, just below the confluence of the east and west Branches and approximately 35 kilometres north of Esk (Figure 2.3). From there, the Brisbane flows south and east and eventually reaches the Wivenhoe Dam. The two sites were separated by three kilometres of winding river. See plate 5.

The other two sites were in the upper Coomera catchment (Figure 2.4), about 30 km southwest of the Gold Coast. This river flows north and east, and reaches the sea south of Brisbane. The two sites were 18 kilometres apart.

A large amount of the vegetation of the upper Brisbane valley is cleared, and minor burning is carried out each year to promote conditions for grazing of (beef) cattle. However, a thin riparian strip, two or three trees wide, remains on most of the river, including trees and shrubs such as *Callistemon* spp.*, Banksia* spp.*, Eucalyptus* spp. and other dry forest species. Both the Lower and Upper Brisbane sites were somewhat affected somewhat by the grazing of cattle, with minor enrichment from faecal inputs and also erosion damage to banks from trampling. Understorey species were reduced and largely included only native and introduced grasses (e.g. *Poa* sp.) and weeds such as the Scotch thistle (*Onopordum acanthium*). The Coomera River flows out of Lamington National Park and the upper site, not far downstream of the park boundary, was largely un-impacted. Riparian vegetation is fern-thicket/hoop pine scrub (e.g. *Araucaria* spp., *Eugenia* spp., and *Eucalyptus* spp.) with some weed species such as *Lantana camara* and exotic vines. There was some erosion damage in places from cattle, although there was little grazing upstream.

The lower Coomera site is located within army land, and is downstream of the Canungra army barracks and a small, associated sewage treatment plant, although the latter has not released waste-water or sewage into the river for some years. Riparian

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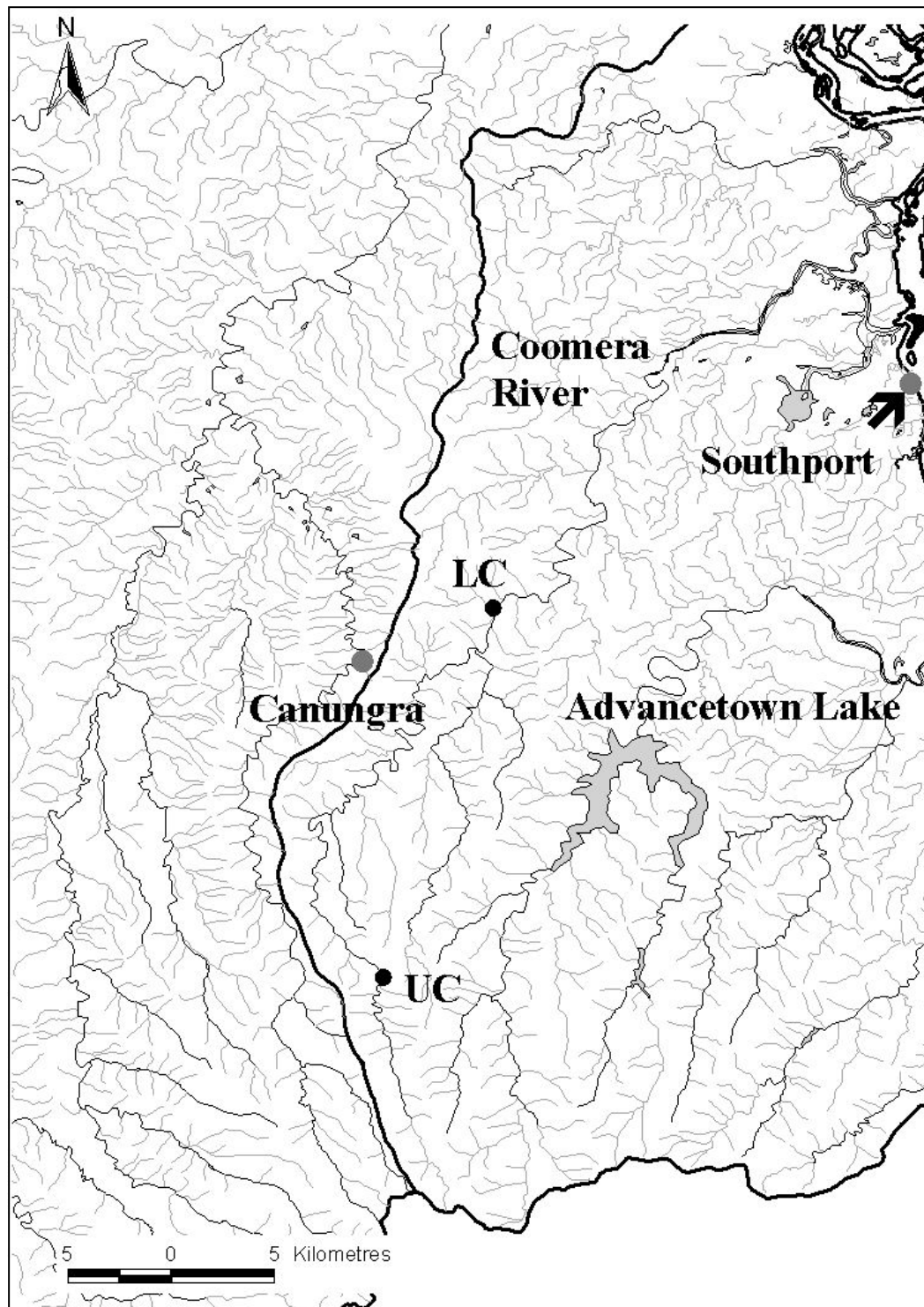
Figure 2.4 Experimental sites in the catchment of the Coomera River. UC= Upper Coomera, LC= Lower Coomera.

vegetation was largely undisturbed medium *Eucalypt* forest and also includes lillipilly (*Eugenia* spp. and *Syzygium* spp.), dogwood and *Acacia* spp. This site is the widest and deepest of the four experimental reaches (Table 2.3).

2.3.3 Site for diet and habitat experiment site

The diet and habitat experiment was carried out in the same geographical area as the survey. However, after four years of drought the water levels were very low, and a new site had to be chosen to provide sufficient numbers of watered cobbles. The Mary River at Conondale (Figure 2.2) was largely open, with only introduced grasses and thistles as vegetation, but received some morning shade from pine trees about 100 m away (see Plate 6). The site received water from tributaries affected by riparian clearing and agriculture. Cattle had access to the site and this had caused obvious erosion damage to banks. The experimental reach (Table 2.4) was wider and deeper than the Kilcoy Creek site also used in this experiment (see 5.2.2; refer to Table 2.2 for habitat information for Kilcoy Creek).

2.4 Flow conditions of study

All sampling was carried out at the end of the dry season (August – November), over a five year period (2000-2004) and during an El Niño-driven drought. Despite the drought, flows did not cease at any site during or shortly before sampling, and the study sites did not become isolated into separate pools. A small flow event occurred three weeks before sampling the enrichment and shading reaches but river levels were estimated to rise only by a maximum of 10% and no rocks were disturbed enough to move or roll; nor was filamentous algal biomass or cover visibly reduced in biomass. Spates did not occur during the 6- 8 months prior to each sampling occasion

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3 - Relationships between the productivity and composition of algae and grazer diversity

3.1 Introduction

The diversity of stream macroinvertebrates can vary considerably across a number of scales (Hart 1981, Crowl & Schnell 1990, Downes *et al.* 1993, Downes *et al.* 2000a, Li *et al.* 2001). Regional diversity is thought to ultimately constrain local diversity in many systems (Ricklefs 1987, Cornell & Lawton 1992, Palmer *et al.* 1996, Caley & Schluter 1997, Vinson & Hawkins 1998). In streams, invertebrate richness may be structured by historical events at the regional scale, and also at smaller scales by local physical, chemical and biological conditions (Vinson & Hawkins 1998).

While there is increasing interest in studying the factors that potentially influence the species richness of macroinvertebrates, significant gaps still remain in the knowledge of such factors and the scales at which they operate. For example, there is little direct evidence with which to judge the influence of algal productivity on consumer diversity in freshwater streams, at any scale (see review by Vinson & Hawkins 1998, Voelz & McArthur 2000). This is despite the fact that it is well established that benthic algal composition, production and biomass influence grazer abundance, growth, composition and production (Lamberti *et al.* 1989, Peterson *et al.* 1993, Hill *et al.* 1995, Wellnitz & Ward 1998, Rosemond 2000).

Evidence from terrestrial systems suggests that there is a relationship between the productivity of resources and the diversity of consumers (e.g. Owen 1988, Siemann *et al.* 1998, Haddad *et al.* 2000). At the local scale, this relationship may be unimodal or 'hump-shaped', but at the regional scale, species diversity often increases monotonically with increasing productivity (Waide *et al.* 1999).

Relationships that do exist in streams between algal productivity and grazer diversity are likely to be confounded by associated variations in the composition of the algal community. Algae are generally more productive where light and nutrients are not limiting (see reviews by Borchardt 1996, Hill 1996). In these conditions, filamentous macroalgae also tend to overgrow more prostrate forms (e.g. diatoms, cyanobacteria) and become more abundant (McCormick 1996).

Filamentous algae may modify clear relationships between productivity of algae and diversity of grazers because they tend to be unpalatable to grazers once established (Brown 1961, Moore 1975). Some taxa with long filaments, such as *Cladophora* or *Spirogyra*, also provide extensive structural complexity to the habitat (Downes *et al.* 2000b), as well as modifying microhabitat conditions such as hydraulic regimes (Dudley *et al.* 1986, Dodds & Biggs 2002).

The relationship of the grazer guild with filamentous algae may be complex; the density of some animals such as *Baetis* can increase in the presence of macroalgae (Dudley *et al.* 1986) whereas other grazers, such as the caddisflies *Leucotrichia pictipes* and *Psychomyia flavida,* have reduced densities (Hart 1992). Some grazers may not eat or digest filamentous algae, while others may be able to consume new growth or decomposing fragments (Gregory 1983, Lodge 1986).

The relationship between grazers and both primary productivity and the presence of filamentous algae may vary with spatial scale, as stream insects can respond to heterogeneity at a number of scales (Hart 1981, Downes *et al.* 2000a). It is predicted that primary productivity will be related to grazer diversity at all scales, but that microhabitat factors such as habitat complexity and algal composition will tend to be more strongly related to grazer variables at the smaller scales within reaches (see 1.5).

Other factors, such as physical and chemical variables, may also influence grazer diversity.

Within reaches, at the scale of cobbles, it is also predicted that mobile grazers will be better able to track variation in productivity and algal composition, and therefore may have stronger relationships with these variables than more sedentary grazers (particularly with respect to their density).

This chapter examines the relationship between primary productivity, filamentous algal cover and the richness, density and composition of macroinvertebrate grazers, at two spatial scales. It also examines whether grazer diversity is related to other physicochemical variables.

Quantitative sampling at ten sites in the upper Mary and Brisbane rivers provided data to examine this relationship at the reach scale, and intensive sampling at one of these sites allowed exploration of patterns at the cobble scale.

This chapter addresses the following questions:

1. What are the natural ranges in grazer diversity between catchments, reaches and cobbles within reaches?

2. What are the relationships between productivity and grazer diversity and community composition at the reach and cobble scales?

3. What are the relationships between the composition and diversity of grazers and filamentous algal cover at these spatial scales?

4. What other (physicochemical) variables are related to grazer diversity at these two spatial scales?

3.2 Methods

3.2.1 Reach scale

Sampling was carried out in early spring (August-September) 2000 when water levels were low but stable after a relatively dry winter (50 mm rainfall from July-September, compared with 200 mm average (Australian Bureau of Meteorology 2003). Measures of physicochemical habitat attributes, benthic community metabolism and algal cover and biomass were taken from each site along with macroinvertebrate samples as described below.

3.2.1.1 Physicochemical attributes

Turbidity and conductivity were measured at each site using a Hach 16800 turbidimeter and a TPS™ conductivity meter. Visual estimates were made of the average cover of silt and detritus within the reach. Depth was taken as an average within the run habitat sampled (n= 5) and surface velocity was estimated by the average time it took for a standard sphere to travel one metre on the surface (n= 5). Temperature was recorded over 24 hours using the TPS™ loggers used to record dissolved oxygen (see below).

3.2.1.2 Benthic metabolism measurements

Benthic community metabolism was measured by monitoring dissolved oxygen within two dome-shaped, Perspex chambers over 24 hours (e.g. Bunn *et al.* 1999) at each reach. The perspex chambers were approximately 29.5 cm diameter and 25 cm high. Each had a dissolved oxygen (DO) sensor (YSI 5739, USA) in the top of each chamber, which was attached to a data-logger (TPS 601) that recorded DO and temperature at five, six or ten minute intervals (intervals varied slightly according to the storage capacity of individual loggers). Water was also circulated within each dome using a 12 V pump. Each DO probe was attached to a data-logger (TPS 601), that recorded DO

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and temperature at five, six or ten minute intervals (intervals varied slightly according to the storage capacity of individual loggers). A cobble was placed in each dome and the chamber sealed by a watertight plastic base. Volume of the water in the chamber was calculating by subtracting the volume of water displaced by the cobble. Surface area of the cobble was measured by wrapping it in aluminium foil and weighing the foil when dry (converting to area by comparing it with the weight of a known surface area). The metabolically 'active' surface area of the cobbles was assumed to be half the total surface area (Bunn *et al*. 1999).

Different components of benthic metabolism were calculated by comparing the rate of O_2 change in the chambers at different times of the day. The mean rate of change at night was taken as the rate of respiration, and daily respiration (R24) was calculated by assuming the rate was constant and multiplying by 24 hours; gross primary production (GPP) was calculated as the sum of the DO production during daylight hours plus the DO consumed by respiration during that period of time based on the night time respiration rate (Fellows *et al.* in review). Changes in dissolved oxygen concentrations over time (mg $O_2.L^{-1}.hr^{-1}$) were multiplied by chamber volume and divided by substrate surface area to obtain values in units of mg $O_2.m^{-2}.hr^{-1}$. The rate was converted into units of carbon by assuming that one mole of C is equivalent of one mole of O_2 for both respiration and photosynthesis (i.e. 1 mg O_2= 0.375 mg C, Bender *et al.* 1987, Bunn *et al*. 1999). Metabolism measures used for each reach were averages of two points, except at reaches where one of the chambers failed. These include Harper's Creek (downstream), Kilcoy Creek, Peters Creek, Chinaman Creek and Geraghty's Creek. Note that two chambers were employed in each sampling area in order to provide data in the case of one chamber failing, but the variation of interest is patch scale therefore chambers were not replicated within treatments more than this.

3.2.1.3 Invertebrate sampling

Five cobbles from each reach were randomly selected from within the run habitat. A 250 μm net was placed downstream of the cobble and the cobble was swiftly removed from the substrate and placed in the net. This technique has been found to yield more precise estimates per unit effort for both density and diversity of invertebrates on stones in some streams than Surber sampling (Death & Winterbourn 1995). Large invertebrates were removed from the cobbles and net with forceps, and cobbles were lightly scrubbed to remove smaller animals. Samples were preserved in 10% formalin and manually sorted in the laboratory. All macroinvertebrates that are known to graze on algae were identified to the lowest taxonomic definition possible, generally species, using the keys described in Hawking (2000). The designation of grazers was made on the basis of the literature, including Chessman 1986, Wells (1997), Davis (1997), Mosisch (1995), McKie and Cranston (1998), Merrit and Cummins (1978) and St Clair (1997). Stable carbon isotope data has previously confirmed an algal diet for these grazers (Bunn, unpublished data), and see also Chapter 5.

3.2.1.4 Algal sampling

Algal samples were taken from different cobbles to those used for invertebrate samples (no algae were left on original cobbles after rocks were scrubbed for invertebrate samples). Ten cobbles from each reach were selected from within the run habitat, by using random numbers as the x and y co-ordinates of a $1m^2$ grid over the stream surface. Before removal the cover of filamentous algae was estimated using a 10 * 10 cm perspex grid, held over the cobble surface. Cobbles were then placed into a plastic tray, and thoroughly scrubbed using a hard nylon-bristled brush; the brush and cobbles were then rinsed into the sample to ensure that any material adhering was collected. Samples

were stored on ice in the dark and transported to the laboratory within 24 hours. On arrival at the laboratory, each sample (one per cobble; ten per site) was made up to one litre, thoroughly shaken, and two aliquots of 40 mL were taken from each sample. The two aliquots were separately filtered through Whitman glass filters (45 μm) and placed into labelled test tubes. One of the filter papers was stored in the freezer for mass determination and the other was placed in 10 mL of 90% acetone for chlorophyll a analysis.

For chlorophyll a determination, the spectrophotometric technique described by Lorenzen (1967) and modified by Parsons $et\ al.$ (1984) was adapted. Samples were extracted overnight in the acetone at 4 °C, after which algal cells were ruptured by sonification for approximately two minutes. Samples were returned to the refrigerator for 0.5 h, followed by centrifugation for three minutes at 3000 g. The absorbances of the resultant supernatants were measured at 665 nm using a Varian Series 634 spectrophotometer, and corrected for phaeophytin by subtracting the absorbance at 750 nm. The final chlorophyll a content of each sample was expressed in mg.m^{-2} for each cobble. Epilithon biomass was expressed as ash-free dry mass (AFDM). Filter papers were dried at 100 °C for at least 24 hours. After weighing, the filter papers were ashed in a muffle furnace at 500 °C for one hour. Weights are expressed as g.m^{-2}.

3.2.2 Cobble scale

In late September 2000, sampling was carried out intensively at one reach in Running Creek. Again, ten cobbles were randomly selected from within the run habitat. Cobbles were removed from the stream and placed in a 250 μm net as described above. All invertebrates were then quickly picked from the cobble surface with forceps and the cobble was placed in a bucket of water at stream temperature for temporary storage (less

than 1 hour). Invertebrates were placed in a labelled vial with 70% alcohol. Benthic metabolism chambers were set into the stream using the same cobbles (see plate 2), and this was carried out as explained above (see 3.2.1.2) for 24 hours. Algal samples were taken at the end of the 24 hour period in the manner described above (see 3.2.1.4). In this way, the algal data and benthic metabolism data from one cobble related directly to the grazer community data from the same cobble.

3.2.3 Data analysis

Reach scale data were used for reach- to catchment-scale analyses of grazer diversity, and for comparisons of grazer diversity with algal variables at this scale.

The replication of sampling of grazers at each reach provided cobble-scale grazer data for each reach, so this fully replicated dataset was used wherever patterns of grazers alone were examined (see also 3.2.3.3). However, variation within algal variables was measured only at one reach (Running Creek), on a separate occasion on which grazer samples were also taken again (from the same cobbles as the algae). Thus only data from this reach were used for comparisons between grazers and algae at the cobble scale.

The first step of the data analysis was to generate sampling curves to ensure that the number of grazer taxa was not a function of the number of samples. Secondly, alpha, beta and gamma diversity variables were compared among the reach and cobble scales in order to relate diversity patterns at the two spatial scales. The degree to which algal and physicochemical variables explained variance in grazer diversity and density was then investigated using linear and unimodal regression analysis. Finally, compositional changes in the grazer community, and their relationship with algal variables and scale, were examined using presence-absence ordinations at both spatial scales.

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3.2.3.1 Accumulation curves

The first aim of the data analysis was to establish the relationship between diversity and abundance, to ensure that the number of taxa per unit (reach or cobble) was accurately represented and was not a function of the number of samples collected. For the cobble scale, diversity is represented by one sample only: that of a cobble. Since the cobble fauna was sampled entirely, it was assumed that the total number of taxa on that cobble was collected. However, this was not the case for the reach scale, where diversity was compared between reaches, as a whole reach could not be sampled. Cobble samples were pooled for each reach in order to create accumulation curves to establish diversity: abundance relationships.

Taxon accumulation curves were created with Ecosim simulation software (Gotelli & Entsminger 2003), according to the methods described by Gotelli and Colwell (2001). A dataset for any one reach represented a total of N individuals and S taxa. Ecosim automatically created S + 3 abundance levels, up to a maximum of 42 abundance levels. The smallest abundance level was an abundance of 1 and the largest abundance level was an abundance of N. The remaining S + 1 samples were evenly spaced between these boundaries (Tipper 1979). As each sample of individuals was added in a cumulative fashion, S was calculated. This process was randomly carried out for 1000 iterations.

Accumulation curves did not reach an asymptote when the entire set of grazer taxa was examined (see Appendix A). For this reason, very rare species were identified, using the criteria of occurring only on one cobble in the entire dataset, with an abundance of one. These were excluded from the dataset. This dataset was used for all further analyses. In addition, the cobble scale dataset at Running Creek had the same rare taxa removed for comparability with the larger scales.

The accumulation curves from data excluding rare taxa (Appendix A) indicate that most species on cobbles are represented even when only relatively low numbers of individuals are collected. If rare taxa are removed in this way, adequate estimates of richness for comparative purposes can be made once only low numbers of invertebrates are gathered, such as, for example, 40 at Cedar Creek, or 57 at Harpers Creek downstream.

3.2.3.2 Diversity measures

Alpha, beta and gamma diversity measures were calculated at two scales following Tockner *et al.* (1999). At the cobble scale, alpha diversity is the diversity of a cobble, and gamma diversity is the diversity of a reach. Beta diversity between cobbles was calculated using two different indices (Harrison *et al.* 1992): ß-1, which measures the amount by which regional (gamma) diversity exceeds the mean diversity of its constituent samples (cobbles); and ß-2, which measure the amount by which gamma diversity (within one reach) exceeds the maximum diversity attained by one sample/cobble.

Thus,

$$ß\text{-}1 = [(\gamma/\alpha)\text{-}1]/(n\text{-}1)*100$$

$$ß\text{-}2 = [(\gamma/\alpha_{max})\text{-}1]/(n\text{-}1)*100$$

where γ is the regional diversity (number of taxa in a reach), α is the mean alpha diversity, α_{max} is the maximum alpha diversity, and n is the number of cobbles sampled within each reach. Data used for this analysis included the full set of samples for every reach.

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At the within-catchment scale, alpha diversity is the diversity of a reach, and gamma diversity is the diversity of a catchment. ß-1 and ß-2 were calculated as above but using these measures, as well as n= number of reaches within a catchment.

To compare diversity measures between scales, the nonparametric Mann-Whitney U test was employed using SPSS 10.05 (1999). Parametric tests could not be used because of the reduced number of replicates of gamma diversity within the catchment scale (two) compared with the reach scale (ten). The Mann-Whitney tested the null hypothesis that a diversity measure was the same at the catchment as at the reach scale; e.g. that γ was the same at both scales. The test produces a value U that is significant below the critical value for the desired α. A significant U meant the rejection of the null hypothesis. The major assumption of the Mann-Whitney test is that variances within each group are equal; this was examined and variables were transformed to improve homogeneity of variance where required (Quinn & Keough 2002).

Data from the Brisbane and Mary river catchments were combined to prevent the low number of reaches (three) in the Brisbane causing an artificial inflation of ß-1 values due to the small denominator term.

3.2.3.3 Regression analysis

Variables

For regression analysis, the diversity measure used was appropriate for the spatial scale. At the cobble scale, the number of taxa per cobble was used as a measure of alpha diversity and the density of individuals on a cobble was used. For the majority of analyses, except where noted, these data were taken from the intensive sampling of Running Creek as this was the source of cobble scale variation of algal productivity and

filamentous algal cover. At the reach scale, the number of taxa per reach was the measure of alpha diversity and the total density of individuals in a reach was used (five measures pooled for each reach). In order to relate the taxonomic turnover within a reach to its overall cover of filamentous algae (which may increase heterogeneity within a reach), linear regressions between FAC and ß-1 and ß-2 were also performed.

For the examination of compositional changes within the grazer guild, the biota were separated into two groups on the basis of mobility and feeding mode (see also 1.1). Highly vagile taxa ('mobile grazers') were defined on the basis of being strong swimmers and crawlers that tend to be readily able to enter the drift of their own volition. These grazers also have brush-type mouthparts. The other defined group of grazers were taxa that were more sedentary in habit ('sedentary grazers'). These move more slowly while feeding and generally have scraping and rasping mouthparts. Most have cases, shells or build silk retreats onto the substrate, and all are less likely to enter the drift. Species were only placed in either group if they clearly displayed all characteristics of that group. Elmids were therefore not grouped, but were still included in the analysis of total abundances and diversity. Elmids comprised only 7% of the total abundance on a cobble and 12% of the total species richness.

Mobile grazer density and sedentary grazer density were included as variables. Numbers of sedentary and mobile grazers, particularly the latter, were too low to exclude rare taxa. Therefore diversity variables were not used alone. However, considering that the number of (non-rare) taxa overall had reached an asymptote, the richness of sedentary and mobile grazers were still used in the form of a ratio between the two. To deal with the problem of zero denominators, mobile grazers were divided by the sum of mobile and sedentary grazers.

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Transformations

Residuals were examined for normality, linearity and homoscedasticity. At both scales, GPP data were transformed as $(x+0.5)^{1/2}$ to correct for platykurtosis, while data on filamentous algal cover, depth and surface area did not require transformation. At the reach scale, chlorophyll a and velocity were transformed as $(x+0.5)^{1/2}$, while AFDM, turbidity, temperature and conductivity needed no transformation. At the cobble scale AFDM and chlorophyll a were both transformed as $\log_{10}(x+1)$.

At the reach scale, grazer diversity and density variables were transformed as $\log_{10}(x+1)$ to correct for mild skew. At the cobble scale, grazer diversity was transformed as $\log_{10}(x+1)$ to correct for skew and leptokurtosis, while grazer density was transformed as $(x+0.5)^{1/2}$ to correct for strong leptokurtosis. ß-1 and ß-2 diversity did not require transformation.

At the reach scale, mobile grazer density was transformed as $\log_{10}(x+1)$ to correct for mild skew, while sedentary grazer density was transformed as $(x+0.5)^{1/2}$ to correct for strong platykurtosis and the ratio of mobile: sedentary taxa was transformed as $(x+0.5)^{1/4}$ to correct for negative skew (Zar 1999). Cobble-scale mobile and sedentary grazer density variables did not require transformation. The ratio of mobile to sedentary taxa did not vary across the reach and therefore was not included in regression analyses.

Linear and unimodal regressions

Simple linear regression was conducted using SPSS 10.05 (1999*)* to examine how much variance in FAC could be explained by GPP. In addition, this approach was used to determine the amount of variance in grazer variables explained by both gross primary production (GPP) and filamentous algal cover (FAC). The amount of variance in grazer diversity explained by physicochemical variables was also investigated. In addition,

the existence of a possible unimodal relationship was explored by applying to the data the model described by Pollock *et al.* (1998).

This tests for nonlinear relationship that fit the generalised curve:

$$y = \beta_0 + \beta_1 * x * e^{(\beta_2 * x^{\beta_3})}$$

where β_0, β_1, β_2 and β_3 are constants, y is the dependent grazer variable, and x is the independent variable (either GPP or filamentous algal cover). This model can be used to describe a line that rises to peak, then exponentially decays to a y= β_0 asymptote. The value of β_1 influences curve amplitude, β_2 influences curve width, and β_3 influences the decay rate on the trailing edge of the curve. Thus, this equation can be used to mathematically describe a wide range of unimodal relationships between two variables (Pollock *et al.* 1998). All regressions performed are listed in Table 3.1. The regression models were checked to ensure that regression residuals were normally distributed with constant variance. With the use of a p< 0.001 criterion for Mahalanobis distance (Tabachnik & Fidell 2001), no outliers among the cases were identified.

3.2.3.4 Ordination

Finally, ordination was used to examine the relationships between algal variables and grazer composition, and to better investigate nonlinear relationships at both scales. A Bray-Curtis dissimilarity matrix was calculated from invertebrate abundance data for each reach, using the software package PATN (Belbin 1993), after transformation to presence-absence data. This transformation was made because it removes abundance information from the ordination and examines only the compositional differences between samples (of particular interest in this case). Semi-strong-hybrid multidimensional scaling ordinations (SSH, Belbin 1993) were calculated from this

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Table 3.1 Regressions performed (untransformed variables listed), r= reach scale regression, c= cobble scale regression. Note that both linear and unimodal regressions were fitted for all instances listed below.

	FAC	$\beta 1$	$\beta 2$	Grazer diversity	Grazer density	Sedentary grazer density	Mobile grazer density	Mobile: sedentary diversity ratio
GPP	r			r,c	r,c	r,c	r,c	r
FAC		r	r	r,c	r,c	r,c	r,c	r
Chlorophyll *a*				r,c				
AFDM				r,c				
depth				r,c				
velocity				r				
turbidity				r				
conductivity				r				
cobble surface area				r,c				
temperature				r				

Bray-Curtis matrix, using 50 iterations and a ratio-ordinal cut value of 0.90 over 100 random starts. Solutions were computed in two, three and four dimensions, and those with a stress less than 0.2 were retained (Kruskal & Wish 1978). The ordination was rotated to a simple structure using Varimax axis rotation to three dimensions. Principal axis correlation was carried out to determine how well the set of taxa and environmental variables could be fitted to the ordination space. Environmental variables were standardised to values from 0 to 1 with the formula:

$$X_{ij} = (X_{ij} - Min_{col})/Range_{col}$$

Significance levels for overall correlations were determined using a Monte-Carlo technique with 1000 random permutations, in three dimensions. The ANOSIM procedure was used to test whether samples clustered in ordination space according to their ranked GPP and/or to their filamentous algae cover. At the reach scale, ANOSIM was also employed to test whether samples clustered within catchments and/or within reaches. All of these procedures were performed using PATN (Belbin 1993).

3.3 Results

3.3.1 Grazers

A total of 1467 individuals from 20 taxa was collected from the orders of Coleoptera, Ephemeroptera, Lepidoptera, Trichoptera, and Gastropoda (Table 3.2; see also Appendix B). Larvae of psephenid beetles, nymphulid moths and baetid mayflies were the most abundant and occurred in most samples. One helicopsychid caddisfly larva (*Helicopsyche cochleatesta*) was also abundant in most samples, but others were rare, with two (*Helicopsyche ptychopteryx* and *Helicopsyche tillyardi*) occurring in only one sample and a further species (*Helicopsyche murrumba*) occurring at only one reach. All other taxa occurred at more than one reach. Nymphulid moth larvae and Baetidae Genus 2 occurred only in the Brisbane catchment, whereas Hydrobiidae and small, unidentified gastropods occurred only in the Mary catchment.

Table 3.2 Grazing taxa collected from all ten reaches. Definitions of sedentary and mobile are supplied above.

Order	Family	Species	Category
Coleoptera	Elmidae larvae	*Austrolimnius* sp.	not assigned
Coleoptera	Elmidae larvae	*Kingolus tinctus**	not assigned
Coleoptera	Elmidae adult	Unidentified	not assigned
Coleoptera	Psephenidae larvae	*Sclerocyphon minimus*	sedentary
Coleoptera	Psephenidae larvae	*Sclerocyphon striatus*	sedentary
Ephemeroptera	Baetidae	Baetidae Genus 1 sp.*	mobile
Ephemeroptera	Baetidae	Baetidae Genus 2 sp. MV5	mobile
Ephemeroptera	Baetidae	*Bungona* sp.	mobile
Ephemeroptera	Leptophlebiidae	*Austrophlebioides* sp. AV11	mobile
Ephemeroptera	Leptophlebiidae	*Tillyardophlebia* sp. AV6	mobile
Gastropoda	Hydrobiidae	Unidentified (small or damaged)	sedentary
Gastropoda	Unidentified	Unidentified (small or damaged)	sedentary
Lepidoptera	Pyralidae	Nymphulinae sp. 18	sedentary
Lepidoptera	Pyralidae	Nymphulinae sp. 3	sedentary
Trichoptera	Helicopsychidae	*Helicopsyche cochleaetesta*	sedentary
Trichoptera	Helicopsychidae	*Helicopsyche murrumba*	sedentary
Trichoptera	Helicopsychidae	*Helicopsyche ptycopteryx**	sedentary
Trichoptera	Helicopsychidae	*Helicopsyche tillyardi**	sedentary
Trichoptera	Helicopsychidae	*Helicopsyche* sp. (early instars)	sedentary
Trichoptera	Tasimiidae	*Tasimia* sp. AV1	sedentary

*grazers excluded from the analysis due to rarity

A total of 129 individuals from 9 taxa were collected from a total of eight cobbles at the Running Creek reach (two samples were damaged). Of these, three taxa occurred on only one cobble (Hydrobiidae, Baetidae Genus 1 and Baetidae Genus 2).

3.3.2 Physicochemical and algal variables

Across reaches, levels of gross primary production (GPP) were low to moderate, varying from 72 to 521 mgC.m^{-2}.day^{-1} (Table 3.3). Filamentous algal cover (FAC) on stones ranged from 0 to 96%. Gross primary production (GPP) at the Running Creek reach varied within the reach from 34 to 469 mgC.m^{-2}.day^{-1} (Table 3.4), which suggests that the mean for this reach used in the reach scale survey (341 mgC.m^{-2}.day^{-1}) was at the higher end of the range available within this reach. Filamentous algal cover (FAC) varied from 25 to 58%, which suggests that some of the algae had senesced in the three weeks between reach and cobble scale surveys, since the mean percentage on the cobbles in the reach was ~70% cover. Data from three replicates had to be discarded due to battery and pump failure.

Table 3.3 Summary of values measured of a) physicochemical variables and b) algal variables from all ten reaches, August-September 2001.

a)

	temperature (°C)	depth (m)	turbidity (NTU)	conductivity (µS.cm^{-1})	detritus cover (%)	velocity (m.s^{-1})
maximum	19.3	0.40	6.9	682	50	0.42
minimum	10.5	0.07	1.5	136	0.0	0.01
mean	14.9	0.22	4.0	328	25	0.20
standard error	0.8	0.03	0.6	62	5.8	0.04

b)

	GPP (mgC.m^2.day^{-1})	FAC (%)	average AFDM (g.m^{-2})	average chlorophyll a (mg.m^{-2})
maximum	520.7	96.0	60.9	61.7
minimum	72.00	0.00	0.37	5.1
mean	340.7	44.4	13.8	23.1
standard error	51.6	11.5	1.6	4.0

Table 3.4 Summary of values measured of algal and physicochemical variables measured at the Running Creek reach in September 2001, n= 10 for all variables except GPP (n= 7).

	average depth (m)	GPP (mgC.m^2.day^{-1})	FAC (%)	AFDM (g.m^{-2})	chlorophyll *a* (mg.m^{-2})
maximum	0.32	468.7	57.8	31.8	25.4
minimum	0.09	34.1	25.0	9.4	7.1
mean	0.18	267.4	38.9	15.9	14.8
standard error	0.02	62.7	4.1	2.1	1.9

The size of the range of GPP did not vary much between scales (Figure 3.1a), but it was lower at cobble scales. There was a smaller range of FAC at the cobble scale (Figure 3.1b).
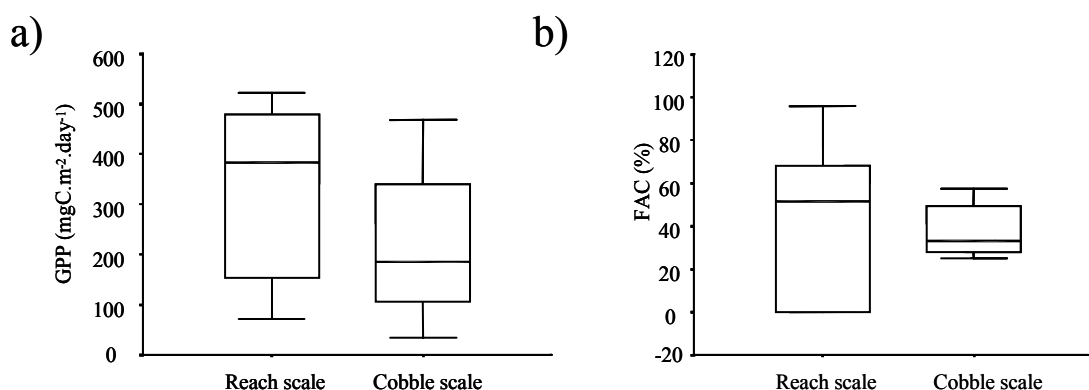
Figure 3.1 Variation in a) GPP and b) FAC between the two scales, n =10 for the reach scale (both variables), and at the cobble scale, n= 6 for GPP and n= 8 for FAC.

3.3.3 Scalar diversity comparisons

Mann-Whitney U tests indicated that the only significant difference in grazer diversity variables between scales was in gamma diversity, which was higher at catchment than at reach scales (Table 3.5). α tended to be higher at the catchment than at the reach scale, and ß-1 and ß-2 also tended to be lower at the catchment scale (between reaches) compared to within reaches (Figure 3.2). These differences were not significant.

Table 3.5 Mann-Whitney U for alpha, beta and gamma attributes of grazer diversity at reach and cobble scales.

	α	ß-1	ß-2	γ
Mann-Whitney U	1.50	1.00	1.30	0.00
Z score	-1.84	-1.93	-1.52	-2.17
Asymptotic Sig. (2-tailed)	0.066	0.053	0.129	0.030
Exact Sig. (2*1-tailed)	0.061	0.061	0.182	0.030*

* indicates significance at p<0.05
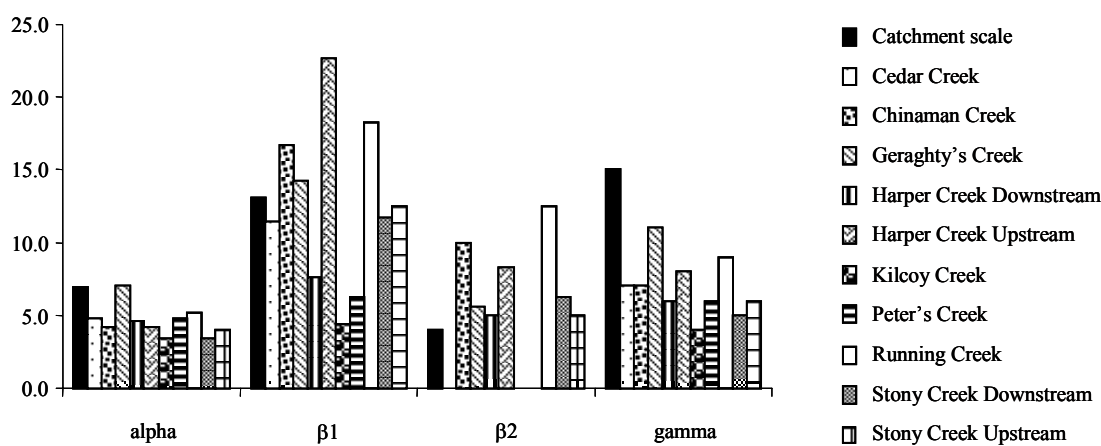
Figure 3.2 Measures of grazer diversity for the reach and cobble scales, for the Brisbane and Mary catchments. Solid bars are used for variables measured at the catchment scale (both catchments combined). Patterned bars are used for variables measured at the reach scale (see legend).

3.3.4 Linear and unimodal regressions

3.3.4.1 Algal variables

Filamentous algal cover explained a significant amount of variance within GPP algal cover both between reaches ($r^2 = 0.52$, $p < 0.001$) and between cobbles ($r^2 = 0.74$, $p < 0.05$). These relationships were both positive.

Figure 3.3 Relationships of grazer variables: a) number of grazer taxa, b) grazer density, c) sedentary grazer density, d) mobile grazer density and e) mobile: sedentary taxa ratio; with gross primary production at the reach scale. Only significant regression lines (p< 0.05) drawn, n= 10, p< 0.001. Regression equations provided in Appendix C.

3.3.4.2 Grazer variables

Reach scale

At the reach scale, regressions indicated that grazer diversity was positively related to both GPP and FAC (Figures 3.3a, 3.4a). Grazer density displayed a u-shaped relationship with GPP (Figure 3.3b). Sedentary grazer density had a much stronger relationship with GPP than did mobile grazer density, and this was also u-shaped (Figure 3.3c). Variance in sedentary grazer density was also explained by a positive regression with FAC (Figure 3.4c). The mobile: sedentary ratio was negatively related to both algal variables (Figures 3.3e, 3.4e).

The downstream reach on Harper Creek had a dense riparian cover (90%) and was downstream of a cleared reach that was heavily impacted by cattle grazing. Although it was not known before the survey, the reach was high in free reactive and total phosphorus (see 2.3.1) and may have had a different algal community than the other sites with an intact riparian canopy, which all flowed directly from relatively unimpacted catchments and thus had lower nutrient levels.

When this site was excluded from the dataset, total and sedentary regressions with GPP 'lost' their u-shapes and became positive and very nearly linear (Table 3.6, see Appendix D). Relationships with FAC were virtually unaffected, apart from the mobile: sedentary grazer ratio, which had a higher r^2 value.
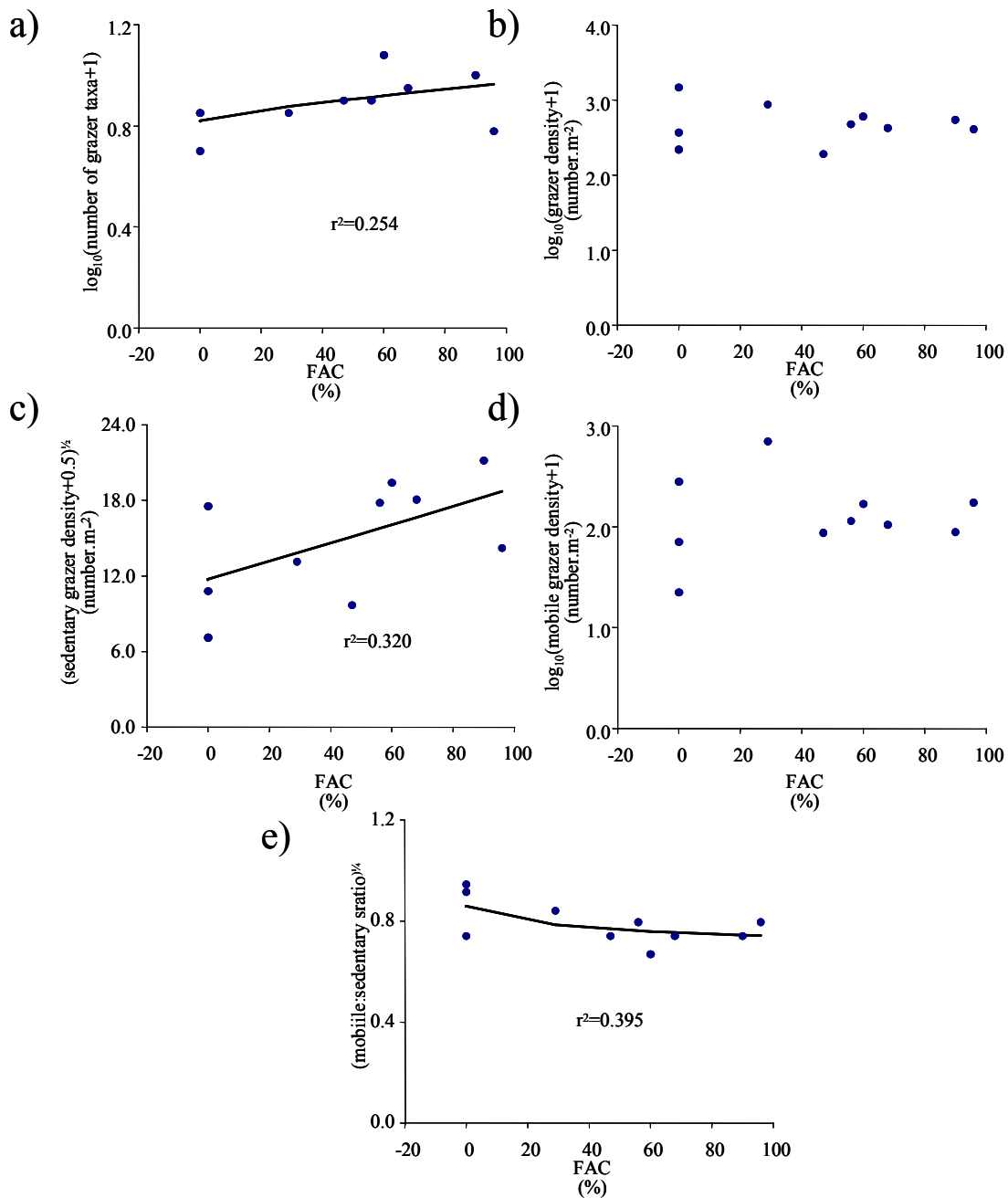
Figure 3.4 Relationships of transformed grazer variables: a) number of grazer taxa, b) grazer density, c) sedentary grazer density, d) mobile grazer density and e) mobile: sedentary taxa ratio; with filamentous algal cover at the reach scale. Only significant regression lines (p< 0.05) drawn, n= 10, p<0 .001. Regression equations provided in Appendix C.

Both ß-1 and ß-2 were strongly related to filamentous algal cover (Figure 3.5). Reaches with no filamentous algae had very low beta diversity, particularly ß-1. Several physicochemical variables explained significant amounts of variation in grazer diversity (Figure 3.6). Grazer diversity was highest at reaches with high chlorophyll *a* concentration and velocity, moderate levels of depth and ashfree dry mass, and low turbidity.

Table 3.6 Results of linear regression of reach scale grazer variables against algal parameters with the exclusion of the downstream Harper's Creek site. Significant regressions only are shown. Variation explained by each variable (r^2) and direction of relationship are provided, $p < 0.005$ for all relationships shown except where marked. Graphs and regression equations provided in Appendix D.

Dependent variable	Independent variable	r^2
Grazer diversity	GPP	0.36 (+)
Grazer density	GPP	0.68 (+)
Sedentary grazer density	GPP	0.58 (+)
Mobile: sedentary diversity ratio	GPP	0.54 (-)*
Grazer diversity	FAC	0.23 (+)
Sedentary grazer density	FAC	0.55 (+)
Mobile: sedentary diversity ratio	FAC	0.57 (-)*

*$p < 0.025$
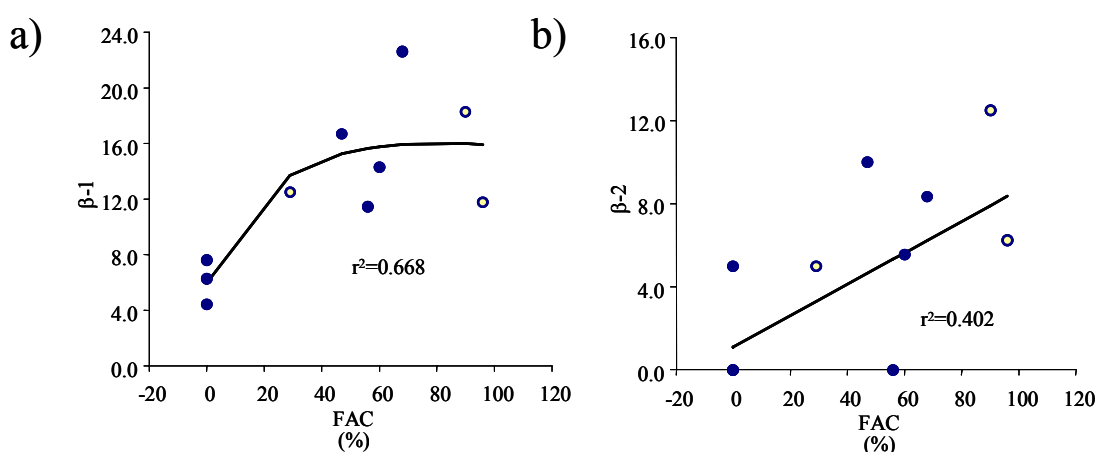
Figure 3.5 Relationship of cobble (within-reach) a) beta-1 (β1) and b) beta-2 (β2) diversity with the average filamentous algal cover of each reach, $p<0.05$. Brisbane reaches (n= 3) are marked with an open circle, Mary reaches (n= 7) have closed circles. Regression equations provided in Appendix C.

Figure 3.6 (opposite) Relationships at the reach scale of grazer diversity with transformed physicochemical variables: a) chlorophyll *a*, b) ashfree dry mass, c) depth, d) velocity, e) turbidity, f) conductivity, g) cobble surface area and h) temperature. Significant regressions (p< 0.05) only drawn, n= 10, p< 0.001 unless indicated. Regression equations provided in Appendix C.
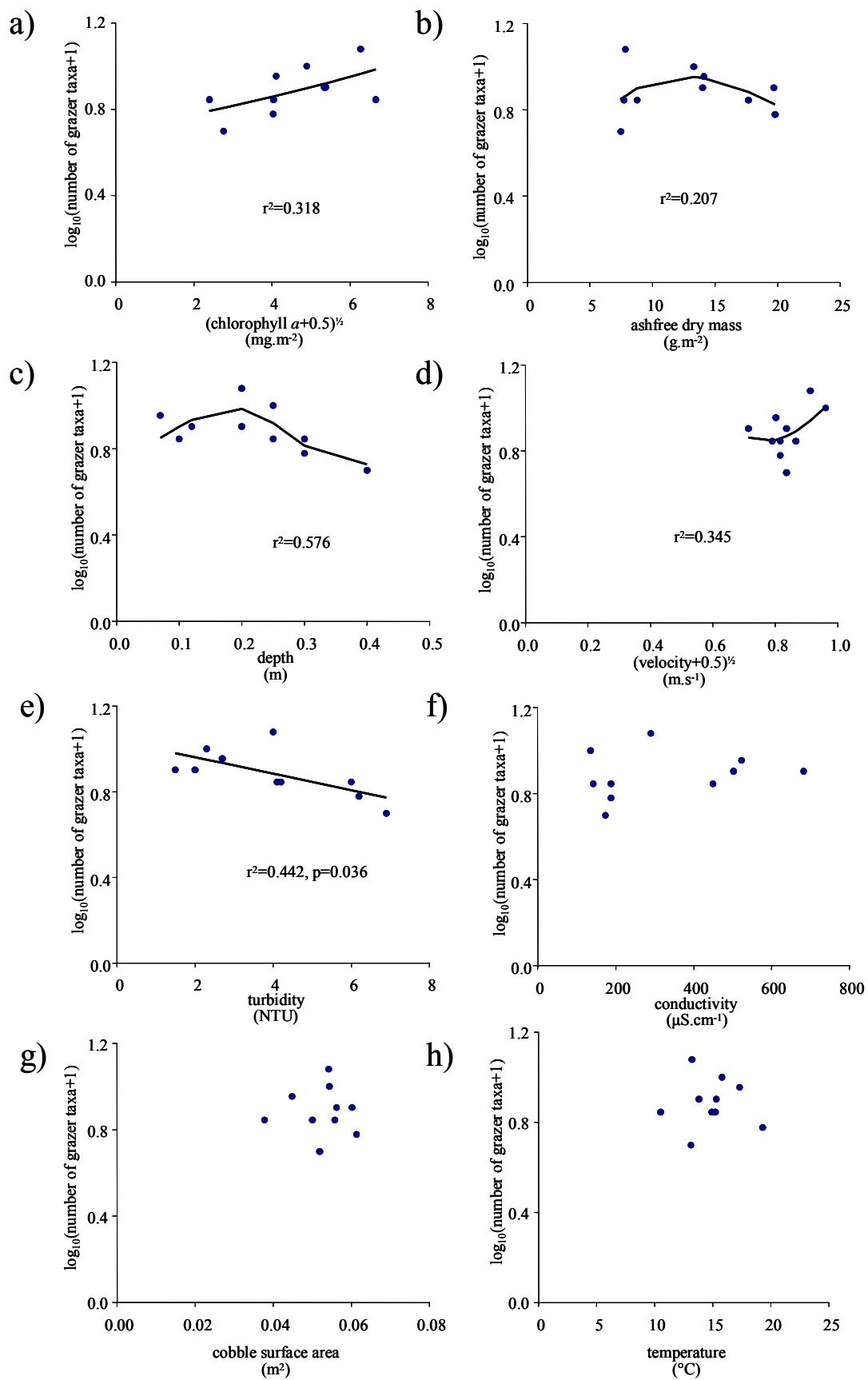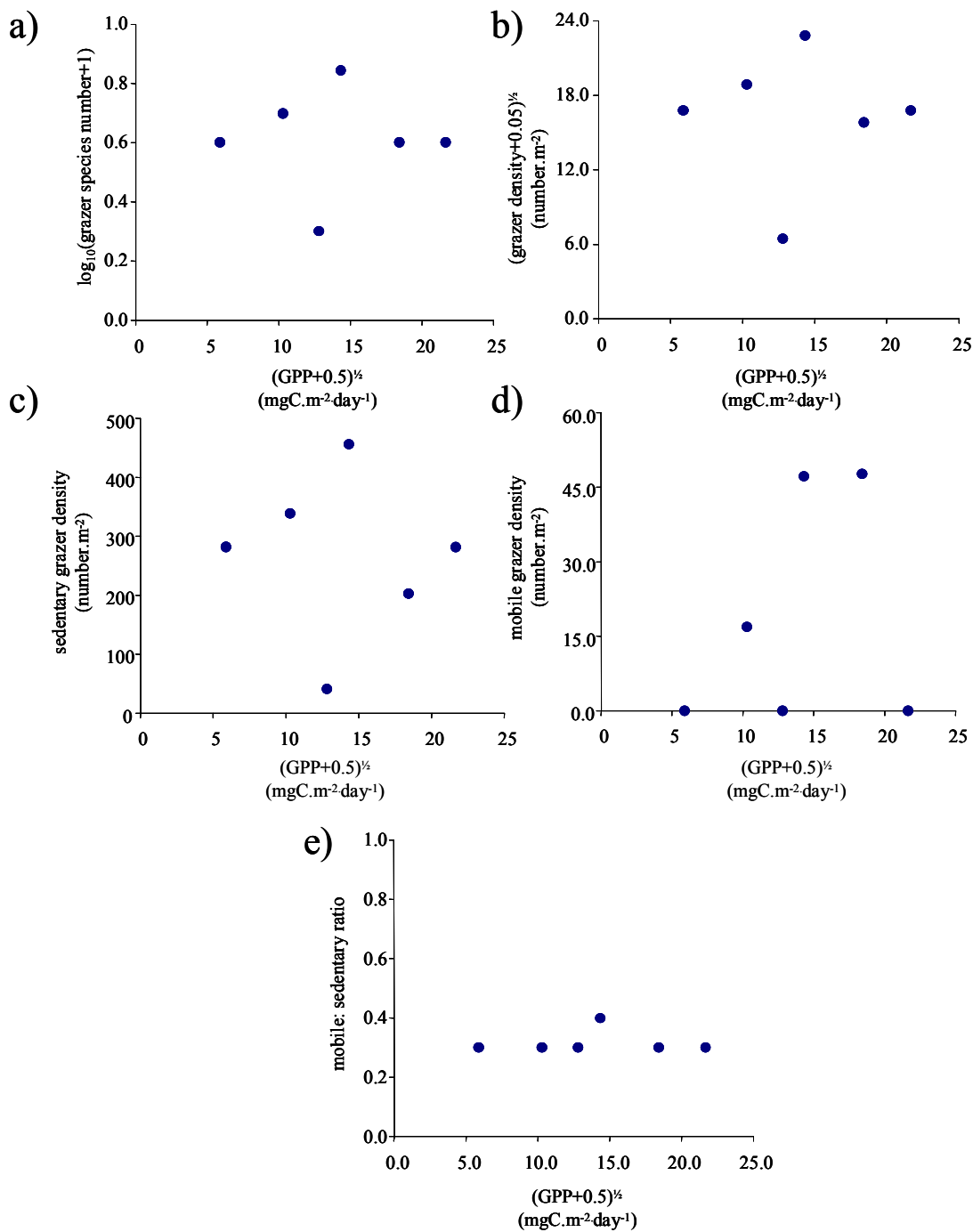
Figure 3.7 Relationships at the cobble scale at Running Creek of transformed grazer variables: a) number of grazer taxa, b) grazer density, c) sedentary grazer density, d) mobile grazer density and e) mobile: sedentary taxa ratio; with gross primary production, n= 8.

Cobble scale

At the cobble scale, there were no significant regressions between grazer variables and GPP (Figure 3.7). However, grazer diversity was inversely related to the cover of filamentous algae (Figure 3.8), as were total and sedentary grazer density. Mobile grazer density was higher on cobbles with moderate cover, but this was not significant. The ratio of mobile: sedentary taxa was virtually identical across all cobbles, and was therefore not subjected to regression analysis, but the data are still portrayed in relation to algal variables (Figure 3.7e, Figure 3.8e).

Several physicochemical variables explained significant amounts of variation in grazer diversity at this scale (Figure 3.9). Grazer diversity peaked at moderate levels of depth, chlorophyll *a* and ashfree dry mass. It is important to note that diversity displayed no significant relationship with cobble surface area, possibly because of the restricted range of cobble sizes that were sampled.

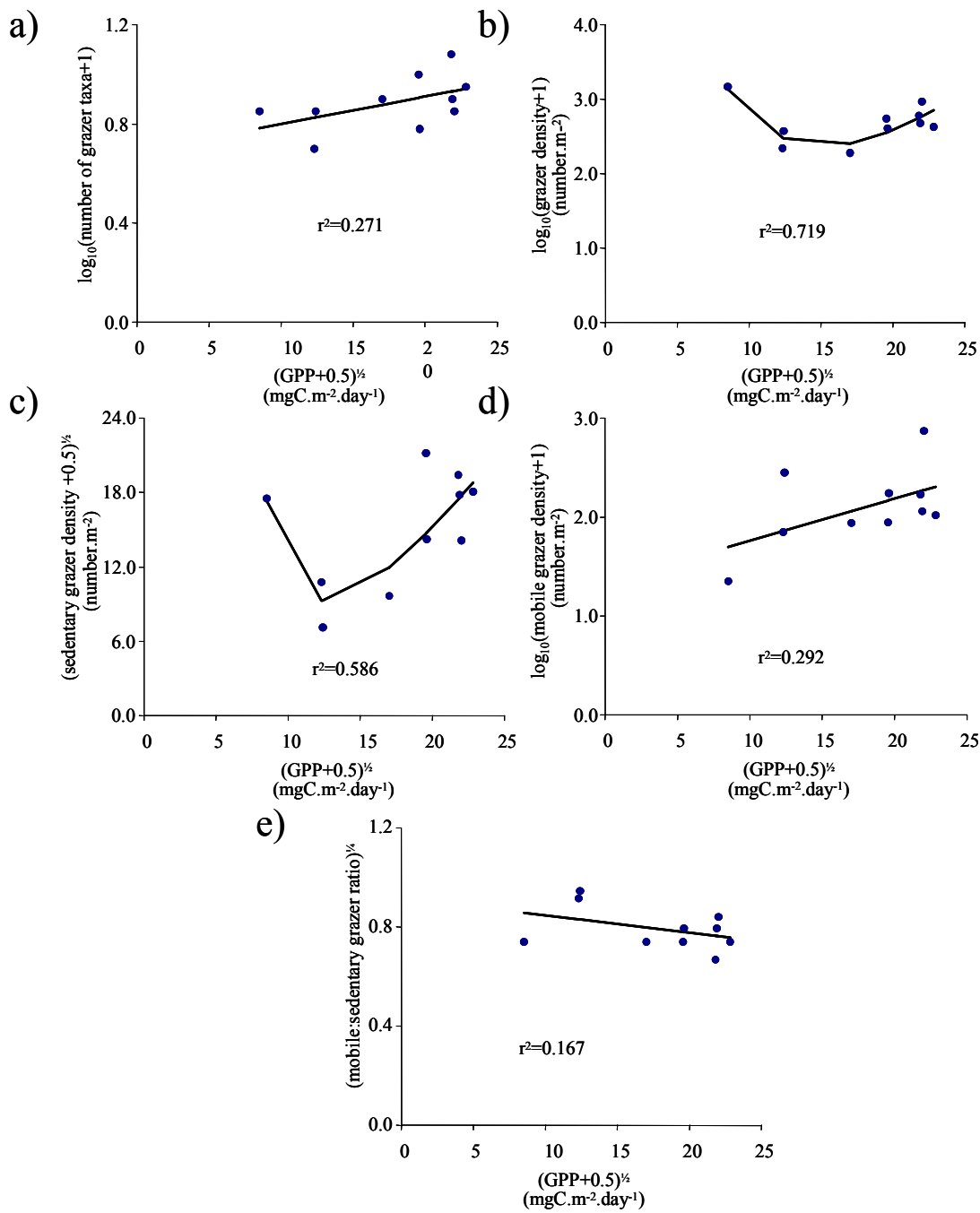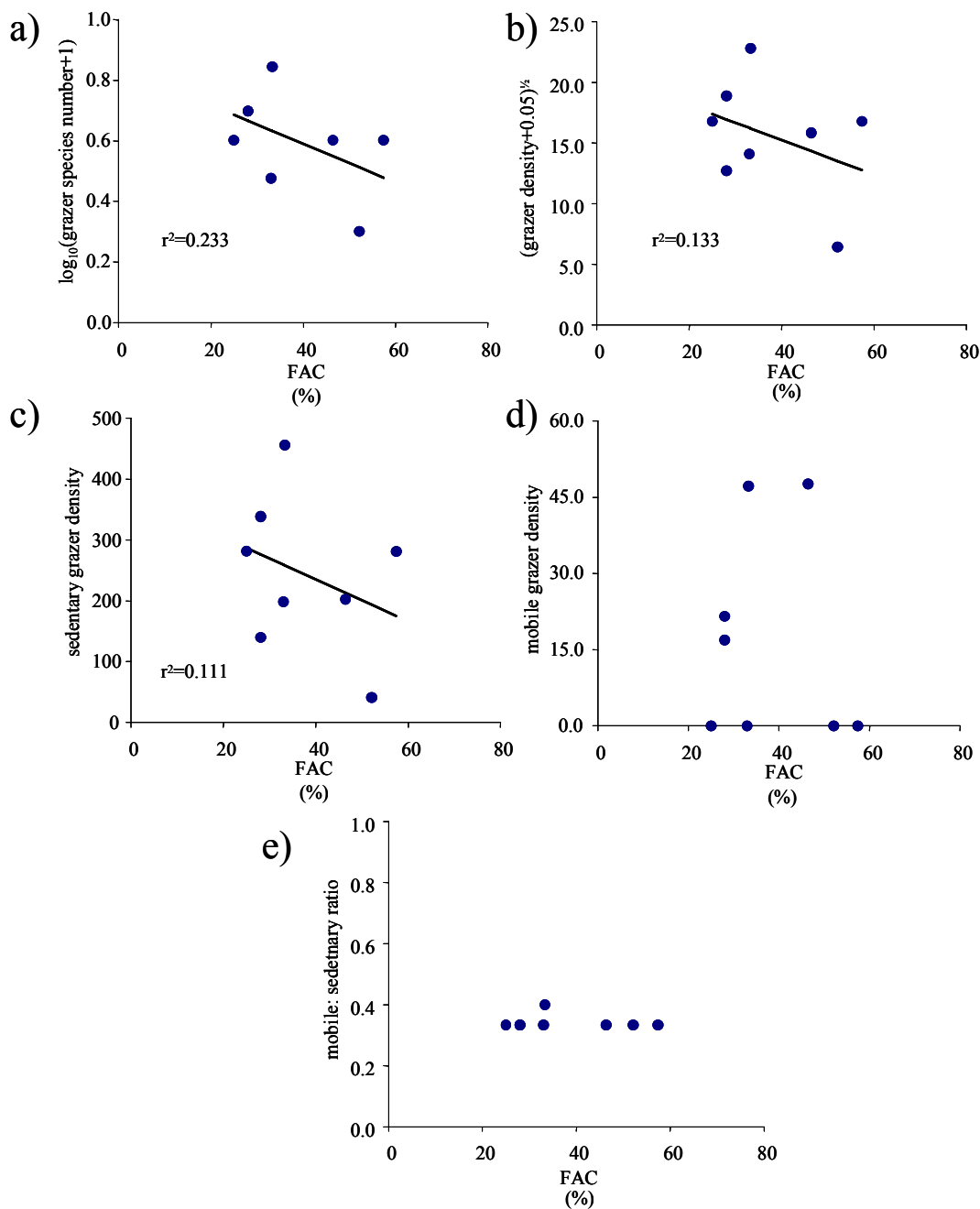**Figure 3.8** Relationships at the cobble scale at Running Creek of transformed grazer variables: a) number of grazer taxa, b) grazer density, c) sedentary grazer density, d) mobile grazer density and e) mobile: sedentary taxa ratio; with filamentous algal cover, n= 8, p< 0.001. Regression equations provided in Appendix C.
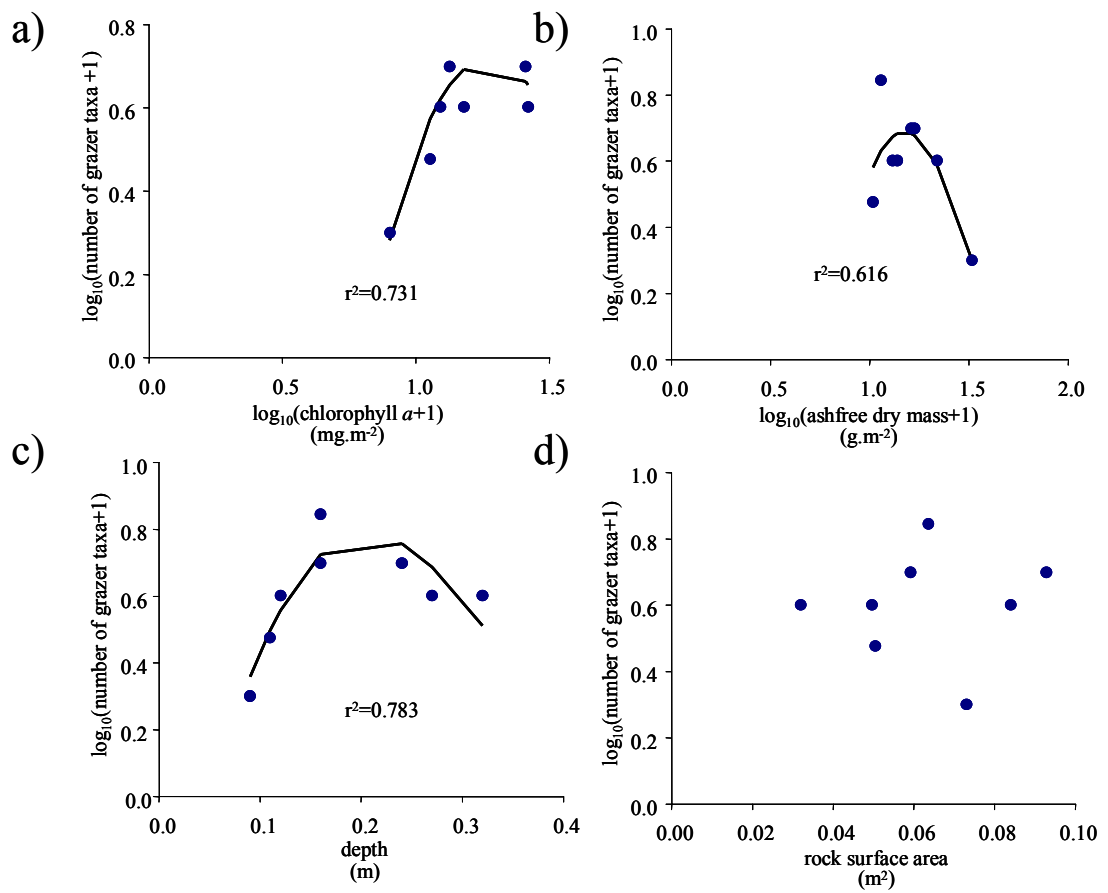
Figure 3.9 Relationships at the cobble scale at Running Creek of grazer diversity with transformed physicochemical variables: a) chlorophyll a, b) ashfree dry mass, c) depth and d) cobble surface area. Only significant regression lines drawn, n= 10, p< 0.001. Regression equations provided in Appendix C.
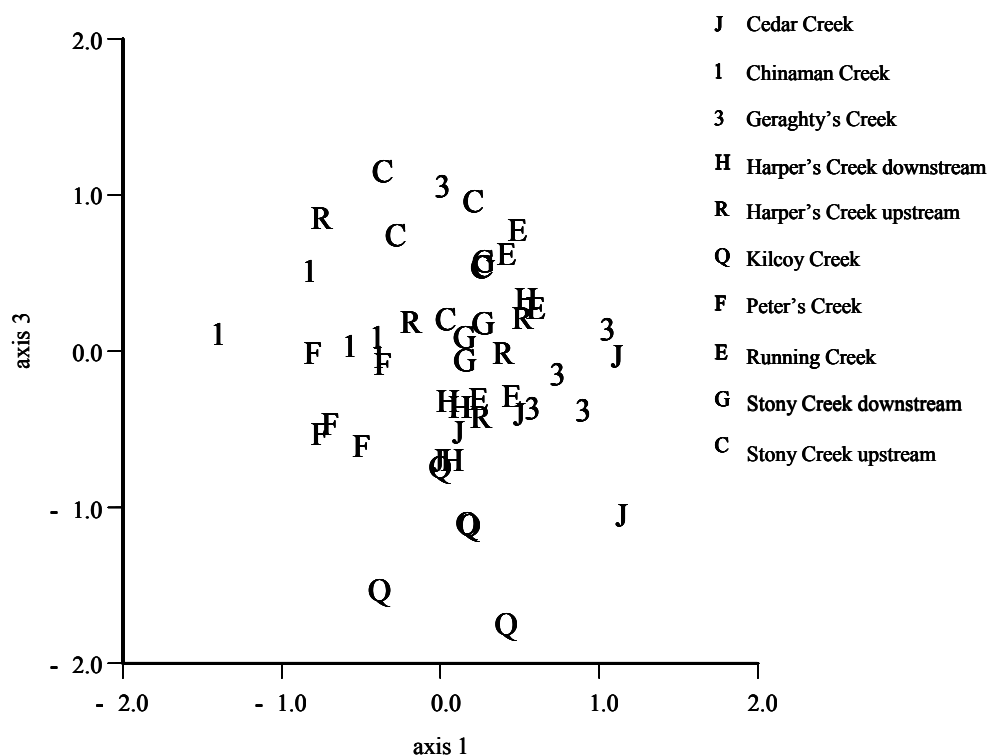
Figure 3.10 Rotated SSH plot for the reach scale on axes 1 vs. 3 of samples. Samples labelled according to reach (shape; see legend) and catchment (filled shapes= Mary catchment, open shapes= Brisbane catchment).
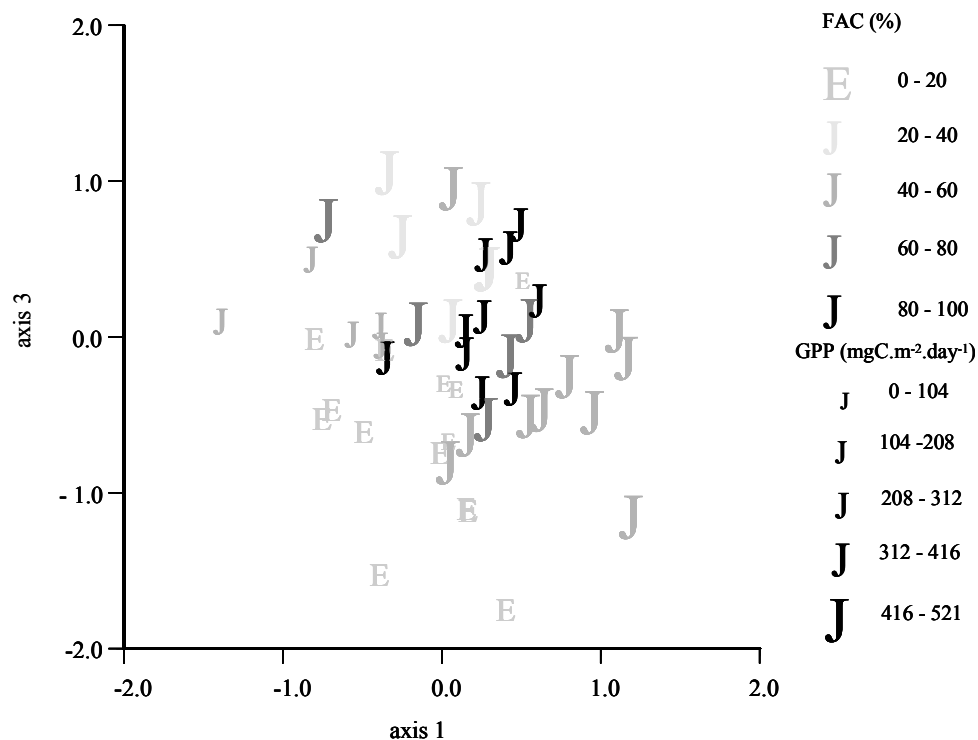
Figure 3.11 Rotated SSH plot on axes 1 vs. 3 of samples. Samples are labelled according to cover of filamentous algae (FAC) and gross primary production (GPP) at the relevant reach on the day of sampling. Size of point denotes GPP and shading denotes FAC.

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3.3.5 Grazer assemblage composition

3.3.5.1 Catchment and reach scale

Ordination of invertebrate data from the full set of 50 samples required three dimensions to adequately describe the data (stress= 0.16). Clearest groupings were seen on axes 1 and 3. Samples grouped on the basis of both reach and catchment (Figure 3.10), and ANOSIM confirmed that these clusters were statistically significant (reach $p< 0.001$, catchment $p< 0.004$).

Samples also clustered on the basis of FAC and GPP (Figure 3.11), and ANOSIM confirmed that these clusters of reaches were significant ($p< 0.001$). Reaches with low levels of GPP (0 - 208 $mgC.m^{-2}.day^{-1}$) were arranged low on axes 1 and 3, and those with higher levels of GPP (208 – 521 $mgC.m^{-2}.day^{-1}$) were arranged high on these axes, particularly on axis 3. Samples from reaches with low filamentous algae were arranged low on axis 3, while those with high filamentous algae were arranged high on this axis.

Of the grazer taxa, 12 correlated significantly with the ordination (Table 3.7). Ordination vectors of sedentary taxa show that they tended to be present high on axis 1, and generally high on axis 3 (Figure 3.12a), while mobile taxa tended to be present low on axis 1 and generally high on axis 3 (Figure 3.12b).

Of the algal or physico-chemical variables, FAC and chlorophyll *a* correlated most strongly with the ordination (Table 3.8), followed by GPP. When these vectors are superimposed over the ordination space, it becomes clear that FAC and GPP were very similar in their relationship to the ordination (Figure 3.13).

Table 3.7 Maximum correlation coefficients in multidimensional space for grazer taxa with ordination vectors derived from the invertebrate assemblage (at the reach scale). Significance levels for overall correlations were determined using a Monte-Carlo technique with 1000 randomisations. Only variables with significant correlations (p< 0.05) are listed.

variable	R	p
Nymphulinae sp. AV18	0.90	<0.001
Helicopsyche cochleatesta	0.84	<0.001
Austrolimnius sp.	0.82	<0.001
Austrophlebioides sp. AV11	0.78	<0.013
Tillyardophlebia sp.	0.77	<0.001
Bungona sp.	0.69	<0.001
Helicopsyche sp.	0.58	<0.001
Sclerocyphon minimus	0.47	<0.008
Elmidae adults	0.45	<0.020
Unidentified gastropoda	0.44	<0.022
Nymphulinae sp. AV3	0.43	<0.008
Helicopsyche murrumba	0.38	<0.048

Table 3.8 Maximum correlation coefficients in multidimensional space for environmental variables with ordination vectors derived from the invertebrate assemblage (at the reach scale). Significance levels for overall correlations were determined using a Monte-Carlo technique with 1000 randomisations. Only variables with significant correlations (p< 0.05) are listed.

variable	R	p
FAC	0.64	<0.001
chlorophyll *a*	0.64	<0.001
GPP	0.58	<0.001
velocity	0.48	<0.003
average temperature	0.40	<0.013
average depth	0.40	<0.044
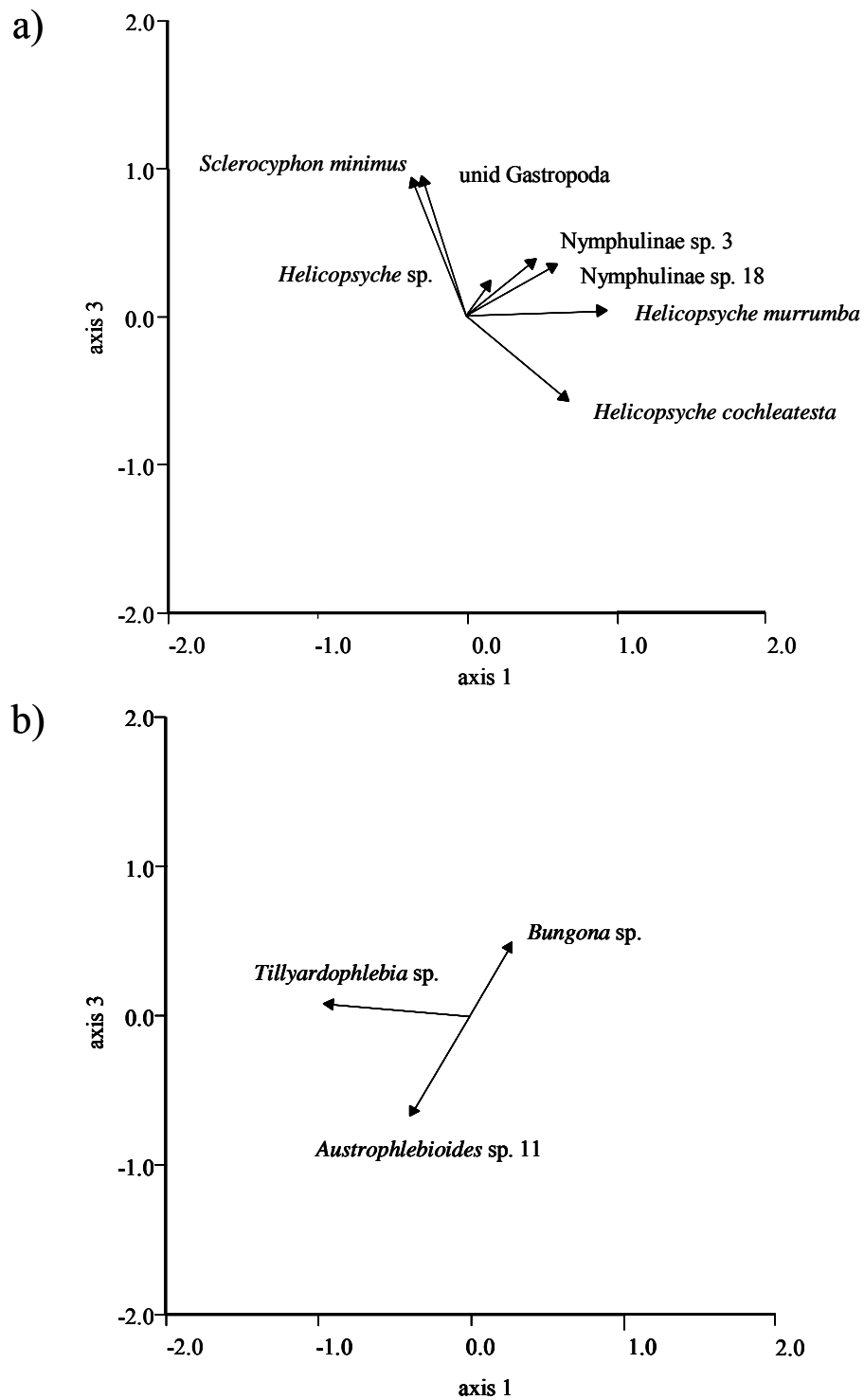
Figure 3.12 PCC vectors of taxa that contributed significantly to the reach-scale ordination, separated into a) sedentary taxa and b) mobile taxa.
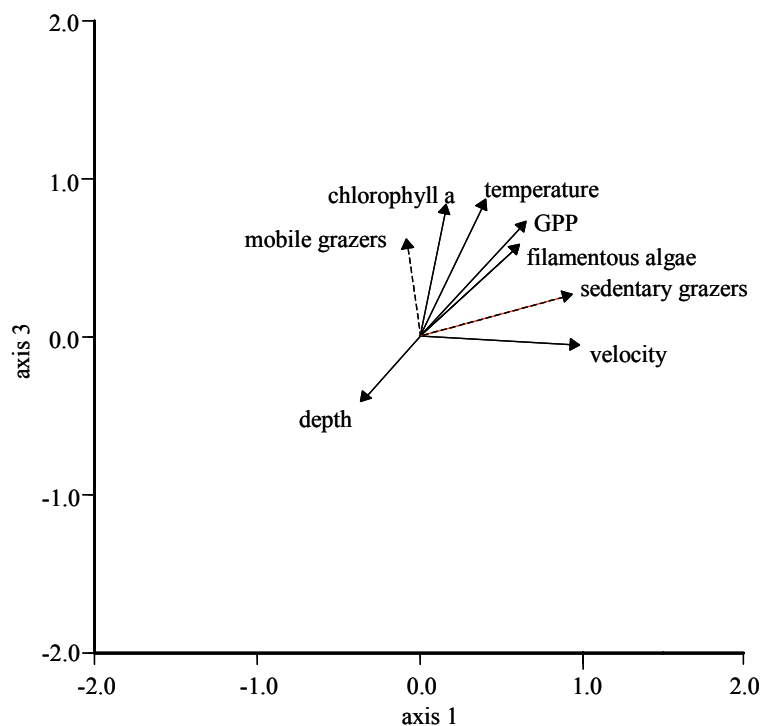
Figure 3.13 PCC vectors of environmental and algal variables that correlated significantly with the reach scale ordination. Sedentary and mobile grazer abundance vectors are superimposed onto the same axes.
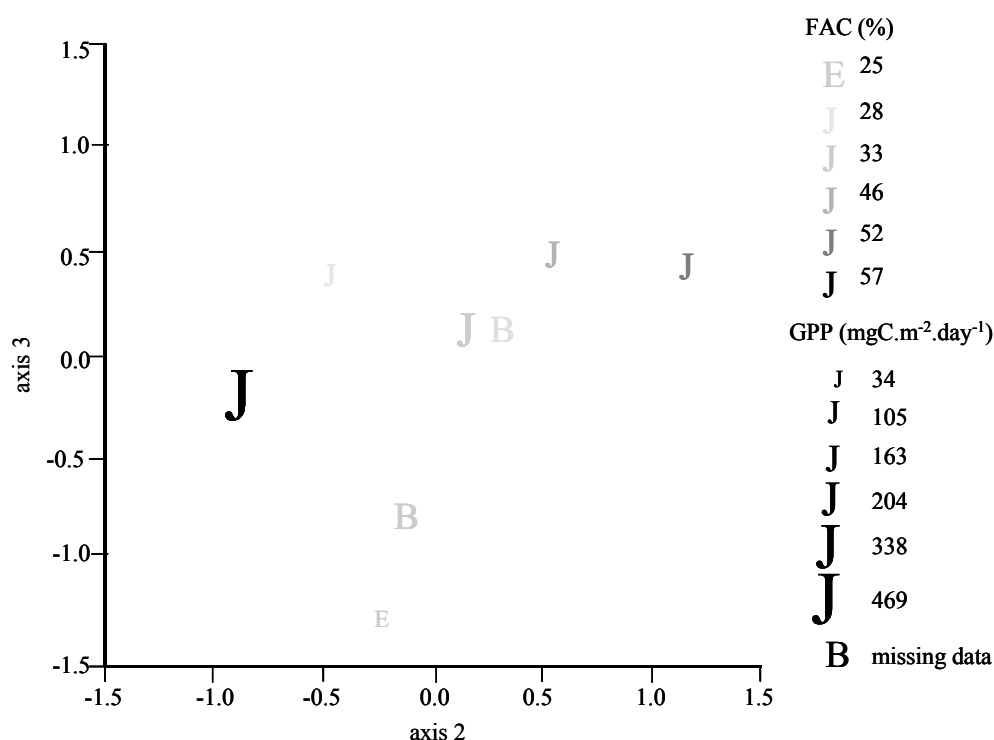
Figure 3.14 Rotated SSH plot for the cobble scale on axes 2 vs. 3 of samples. Samples are labelled according to cover of filamentous algae (FAC) and gross primary production (GPP) at the reach on the day of sampling. Size of point denotes GPP and shading denotes FAC. Open circles indicate cobbles where no GPP data are available.

The vector for sedentary grazer density (r= 0.60, p< 0.001) was in a similar direction to both of these vectors, while the vector for mobile grazer density, while not significantly related to the ordination as a group (r= 0.23, ns), tended to fall more closely to the vectors for chlorophyll *a* and depth. (Note that all of the individual mobile grazer taxa shown in Figure 3.12b correlated significantly with the presence-absence ordination).

3.3.5.2 Cobble scale

The cobble scale ordination showed no clear gradient or grouping with GPP or FAC (Figure 3.14). There were no significant correlations of algal or physicochemical variables with the ordination at this scale.

3.4 Discussion

3.4.1 Between-catchment and reach scales

Ordination results strongly indicate that the composition of grazers on a cobble was related to the composition of grazers within the catchment and the reach of the river. Similarly, comparison of diversity measures at these scales indicates that the diversity of grazers was higher at the reach scale than at the cobble scale. This suggests that regional diversity ultimately constrained local diversity, as has been predicted to occur in most communities (Ricklefs 1987, Cornell & Lawton 1992, Palmer *et al.* 1996, Caley & Schluter 1997, Vinson & Hawkins 1998). It also supports the assertion of Vinson and Hawkins (1998) that that local species pools in streams are subsets of regional pools.

Local species pools may be smaller samples of regional pools because of local conditions that constrain the establishment of species (Poff & Ward 1990, Vinson & Hawkins 1998), and some of these factors are discussed below. However, in these streams there were also a few taxa that have very limited broad-scale dispersal abilities

(e.g. limpets and snails). These animals may have found it difficult to colonise every reach whether or not conditions suited them. In other words, these taxa may have been limited by dispersal abilities and not just by local conditions. This limited dispersal ability is reflected in the fact that snails as a whole group were found in one catchment (the Mary) and not the other catchment, a pattern also shown for nymphulid moths.

Indeed, the composition of grazer communities grouped clearly in the ordination analysis according to catchment as well as to reach. This is in contrast to the Victorian study of Downes *et al.* (2000a) who found little variance in species richness, composition or abundances between sub-catchments (within a 650 km^2 larger catchment), although considerable difference in all these variables between reaches.

However, Li *et al.* (2001) found that more widely separated streams (in different ecoregions) varied strongly in species richness and in composition, with considerably less variation within streams. Winterbourn and Collier (1987) also found that streams in close proximity tended to have similar faunas. This suggests that aquatic connectivity, and distance between, river systems affects the similarity of macroinvertebrate communities (see also Tockner *et al.* 1999, Sheldon *et al.* 2002).

Thus, the lack of connectivity between the Brisbane and the Mary rivers may be enough to cause significant differences in diversity and composition (these small streams at the top of the catchments are separated by an aquatic distance of over 700 km; Schmidt *et al.* (1995)). This is supported by Woolschot *et al.* (1999), Hancock (1995) and Hughes *et al.* (1995). These authors studied shrimps in these catchments, and found that shrimps, which lack adult flight, had very limited dispersal abilities and strong genetic differentiation between populations in different catchments.

3.4.1.1 Algal productivity and composition

In attempting to explain the diversity patterns found across reaches and between cobbles within reaches, the aim of the chapter was to determine the potential influences of algal productivity and composition. At both between- and within-reach scales, it was not clear whether the patterns in grazers were most related to productivity or to algal community structure. It is still clear, however, that at the reach scale, there was a positive relationship between the number of grazer taxa and both primary production (as either GPP or chlorophyll *a*) and filamentous algal cover. The positive nature of this relationship is somewhat unusual; Mittelbach *et al.* (2001) reviewed 28 studies examining the relationship between productivity and aquatic invertebrate diversity, and found that less than 10% of studies showed a positive relationship. Of 42 studies investigating productivity: animal diversity at the across-community scale, less than 20% established a positive relationship.

However, GPP levels were not particularly high in this study, at a maximum of only 469 $mgC.m^{-2}.day^{-1}$. For example Bunn *et al.* (1999) recorded GPP values of over 2000 $mgC.m^{-2}$ day^{-1} at some sites in the Mary River catchment. It is possible, therefore, that a hump-shaped relationship between invertebrate grazer diversity and productivity might emerge if reaches with a higher GPP were included.

Of the mechanisms listed in Chapter 1 that explain positive relationships between GPP and grazer diversity, the one that may be most likely to explain the observed pattern is that which attributes the relationship to an increase in the diversity of resources (see also Abrams 1995). The lack of a positive relationship between GPP and grazer density reduces the likelihood that the relationship with diversity was due to the increase in the abundance, and thus occurrence, of rare taxa to the point where they become less rare

(and are no longer excluded from the data). The lack of a negative GPP: grazer density relationship also suggests it is unlikely that GPP: diversity relationships were due to an increase in intra-specific density dependence (cf. Abrams 1995, Siemann 1998).

It is also possible that the positive relationships were in fact due largely to filamentous algal cover rather than to GPP. While the influence of filamentous algae on the density and richness of invertebrates has been documented (e.g. Dudley *et al.* 1986, Downes *et al.* 1998, 2000b), to date researchers have examined the effects only at the microhabitat scale.

However, benthic algal communities are inherently heterogeneous in composition, biomass and productivity (Stevenson 1997 and references within), and the effect of this is particularly dramatic with algae that dominate vertical as well as horizontal space. This heterogeneity of habitat was clearly related to the *variation* in grazer diversity within a reach, with considerably more homogeneous distributions within reaches where there is no filamentous algal cover. There is therefore also likely to have been a positive relationship between this habitat heterogeneity and macroinvertebrate diversity (e.g. Brown 2003). As well as algal variables, other, physicochemical variables were also related to grazer diversity, including depth, velocity and turbidity.

The density of grazers at a reach, and of sedentary grazers in particular, also appeared to be high where GPP and FAC were high, but this relationship was a positive one only if one of the study sites was removed from the analysis. The unusual reach, Harpers Creek downstream, most likely differed from other reaches with intact riparian zones in its composition of diatoms and other adnate algae (no filamentous algae were present), due to its unusual combination of high shade and high nutrients. If this was the case, it suggests the possibility of a key relationship between algal composition and grazer taxa diversity.

The relationship between mobile grazer density and primary productivity/filamentous algal cover was less clear from the regression analysis. Ordinations indicated that mobile grazers were present at lower to moderate levels of both factors. In addition, their mean density and coefficient of variation were both considerably higher below 20% FAC (279.1 and 118%) than above 20% (122.3 and 30%), which implies that filamentous algae might have a negative effect on these grazers above this threshold of cover. Mobile grazers showed no relationship with GPP once the Harpers Creek downstream reach was removed. This reach may have had different algal composition to other covered sites (see above), and the lack of relationship across sites of more similar algal community composition suggests that the relationship originally displayed with GPP may have actually been a relationship with algal composition.

Finally, at the reach scale, the ratio of mobile to sedentary grazer taxa was low where FAC and GPP values were high. This adds supports the suggestion that where these variables were high at a reach, the grazer community switched from vagile mayflies toward sedentary taxa such as pyralid larvae, snails and caddisflies.

3.4.2 Cobble scale

At the cobble scale, there was no apparent relationship of productivity and diversity or density. A hump-shaped relationship was suggested, but this was not significant, possibly due to the low level of replication, although note that an asymptote of species richness was reached at eight samples (see Appendix A). .

Grazer diversity tended to be low on cobbles with high FAC at this scale. This result is in contrast to the findings of Downes *et al.* (2000b) at a similar scale, and to the broader literature that suggests that more complex habitats contain more species (see reviews by Douglas & Lake 1994 and McKenny 1995, also Brown 2003 and references within).

The density of grazers and sedentary grazers also were low on cobbles with high filamentous algal cover, but mobile grazers tended to be most dense at moderate levels of cover. The negative relationship of sedentary grazer density with FAC was unexpected, considering the relationship it had with FAC at the reach scale. It is also interesting that there was no change in the ratio of mobile: sedentary taxa across a reach, suggesting that any density differences were not reflected in numbers of taxa.

Finally, it could be argued that the lack of relationship between productivity and grazer variables at the cobble scale may have been due to the reduced amount of variation in algal variables at the cobble scale. This is only a possibility for filamentous algal cover, as variation in gross primary production was not lower at the smaller scale.

3.4.3 Conclusions

The strong relationship between primary productivity and filamentous algal cover can obscure the conclusions that can be drawn from a correlative study about the relative importance of algal composition versus productivity on grazer diversity. The considerable impact that filamentous algal cover has on the complexity of a microhabitat and the heterogeneity of a reach means that it may have as strong as, or greater, influence on grazer diversity than productivity at these spatial scales. This is perhaps evidenced by the fact that filamentous algal cover, and not primary production, was positively related to grazer variables at the cobble scale. Experimental manipulation of filamentous algal cover and primary production would be required to determine their relative influence on grazer diversity (see Chapter 4).

Strongest relationships between grazers and algal variables were found at the reach scale, and these were generally monotonic and positive. There was also a clear suggestion of shifts in grazer composition that may have been related to algal variables:

there were fewer mobile grazers and more sedentary grazers at reaches with high productivity and filamentous algal cover, and vice versa. At a smaller spatial scale (between cobbles), patterns were less clear, and require investigation with more extensive replication (see Chapter 5)

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4 - Grazer response to manipulated treatments of different algal composition and production

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4.1 Introduction

It is well established that the abundance and distribution of macroinvertebrate grazers in lotic systems is influenced by benthic algae (e.g. Lamberti & Moore 1984, Vaughn 1986, Wallace & Webster 1996, Álvarez & Peckarsky 2005). Algal productivity could be expected to be related to grazer diversity, given the evidence in other systems that suggests diversity can increase or display a hump-shaped response (peaking at moderate productivity) as productivity increases (see reviews by Waide *et al.* 1999, Mittelbach *et al.* 2001). There is, however, little evidence concerning the influence of algal productivity on grazer diversity in streams. Grazer density and growth have been shown to increase in response to enhanced primary production (Hill & Knight 1988b, Lamberti *et al.* 1989, Peterson *et al.* 1993, Hill *et al.* 1995). The number of grazer taxa may also increase, possibly due to such factors as a rise in the number of rare taxa or in the diversity of resources (Abrams 1995, see Chapter 1).

Often associated with increased algal production is a change in the composition of algal communities. One such change that may have major impacts on grazers is the shift towards a dominance of the community by filamentous algae. The structural complexity of some forms of filamentous algae may provide additional habitat, more resources and/or more niches for grazers and thus may lead to a higher number of taxa being able to coexist (Dean & Connell 1987a, b, O'Connor 1991, Downes *et al.* 1998, 2000a).

However, it may also have negative effects through the reduction of the availability of other, more edible, algal forms through its dominance of space (McCormick 1996, Wellnitz & Ward 1998).

Because changes in productivity are closely associated with changes in filamentous algal cover, it can be difficult to separate their effects on grazer communities (Chapter 3). One way to separate these two characteristics of algal communities may be to experimentally manipulate the habitat variables within the stream that influence these parameters. Two variables commonly and easily manipulated in streams to influence algal communities are light and limiting nutrients (see reviews by Hill 1996 and Borchardt 1996; also Mosisch *et al.* 1999, Rosemond *et al.* 2000, Stelzer & Lamberti 2001).

Both light and nutrients play important roles in controlling the levels of production and filamentous algal cover (e.g. Lowe *et al.* 1986). For example, filamentous chlorophytes have higher light requirements than those of diatoms or benthic cyanobacteria (Hill 1996), and also require relatively high in-stream concentrations of nitrogen and phosphorus (Borchardt 1996). The level of irradiance also plays an important role in controlling rates of algal production (Lamberti *et al.* 1989, Steinman 1992, Hill *et al.* 1995).

Similarly, the addition of limiting nutrients increases production in diatoms and filamentous chlorophytes (Peterson *et al.* 1993, Rosemond 1993, Rosemond 1994). Limiting nutrients can be either nitrogen (Hill & Knight 1988b, Lohman *et al.* 1991), phosphorus (Pringle & Bowers 1984, Pan & Lowe 1994), a combination of nitrogen and phosphorus (Tate 1990, Winterbourn 1990) or micronutrients (e.g. Pringle *et al.* 1986, Carrick *et al.* 1988). Addition of limiting nutrients can increase diatom production even

under conditions of reduced light (e.g. Winterbourn 1990, Rosemond *et al*. 2000, Stelzer & Lamberti 2001).

As well as productivity and filamentous algal cover, the taxonomic and morphological composition of algal communities may also be important to grazer diversity, as some taxa are more successfully grazed than others (see review by Steinman 1996). Some large, stalked diatom taxa (e.g. *Cymbella* and *Gomphonema*) may be more successfully ingested than small, adnate forms such as *Achnanthes* and *Cocconeis* (Jacoby 1987, Peterson 1987, McCormick & Stevenson 1989, Wellnitz & Ward 1998). In addition, some species of blue-green algae may be avoided by grazers if they produce toxins, mucilaginous sheaths, or chemical deterrents (McCullough *et al.* 1979, Dudley & D'Antonio 1991).

Algal diversity may also affect grazers. Because a greater number of resources should support a greater number of consumer species, most models predict that plant diversity should determine herbivore diversity (see Chapter 1). Plant: animal diversity relationships have been demonstrated at local spatial extents by both correlative and experimental studies (Siemann *et al.* 1998 and references therein, Knops *et al.* 1999, Haddad *et al.* 2001). However, there is little empirical evidence concerning the nature of the possible influence of changes in algal diversity on freshwater macroinvertebrates.

In this chapter, variation in algal characteristics was created by manipulating light and nutrients at the patch (10^0-10^1m) scale across replicate stream reaches. In manipulating these variables, the following responses were predicted:

1. that primary production would be low in patches with low light and nutrients, moderate where light was low and nutrients high, and highest in patches with high light and nutrients (Table 4.1); and

2. that treatments with low light would result in little or no filamentous algae (while still maintaining a diatom community, albeit with lower productivity), and that nutrient addition would enhance filamentous algal growth in unshaded treatments; and

3. that algal diversity would be affected by enrichment, although the direction of the response could be either positive (Pringle 1990, McCormick & Stevenson 1991) or negative (Carrick *et al.* 1988, Peterson & Grimm 1992).

Table 4.1 Predicted outcome of experimental manipulation of light and nutrients.

Treatment	Predicted GPP	Predicted FAC
Low light, low nutrients	Low	Very low
Low light, high nutrients	Moderate	Very low
High light, low nutrients	Moderate - high	Moderate
High light, high nutrients	High	High

Grazer diversity and density were expected to vary considerably in association with algal changes, since some taxa are able to rapidly disperse at the scale of reaches and of patches within reaches (Chapters 1, 3) using aerial flight. Mobile grazers (as defined in Chapter 3) might be expected to show stronger relationships with algal variables at the patch scale, due to their added ability to track algal variation by moving into the drift or by swimming (Mackay 1992). Sedentary grazers, on the other hand, generally have heavy cases or shells and are not able to readily enter the drift (Mackay 1992). The slow crawling speeds exhibited by this group in these streams mean that they may not be able to rapidly track variation in algal variables, and their smaller home ranges may mean that they do not perceive heterogeneity at this scale (cf. Kotliar & Wiens 1990).

This chapter seeks to address the following questions:

1. Is there a relationship between algal variables and the diversity and composition of grazers at the patch (10^0-10^1 m) scale?

2. Can such relationships be attributed clearly to one aspect of the algal community (productivity vs. filamentous algal cover) through the use of experimental manipulation?

3. Does the mobility of grazers affect their responses to algal variation at the patch scale?

What are the relationships between diversity and composition of algae and grazers at the reach, patch and cobble scales?

4.2 Methods

4.2.1 Experimental setup

At each of four reaches (two sites on each of two streams), there were four treatments (three manipulations and a control; Table 4.2). Each treatment was located in a run habitat separated by a riffle/pool sequence or by at least five metres. The sampling area for each treatment was between 5.3 and 6.8 m^2 (in a rectangle perpendicular to the flow, as was most appropriate in streams of this width; see Appendix E). The treatments subject to nutrient addition were always located downstream of those not subject to enrichment, by at least five metres (Appendix E). The experiment was allowed to run for at least fifty-six days at each site.

Table 4.2 Experimental manipulations undertaken in this study

Treatment	Shadecloth	N + P added
Control*	No	No
Unshaded N + P	No	Yes
Shaded, no nutrient added	Yes	No
Shaded, N + P added	Yes	Yes

* Unshaded, no nutrient added

Samples were taken from the centre of each patch to avoid edge effects. Shade was provided by stringing shadecloth from steel posts at about $1 - 1.5$ m from the water surface (see Plate 5). Two layers of 75% green shadecloth were used and this provided a large central area (approximately 5 m^2) reduced in light by $90 - 95\%$ (Figure 4.1). Samples were taken within the central area that remained out of reach of any direct sunlight entering from the sides. Light was logged over 24 hours at three or four points at each site at the water surface, both beneath the shadecloth and in full light conditions, using Odyssey light loggers.
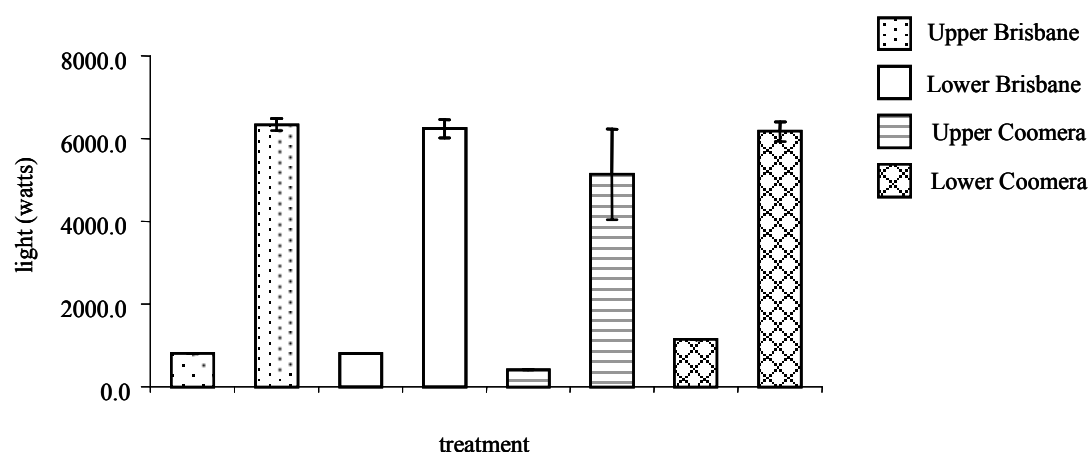
Figure 4.1 Maximum light levels in shaded and unshaded treatments at each site. Mean ± 1 S.E. provided. For all shaded treatments n= 1. For all unshaded treatments n= 3 except for the Upper Coomera where n= 2.

In order to characterise the nutrient status of each site, water samples were collected (see 2.2.1). This was carried out before enrichment or shading treatments were established. Samples were stored and analysed for total Kjeldahl nitrogen and phosphorus. Analyses were undertaken by Queensland Health Scientific Services as described in 2.3.1. The Upper Coomera had the lowest levels of ambient nutrients (Figure 4.2), while the other sites did not vary greatly from each other. Nutrients were added by seeding patches with $N + P$ Osmocote™, which is a slow diffusing, gel-coated fertiliser that is resistant to drag and which could be clearly seen to remain on the cobbles throughout the experiment. This fertiliser contains 19% N, 2.5% P and 10% K by weight, and about 0.74 kg was added per m^2, which amounts to 19g of N and 2.5g of P per m^2. This was calculated in accordance with Redfield ratios (Redfield 1958) to provide slightly more than the requirements of a site producing an estimated 3000 $mgC.m^{-2}.day^{-1}$; the approximate median of South-east Queensland cobble streams of a similar size and open riparian canopy (Udy et $al.$ 2001).
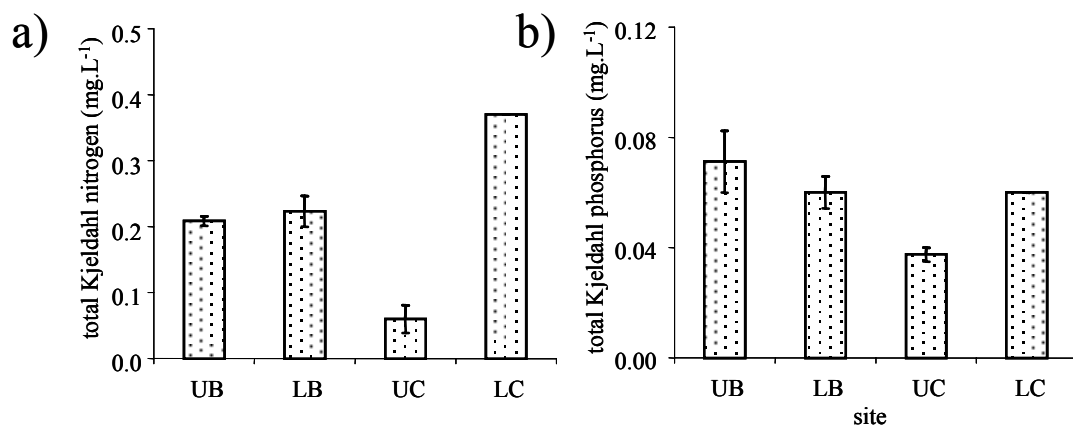
Figure 4.2 Ambient nutrient levels at each reach before commencement of experiment: a) total nitrogen; and b) total phosphorus; n= 4 except at the Lower Coomera where n= 1. U= Upper, L= Lower; B= Brisbane, C= Coomera.
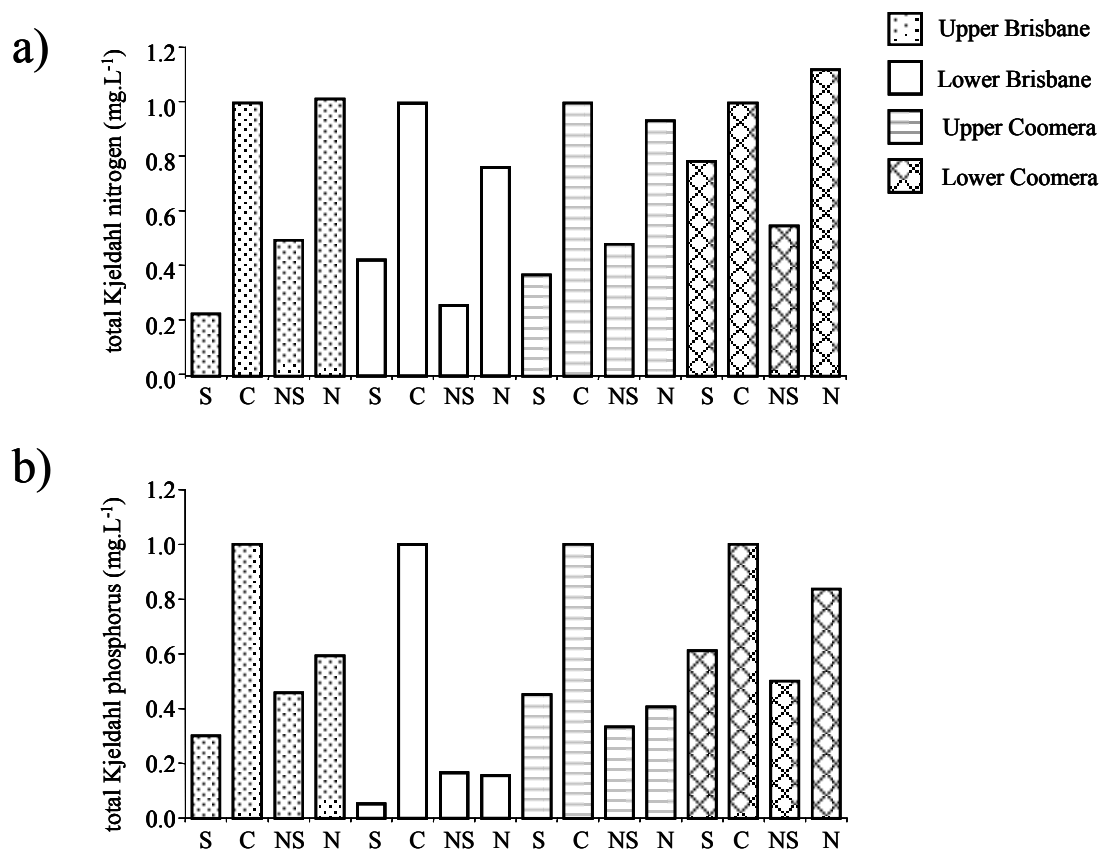
Figure 4.3 Water nutrient levels of each treatment at each reach: a) total nitrogen; and b) total phosphorus. Treatments are described using S= Shade, N= Nutrient and C= Control.

In order to characterise the nutrient status of each patch at the end of the experiment, water samples for nutrient analysis were collected from each patch, stored, and analysed for total Kjeldahl nitrogen and phosphorus, as described in 2.2.1. Data for some Upper Coomera samples were not available (Figure 4.3).

4.2.2 Invertebrate sampling

At the start of the experimental treatment, five cobbles from each reach were randomly selected from within the sampling area. A 250 μm net was placed downstream of the cobble and the cobble was swiftly removed from the substrate and placed in the net. All invertebrates were removed from the cobble, tray and net with forceps and placed in labelled vials with 70% ethanol. All grazing macroinvertebrates were identified to the lowest taxonomic definition possible, generally to species. Grazers were again separated into sedentary and mobile taxa (see 3.2.3.3). Elmids were again excluded for reasons discussed in 3.2.3.3; they comprised an average of 2% of the total abundance and 3% of the total species richness on a cobble and in a treatment.

4.2.3 Algal sampling and metabolism measurement

The cobbles were each thoroughly brushed using a hard nylon-bristled brush to remove algal filaments and then scrubbed with a wire brush to remove tightly adhering diatoms. The brushes and cobbles were then rinsed into the sample. Samples were stored on ice in the dark and processed within one hour. Each sample was made up to a standard volume, thoroughly shaken, and three aliquots taken. Two of these aliquots were separately filtered through Whitman glass filters (45 μm) and placed into labelled test tubes. One of the filter papers was stored in the freezer for mass determination and the other was placed in 10 mL of 90% acetone for chlorophyll *a* analysis. The third aliquot was stored in 1% Lugol's solution for later identification.

Of the five algal samples, three were identified and algal cells and colonies counted. A micropipette was used to extract 100 µl of sub-sample and this was evenly spread on a slide with a 22 x 50 mm cover slip. Each cover slip was divided into a grid of 10 x 5 mm and 10 randomly chosen points were selected for each slide. This procedure was duplicated for each sample, so that 0.15 µl of solution was actually examined. Calculation of the volume of sample examined is provided in Appendix F. Diatoms were identified to species and the remainder of taxa were identified to genus.

Methods used for chlorophyll *a* analysis and ash-free dry mass determination are described in detail in 3.2.1.4. Benthic metabolism was measured over 24 hours using the chamber method described in 3.2.1.2. Note that two chambers were employed in each sampling area in order to provide data in the case of one chamber failing. The variation of interest is at the patch scale, therefore chambers were not further replicated within treatments. Different cobbles were used within chambers (compared with sampled cobbles) to prevent disturbing invertebrates and algae. Different components of benthic metabolism were calculated by comparing the rate of O_2 change in the chambers at different times of the day. The rate of change at night was used as the rate of respiration and was assumed to occur over 24 hrs. Gross primary production (GPP) was calculated by summing the daily O_2 production plus the estimated O_2 consumed by respiration during the day. This method is slightly different to that described in 3.2.1.2, and is based on fewer assumptions. The resulting rate is an average rather than a maximum rate of gross primary production. Changes in dissolved oxygen concentrations over time (mg $O_2 l^{-1}.day^{-1}$) were converted to a rate of carbon fixation as described in 3.2.1.2.

4.2.4 Data analysis

The first step within the data analysis was to generate sampling curves to ensure that the number of grazer taxa was not simply a function of the number of samples. Secondly, ANOVA was carried out on algal variables to determine whether shading and nutrient treatments altered productivity, algal diversity and density, or filamentous algal cover. Alpha, beta and gamma diversity variables (grazers) were compared between the within and among reach scales in order to relate diversity patterns at the two scales. Linear and nonlinear regression analysis was carried out to examine the amount of variance in grazer variables by algal variables, at the treatment scale. Finally, compositional changes in the algal and grazer communities were examined using presence-absence ordinations.

4.2.4.1 Accumulation curves

The first aim of the data analysis was to establish the relationship between diversity and abundance for both grazers and algae, to ensure that the number of taxa per unit was accurately represented and not simply a function of the number of samples collected.

For both grazers and algae, cobble samples were pooled for each treatment and for each reach in order to create accumulation curves to establish diversity: abundance relationships. Accumulation curves were created using 'Ecosim' software (Gotelli & Entsminger 2003) as for 3.2.3.1. Very rare grazer taxa were identified using the criteria of occurring only on one cobble in a reach, and with an abundance of one, and were excluded from the dataset for all further analyses (see Appendix G for the resulting accumulation curves). For algae, curves did not reach an asymptote using these criteria, so that taxa were excluded when they occurred on only two cobbles within a reach (see Appendix H for the resulting accumulation curves). Because the number of (non-rare)

grazer taxa overall had reached an asymptote, the richness of sedentary grazers and of mobile grazers were again used in the form of a ratio between the two (see 3.2.3.3).

4.2.4.2 ANOVA

The experiment was designed so that reach was a random factor with four levels. Nutrient treatment was a fixed factor with two levels, and shading treatment was a fixed factor with two levels. Variations between reaches were expected *a priori*, and were not of interest in this context, therefore reach was used as a block in a randomised block design (Zar 1999). A mixed model ANOVA was used to test for the effects of treatment (SPSS 10.05, 1999) on GPP, FAC, algal genus richness, and total algal cell density.

Because the patch scale was of interest, rather than the cobble scale, the average cover of filamentous algae and GPP were used for each treatment. Therefore, only one replicate of each variable was available from each treatment, and so no statistical test of interactions was possible (Zar 1999). However, cell mean plots and residual plots were examined to detect any interactions that may have occurred (Quinn & Keough 2002). Reach, as a random factor, also had to be tested with caution as the probability of Type II error (i.e. the probability of incorrectly retaining the null hypothesis) was increased (Zar 1999).

Transformations

Transformations of data were carried out as required (Zar 1999; see Table 4.3).

Table 4.3 Transformations used for algal variables in analysis of variance.

Variable	Transformation
average gross primary production	$\log_{10}(x+1)$
filamentous algal cover	none
total algal density	$(x+0.5)^{1/2}$
algal genus richness	$(x+0.5)^{1/2}$

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4.2.4.3 Diversity measures

Alpha, beta and gamma diversity measures were calculated for grazers at several spatial scales following Tockner *et al.* (1999). At the within-treatment scale, α diversity was the diversity of a cobble, and γ diversity was the diversity of a treatment. Beta diversity between cobbles was calculated using two different indices (Harrison *et al.* 1992; see 3.2.3.2): ß-1, which measures the amount by which regional (gamma) diversity exceeds the mean diversity of its constituent samples (cobbles); and ß-2, which measures the amount by which gamma diversity (within one reach) exceeds the maximum diversity attained by one sample/cobble.

At the within-reach scale, α diversity was the diversity of a treatment, and γ was the diversity of a reach. For the within-catchment scale, γ was catchment diversity and α was reach diversity. These groups of diversity variables were examined for heterogeneity of variance (across scale groups). Alpha and β-1 grazer diversity were transformed as $\log_{10}(x+1)$, ß-2 grazer diversity as $\log_{10}(x+0.1)$ and gamma diversity was not transformed (Quinn & Keough 2002).

To compare diversity measures between the three spatial scales, the non-parametric Kruskal-Wallis test was employed within SPSS 10.0 (1999). Parametric tests could not be used because of the varying number of gamma diversity replicates at each scale. The test is an extension of the Mann-Whitney test used in Chapter 3 (Quinn & Keough 2002). It tests the null hypothesis of no difference in the location of the distributions between groups and is based on ranking the pooled data, determining the rank sums within the group, and calculating the H statistic that follows a chi-squared distribution with (p-1) degrees of freedom (where p= number of groups). Variances within each

group were examined and variables were transformed to improve homogeneity of variance where required (Quinn & Keough 2002).

4.2.4.4 Regression analysis

In order to examine relationships between algal variables and grazers at the patch scale, measures of each variable taken from a site were relativised to the control at that site (i.e. $x_{treatment}/x_{control}$). In this way, inter-site variance was removed, and only inter-patch variance was explored. This was not, however, performed for the ratio of sedentary: mobile grazers as this was already a proportion.

Simple linear regression was used within SPSS 10.05 (1999*)* to investigate the amount of variance in grazer variables described by algal variables, as described in 3.2.3.3. In addition, the existence of a possible unimodal relationship was explored, by applying to the data the model described by Pollock *et al.* (1998) and outlined in 3.2.3.3. This tests for nonlinear relationships that fit the generalised curve:

$$y = \beta_0 + \beta_1 * x * e^{(\beta_2 * x^{\beta_3})}$$

where β_0, β_1, β_2 and β_3 are constants, y is the dependent grazer variable, and x is the independent variable (either GPP or filamentous algal cover). The regression models were checked to ensure that regression residuals were normally distributed with constant variance. All regressions performed are outlined in Table 4.4.

Table 4.4 Regressions performed (untransformed variables listed). Note that both linear and unimodal regressions were conducted for all instances listed.

	FAC	Algal diversity	Grazer diversity	Grazer density	Sedentary grazer density	Mobile grazer density	Mobile: sedentary diversity ratio
GPP	*	*	*	*	*	*	*
FAC		*	*	*	*	*	*
algal diversity			*	*	*	*	*

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Transformations

No transformation was required for parametric analysis of any of the relativised algal variables. Data from the Lower Coomera site were removed from the analysis for regression analysis with mobile grazers and with the mobile: sedentary grazer ratio, because mobile grazers were not found at this site, and the zero abundances and diversities created problems with zero denominators. Of the relativised grazer variables, grazer density and sedentary grazer density were transformed as $(x+0.5)^{\frac{1}{2}}$.

4.2.4.5 Ordinations

Finally, ordination was used to examine the relationships between algal variables and grazer composition, and to better investigate nonlinear relationships.

Using the software package PATN (Belbin 1993), a Bray-Curtis dissimilarity matrix was calculated from algal abundance data, after transformation to presence-absence data. This transformation removes abundance information from the ordination and examines only compositional differences between samples (abundance/density patterns have already been investigated with regression analysis and ANOVA). Semi-strong-hybrid multidimensional scaling ordinations (SSH, Belbin 1993) were calculated from this Bray-Curtis matrix, using 50 iterations and a ratio-ordinal cut value of 0.90 over 100 random starts. Solutions were computed in two, three and four dimensions, and those with a stress less than 0.2 were retained (Kruskal & Wish 1978). The ordination was rotated to a simple structure using Varimax axis rotation to three dimensions.

Principal axis correlation was carried out to determine how well the set of taxa and environmental variables could be fitted to the ordination space. Environmental variables were standardised to values from 0 to 1 with the formula:

$X_{ij} = (X_{ij} - Min_{col})/Range_{col}$

Significance levels for overall correlations were determined using a Monte-Carlo technique with 1000 random permutations in three dimensions. ANOSIM was employed to test whether there were significant clusters of samples within catchments, reaches and/or treatments (patches). All of these procedures were performed using PATN (Belbin 1993), and were repeated for invertebrate data.

4.3 Results

4.3.1 Algae

The maximum GPP value recorded was almost three times higher in this experiment than that recorded at the most productive site in Chapter 3 (1773 mg $C.m^{-2}.day^{-1}$ compared with 521 mg $C.m^{-2}.day^{-1}$). The maximum cover of any treatment by filamentous algae was 81%, which is lower than the maximum cobble cover of 96% in the sites described in Chapter 3. However, the maximum cobble cover in this experiment was comparable at 100%. Minima were similar to those detailed in Chapter 3, with 1% FAC and 132 mg $C.m^{-2}.day^{-1}$, both of which occurred at the Upper Coomera site. Variation in algal variables was high between sites, with Brisbane sites recording higher means for all variables, and the Upper Coomera site recording lowest means (Figure 4.4). Note that due to the failure of some chambers, only one value of GPP was available for some treatments; for other treatments the mean GPP was used.

Twenty genera of filamentous algae were collected, the most abundant being the greens *Ulothrix, Cylindrocapsa* and *Hyalotheca* as well as the blue-greens *Anabaena, Lyngbya, Schizothrix* and *Rivularia*. The Upper Coomera reach had only two genera of filamentous algae and there were only four cobbles at this reach with any cover. Twenty-four diatom species were collected, seven of which only occurred at the Lower

Coomera. *Staurosira*, *Fragilaria* and *Epithemia* were the most abundant. A total of 56 genera of algae were collected.

ANOVA indicated that GPP and FAC varied significantly with reach (as expected), but more importantly decreased with shade treatment (Table 4.5a and b, Figure 4.5a and b). Nutrient treatment had no predictable effect on GPP (Table 4.5a; Figure 4.5b), but a modest, but not statistically significant, negative effect on FAC (Table 4.5a).

Algal diversity did not vary with any treatment (Figure 4.6c) and algal density did not significantly vary with any factor (Table 4.5c and d), although algal density was very low at the Upper Coomera (Figure 4.5d).

4.3.2 Grazers

A total of 752 grazing macroinvertebrates from 20 taxa was collected from the orders Coleoptera, Ephemeroptera, Lepidoptera, Trichoptera, and Gastropoda (Table 4.6). Eight taxa occurred at only one reach. Total abundances were generally low, ranging from 0 to 27 grazers (per cobble), and this translates to a density range of 0 to 777 grazers per m^2. Up to seven taxa were found per cobble. Note that an asymptote in species accumulation curves per treatment was always reached (Appendix G). Grazer taxon number was not related to cobble surface area (Pearson's correlation coefficient two-tailed = 0.006, p= 0.960).
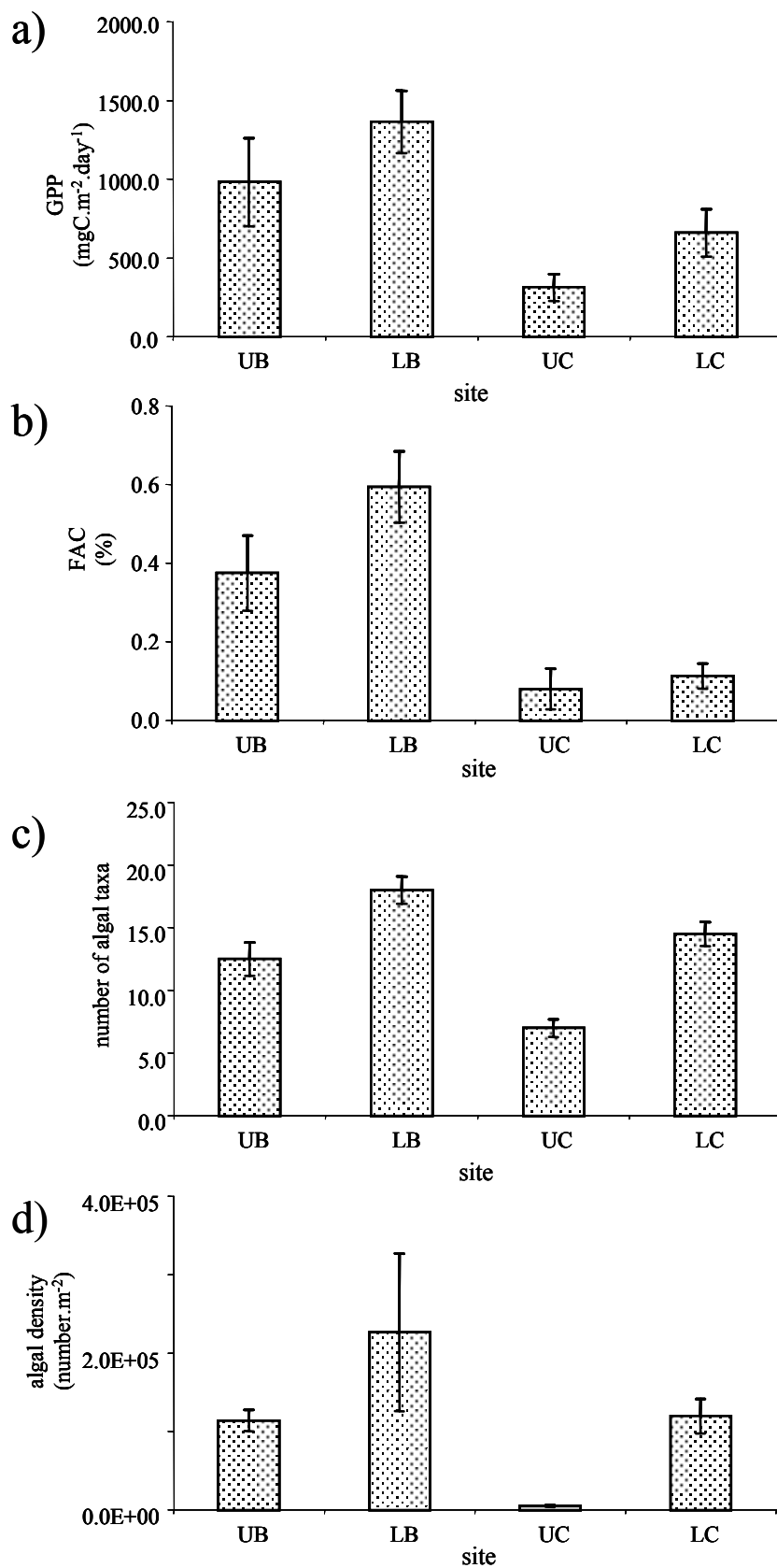
Figure 4.4 Means ± 1 S.E. of a) GPP, b) FAC, c) algal diversity and d) algal density of treatments at each site, n= 4 at each site.

Table 4.5 Results of randomised block ANOVA for algal variables: a) $\log_{10}(GPP+1)$, b) FAC, c) (algal genus richness $+0.5)^{\frac{1}{2}}$ and d) (total algal density$+0.5)^{\frac{1}{2}}$.

a)

Source		df	Mean Square	F	p
REACH	Hypothesis	3	0.326	21.985	0.000
	Error	10	$1.48*10^{-2}$		
SHADE	Hypothesis	1	0.535	36.106	0.000
	Error	10	$1.48*10^{-2}$		
NUTRIENT	Hypothesis	1	$2.50*10^{-7}$	0.000	0.997
	Error	10	$1.48*10^{-2}$		

b)

Source		df	Mean Square	F	p
REACH	Hypothesis	3	0.232	26.26	0.000
	Error	10	$8.85*10^{-3}$		
SHADE	Hypothesis	1	0.137	15.47	0.003
	Error	10	$8.85*10^{-3}$		
NUTRIENT	Hypothesis	1	$3.06*10^{-2}$	3.459	0.093
	Error	10	$8.85*10^{-3}$		

c)

Source		df	Mean Square	F	p
REACH	Hypothesis	3	1.75	17.49	0.000
	Error	10	0.100		
SHADE	Hypothesis	1	1.55	0.155	0.703
	Error	10	0.100		
NUTRIENT	Hypothesis	1	2.39	0.024	0.880
	Error	10	0.100		

d)

Source		df	Mean Square	F	p
REACH	Hypothesis	3	$9.08*10^{5}$	3.554	0.055
	Error	10	$2.55*10^{4}$		
SHADE	Hypothesis	1	$2.84*10^{2}$	0.011	0.918
	Error	10	$2.55*10^{4}$		
NUTRIENT	Hypothesis	1	$2.42*10^{2}$	0.095	0.765
	Error	10	$2.55*10^{4}$		
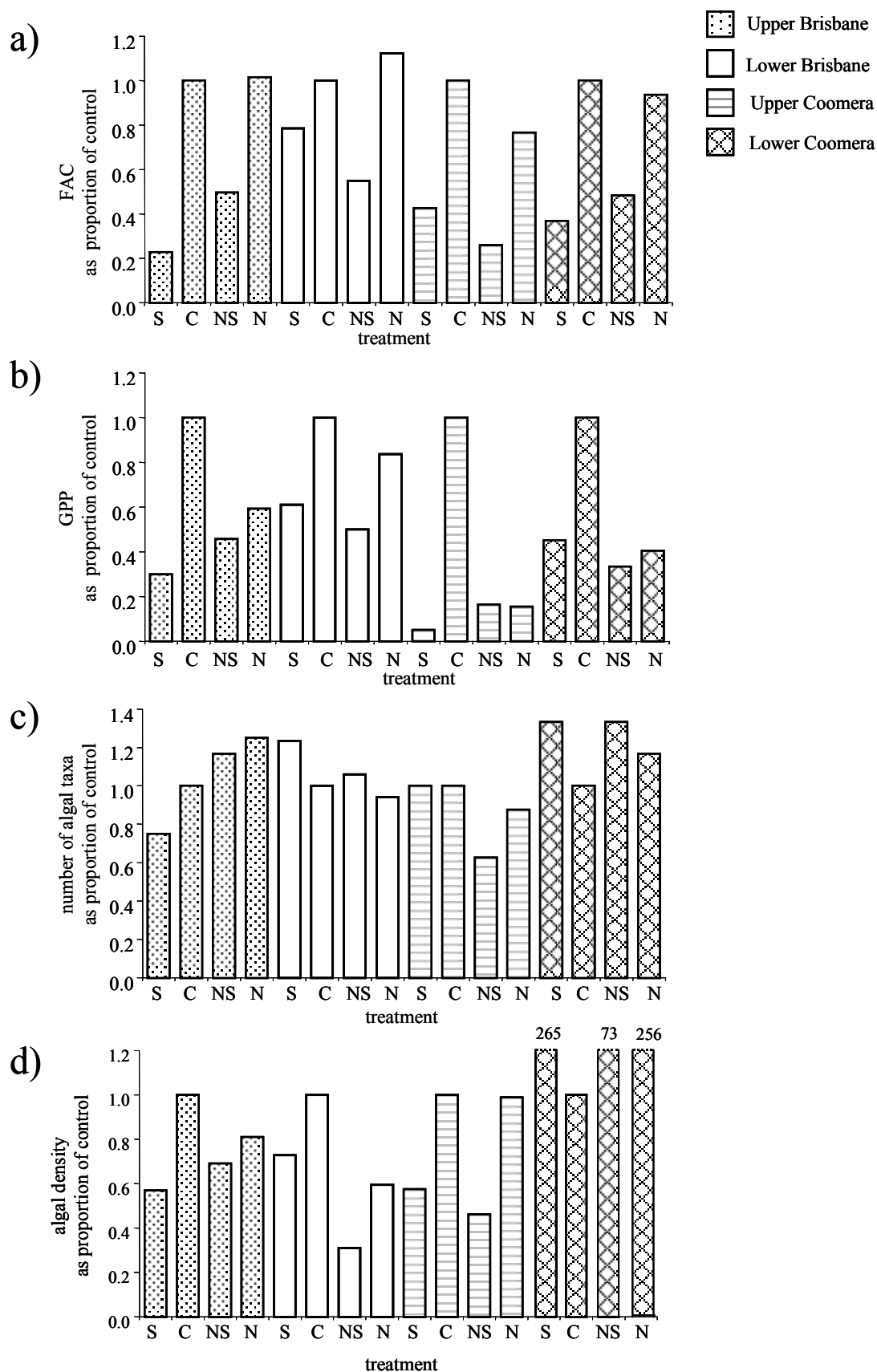
Figure 4.5 a) GPP, b) FAC, c) algal diversity and d) algal density as proportions of the control for each reach. C= Control, S= Shade, N= Nutrients.

4.3.2.1 Scalar diversity comparisons

For grazers, alpha, beta and gamma diversity were calculated between reaches, between treatments, and between cobbles.

The Kruskal-Wallis test indicated that α and γ varied with scale, while ß-1 and ß-2 did not (Table 4.7). ß-1 tended to be lower between reaches than at the smaller scales, and ß-2 tended to be lower between reaches than between cobbles in a treatment (Figure 4.6), but these differences were not significant.

4.3.3 Regression analysis

GPP displayed a strong, positively linear relationship with FAC (Figure 4.7a), while algal diversity was highest at moderate levels of GPP and FAC (Figure 4.7b,c).

Grazer diversity and density were highest at mid-range GPP (Figure 4.8 a, b), and grazer diversity was also highest at midrange FAC (Figure 4.9a). Mobile grazer density was also highest at mid-range GPP, but was lowest at a moderate cover of FAC (Figures 4.8d and 4.9d). Variance in sedentary grazer density was not explained by any significant regressions with either algal variable (Figures 4.8c and 4.9c).

Grazer diversity displayed a positive relationship with algal diversity, and mobile grazer density was highest at mid-range algal diversity (Figure 4.10a, d). Variance in the density of total and sedentary grazers was not explained significantly by any regression with algal diversity (Figure 4.10b, c). The ratio of mobile : sedentary grazers did not display any significant relationships apart from a weakly hump-shaped relationship with algal diversity (Figure 4.10e).

Table 4.6 Grazing taxa collected across all reaches. Definitions of sedentary and mobile are supplied in Chapter 3.

Order	Family	Species	Category
Coleoptera	Elmidae adult	Unidentified	not assigned
Coleoptera	Elmidae larvae	*Austrolimnius* sp.	not assigned
Coleoptera	Psephenidae larvae	*Sclerocyphon* larval form B	sedentary
Coleoptera	Psephenidae larvae	*Sclerocyphon striatus*	sedentary
Ephemeroptera	Baetidae	*Bungona* sp.	mobile
Ephemeroptera	Baetidae	*Cloeon* sp.*	mobile
Ephemeroptera	Leptophlebiidae	*Tillyardophlebia* sp. AV6	mobile
Ephemeroptera	Leptophlebiidae	*Koorrnonga* sp. AV2	mobile
Gastropoda	Ancylidae	*Ferrissia* sp.*	sedentary
Gastropoda	Hydrobiidae	Unidentified	sedentary
Gastropoda	Lymnaeidae	*Pseudosuccinea columnella*	sedentary
Gastropoda	Planorbidae	*Gyraulus* sp.	sedentary
Gastropoda	Thiaridae	*Thiara* sp.	sedentary
Lepidoptera	Pyralidae	Nymphulinae sp18	sedentary
Trichoptera	Helicopsychidae	*Helicopsyche cochleaetesta*	sedentary
Trichoptera	Helicopsychidae	*Helicopsyche* sp. (early instars)	sedentary

*grazers excluded from the analysis due to rarity

Table 4.7 Results of Kruskal-Wallis test for differences in alpha, beta and gamma attributes of grazer diversity with spatial scale (catchment, reach and treatment).

	α	ß-1	ß-2	γ
Chi-square	10.45	4.27	1.43	7.86
df	2	2	2	2
Asymptotic significance	0.005	0.118	0.488	0.020
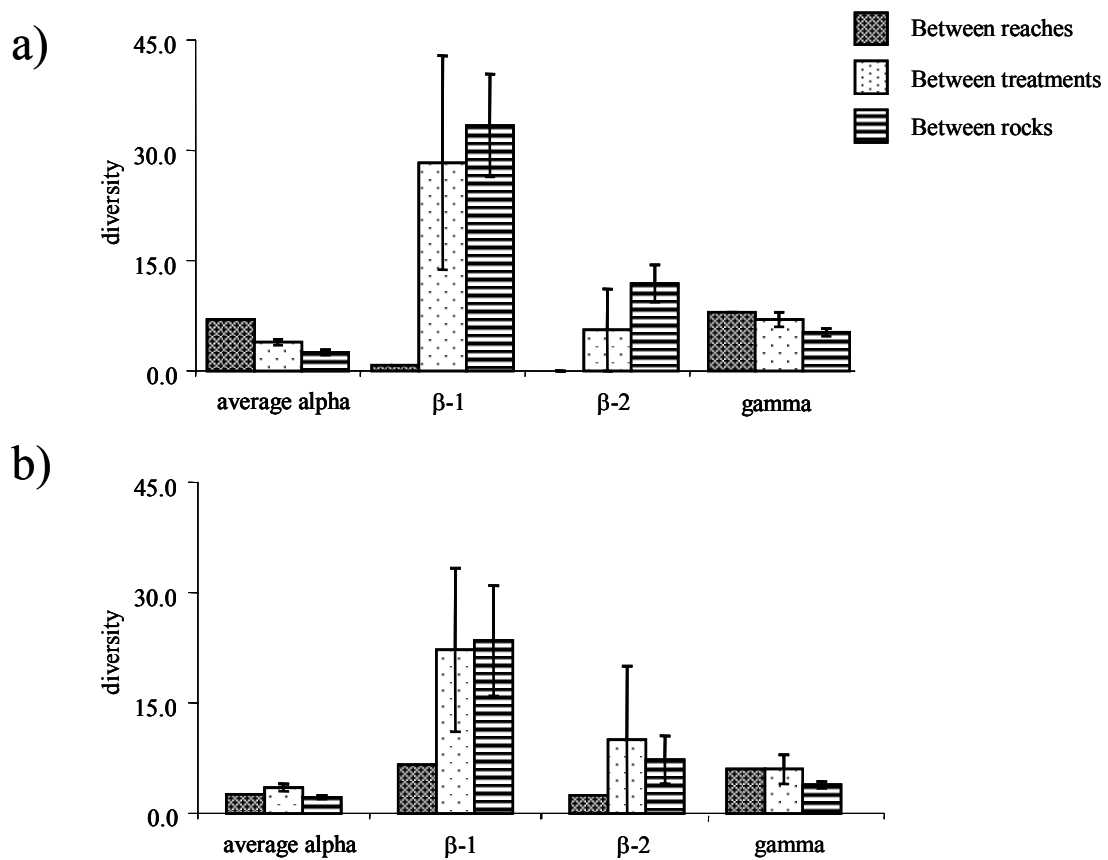
Figure 4.6 Grazer diversity measures for the reach, treatment and cobble scales, for the a) Brisbane and b) Coomera catchments. Mean ± 1 S.E. provided.
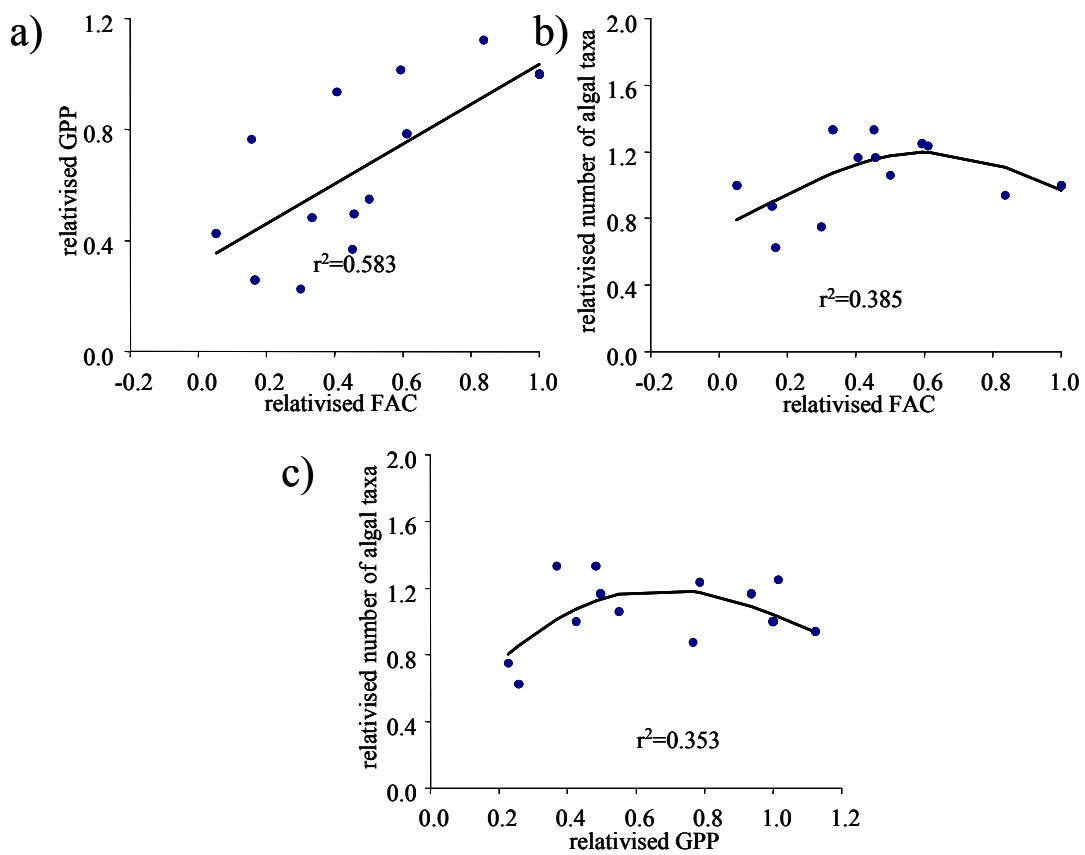
Figure 4.7 Treatment scale relationships of relativised algal variables: filamentous algal cover and a) gross primary production and b) algal diversity; and c) of gross primary production and algal diversity. Only significant regressions (p< 0.05) drawn, n =16, p< 0.001. Regression equations provided in Appendix I.
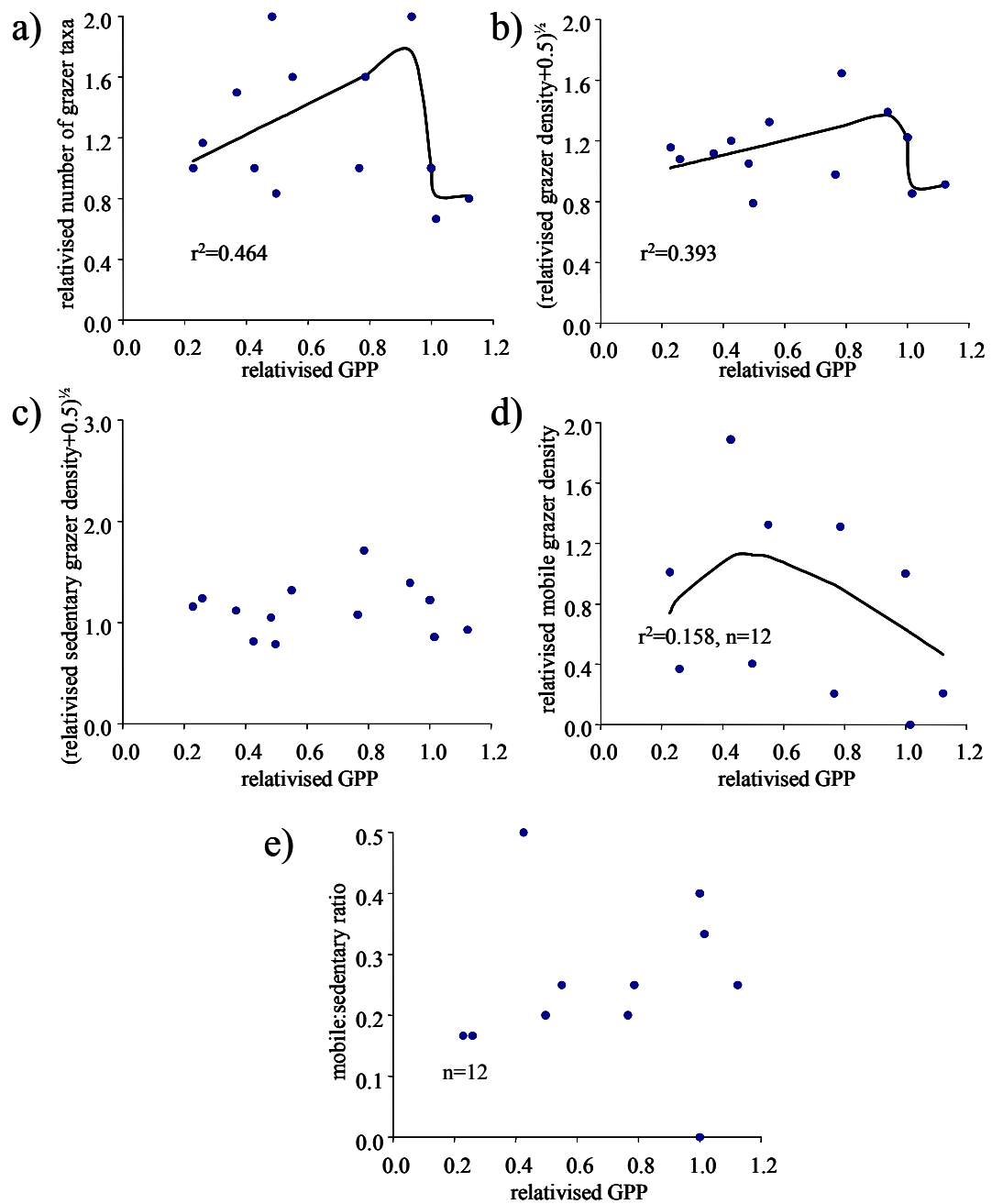
Figure 4.8 Relationships of grazer variables with gross primary production at the treatment scale. Only significant regressions (p< 0.05) drawn, n= 16 except where indicated, p< 0.001. Regression equations provided in Appendix I.
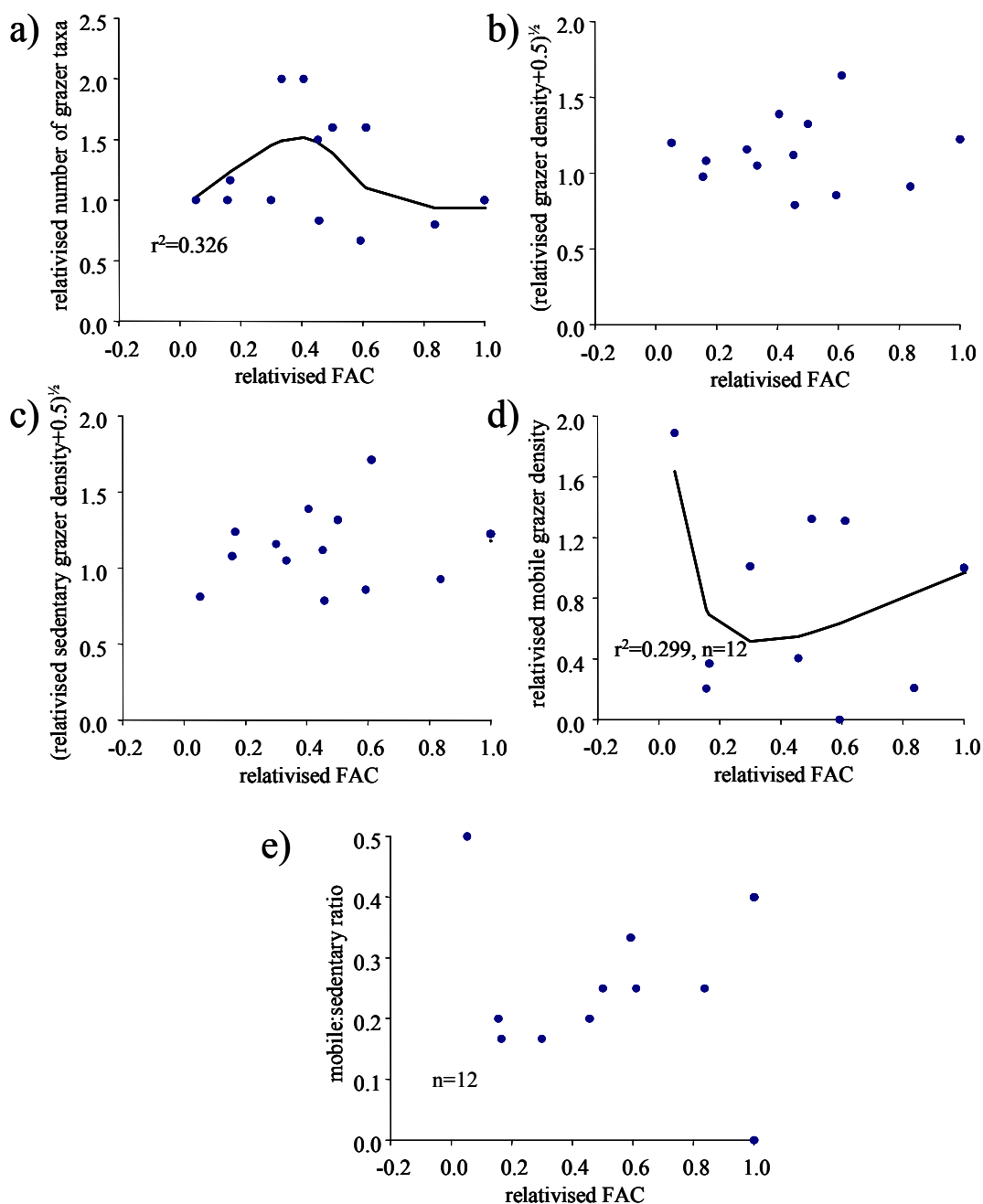
Figure 4.9 Relationships of grazer variables with filamentous algae at the treatment scale. Only significant regressions (p< 0.05) drawn, n= 16 except where indicated, p< 0.001. Regression equations provided in Appendix I.
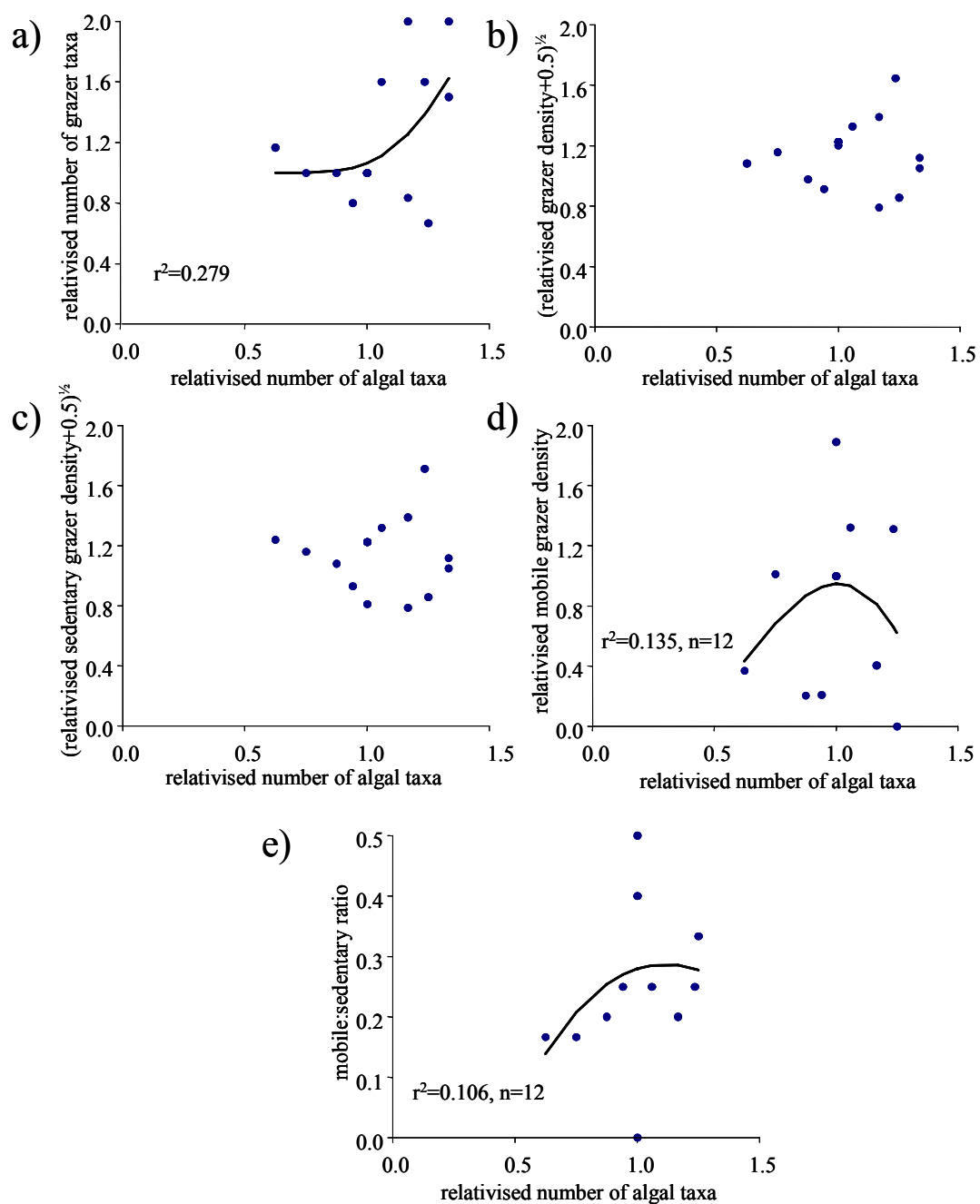
Figure 4.10 Relationships of grazer variables with algal diversity at the treatment scale. Only significant regressions (p< 0.05) drawn, n= 16 except where indicated, p< 0.001. Regression equations provided in Appendix I.
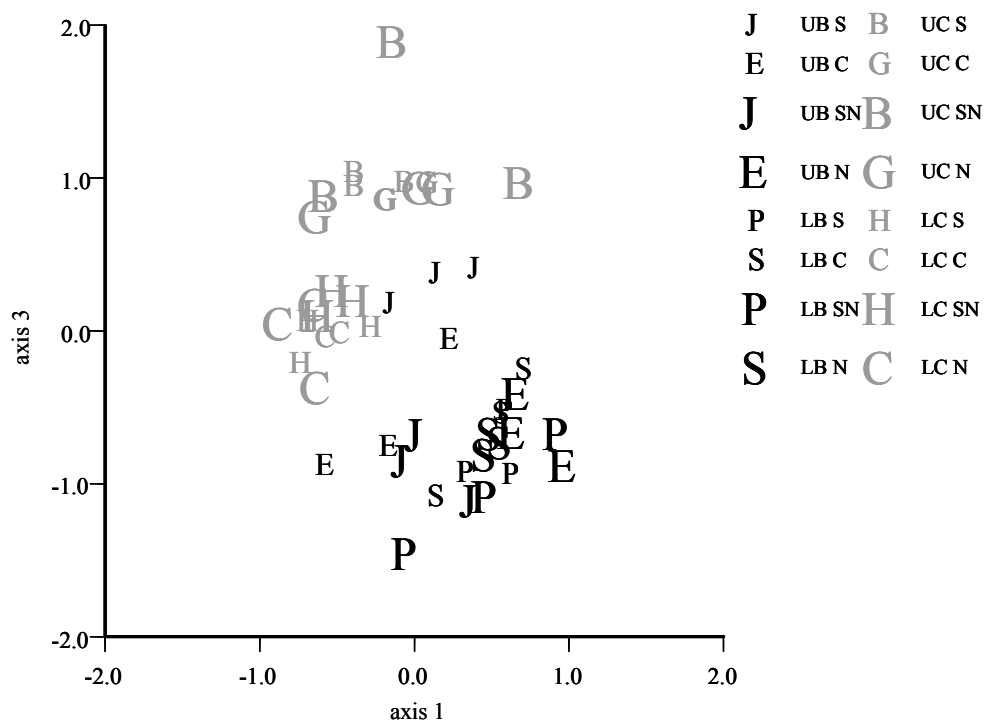
Figure 4.11 Rotated semi-strong hybrid (SSH) plot for algae on axes 1 vs. 3. Samples are labelled according to reach (U= Upper, B= Brisbane and C= Coomera) and treatment (S =shade addition, C= control, N= nutrient addition).

Figure 4.12 Rotated semi-strong hybrid (SSH) plot on axes 1 vs. 3 of samples. Samples are labelled according to FAC (shading) and GPP (size) at the reach on the day of sampling. PCC vectors of variables that correlated significantly with the ordination are superimposed onto the same axes.

4.3.4 Community composition

4.3.4.1 Algae

Ordination of algal genera data from the 48 samples required three dimensions to adequately describe the data (stress= 0.134). Clearest groupings were seen on axes 1 and 3. Samples grouped on the basis of both reach and catchment (Figure 4.11), and ANOSIM confirmed that these clusters were significant ($p < 0.001$ for both). In particular the Upper Coomera samples formed a distinct group distinct from the rest of the ordination. The two Brisbane reaches were much more similar than the two Coomera reaches. The samples did not cluster significantly with treatment across all reaches, but did significantly cluster with treatment within reaches ($p < 0.0001$).

Reaches with low levels of GPP ($0 - 709$ mg $C.m^{-2}.day^{-1}$) were high on axis 3, and those with higher levels of GPP ($710 - 1773$ mg $C.m^{-2}.day^{-1}$) were low on this axis (Figure 4.12). PCC analysis confirms that this gradient of GPP was statistically significant (Table 4.8). Samples from reaches with moderate to high filamentous algae ($> 40\%$) were low on axis 3 (Figure 4.12), and there was a significant gradient of FAC across the ordination (Table 4.8). Mobile grazer density again tended to be highest where FAC and GPP were low.

Twenty-nine algal genera correlated significantly with the ordination (Table 4.9). This included a range of filamentous greens, filamentous blue-greens and diatom taxa, as well as a few colonial genera. Filamentous greens tended to be present low on axis 2 (Figure 4.13), as did blue-greens (Figure 4.14). Mobile grazer density increased on a vector quite similar to that of *Rhoicosphenia,* and the next closest vector was that of *Cocconeis* (Figure 4.15). *Ulothrix, Epithemia* and *Anabaena* were present at reaches where mobile grazers were lowest.

Table 4.8 Maximum correlation coefficients in multidimensional space for environmental variables with ordination vectors derived from the algal assemblage. Significance levels for overall correlations were determined using a Monte-Carlo technique with 1000 randomisations. Only variables with significant correlations are listed, $p < 0.0001$.

variable	r
GPP	0.824
AFDM	0.762
chlorophyll *a*	0.748
FAC	0.747
average depth	0.607
mobile grazer density	0.542

Table 4.9 Maximum correlation coefficients in multidimensional space for algal genera with ordination vectors derived from the algal assemblage. Significance levels for overall correlations were determined using a Monte-Carlo technique with 1000 randomisations. Only variables with significant correlations are listed, $p < 0.001$ unless indicated.

Genus	r	Form
Rivularia	0.867	Filamentous blue-green
Hyalotheca	0.849	Filamentous green
Ulothrix	0.830	Filamentous green
Cocconeis	0.810	Diatom
Rhopalodia	0.799	Diatom
Schizothrix	0.754	Filamentous blue-green
Microspora	0.738	Filamentous green
Lygnbya	0.734	Filamentous blue-green
Cylindrocapsa	0.728	Filamentous green
Unidentified colonial genus 2	0.715	Colonial
Epithemia	0.713	Diatom
Unidentified filamentous genus 1	0.707	Filamentous green
Fragilaria	0.706	Diatom
Nitzschia	0.701	Diatom
Gomphonema	0.672	Diatom
Trachelomonas	0.667	Colonial
Achnanthes	0.632	Diatom
Synedra	0.620	Diatom
Phormidium	0.603	Filamentous blue-green
Zygnema	0.597	Filamentous green
Anabaena	0.588	Filamentous blue-green
Navicula	0.546	Diatom
Denticula	0.496	Diatom
Unidentified colonial genus 5	0.486*	Colonial
Rhoicosphenia	0.485*	Diatom
Dichothrix	0.461*	Filamentous blue-green
Groenbladia	0.460*	Filamentous green
Encyonema	0.401**	Diatom

* $p < 0.01$ ** $p < 0.025$

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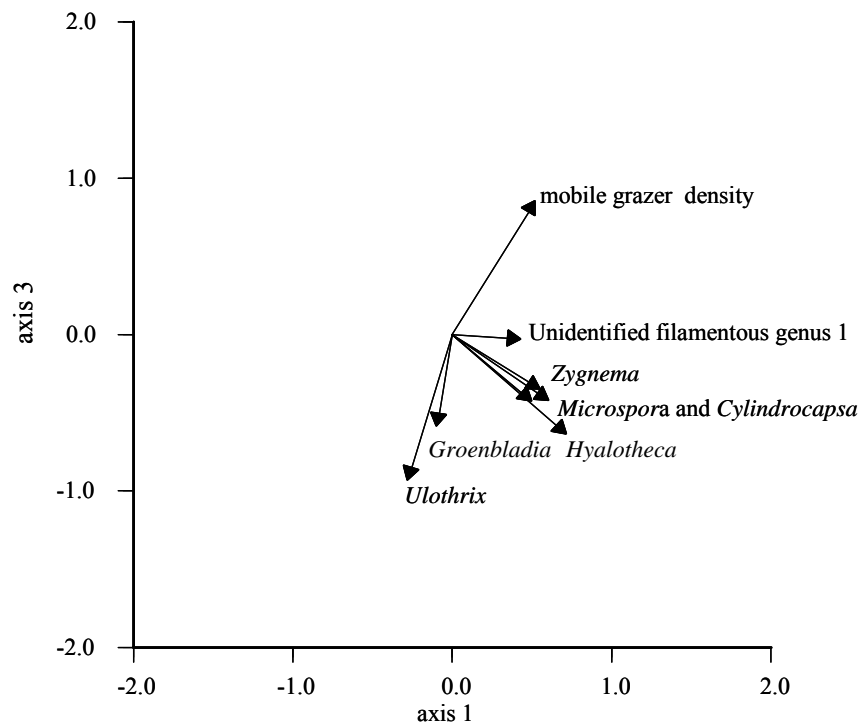
Figure 4.13 PCC vectors of filamentous green algal genera that contributed significantly to the ordination of the algal assemblage. Mobile grazer density vector is superimposed onto the same ordination space.
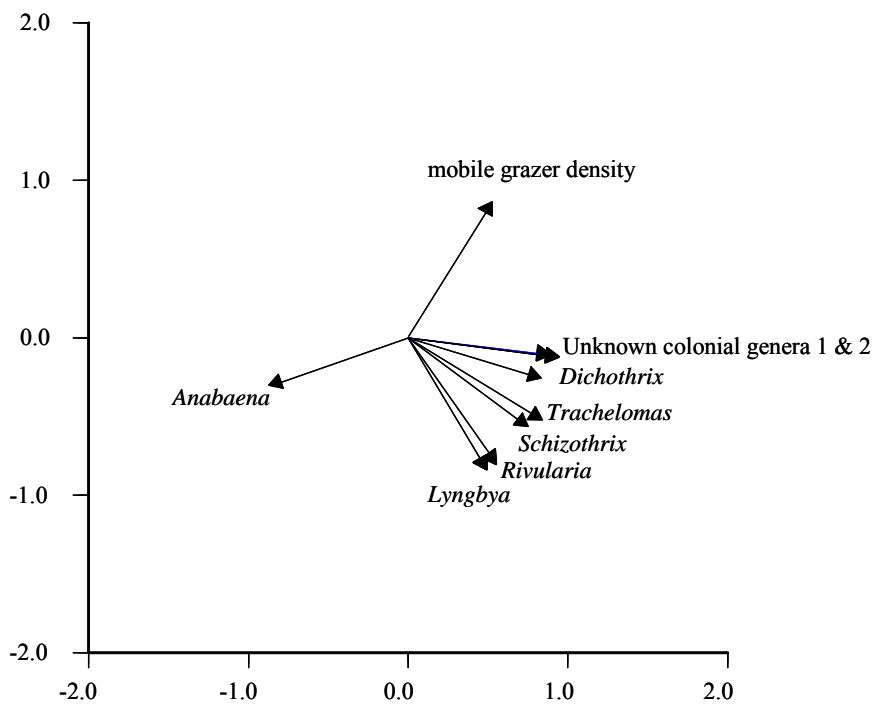
Figure 4.14 PCC vectors of blue-green algal genera that contributed significantly to the ordination of the algal assemblage. Mobile grazer density vector is superimposed onto the same ordination space.
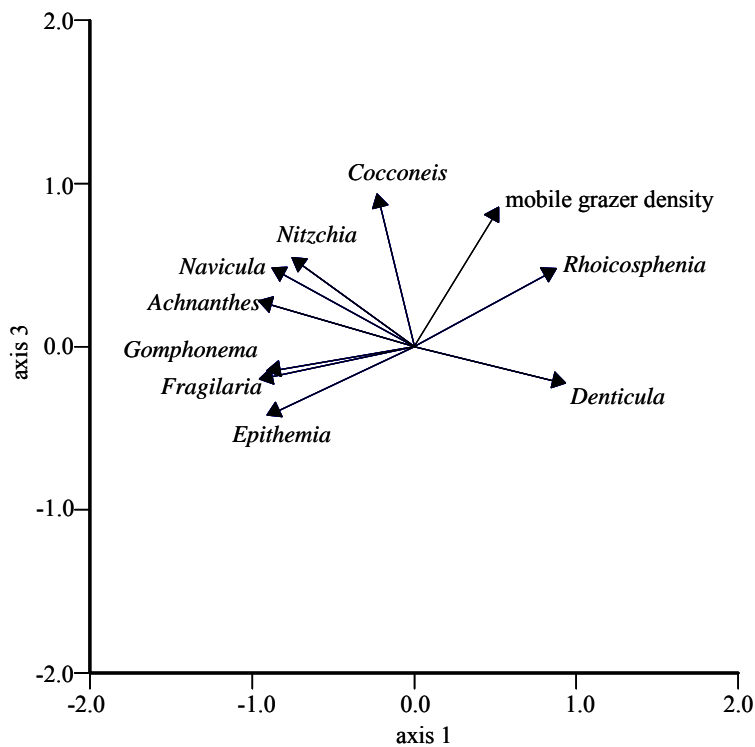
Figure 4.15 PCC vectors of diatom genera that contributed significantly to the ordination of the algal assemblage. Genera only shown if vectors are sufficiently long on these axes. Mobile grazer density vector is superimposed onto the same ordination space.
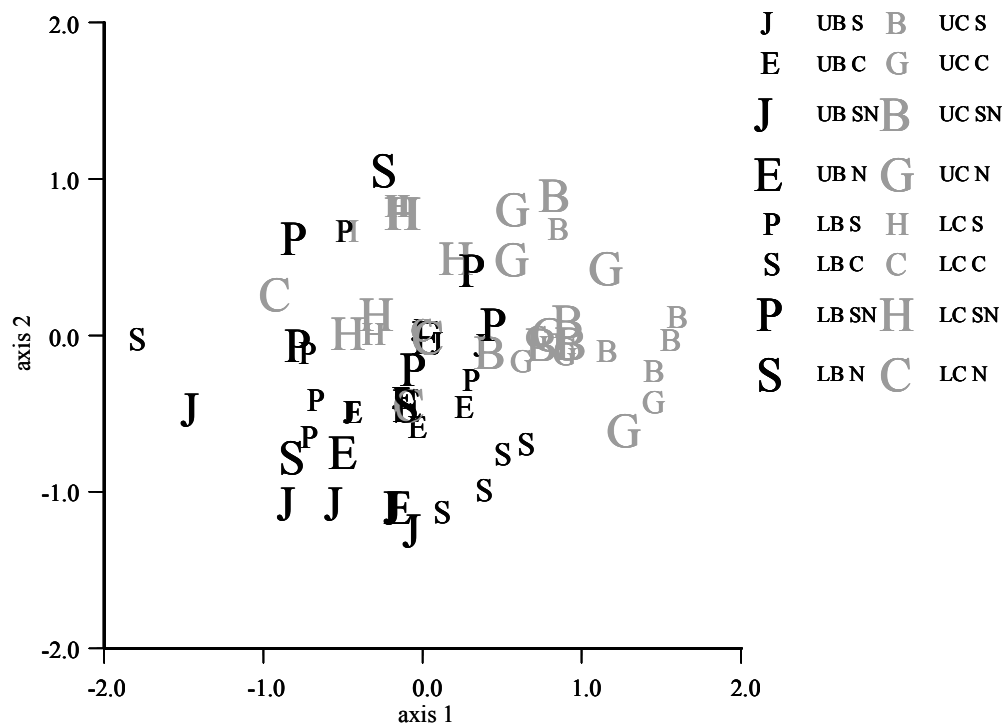
Figure 4.16 Rotated SSH plot for the grazer assemblage on axes 1 vs. 2. Samples labelled according to reach (U= Upper, B= Brisbane and C= Coomera) and treatment (S= shade addition, C= control, N= nutrient addition).
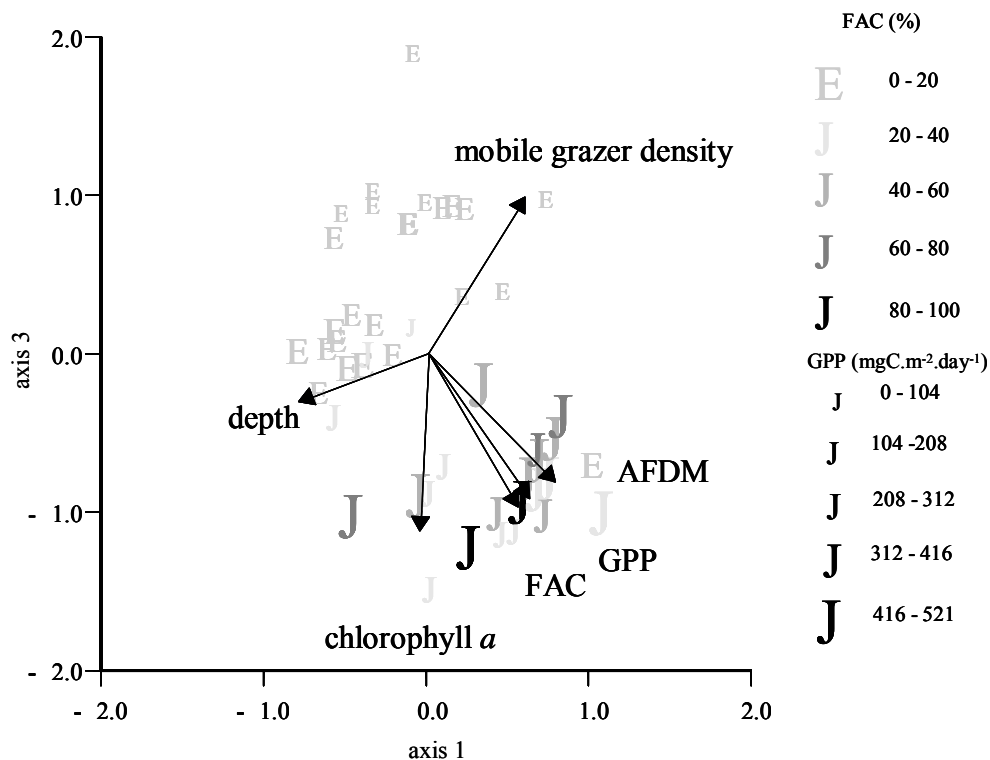
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4.3.4.2 Grazers

Ordination of invertebrate data from the 80 samples required three dimensions to adequately describe the data (stress= 0.164). Clearest groupings were seen on axes 1 and 2. Samples grouped on the basis of both reach and catchment (Figure 4.16), and ANOSIM confirmed that these clusters were significant (p< 0.0001 for both). The Coomera reaches grouped at the top of the ordination, with the Lower Brisbane samples forming the least distinct group.

Across all reaches, the samples clustered significantly with treatment (p< 0.012). Control reaches formed the tightest cluster in the bottom right hand corner of the ordination. Samples from shaded treatments tend to fall high on axis 2 and low on axis 1, and this was a significant grouping within the ordination (p< 0.006).
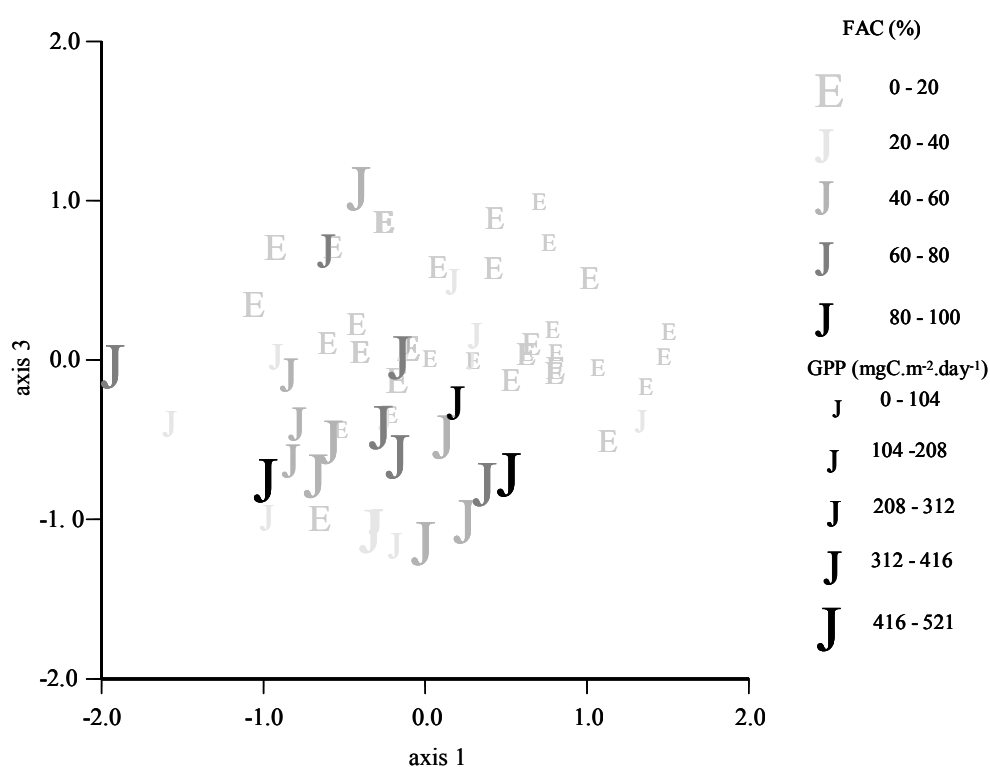
Figure 4.17 Rotated SSH plot on axes 1 vs. 2 of samples (derived from grazer assemblage). Samples are labelled according to cover of FAC (shading) and GPP (size) at the reach on the day of sampling.

Table 4.10 Maximum correlation coefficients in multidimensional space for environmental variables with ordination vectors derived from the grazer assemblage. Significance levels for overall correlations were determined using a Monte-Carlo technique with 1000 randomisations. Only variables with significant correlations are listed, p< 0.0001 unless indicated.

variable	R
algal genus richness	0.592*
AFDM	0.588
total algal density	0.582*
GPP	0.578
filamentous algal cover	0.572
chlorophyll *a*	0.540
depth	0.380**

*p< 0.005 **p< 0.01
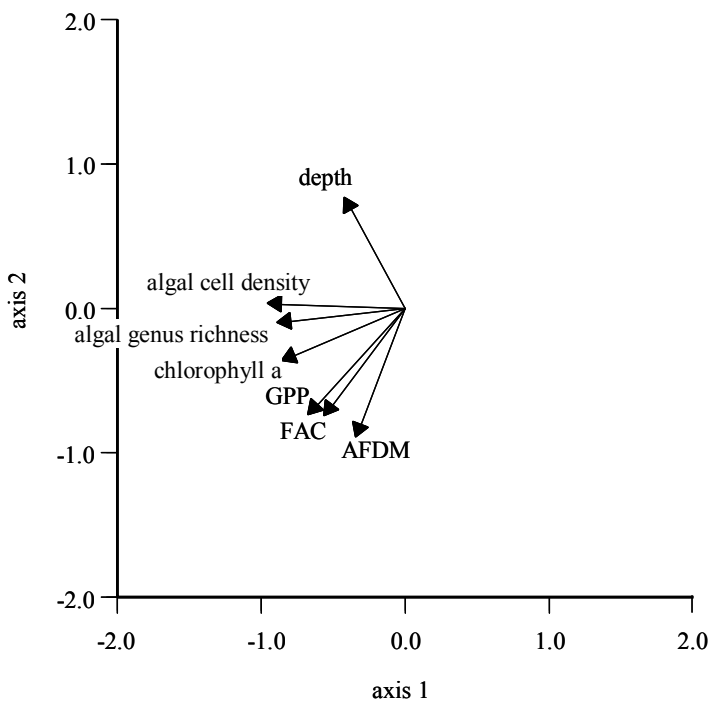
Figure 4.18 PCC vectors of environmental variables that correlated significantly with the ordination derived from the grazer assemblage.

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Treatments without nutrient addition tended to fall low on axis 2 and high on axis 1, but this was not a significant cluster (p< 0.186). Within reaches, samples clustered significantly with both treatments (p< 0.0001 for both), although there was no pattern in treatment arrangement that was similar between reaches.

GPP and FAC showed the strongest clustering at the reach scale. Reaches with low levels of GPP $(0 – 709 \text{ mg C.m}^{-2}.\text{day}^{-1})$ were arranged high on axes 1 and 2 (corresponding largely with Upper Coomera reaches), and those with higher levels of GPP $(710 – 1773 \text{ mg C.m}^{-2}.\text{day}^{-1})$ were arranged low on these axes (Figure 4.17). PCC analysis confirmed that this gradient of GPP was significant (Table 4.10). There was no clear grouping of samples from cobbles with high FAC, although samples with low FAC tended to form a large cluster at the top of the ordination (corresponding closely with Coomera reaches). There was a significant gradient of FAC across the ordination (Table 4.10). Of these variables, chlorophyll *a*, GPP and AFDM were highest at a very similar part of the ordination (low on axes 1 and 2), as were the density and richness of the algal community (low on axis 1; Figure 4.16).

Eleven grazer taxa correlated significantly with the ordination (Table 4.11). Mobile taxa generally occurred high on axis 1, while those of sedentary taxa almost all occurred lower on this axis (Figure 4.19), with snails in particular occurring when the algal variables were also at a maximum (Figures 4.18, 4.19).

Table 4.11 Maximum correlation coefficients in multidimensional space for grazer genera with ordination vectors derived from the grazer assemblage. Significance levels for overall correlations were determined using a Monte-Carlo technique with 1000 randomisations. Only variables with significant correlations are listed, $p < 0.0001$ unless indicated.

Taxon	R
Bungona sp.	0.834
Nymphulinae sp. AV 18	0.703
Thiara sp.	0.657
Unidentified Hydrobiidae	0.655
Sclerocyphon minimus	0.651
Sclerocyphon striatus	0.635
Koorrnonga sp.	0.617
Gyraulus sp.	0.503
Pseudosuccinea columnella	0.443*
Tillyardophlebia sp.	0.354**
Unidentified Baetidae	0.338**

* $p < 0.005$ ** $p < 0.025$
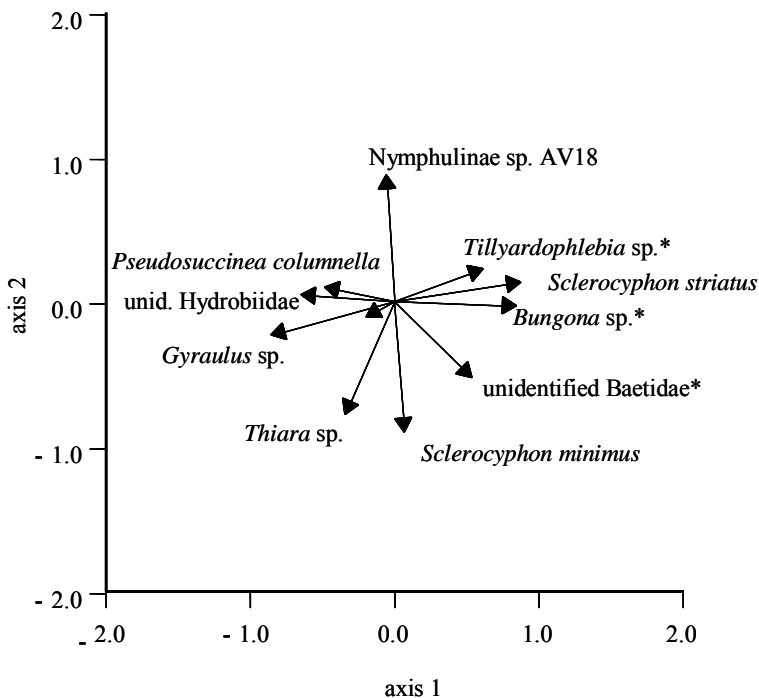
Figure 4.19 PCC vectors of grazer taxa that contributed significantly to the ordination derived from the grazer assemblage. Mobile grazers are indicated with *; sedentary grazers are unmarked.

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4.4 Discussion

4.4.1 Algal responses to treatments

The experimental manipulation of patches did not produce a clear separation between primary productivity (GPP) and filamentous algal cover (FAC). Graphs of the means of algal variables in each treatment, along with the ordination of algal taxa, indicated that treatments did not have consistent effects on algal composition and production, and had no effect on algal diversity. However, the experiment did increase the variability of these parameters, allowing an examination of their relationships with grazer diversity and composition.

Shading did have an effect on GPP (causing a significant reduction), but nutrient addition did not have any effect, even in unshaded treatments or in the Upper Coomera reach that had the lowest level of ambient nutrients. The Redfield ratio at this site was 3.5: 1, suggesting that nitrogen should be limiting. The nitrogen level of this reach was 0.060 ± 0.021 mg.L^{-1}, which is below the threshold of 0.10 mg.L^{-1} reported by Lohman (1991) for enrichment to enhance production, and is close to the threshold of 0.055 mg.L^{-1} proposed by Grimm and Fisher (1986). These factors suggest that GPP should have responded to nutrient enrichment.

Filamentous algal cover responded similarly to GPP, with shading causing a dramatic reduction in cover. This accords with most of the literature (but see Chessman *et al.* 1992, Mosisch *et al.* 1999), although an effect of enrichment might have been expected in unshaded treatments, particularly in the Upper Coomera where nutrients were at very low levels. However, at this reach filamentous algal taxa were very rare; there was only one occurrence of a filamentous chlorophyte in of all the 48 samples taken. There may

not have been sufficient opportunity for algal species from higher productivity sites to disperse into the treatments or for species to adapt to the new productivity conditions (Mittelbach *et al.* 2001). This may have particularly been the case in the headwaters of a catchment, downstream of pristine conditions where filamentous taxa would be rare. In a comparable experiment, using agar pots, enrichment by nitrogen and phosphorus did not cause an increase in filamentous algal growth in other tributary streams of the eastern Upper Brisbane (Mosisch *et al.* 1999).

ANOVA results also indicated that generally, treatment-scale variation in algal and grazer variables was not as great as that at the reach scale. Beyond this, scalar analysis suggested that (as in Chapter 3) the treatment level diversity of grazers was constrained by reach level diversity, with greater gamma diversity and lower turnover at the reach scale. Ordinations showed that a similar pattern for the composition of algal and grazer communities, with a nested effect of reach composition constraining treatment composition, which in turn constrains cobble composition (cf. predictions of Caley & Schluter 1997).

Within each site, the experimental manipulation did provide greater variation in GPP and FAC at the treatment scale than would occur in an unaltered system. By keeping values of all variables at each treatment relative to the control (the ambient level of a value), it was possible to look at grazer relationships with these algal variables at the treatment, or patch, scale.

4.4.2 Grazer relationships

Grazer diversity displayed a hump-shaped relationship with GPP and FAC at the treatment or patch scale. This is in accord with only about 20–25% of within-community studies of animals (Waide *et al.* 1999, Mittelbach *et al.* 2001). It is,

however, commonly found where the productivity: diversity relationship has been studied in aquatic systems (Dodson *et al.* 2000, Mittelbach *et al.* 2001). Such unimodal relationships may be best understood by looking at the increase and decrease phases of the hump.

One explanation for the increase phase of the hump is that increased productivity raised the abundance of rare species, reducing their extinction rates (Abrams 1995). At the treatment scale, grazer density had a strong positively linear relationship with grazer diversity (r^2= 0.301, p< 0.001; see Appendix I), and peaked at the same moderate level of primary productivity. While the rarest taxa were excluded from the data set for each treatment, it is possible that high abundances associated with high productivity at a reach allowed them to become sufficiently common to be counted in the dataset for that treatment (Dean & Connell 1987a, b).

Another explanation is that increased productivity increased the abundance of rare resources or combinations of resources and conditions that were required by specialist species (Schoener 1974, Abrams 1995, cf. Haddad *et al.* 2001). For example, algal diversity had a strong, positive relationship with grazer diversity at this scale, and peaked at the same levels of productivity. Plant diversity has been shown to relate to herbivore diversity in terrestrial systems (e.g. Siemann *et al.* 1998, Knops *et al.* 1999, Haddad *et al.* 2001).

The resources that may have increased with algal diversity could have been food- and/or habitat complexity-related. A greater diversity of algal species across a patch may have increased the range of food types and therefore the number of grazer taxa. Grazers exhibit differences in modes of feeding, behavioural adaptations, consumptive abilities and mouthpart morphology (see Gregory 1983, Lamberti & Moore 1984), and these

may lead to various 'preferences' for particular algal taxa (cf. Jacoby 1987, Peterson 1987, Hill & Knight 1987, 1988a, Blinn *et al.* 1989, McCormick & Stevenson 1989, Karouna & Fuller 1992, Wellnitz & Ward 1998).

A greater diversity of algae may also have maximised the structural heterogeneity and/or complexity at the treatment scale. A greater diversity of algal species across a treatment or patch occurred where filamentous algal cover was moderate. It is possible that maximum habitat heterogeneity was reached at this moderate level of FAC, where the cover of individual cobbles was most variable. Lower heterogeneity may have been found at either high or low levels of cover, where cobbles were either all covered, or devoid of filamentous taxa. Habitat heterogeneity has been shown to be related to invertebrate diversity at this scale (e.g. Brown 2003) and at the microhabitat scale (e.g. O'Connor 1991, McKenny 1995, Robson & Barmuta 1998, Downes *et al.* 1998, 2000a & b).

Alternatively, filamentous algal cover may explain the decrease phase of the algal productivity: grazer diversity hump. Filamentous algal cover may have reduced the variety of food resources by out-competing other algal taxa and reducing algal diversity (see review by Hill 1996). This is supported by the low algal diversity at high levels of FAC. If it did reduce the number of total algal species in this way, the number of preferred algal food species would probably therefore also be reduced, and thus there may be fewer grazer taxa supported by such algal communities (cf. Siemann *et al.* 1998).

However, not all grazers responded to algal variables at this scale. A relevant example is provided by sedentary taxa, which displayed no strong relationships with any algal variables at this scale. This supports initial predictions about this group (see 4.1), which

were based on the lack of ability of sedentary grazers to swim or voluntarily enter the drift and thus to disperse rapidly at the scale of patches. Notably, at the reach scale, ordination of grazer taxa showed that sedentary grazer taxa (particularly snails) were more abundant where GPP, FAC and algal diversity were high (see also Chapter 3). However, the time provided for colonisation was at least fifty-six days, which may be considered long enough for sedentary grazers to move distances of 10^1-10^2 m. Addicott *et al.* (1987) discuss the importance of understanding heterogeneity in relation to the target organism. The perception of heterogeneity by organisms can be is discussed in terms of grain or extent (Kotliar & Wiens 1990). "Grain" is the smallest scale at which an organism responds to patch structure by differentiating between patches. "Extent" is the largest scale of heterogeneity to which an organism responds, and this upper limit is determined by the home range of the individual. It is possible that the patch scale of heterogeneity is not one that is perceived by sedentary species at the larval stage, as it is at or close to their "extent" of perception, while cobble scale heterogeneity is more relevant to their grain of perception. The responses of sedentary grazers to reach scale heterogeneity (seen in Chapter 3 and the ordinations of this chapter) are likely to be due to winged adults, which will have larger home ranges than the sedentary larvae (10^3-10^4 m compared to 10^2 m).

Mobile grazers, on the other hand, showed some relationships with algal variables at the treatment scale. The density of these grazers was highest at moderate levels of GPP and algal diversity, and displayed a u-shaped (inverse 'hump') relationship with filamentous algal cover. It is interesting that the relationship is different with FAC, given the strong, positively linear relationship of FAC with GPP. However, the r^2 values for both relationships are low, suggesting that the grazers also do not display strong responses at this scale.

Broadly, these relationships are somewhat similar to those indicated by the ordination, which provides a more reach-scale perspective. Mobile grazers tended to be higher at reaches with low to moderate levels of GPP and algal diversity. In addition, they tended to be higher at reaches with low abundance of filamentous algal taxa and with moderate to high abundance of the diatoms *Cocconeis* and *Rhoicosphenia*. At this scale these distribution patterns may be due to the oviposition choices of winged adults, although larval mayflies have often been shown to track smaller-scale periphyton distributions (e.g. Kohler 1984, Richards & Minshall 1988, see also Chapter 5), and are readily able to enter the drift to move larger distances (Mackay 1992).

Also notable is that the ratio of mobile to sedentary grazers showed no strong relationships at the treatment scale, indicating that density changes in mobile grazers were not also mirrored by diversity changes.

4.4.3 Conclusions

A different suite of relationships between grazer and algal variables was found at the treatment scale from those found at the reach and catchment scales in Chapter 3 (Table 4.12).

At the scale of patches, grazer diversity displayed a clearly hump-shaped relationship with GPP. This is similar to the trend shown at the cobble scale, but different to the linearly positive relationship displayed by grazer diversity with GPP at the reach scale (Chapter 3). Grazer diversity displayed different relationships with filamentous algae at all three scales.

Table 4.12 Relationships of GPP and FAC with grazer variables at reach, patch (treatment) and cobble scales from this chapter and Chapter 3. Shape of relationships are indicated using L= linear, H= hump-shaped and direction indicated with + (positive) and – (negative).

Independent variable	Dependent variable	Reach scale	Patch scale	Cobble scale
Grazer diversity	GPP	L +	H +	ns (H +)
	FAC	L +	H +	L -
Grazer density	GPP	H -	H +	ns (H+)
	FAC			L -
Sedentary grazer density	GPP	H -		ns (H+)
	FAC	L +		L –
Mobile grazer density	GPP	L +	H +	ns (H+)
	FAC		H -	ns (H+)
Mobile : sedentary ratio	GPP	L -		
	FAC	L -		

Sedentary grazer density was not related to algal variables at this spatial scale. This differed to the significant relationships shown at the reach and cobble scales (which were opposite in direction; Chapter 3). Mobile grazer density was, however, related to algal variables, with similar relationships with GPP as at the cobble scale (hump-shaped). No relationships to algal variables were shown for the ratio of mobile to sedentary grazers, as was also the case at the cobble scale.

5 - Diet and habitat choice of mobile and sedentary grazers

5.1 Introduction

Fine scale patchiness in periphyton abundance is known to structure the micro-distribution of grazers in streams. Examples include the mayfly *Baetis* (Kohler 1984, Richards & Minshall 1988, Álvarez & Peckarsky 2005), the caddisflies *Helicopsyche borealis* (Lamberti & Resh 1983, Vaughn 1986) and *Dicosmoecus gilvipes* (Hart 1981), and the chironomid *Paratanytarsus dubius* (Gresens & Lowe 1994). While the debate on whether herbivores exhibit true selection for algal taxa remains unresolved (see reviews by Gregory 1983, Steinman 1996), the active selection of particular forms, or taxa, of plants by freshwater herbivores has been observed in a number of studies. For example, some snails are attracted to or repelled from plants depending on their nutritional status (Sterry *et al.* 1983, Brönmark 1985) or their taxonomic identity (Lodge 1986). In addition, the chironomid *Paratanytarsus dubius* has been shown to prefer grazing on patches of diatoms rather than on those comprising the filamentous green alga *Stigeoclonium* (Gresens & Lowe 1994).

Whether true selectivity occurs, it is clear that grazers are better able to graze some algal taxa according to the form and size of the alga and the degree of its adherence to the biofilm, as well as to their feeding mode and the morphology of their mouthparts (e.g. Sumner & McIntire 1982, Hill & Knight 1988a, McCormick & Stevenson 1988, Blinn *et al.* 1992, Karouna & Fuller 1992, Wellnitz & Ward 1998). Those grazers with brushing mouthparts (e.g. *Ameletus, Epeorus* and *Ecdonyurus* mayflies; all 'mobile' grazers as defined by Chapter 3) may be more able to ingest large, high-profile, loosely attached diatom taxa (e.g. *Cymbella* and *Gomphonema*) compared with small,

adnate, adherent forms such as *Achnanthes* and *Cocconeis* (Karouna & Fuller 1992, Wellnitz & Ward 1998). Grazers that feed with scraping mouthparts, such as the caddisfly *Neophylax* and the limpet *Ferrissia* (both 'sedentary' grazers), are able to consume adnate diatoms (Hill & Knight 1988, Blinn *et al.* 1989), and Blinn *et al.* (1989) suggested that the low shell of *Ferrissia fragilis* may push aside upright and stalked diatoms so that they are not consumed.

Some grazers are able to eat filamentous macroalgae, particularly when it is in the early stages of establishment (e.g. Brown 1961, Dudley *et al.* 1986, Feminella & Resh 1991, Hill *et al.* 1992, Sarnelle *et al.* 1993). In addition, some grazers (e.g. *Baetis*, *Agapetus*) are able to consume epiphytes that grow on macroalgae, including diatom taxa such as *Gomphonema*, *Rhoicosphenia* and *Epithemia* (Dudley 1992).

Not all algal material consumed by grazers is necessarily absorbed and assimilated. For example, Petersen (1987) found that 42% of diatoms eliminated in caddisfly (*Neophylax fuscus*) faeces were still viable. Later work by Petersen *et al.* (1998) found that mayflies (*Ameletus* sp.) may digest diatoms more efficiently than caddisflies (*Ecclisomyia* sp.). In addition, *Ecclisomyia* appeared to digest some diatoms more efficiently than others.

Stable isotope analysis is one means of examining the food actually assimilated by macroinvertebrates. The analysis of $\delta^{13}C$ and $\delta^{15}N$, along with C: N ratios, was used to separate invertebrate grazers and shredders in an upland Swiss stream (Zah *et al.* 2001). The $\delta^{13}C$ signatures of many grazers suggested that the diet of these species was dominated by the filamentous gold alga *Hydrurus foetidus*. Stable isotope analysis can be used successfully to investigate macroinvertebrate diets whenever there are site-specific differences in the isotopic compositions of potential food sources (Doucett *et al.* 1996).

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As well as feeding behaviours and preferences shaping invertebrate responses to the heterogeneity of algal composition, other aspects of the microhabitat that are influenced by algal composition may be important to invertebrates. The long strands of established communities of filamentous algae can provide flow and predation refugia (Dodds & Biggs 2002, Warfe & Barmuta 2004), and increased surface area for the colonisation of epiphytic food species (Dudley *et al.* 1986). The algae may also compete for space with grazers and their preferred food species, and cause mechanical interference with invertebrate movement and feeding (Dudley *et al.* 1986).

In streams of this study, earlier work suggested that mobile grazers tended to be most dense on cobbles with a moderate cover of filamentous algae, while the density of sedentary grazers was inversely related to the degree of filamentous algal cover (Chapter 3). At the reach scale there was a compositional shift in the grazer community that occurred in places where filamentous algae dominated algal composition and where benthic productivity was high. Mobile grazers occurred at lower densities, while sedentary grazers were relatively more abundant in such locations (Chapters 3 and 4). It is possible that these changes were due to preferences for particular algal taxa as food. Mobile grazers were most densely populous where algal taxa such as *Rhoicosphenia* and *Cocconeis* were abundant (Chapter 4).

The primary goal of this chapter is to identify whether grazing invertebrates do respond to particular features of the algal communities in streams. In order to answer this question, an experiment was conducted in the laboratory in late 2002. However, due to a severe drought in South-east Queensland streams during this time, abundances of animals of suitable species were greatly reduced, and replication was low. This experiment was therefore used as a preliminary investigation only, and was followed by a field experiment in October 2004.

The chapter firstly investigates whether mobile and sedentary grazers prefer an epilithon layer dominated by diatoms or a community dominated by filamentous algae, at the cobble scale. Secondly, it examines what grazers consume on cobbles in order to understand more about the exact reasons for their choices of feeding sites. Thirdly, it investigates which of these food sources is actually assimilated.

The following questions are addressed:

1. Do sedentary grazers and mobile grazers actively select cobbles with particular algal communities?

2. What types of algae do sedentary grazers and mobile grazers eat, and do both grazer sub-guilds eat it in the same proportions?

3. What food sources are actually assimilated by grazers?

4. If selection of cobbles with particular algal communities is observed (1), is this likely to be a result of food or habitat preference?

5.2 Methods

5.2.1 Laboratory experiment

5.2.1.1 Experimental setup

Grazers

Two common grazers were selected for this study, *Helicopsyche murrumba* and Baetid genus 2 sp. MV3. These species were selected to provide typical responses of their mobility group (sedentary or mobile, as defined in this thesis) and because they were two of the few species sufficiently abundant in the study areas at this time of drought (October 2002). Baetids, representing the mobile grazer group, could not be retrieved

from the experimental substrates in large enough numbers, and were discarded from the analysis. The sedentary grazer, *Helicopsyche murrumba*, is a common insect in streams of South-East Queensland. Larvae construct a distinctive helical case of sand particles. The ballast provided by their mineral cases limits the ability of *Helicopsyche* sp. to drift in the water column (e.g. Mackay 1992). Larvae feed using their mandibles and forelegs to scrape adherent algal cells from cobble surfaces (Resh & Rosenberg 1984).

Experimental animals were collected on Thursday 12th December 2002 from a long 'run' habitat of the Brisbane River at Burton's Bridge (27° 30′ 7″ E, 152° 41′ 24″ N), about 30 km downstream of the Wivenhoe Dam. Two 10 metre kick samples were conducted for collection and in addition over 20 cobbles were also thoroughly washed into nets at the site. The number of individuals that could be collected as replicates was still low (see below).

After collection, animals were brought, under cool, stable conditions, to the laboratory where they were acclimated to experimental conditions for 24 hours before the start of the experiments. For acclimation, animals were placed in perspex trays in aerated river water, with a small algal-covered cobble for food and shelter. A constant temperature was maintained that was similar to local stream temperature (19 °C), and a light: dark regime of 14: 10 hours approximated the natural regime. Food sources were removed from trays to starve the animals for 24 hours before the experiment began. Experimental animals were chosen to be as uniform in size as possible.

5.2.1.2 Experimental substrates

Two types of algal food were offered during the experiment: filamentous turf and diatom film. Natural stream stones, with both types of food, were taken from the same reach of the Brisbane River as the animals, and maintained in experimental trays for five days before the experiment began. Cobbles were chosen carefully to be of similar size and to have as uniform growth of algae as possible. These cobbles were then buried in fine aquarium gravel to provide a flat surface of a similar area (124 ± 7 cm^2). Four cobbles (two of each type of algae) were collected at the same time to provide an ungrazed algal substrate for determination of composition and biomass.

5.2.1.3 Post-experiment processing

Experimental trays contained a representative of both algal community types, with cobbles about two centimetres apart within the gravel to allow the grazers ease of movement between them. Three replicates (trays) were used for each species.

At the start of the experiment, animals were supplied to the trays at the approximate densities in which they occurred in the correlative survey (Chapter 3), with four caddisflies per replicate. Animals were handled carefully with broad, flat-ended forceps to minimise injury. Individuals were added, one at a time, to the water between the two cobbles. Trays were aerated throughout the experiment.

Animals were left undisturbed to feed for six hours. Care was taken with the position of the observer to prevent shadows from falling on the animals during the experiment (previously observed to cause animals to fall from cobbles into surrounding substrates). Notes were made of the location of each animal in relation to experimental substrates.

At the end of the experiment, all animals were removed from each tray into separate perspex containers, and the head capsule width of each animal was measured. Guts were then immediately removed from live animals under magnification (as per Cowan & Peckarsky 1990) and placed in 1% Lugol's solution. Experimental and ungrazed cobbles were removed into white perspex trays and the surfaces that had been exposed were scrubbed lightly with a toothbrush and then more vigorously with a wire brush to remove adherent algae. The resultant slurry was made up to a known volume (600–900 mL) and thoroughly shaken, and a standard aliquot was taken and stored in 1% Lugol's solution for later determination of composition.

The composition of the gut content samples was measured as described in Lodge (1986). Two drops of suspension (120 μL) were placed on a microscope slide, covered with a 22 x 22 mm coverslip, and examined at 250 times magnification. Items in the guts of invertebrate larvae are difficult to identify to species level, so algae were grouped by their morphology. Particles were thus classified into one of six groups: organic detritus, inorganic detritus, diatoms, unicellular greens, cyanobacteria and filamentous algae. The proportion of particles from each of the groups was estimated from their percentage cover in each field of view. Five random fields of view were examined for each sample.

Due to the dilute nature of the samples of algae from experimental substrates, a slightly different technique was employed to determine composition. Two drops of suspension were placed on a microscope slide, covered with a 22 x 22 mm coverslip, and examined at 250 times magnification. Five transects were taken across the coverslip, recording number of times each particle type occurred. This was carried out for three separate aliquots from each sample. The average size for each particle type was calculated (using

an ocular graticule) and this was used with the abundance data to generate a final proportion of each particle type.

While the two methods of calculation were slightly different for cobble and gut samples, both methods provided an assessment of the same parameter: the proportion of each type of particles in a sample.

5.2.1.4 Data analysis

The first aim of the experiment was to examine whether the animals actively selected cobbles with particular algal communities. The number of replicates (n= 3) ruled out the possibility of using ANOVA. Instead, the nonparametric Mann-Whitney test was employed within SPSS 10.0 (1999) to test the null hypothesis that helicopsychids were found in equal quantities on both type of experimental substrate within each tray. The test produces a value (U) that is significant below the critical value for the desired α. A significant U means the rejection of the null hypothesis. Variances were examined for heterogeneity to meet the assumptions of this test (Quinn & Keough 2002).

Due to the low grazer densities and short time frame of the experiment, it was expected that the grazed cobbles would not significantly change in algal community structure and therefore would remain a valid comparison against gut content samples. This assumption was tested using Mann-Whitney's U, with the test being how many times the proportion of the algal group of interest (for example, cyanobacteria) on the grazed cobbles exceeded the proportion on ungrazed cobbles.

In order to examine whether helicopsychids grazed algal forms in the same proportions as which they occurred, the proportions of diatoms, cyanobacteria and filamentous algae were compared between grazed cobbles of each type (diatom film and filamentous algae) and gut contents. Due to uneven variances and numbers of samples, a Mann-

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Whitney test was employed. This tested the number of times the proportion of the algal group of interest in the cobble samples exceeded the proportion of the algal group in the gut samples.

5.2.2 Field experiment

A field experiment was set up in October 2004, with two treatments: *algae* and *time*. *Algae* had two levels, *filamentous* and *diatom*, and time had two levels, *10 days* (colonisation) and *3 days*. The experiment was originally designed with *site* as a third, random factor, with filamentous cobbles placed at Kilcoy Creek as well as diatom-dominated cobbles placed at Mary River at Conondale (Figure 5.1). However, a bushfire occurred in the headwaters of Kilcoy Creek at day -2 and large amounts of carbonaceous material and ash were deposited as silt over the experimental habitat, smothering algae. *Site* was therefore abandoned as a treatment and the cobbles placed at Kilcoy Creek were not sampled. The original design explains the length of the colonisation time allowed for macroinvertebrates, as ten days was chosen as the longest possible interval in filamentous algae that could be certain to remain viable in the high shade conditions of Kilcoy Creek (from previous observations). In addition, it was judged a short enough length of time for filamentous algae not to become abundant on diatom treatment cobbles. The timing proved fortuitous, as it meant that sampling occurred before a high rainfall event two days later, marking the arrival of the wet season and causing a spate in the Mary River.

5.2.2.1 Experimental methods

At Day -10, eight transects were set up across Kilcoy Creek at random points along a 20 metre stretch (points assigned using a random number table). Starting downstream, one cobble was randomly selected from each transect. All invertebrates were picked or
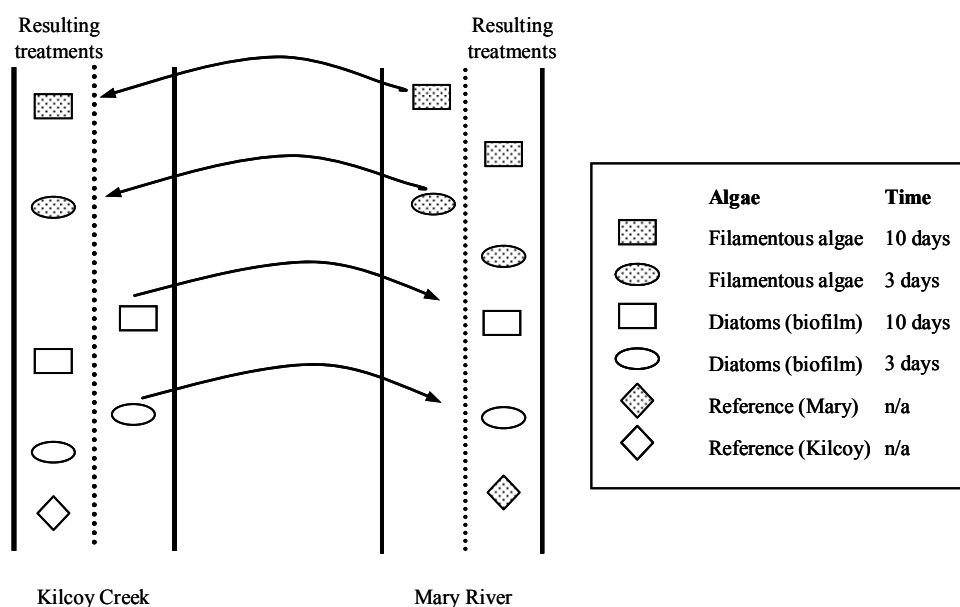
Figure 5.1 Original design of field experiment, where the levels of *site*= 2. Arrows indicate translocation of treatments (from random sampling throughout reach). Final design was the same but without Kilcoy Creek; for each treatment n= 8.

rinsed off each cobble using forceps and water, taking care to cause minimal disturbance to algae. A corner of each cobble was dried using paper towel and marked with coloured zinc cream. Each cobble was placed in a small bucket of stream water for transport to the Mary River site.

This procedure was repeated at the Mary River at Conondale. A different coloured zinc cream was used to mark all cobbles, and these were then replaced at the same grid points with their locations recorded. At the same time, all cobbles collected from Kilcoy Creek were placed randomly on the grid in the Mary River (according to a random number table) and the location of each cobble recorded. The procedure was also repeated on Day -3 at each site. Two different colours were used to distinguish between those taken from each site and on which day.

On the final day, all marked cobbles were collected from downstream to upstream. A further eight cobbles were selected as reference cobbles using a random number table and pre-existing transects. Each cobble was lifted into a 250 μm dip net, scooping all stirred material to minimise loss of fauna. All invertebrates were picked off the cobble using forceps and placed in ethanol. The cobble was then rinsed and scrubbed of remaining algae and this residue was put through a 250 μm sieve; the contents retained on the sieve were preserved in ethanol. In the laboratory all macroinvertebrates were identified to the lowest taxonomic definition possible, generally to species. The grazer guild was again separated into sedentary and mobile taxa (see 3.2.3.3). Invertebrates were sampled from the Mary River site a second time, in early February 2005, to further clarify their dietary preferences.

5.2.2.2 Collection of primary sources and consumers

Major primary sources of organic carbon (terrestrial and aquatic) were collected from both sites at the start of the experiment (Day -10). Separate samples of filamentous algae and biofilm were scraped from the surface of cobbles with razor blades, stored in zip lock bags, then frozen. Leaf packs and other benthic detritus were collected by hand and wet-sieved into fine (250 μm – 2 mm) and coarse (>2 mm) particulate organic matter fractions. Macrophytes were collected by hand, stored in zip lock bags and frozen. Grazers were collected by selecting cobbles and removing targeted taxa with forceps. Individuals from the same taxonomic groups were put in zip lock bags, placed on ice then frozen on return to the laboratory (on the same day).

Algae, CPOM and FPOM samples in the lab were rinsed with distilled water, and dried in the oven for 24- 48 hours before being ground to a powder-like consistency using a ring grinder.

Invertebrate taxa were identified to lowest possible taxonomic level. Guts and their contents were removed to prevent contamination from non-assimilated sources, and gastropod shells were removed to prevent possible contamination from non--dietary carbohydrates. Invertebrates were then cleaned with distilled water and dried in the oven for 24- 48 hours. Individuals of the same taxa from the same site were grouped together to maximise the sample size and weight. Where possible, three replicates of sources and consumers were prepared. Due to naturally very low abundances (see elsewhere, e.g. Chapter 2), generally only sufficient animals were available for one replicate. For example, one baetid sample required up to 30 animals. However, samples consisted of pools of individuals from several cobbles right across the reach, in order to maximise the likelihood that a sample represents the population. All dried samples were then ground to a powder-like consistency using a mortar and pestle. Sampling was repeated at the Mary River at Conondale site in early February 2005 during a period of stable flow in order to further clarify dietary preferences.

5.2.2.3 Stable isotope analysis

Dried, ground samples were oxidised at high temperature and the resultant CO_2 and N_2 were analysed for percentage carbon (C), nitrogen (N) and the stable isotope ratios $^{13}C/^{12}C$ and $^{15}N/^{14}N$ using an elemental analyser (Eurovector 3000) and mass spectrometer (Micromass Isoprime).

Ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ were expressed as the relative per million (‰) difference between the sample and conventional standards (PDB carbonate and air N_2) where:

$$\delta X\ (‰) = (R_{sample}/R_{standard} - 1)*1000$$

where $X = {}^{13}C$ or ^{15}N and $R = {}^{13}C/^{12}C$ or $^{15}N/^{14}N$.

5.2.2.4 Gut contents

Individual grazers were dissected in ethanol in a small glass dish, with the entire gut extracted from the animal using fine forceps. The contents were placed on a microscope slide with a 22 x 22 mm coverslip. The composition of the gut content samples was measured as described above (5.1.2), with particles classified into one of six groups and the proportion of particles from each of the groups estimated from their percentage cover in each field of view. Between four and six random fields of view were examined for each sample. Organic detritus in this study always consisted of fine, particulate matter that could not be further distinguished, and material that was clearly of terrestrial origin was not seen in the guts of any grazer examined.

5.2.2.5 Data analysis

ANOVA

Power analysis

Data from chapter 3 on abundances of key grazer species (*Bungona* sp., *Austrophlebioides* sp. 11, *Helicopsyche cochleatesta*) in similar stream sites to the ones used in this chapter (Cedar Creek as a similar site to the Mary at Conondale, and Kilcoy Creek as the shaded site) were used to provide estimates of variance between and within treatments. These estimates were used in the software designed by Russel Lenth (http://www.stat.uiowa.edu/~rlenth/Power/). Effect size was determined as the average difference between abundances for key grazer species (*Bungona* sp., *Austrophlebioides* sp. 11, *Helicopsyche cochleatesta*) on filamentous cobbles (at the Cedar Creek site) and on diatom cobbles (at Kilcoy Creek), and ranged from 1.5 to 4. The most conservative sample to power curve is provided below (Figure 5.2). The number of replicates was chosen as eight. This gave a minimum estimate of power of about 0.5, and allowed the

sampling to be conducted within a day rather than over more than one day (which would allow some replicates longer colonisation time, and could affect abundances). In addition, the sizes of the experimental reaches were such that sampling more cobbles would have meant a very high proportion of available cobbles would have been sampled.
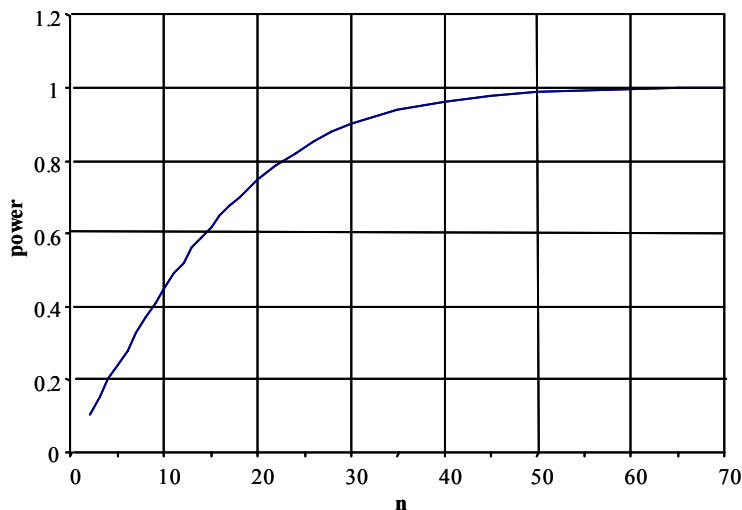
Figure 5.2 N vs power curve for an effect size of 4 (for *Bungona* sp.).

Design

Total abundance, sedentary abundance and mobile abundance were calculated (groupings as described in 3.2.3.3). The three species with sufficient abundance data to analyse individually were *Centroptilum* sp. (Ephemeroptera: Baetidae), Nymphulinae sp. 18 (Lepidoptera: Pyralidae), and *Thiara* sp. (Gastropoda: Thiaridae).

The experiment was designed so that algal treatment was a fixed effect with two levels (diatom cover and filamentous cover), and time was a fixed effect with two levels (three days and ten days colonisation). A fixed-effects (model 1) ANOVA was used to test for the effects of treatment (SPSS 10.05, 1999) on the abundances of the three species.

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Transformations

Total, sedentary and mobile abundance all required a square root transformation ($x^{\frac{1}{2}}$) to improve skew, kurtosis and heterogeneity of variance. Nymphulinae sp. 18 abundance required a fourth root transformation ($x^{\frac{1}{4}}$) to correct for left-hand skew and leptokurtosis and to improve homogeneity of variance. *Centroptilum* sp. and *Thiara* sp. abundances required a square root transformation ($x^{\frac{1}{2}}$) to correct less extreme leptokurtosis and skew, and heterogeneity of variance. Cell mean plots and residual plots were examined to detect any interactions that may have occurred (Quinn & Keough 2002).

Gut content analysis

Between treatments

Only *Thiara* sp. and Nymphulinae sp. 18 were sufficiently abundant on experimental substrates to compare gut contents between treatments. Of the Psephenidae and Baetidae collected, 65% were too small to dissect, and 7% had empty digestive tracts.

For each grazer, ANOVA could not be used to compare the proportions of algal types consumed between treatments for each group, due to the unequal number of replicates in each group, so the non-parametric Kruskal-Wallis test was used (within SPSS 10.0 1999; Quinn and Keough 2002). The test is described in 4.2.4.3. Variances within each group were examined and variables were transformed to improve homogeneity of variance where required (Quinn and Keough 2002). For *Thiara*, diatom proportions were transformed by arcsin($x^{\frac{1}{2}}$). For Nymphulinae sp. 18, the same transformation was used for filamentous proportions, while diatom proportions did not require transformation.

Between grazers

In February 2005, along with *Thiara* sp. and Nymphulinae sp.18, the baetids *Centroptilum* sp. were sufficiently abundant to test the null hypothesis that each species

ate the same proportion of algal groups. In both October and February, there was an unequal number of replicates in each group, so ANOVA could not be used. Instead, the nonparametric Mann-Whitney (October data) and Kruskal-Wallis (February data) tests were conducted using SPSS 10.0 (1999). In order to meet the assumptions of variance heterogeneity (Quinn & Keough 2002), diatom proportion was transformed using $\arcsin(x^{\frac{1}{2}})$ for the October data, and the same transformation was used for both diatom and filamentous algal proportions for February.

Stable isotope analysis

Linear regression was conducted using SPSS 10.05 (1999) to investigate the relationship between the isotope ratios (both $\delta^{13}C$ and $\delta^{15}N$) of grazers and biofilm, and of grazers and filamentous algae from all sites and times combined. If grazers are selectively feeding on and assimilating biofilm rather than filamentous algae, it could be expected that the observed spatial variation in grazer isotope ratios would be explained by variation in biofilm $\delta^{13}C$ and $\delta^{15}N$ signatures. Slopes of relationships would be expected to be similar to 1.

5.3 Results

5.3.1 Laboratory experiment

Typical diatoms on cobbles included species of *Cocconeis, Cymbella, Gomphonema, Rhoicosphenia, Tabularia* and small numbers of *Amphora, Aulocoseira* and *Cyclotella.* Cyanobacteria included species of *Heteroleibleinia* (previously classified within the *Lyngbya* genus) and small amounts of *Spirulina.* Filamentous greens were almost entirely represented by *Spirogyra* and *Cladophora.*

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The proportion of filamentous chlorophytes was higher on cobbles selected for filamentous algae, as were the proportions of both diatoms and cyanobacteria (Figure 5.3). Many epiphytic diatoms, particularly *Rhoicosphenia,* were observed in these samples, either attached or semi-detached and tangled in filaments. Organic detritus was in lower proportions than on cobbles selected for diatoms, as was the group comprised of unicellular greens.
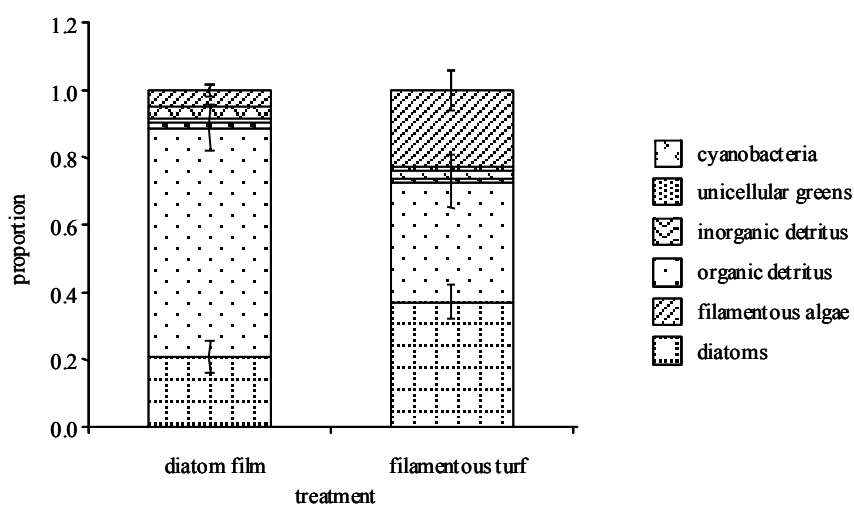
Figure 5.3 Proportion of algal samples represented by each 'particle' type, for cobbles covered with diatom film and for cobbles covered by filamentous turf used in the laboratory feeding experiment.

Proportions of algal species did not vary significantly between grazed and ungrazed cobbles (Table 5.1). Grazed cobbles therefore can be used to compare algal proportions between available communities (on cobbles) and what was eaten (gut contents).

5.3.1.1 Grazer cobble choice

Helicopsychid individuals all chose one cobble within the first half hour and remained there throughout the experiment (Table 5.2). All larvae were retrieved at the end of the

experiment. Although there was an apparent majority of animals on diatom-covered cobbles, this difference was not significant (U= 0.5, p= 0.077).

Table 5.1 Mann-Whitney U of comparisons of proportions of algal groups for grazed (each n= 6) and ungrazed cobbles (each n= 2) used for laboratory feeding experiment.

Comparison	Diatoms	Cyano-bacteria	Filamentous algae
Diatom grazed vs. diatom ungrazed	4.0	4.5	5.5
Filamentous grazed vs. filamentous ungrazed	1.0	3.0	4.0

* p = 0.046

Table 5.2 Locations of all *Helicopsyche murrumba* retrieved from experimental trays, at the time of removal.

Tray	Number added	Number on or near diatom cobble	Number on or near filamentous algal cobble
1	4	4	0
2	4	3	1
3	4	2	2

5.3.1.2 Gut contents

Helicopsyche murrumba consumed more organic detritus than anything else (Figure 5.4). The minimum proportion for all variables was 0%, except for organic detritus which was 15%. Maximum proportions of diatoms and organic detritus were over 85%, and the highest proportions of both cyanobacteria and unicellular greens were around 36%. Inorganic detritus was always less than 10%. No filamentous algae were found in any of the guts.

Data for cyanobacteria were transformed as $\log_{10}(x+1)$ to correct for heterogeneity of variance (Quinn & Keough 2002). Filamentous algal proportions were significantly lower in helicopsychid gut contents compared with both cobble types (Table 5.3). Diatom proportions were lower in the gut contents compared to their representation on cobbles with filamentous algae.

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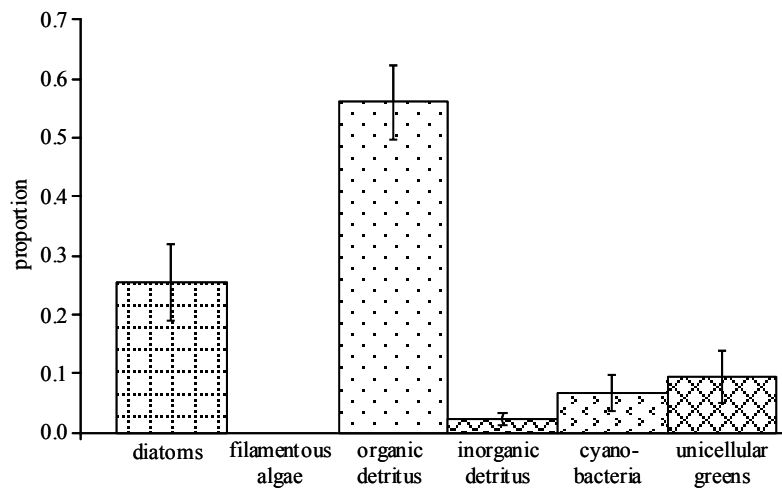
Figure 5.4 Proportion of matter in guts of *Helicopsyche murrumba* represented by each 'particle' type.

Table 5.3 Mann-Whitney U of comparisons of proportions of algal groups for cobbles and gut contents. Letters indicate whether proportions were higher on cobbles (R) or in gut contents (G), for significant comparisons only.

Comparison	Diatoms	Cyanobacteria	Filamentous algae
Diatom cobbles vs helicopsychid guts	35	34	12*(R)
Filamentous cobbles vs helicopsychid guts	11*(R)	29	0*(R)

* p<0.05

5.3.2 Field experiment

Filamentous algae at the Mary River consisted largely of chlorophytes such as *Stigeoclonium* with some *Cladophora* and tangled filaments of *Hyalotheca* also present. *Gomphonema, Rhoicosphenia* and *Synedra* were common epiphytes, and other common diatoms at this site included *Epithemia, Fragilaria, Nitzchia* and *Tabularia*. Diatoms on cobbles from Kilcoy Creek included *Achnanthes, Gomphonema, Navicula, Nitzchia, Tabularia,* and *Encyonema,* and filamentous algae at this site was dominated by the rhodophyte *Batrachospermum.* The most abundant grazers were thiarid snails and larval pyralids, baetids, and psephenids (see Table 5.4).

Table 5.4 Most abundant grazers sampled at Mary River at Conondale.

Order	Family	Taxon	% of total grazer abundance
Gastropoda	Thiaridae	*Thiara* sp.	58
Lepidoptera	Nymphulinae	Nymphulinae sp. 18	16
Ephemeroptera	Baetidae	*Centroptilum* sp.	8.2
Coleoptera	Psephenidae	*Sclerocyphon* sp.	6.0

Abundances were even lower than in previous years, with one reference cobble only yielding one grazer, and with the highest number of grazers on a cobble being ten (Figure 5.5). Species richness ranged from one to three.
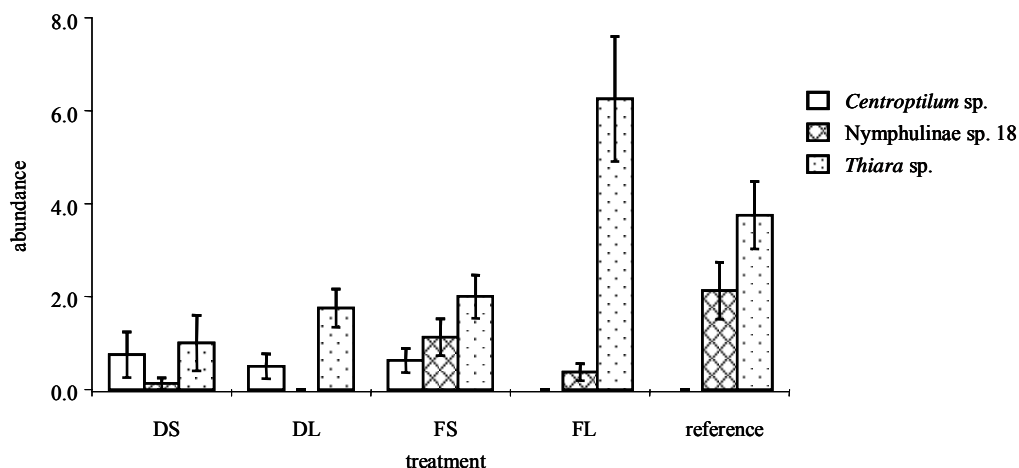
Figure 5.5 Abundances of dominant grazer species on each treatment. DS = Diatom, 3 days; FS = Filamentous, 3 days; DL = Diatom, 10 days; FL = Filamentous, 10 days. Mean ± 1 S.E. provided, for each treatment, n = 8.

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5.3.2.1 ANOVA

Total grazer abundances were significantly higher on filamentous algal substrates (Figure 5.6, Table 5.5a), and mobile grazer abundances were significantly lower (Figure 5.6, Table 5.5c). Neither varied significantly over time. However, sedentary grazer abundances were significantly higher on filamentous algal substrates, and also significantly higher after ten days colonization (Figure 5.6, Table 5.5b).

Centroptilum sp. was more abundant on diatom cobbles (Table 5.6a, Figure 5.5), while Nymphulinae sp.18 was more abundant on filamentous cobbles (Table 5.6b, Figure 5.5). The time that treatments were in place for colonisation had no effect on either species. In contrast, *Thiara* sp. was more common on filamentous algae cobbles (Table 5.6c, Figure 5.5), and more common on cobbles that had been colonised for ten days. No interaction terms were significant for any of the three species.

5.3.2.2 Gut analysis

Thiara sp. was found on all treatments and consumed almost no filamentous algae (Figure 5.7). Nymphulinae sp. 18 individuals were found only on reference and filamentous treatments but not on diatom treatments. They consumed a noticeable amount of filamentous algae (Figure 5.7). For both species, there were no significant differences in the dominant algal groups consumed between the treatments (Table 5.7).

In October and February, there were significant differences in the proportions of both filamentous algae and diatoms consumed by each grazer species (Table 5.8, Figure 5.8). Nymphulinae sp. 18 consumed more diatoms and more filamentous algae than *Thiara* sp, and in February, *Centroptilum* sp. consumed fewer diatoms and more filamentous algae than both species.
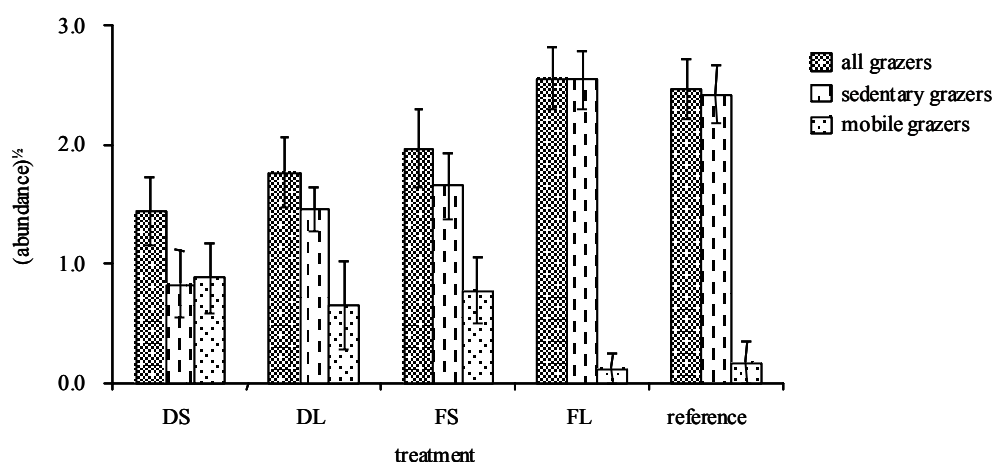
Figure 5.6 Abundances of grazer groups on each treatment. DS= Diatom, 3 days; DL= Diatom, 10 days; FS= Filamentous, 3 days; FL= Filamentous, 10 days. Mean ± 1 S.E. provided. For each treatment n= 8.

Table 5.5 Results of fixed effects ANOVA for grazer abundances: a) (total grazer abundance)$^{1/2}$, b) (sedentary grazer abundance)$^{1/2}$ and c) (mobile grazer abundance)$^{1/2}$.

a)

Source		df	Mean Square	F	p
Model	Hypothesis	4	31.25	46.06	0.000
ALGAE	Hypothesis	2	61.59	90.76	0.000
TIME	Hypothesis	1	1.698	2.503	0.125
ALGAE * TIME	Hypothesis	1	0.134	0.198	0.660
	Error	28	0.679		

b)

Source		df	Mean Square	F	p
Model	Hypothesis	4	24.05	48.82	0.000
ALGAE	Hypothesis	2	45.73	92.83	0.000
TIME	Hypothesis	1	4.609	9.356	0.005
ALGAE * TIME	Hypothesis	1	0.131	0.265	0.611
	Error	28	0.493		

c)

Source		df	Mean Square	F	p
Model	Hypothesis	4	3.665	5.918	0.001
ALGAE	Hypothesis	2	6.370	10.285	0.000
TIME	Hypothesis	1	1.557	2.514	0.124
ALGAE * TIME	Hypothesis	1	0.364	0.588	0.450
	Error	28	0.619		

Table 5.6 Results of fixed effects ANOVA for grazer abundances: a) (*Centroptilum* sp. abundance)$^{1/2}$, b) (Nymphulinae sp. 18 abundance)$^{1/4}$ and c) (*Thiara* sp.)$^{1/2}$.

a)

Source		df	Mean Square	F	p
Model	Hypothesis	4	1.47	4.529	0.006
ALGAE	Hypothesis	2	2.33	7.154	0.003
TIME	Hypothesis	1	0.781	2.402	0.132
ALGAE * TIME	Hypothesis	1	0.458	1.408	0.245
	Error	28	0.325		

b)

Source		df	Mean Square	F	p
Model	Hypothesis	4	1.33	7.062	0.000
ALGAE	Hypothesis	2	2.39	12.75	0.000
TIME	Hypothesis	1	0.427	2.272	0.143
ALGAE * TIME	Hypothesis	1	0.090	0.478	0.495
	Error	28	0.188		

c)

Source		df	Mean Square	F	p
Model	Hypothesis	4	17.6	27.95	0.000
ALGAE	Hypothesis	2	32.6	51.71	0.000
TIME	Hypothesis	1	4.84	7.691	0.010
ALGAE * TIME	Hypothesis	1	0.427	0.679	0.417
	Error	28	0.629		
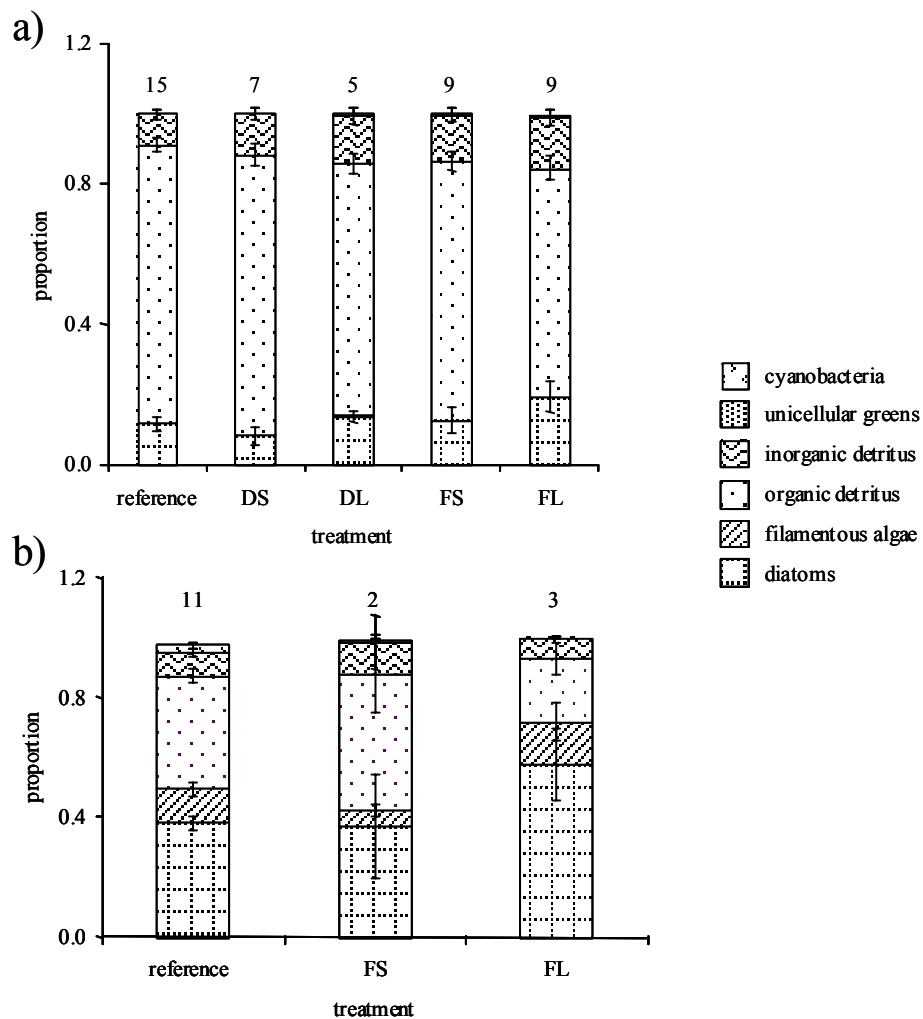
Figure 5.7 Proportion of matter in guts of a) *Thiara* sp. and b) Nymphulinae sp. 18 represented by each 'particle' type, with treatment. DS= Diatom, 3 days; DL= Diatom, 10 days; FS= Filamentous, 3 days; FL= Filamentous, 10 days. Mean ± 1 S.E. provided; relevant number of replicates given at the top of each column.

Table 5.7 Results of Kruskal-Wallis test for differences in gut proportions of dominant algal groups between treatments (not including reference).

	Thiaridae	**Nymphulinae sp. 18**	
	arcsine (diatom proportion$^{\frac{1}{2}}$)	**diatom proportion**	**arcsine (filamentous proportion$^{\frac{1}{2}}$)**
Chi-square	3.54	0.625	3.16
df	3	1	1
Asymptotic significance	0.316	0.429	0.076
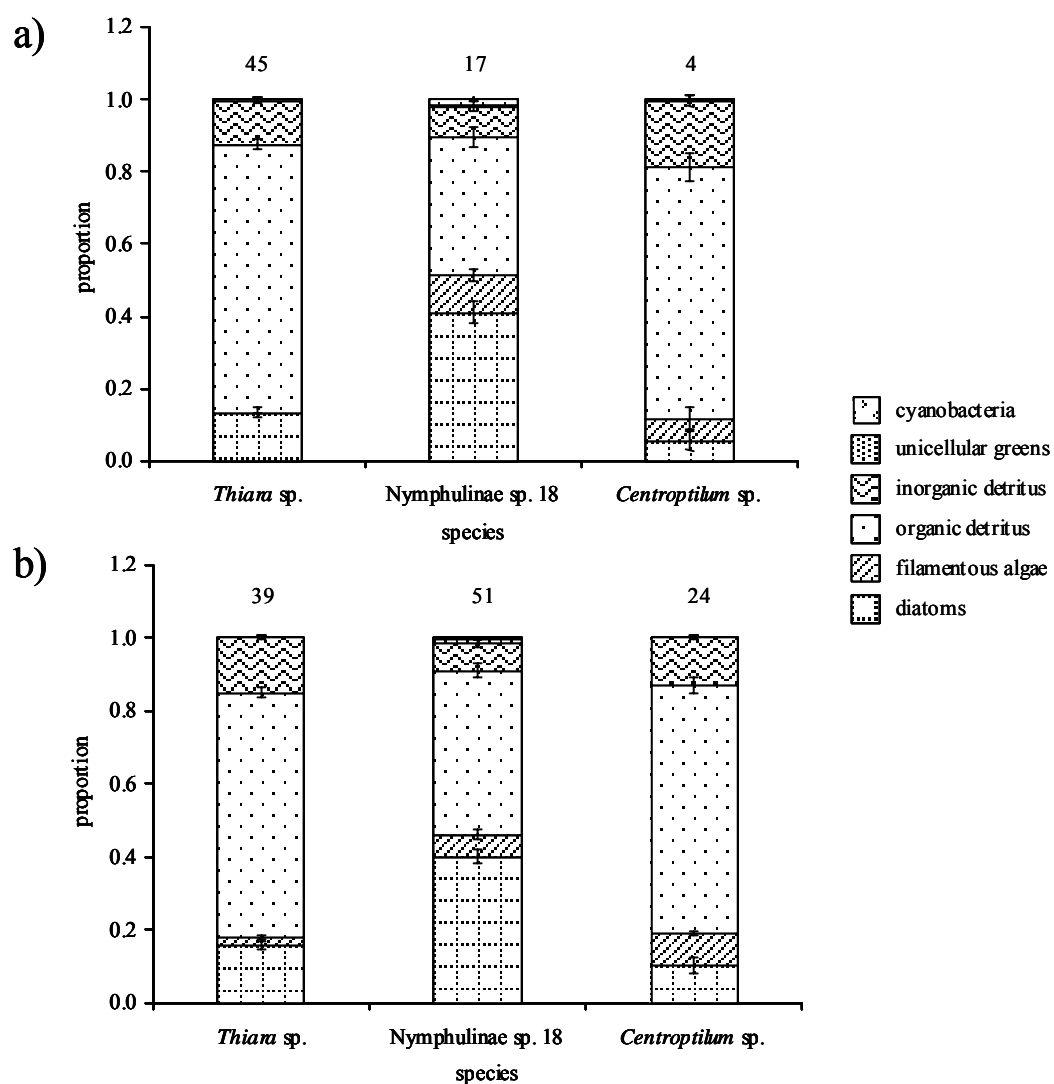
Figure 5.8 Proportions of matter in guts represented by each 'particle' type for a) October and b) February. Mean ± 1 S.E. provided. Relevant number of replicates provided at the top of each treatment column.

Table 5.8 Results of statistical tests for differences in gut proportions of dominant algal groups, for a) October and b) February.

a)

	arcsin(diatom proportion^{½})	filamentous proportion
Mann-Whitney U	20.00	46.00
Z score	-5.721	-6.905
Asymptotic Sig. (2-tailed)	.000*	.000*

* indicates significance at p<0.05

b)

	arcsin(diatom proportion^{½})	arcsin(filamentous proportion^{½})
Chi-square	29.20	67.62
df	2	2
Asymptotic significance	0.000*	0.000*

* indicates significance at p<0.05

5.3.2.3 Stable isotope analysis

On average, grazer δ^{13}C signatures were about 3‰ enriched relative to biofilm δ^{13}C and 4‰ relative to filamentous algae (Table 5.9). On average, grazer δ^{15}N were ^{15}N-enriched about 4‰ relative to biofilm δ^{15}N and 2‰ relative to filamentous algae. Isotopic signatures of filamentous algae and biofilm did not change markedly between October and February at the Mary River site (Figure 5.9). At this site, filamentous algae and biofilm had very similar signatures, making it difficult to clarify the likely diets of grazers (Figure 5.9a, c).

However, filamentous algae were clearly separated from biofilm at the Kilcoy Creek site (Figure 5.9b), as it was very depleted in ^{13}C. Grazer δ^{13}C signatures were close to or slightly enriched compared with biofilm, within the range of 0- 3‰ enrichment expected for consumers relative to their diets (Bunn & Boon 1993, see also Peterson & Fry 1987, Vander Zanden & Rasmussan 2001, McCutchan 2003).

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Table 5.9 Stable isotope ratios of grazing consumers and major sources of organic carbon from Mary at Conondale in October and February, and Kilcoy Creek in October. Mean ± 1SE and number of replicates provided.

	δ^{13}C (‰)	δ^{15}N (‰)	n
grazers	-22.1 ± 1.6	6.2 ± 0.8	14
biofilm	-24.9 ± 2.6	2.5 ± 0.6	6
filamentous algae	-26.2 ± 3.2	4.1 ± 0.6	9
FPOM	-29.0	0.23	1
CPOM	-28.5 ± 0.4	-0.08 ± 1.1	3
macrophytes	-18.3 ± 6.0	1.6 ± 0.9	2

It should also be noted that at the Mary River in February, *Helicopsyche cochleatesta* and *Thiara* sp. were depleted in δ^{13}C compared with both algal sources. In addition, across the various sites and times grazers were always enriched in ^{15}N by 5- 15‰ relative to CPOM and FPOM, which is considerably more than the 0- 3‰ fractionation generally reported between primary producers and consumers (Petersen & Fry 1987, Vander Zanden & Rasmussan 2001, McCutchan 2003).

There were significant relationships between grazer isotope ratios (both C and N) with isotope ratios of biofilm (Figure 5.10a, c), and slopes were quite close to 1. While variation in grazer δ^{13}C was significantly related to variation in filamentous δ^{13}C, the slope was not close to 1, and there was no significant relationship for δ^{15}N.
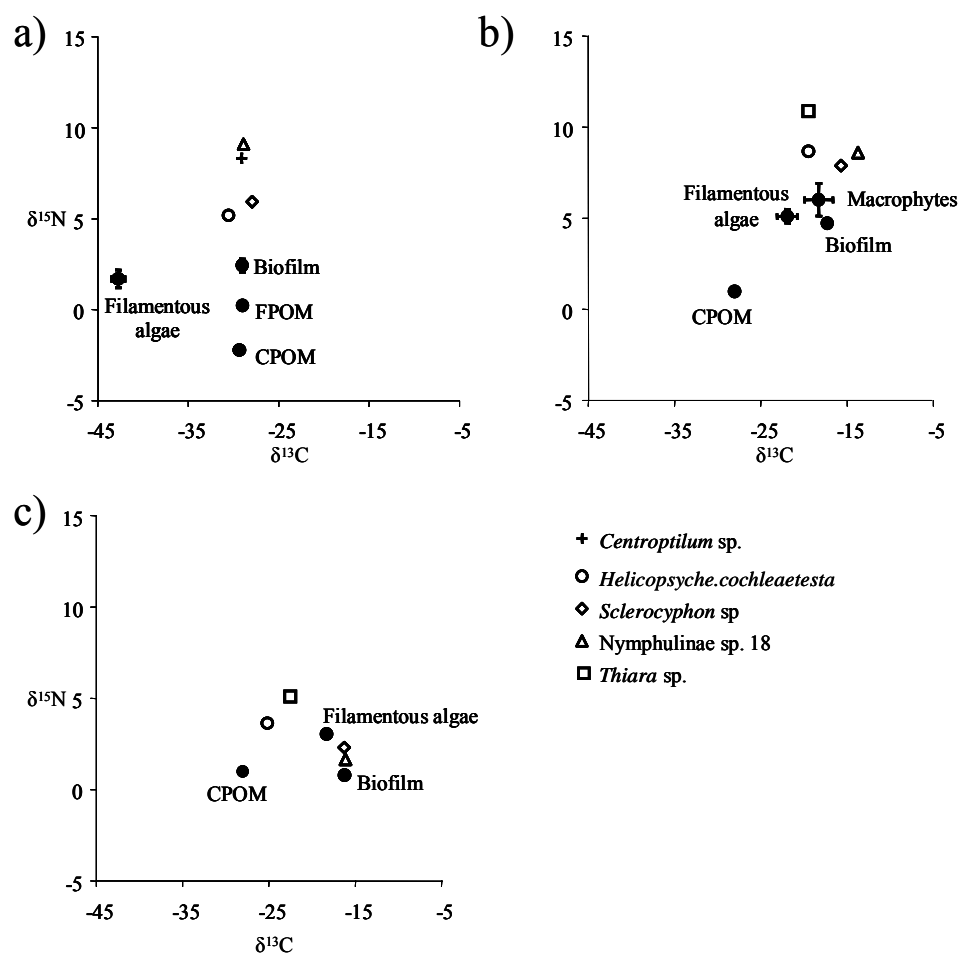
Figure 5.9 δ^{13}C and δ^{15}N signatures of potential food sources and grazers at a) Mary River in October; b) Kilcoy Creek in October; and c) Mary River in February. Mean ± 1 SE shown where n> 1. For Mary River, October n= 6 for filamentous algae, n= 2 for macrophytes; for Kilcoy Creek n= 4 for biofilm, n= 2 for filamentous algae.
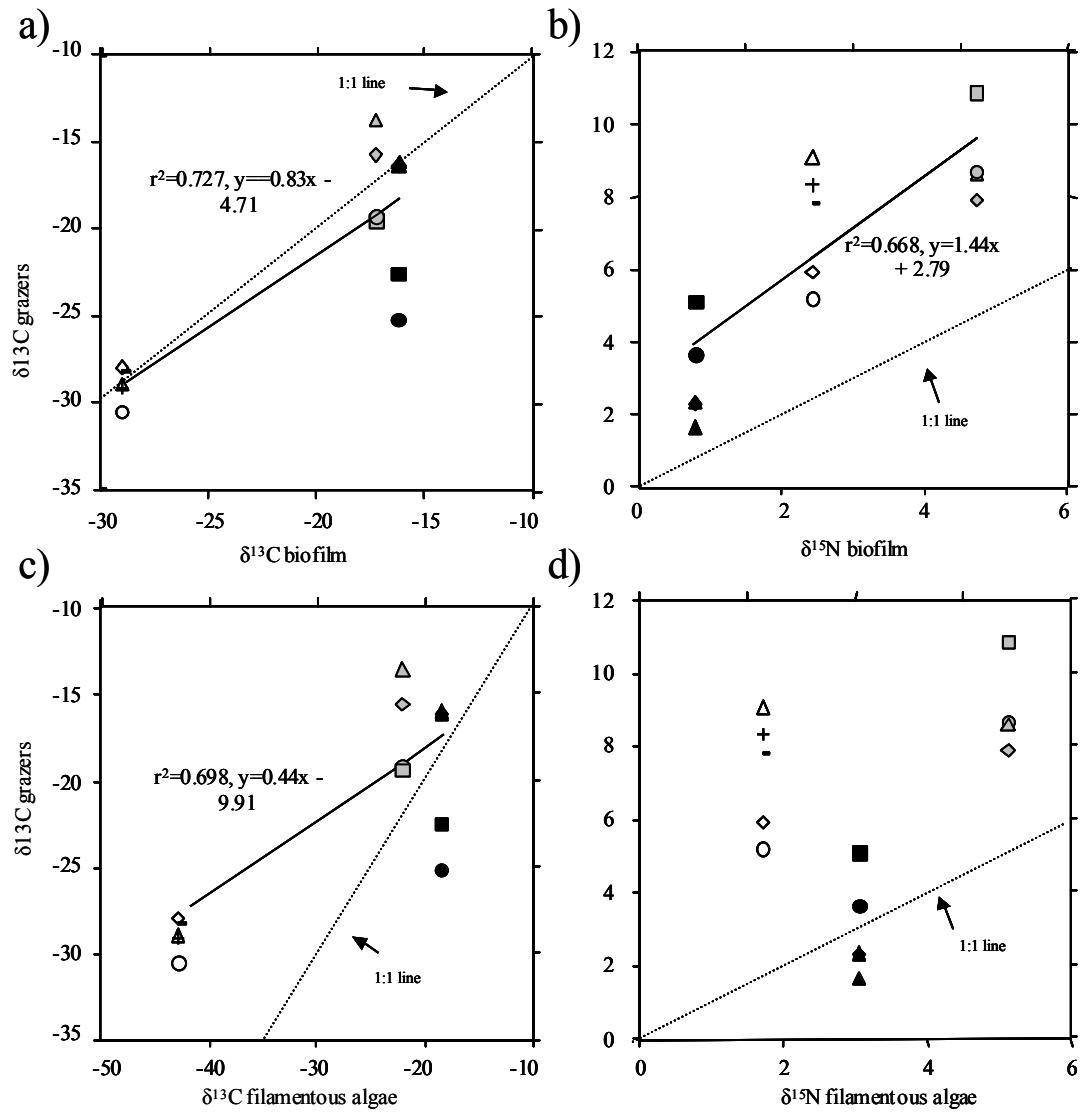
Figure 5.10 Relationships between a) biofilm and grazer $\delta^{13}C$; b) biofilm and grazer $\delta^{15}N$; c) filamentous algae and grazer $\delta^{13}C$; and d) filamentous algae and grazer $\delta^{15}N$. Open shapes = Mary River, October; grey shapes= Mary River, February; black shapes= Kilcoy Creek, October. Plus sign= *Centroptilum* sp.; dash= *Austrophlebioides* sp.; triangles= Nymphulinae sp. 18; circles= *Helicopsyche cochleatesta*; squares= *Thiara* sp.; diamonds= *Sclerocyphon* sp. Significant regressions only (p< 0.05) shown.

5.4 Discussion

Sedentary grazers as a group were more abundant on cobbles with a dominance of filamentous algae, while mobile grazers were more abundant on cobbles with a dominance of diatoms. These patterns are similar to those seen at the reach scale and those suggested by the community ordinations of Chapter 3. They are different to the trends shown by the grazers at the cobble scale of Chapter 3, but the comparatively higher replication in this chapter suggests that these patterns may be more reliable. Alternatively, the difference could be due to the different responses of the particular species that made up the mobile sub-guild in Running Creek as compared with the Mary River, as for example the particular mobile species analysed in the field experiment of this chapter (*Centroptilum* sp.) was more abundant on cobbles with filamentous algal cover (as were the two sedentary species).

While there were some differences in feeding between the individual species studied, their colonisation behaviour was consistent with their mobility group in all cases. Sedentary grazers were more abundant after a longer colonisation time, and this was most obvious for thiarids. Nymphulinae did not display a significant change in abundance between the two colonisation periods, but they were more abundant on reference cobbles, which presumably had much longer colonisation times ($F= 8.51$, $p< 0.05$). Mobile grazers, on the other hand, appeared to decrease slightly with time, particularly on filamentous rocks, but this was not significant (and neither was the interaction effect) for the group or for *Centroptilum* sp.

The increased abundance on filamentous rocks of the sedentary grazer group and the three most abundant individual species studied may be due to a number of benefits conferred by filamentous algae. Filamentous algae may provide food, either directly

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(e.g. Feminella & Resh 1991, Sarnelle *et al.* 1993) or as structure for the epiphytes that grow on its filaments (e.g. Dudley 1992). The algae may also provide increased complexity and living space (Downes *et al.* 2000b), and refuge from flow (Dudley *et al.* 1986, also cf. Gregg & Rose 1982) and predation (cf. Mattila 1992, Williams 1993).

In order to elucidate the likely reasons for the preference of grazers for filamentous algal cover, it is necessary to examine their diets. Stable isotope analysis indicates that grazers as a group probably assimilate carbon largely from biofilm. Not only were grazers signatures more similar to those of biofilm where filamentous algae and biofilm had differing signatures (Kilcoy Creek in October), but both grazer $\delta^{13}C$ and $\delta^{15}N$ signatures tracked those of biofilm across time and space. Indeed, grazer $\delta^{15}N$ signatures had no relationship with filamentous $\delta^{15}N$ signatures.

Examining the gut contents of individual grazer species provides further information about their feeding behaviour. Nymphulinae sp. 18, which have biting and chewing mandibles, consumed a considerable amount of filamentous algae. Bergey (1995) found that the pyralid *Petrophila confusalis* maintains a particular community of algae in a clearly demarcated area around the outside of their retreats, by 'gardening' in a manner similar to that described for *Leucotrichia* sp. by Hart (1991). It is possible that Nymphulinae sp. 18 consume filamentous algae as they clear space for more preferred species of algae, and that these are 'by-catch' rather than being assimilated as food.

Thiara sp. consumed no filamentous algae, which is a similar pattern to that shown by *Helicopsyche murrumba* in the laboratory experiment. The lack of filamentous algae in either species' guts could be due either to their non-consumption of these taxa, or to the rapid destruction of filaments during feeding and by gut enzymes. Several factors argue against the latter hypothesis. Firstly, if the digestive system quickly destroyed all

filaments, some evidence of damage should be observed to other algae within the guts. However, a large proportion of diatom frustules found in the gut were intact. Secondly, even if large portions of filaments were ingested, it could be expected that recognisable detritus would remain (Hart 1985). This was not the case.

Instead, it is more likely that animals were either unable to, or 'selected' not to, eat filamentous algae. Steinman (1996) asserts that true selectivity is unlikely in invertebrate grazers, as they lack the sensory equipment necessary for discriminating algal taxa, and due to their small size relative to algal prey. Instead, they may be unable to eat filaments due to their mouthpart structure and feeding mechanisms, particularly since the algae were largely present only at an advanced stage of development, with thick and long filaments. While many macroalgae are susceptible to grazing in their juvenile stage, they may escape in size from small herbivores (Lubchenco 1983, Steinman *et al.* 1987). *Helicopsyche murrumba* has scraping mandibles which enable individuals to remove small, tightly adherent algae from epilithic surfaces (Resh & Rosenberg 1984), and may be unable to harvest filaments of large girth (Feminella & Resh 1991). *Thiara* sp. has a taenioglossid radula, which is equipped to consume detritus and small periphytic algae such as diatoms and is likely to be similarly unable to consume mature filaments of algae (Sheldon & Walker 1997).

In addition, the mouthparts of both groups are inadequate for processing CPOM. This suggests that the δ^{13}C of both *Helicopsyche cochleatesta* and *Thiara* sp. at the Mary River in February, which was depleted compared with that of algal sources, is unlikely to indicate a dependence on CPOM. Rather, the two species may be expressing a signature from an algal source not collected at the time of sampling. Algal signatures can vary in space (Finlay *et al.* 2002, Zah *et al.* 2001), so it is possible that the particular

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source consumed was missed on the day of sampling, although sampling aimed to be comprehensive across the reach. More likely is that algal δ^{13}C signatures had changed in the recent past, as they can vary through time (McCutchan & Lewis 2002), and consumer signatures can lag behind changes in algal signatures as material is assimilated (McCutchan & Lewis 2002, McCutchan *et al.* 2003).

Baetids may also be unable to harvest filamentous growth once it reaches a certain advanced stage of development (Wellnitz & Ward 1998), since they feed by gathering algae with setae on their brush-like mouthparts in a sweeping motion (Lamberti *et al.* 1987, DeNicola *et al.* 1990, Dudley 1992). In this study, *Centroptilum* sp. did consume a noticeable amount of filamentous algae along with a large amount of FPOM. Again, filamentous algae and POM were not assimilated, and the filamentous algae in guts consisted of small, short fragments. It is possible that both filamentous algae and POM were gathered during indiscriminate feeding on biofilm surfaces and/or epiphytes on filamentous algae. Mayflies with brushing mouthparts have previously been shown to be able to prevent the establishment of the filamentous *Cladophora*, an ability attributed to their feeding mode that reduces the loose overstory layer of periphyton (Hill and Knight 1988a, Dudley & D'Antonio 1991).

There are at least two ways in which the habitat aspects of filamentous algae can be important to invertebrates. The long filaments of algae may provide refugia from predation and flow. It is well established that complex substrates can reduce the foraging efficiency of both invertebrate and fish predators (e.g. Hildrew & Townsend 1977, Brusven & Rose 1981, Williams *et al.* 1993, Manatunge *et al.* 2000, Warfe & Barmuta 2004). It is also widely accepted that aquatic plants can reduce water velocity in streams (see review by Dodds & Biggs 2002), and filamentous algae may be even

more effective at this than macrophytes, reducing flow by, for example, as much as 40% (Dudley *et al.* 1986). Small-scale hydraulic characteristics in streams can affect micro-distributions of macroinvertebrates (Brooks *et al.* 2005), and are thought to influence the metabolism, feeding and behaviour of macroinvertebrates (Statzner *et al.* 1988). This is not surprising, given that high velocities are associated with increased drag on organisms that can result in high metabolic requirements for movement and attachment (Brooks *et al.* 2005 and references therein). For example, Bournard (1975) reported that movements of the caddisfly *Micropterna* sp. against flow require so much energy that a large part of the whole energy budget is expended simply in dealing with flow forces.

An alternative explanation for the preference of some grazers for rocks with filamentous algal cover might be that the algal filaments provide an increased surface area for epiphytic diatoms and cyanobacteria (Dudley *et al*. 1986), which are grazed by many macroinvertebrates as food. However, filamentous algae can also have negative effects on some diatom species by overgrowing them and causing significant shading impacts (see review by Hill 1996). Using Chapter 4 treatment-scale data, linear regression between filamentous algae and diatom density indicates that there is a simple linear decline in diatom density with filamentous algal cover at this scale (r^2= 0.419, p= 0.007; diatom density transformed as $x^{1/4}$ to improve normality and heterogeneity of variance). This suggests that filamentous algae in these systems is unlikely to be of benefit to grazers due to any augmentation of epiphytic food resources.

5.4.1 Conclusions

Patterns of sedentary and mobile grazers were generally as expected from earlier chapters, with more sedentary grazers on cobbles with filamentous algae, and more mobile grazers on cobbles with diatoms. The gut contents data and stable isotope

analysis together provide evidence that offers explanation for the possible reasons for these patterns. It is unlikely that any of the most abundant species consume filamentous algae as a preferred food source. Filamentous algal filaments are also unlikely to augment ephiphytic diatoms, and may in fact be associated with reduced food resources. This suggests that filamentous algae confers an advantage on grazing macroinvertebrates that is not due to its direct or indirect effect on food availability, but rather is associated with the provision of refugia from predation and/or flow.

It is worth noting that the combination of gut content investigation and stable isotope analysis together allow for better elucidation of the dietary preferences of macroinvertebrates. Alone, gut content investigation can allow for under- or over-estimation of components of algal material, depending on differing digestions and digestibility, and results can be a reflection of consumed matter that have little correspondence with assimilation and growth (Fürerder *et al.* 2003). Stable isotope analyses are not always clear in cases where primary sources have similar isotopic signatures, but integrate food assimilation over time, and in conjunction with gut content investigation provide an excellent method for the investigation of the dietary preferences of macroinvertebrates.

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6 – General discussion

Observed relationships between productivity and diversity are not easily explained in many systems. Factors such as disturbance and habitat stability (Hildrew & Townsend 1987, Death & Winterbourn 1995, Cardinale *et al.* 2005), resource heterogeneity (Abrams 1995, Hall *et al.* 2000) and resource diversity (Abrams 1995, Siemann 1998), amongst others, are evoked to explain these relationships (see review by Rosenzweig & Abramsky 1993), but can often be confounding (e.g. Abramsky 1978, Death & Winterbourn 1995, Siemann 1998, Dodson *et al.* 2000, Haddad *et al.* 2000). For example, where the productivity of plants and diversity of herbivores are the variables of interest, the diversity and composition of plants may need to be investigated to tease apart the bottom-up forces controlling animal diversity (Siemann 1998). This study proved no exception, as it showed that the relationships seen between algal productivity and the diversity of grazing consumers in small sub-tropical streams of South-east Queensland cannot be understood without also clarifying the role of species composition; and especially the structural attributes of assemblages.

This study sought to tease apart this inter-relationship. In particular, the study aimed to:

a) examine relationships between the productivity of algae and diversity of grazing consumers;

b) separately manipulate filamentous algae and algal productivity in order to determine their roles and relative importance to grazing consumers; and

c) investigate the dietary preferences of grazing consumers in order to clarify their relationships with algal species composition.

In addition, two other factors were involved in this study: mobility, and scale. Grazers in the study streams differed in their degree of mobility or modes of dispersal, and this may have affected their responses to algal communities at different scales. Therefore the above questions were posed at various scales, and grazers were assigned to one of two groups wherever their modes of dispersal were clearly one (mobile) or the other (sedentary).

6.1 Detail of findings

The study found relationships at various scales between grazer diversity and primary productivity, algal diversity and algal species composition, along with some physico-chemical variables. These are summarised in a modification of the initial conceptual model (Figure 6.1). The model is not intended to be comprehensive, and variables not measured, such as competition, predation and disturbance, have not been included in the revised model (but see Chapter 1 for full model). It is, rather, intended to show inter-relationships of the variables of interest across various scales.

As predicted by the conceptual model, regional processes largely constrained the diversity and composition at local scales. The diversity and composition of grazer taxa in the study catchments (including the eastern Upper Brisbane and Mary catchments, and the western Upper Brisbane and the Upper Coomera catchments) were primarily structured at catchment (10^4-10^5 m) and reach (10^2-10^3 m) scales. The beta diversity of grazers tended to be lowest between reaches, and reaches close together had low turnover and similar faunal composition, whereas those further apart exhibited more differences in grazer communities.

However, also as predicted, the conditions at a reach also appeared to determine which taxa successfully colonised from the catchment pool. Productivity and composition of algal communities were important factors contributing to the explained variation of grazer diversity at a reach, in a patch, and on a cobble.
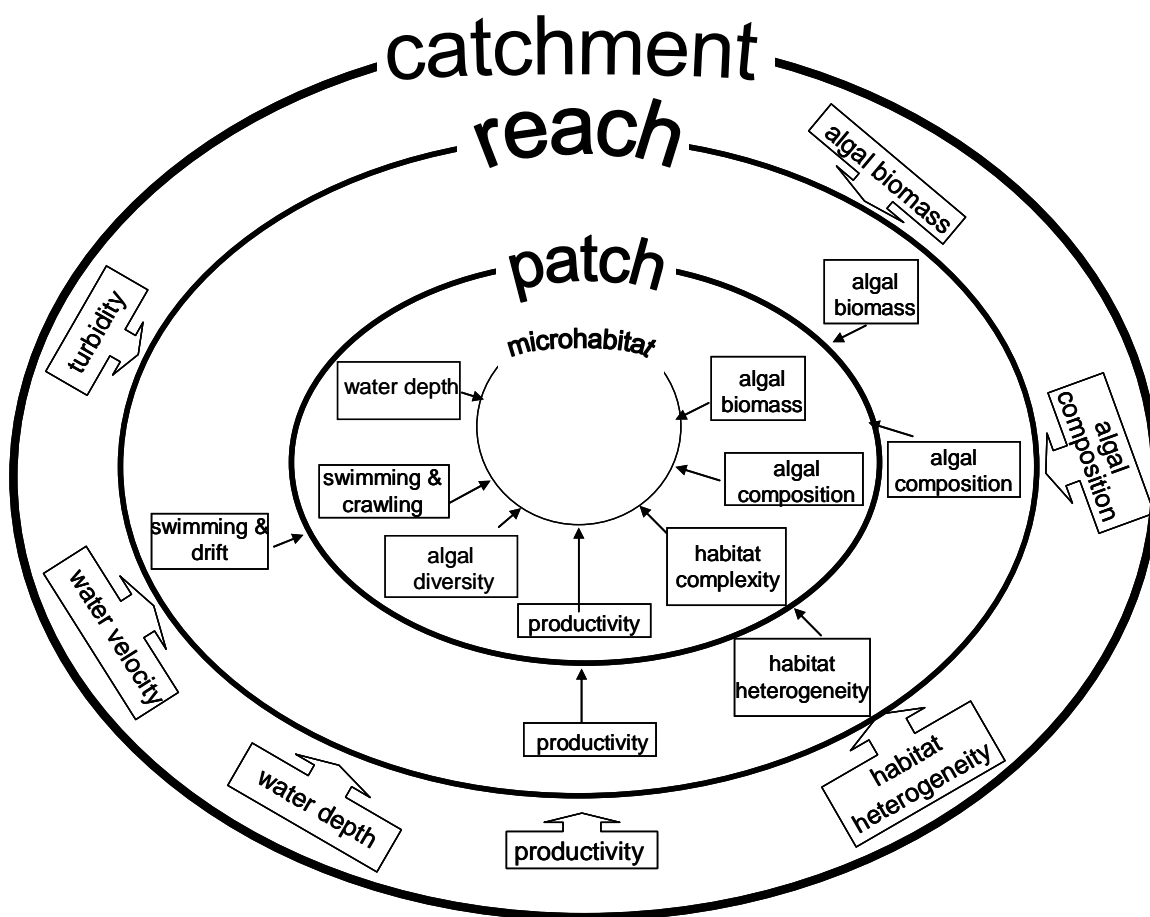
Figure 6.1 Revised conceptual model of the nested factors of interest that influence macro-invertebrate grazer diversity in study streams (cf. Figure 1.4). Each ring represents diversity at the nominated scale. Arrows indicate factors that may influence diversity at this scale. Only factors found to be related to diversity in this study are included.

The relationships of algal productivity and composition with grazer diversity are shown in more detail below (Figure 6.2). At the reach scale, there was a strongly positive relationship of grazer diversity with primary productivity (GPP)/ filamentous algal cover (FAC; see Chapter 3). At the patch scale (10^0-10^1 m), the relationship was clearly hump-shaped (Chapter 4). Most cobble-scale (10^{-2} m) relationships were not significant, although there was a negative linear relationship between grazer diversity and FAC (Chapter 3).
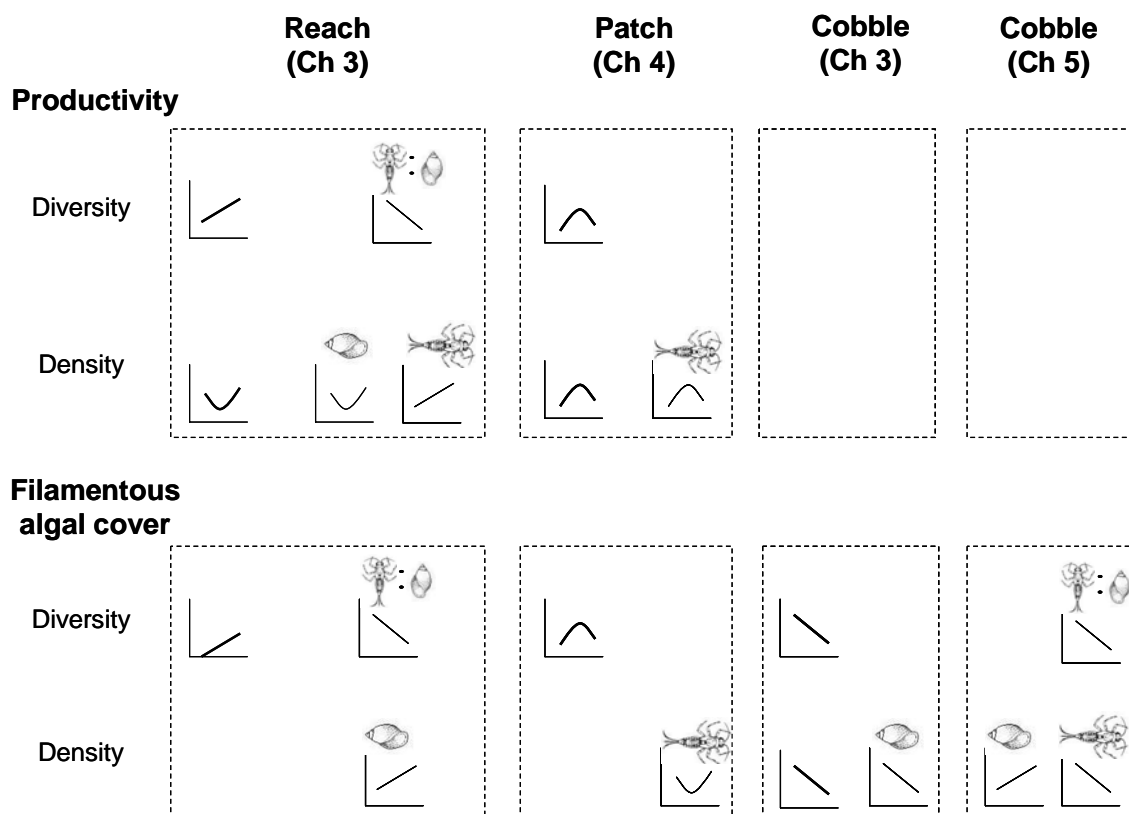
Figure 6.2 Stylised relationships of algal productivity and composition with grazer diversity and density found in this thesis. Shells indicate sedentary grazer relationships, mayflies indicate mobile grazer relationships, and the mobile: sedentary ratio (ratio of number of species in each group; see chapter 3) is also indicated. Unmarked relationships are for total grazer community.

At the reach scale, it was unlikely that the relationship between grazer diversity and GPP/FAC was due to an increase in intra-specific density dependence or abundance of rare species (cf. Abrams 1995, Siemann 1998; see 3.4.1.1). In fact, at all scales it is suggested that the increasing phase of the relationship was due to the increasing diversity of available food species and/or the heterogeneity or complexity of habitat, all of which were related to increases in primary productivity (Chapters 3,4).

At high levels of gross primary productivity, the diversity of algae was also high (Chapter 4), along with the range of algal forms or types. Grazers can feed more effectively on certain algal taxa according to the characteristics and form of the alga, and to their modes of feeding, consumptive abilities and mouthpart morphology (e.g. Sumner & McIntire 1982, McCormick & Stevenson 1988, Wellnitz & Ward 1998). Thus at high levels of productivity, there may have been more 'preferred' food taxa for a wider range of grazer taxa, and this may have allowed the local persistence of more species (cf. Schoener 1974, Abramsky 1978, Siemann 1998, Haddad *et al.* 2000).

Alternatively, sites with high productivity were also associated with higher filamentous algal cover, and thus the heterogeneity of habitat may have been higher at these sites. Increasing habitat heterogeneity and complexity can provide a greater variety of living conditions and increased surface area (O'Connor 1991), and may have conferred benefits, such as reduced predation, that may allow rarer species to persist (e.g. Brusven & Rose 1981, Hildrew & Townsend 1977, 1982). The alternative explanation that filamentous algae provided more food resources either directly or by providing increased surface area for epiphytic diatoms was not well supported. Diet analysis, particularly using stable isotope ratios, suggested that filamentous algae did not contribute significantly to the food assimilated by grazers (Chapter 5), and it did not appear to augment the density of the likely preferred food source, diatoms (Chapter 4,5).

While filamentous algae may therefore have had a positive influence up to a certain level of cover, at the patch and reach scales this was not the case at high FAC levels, as grazer diversity was lower under such conditions (Chapter 4). There was also lower algal diversity, as filamentous taxa dominated the community. It is possible, therefore, that the low diversity of grazers was due to a lower diversity of food resources (cf. Siemann 1998, Haddad *et al.* 2000). Alternatively, since diatom density declined with increasing FAC, the low grazer diversity could have been due simply to a reduced amount of food available (cf. Stevens & Carson 2002).

There is some possibility that at the reach scale, the lack of a declining phase in the GPP: diversity relationship, and thus the lack of a hump-shaped pattern, may have been attributable to the reduced range of productivity. Several authors have suggested that surveys of species richness conducted over limited productivity ranges are less likely to detect a hump-shaped relationship than studies conducted over a broader productivity range (e.g. Begon *et al.* 1990, Rosenzweig 1992, 1995, Huston 1994, Guo & Berry 1998).

However, another explanation for the lack of a hump-shaped pattern in grazer diversity is that, at this scale, any negative effects of very high filamentous algal cover were outweighed by other benefits, at least to most species. For example, there were higher densities of sedentary grazers at reaches with high GPP/ FAC (Figure 6.2, Chapter 3), and these animals also were more abundant on cobbles with high FAC compared with those with no FAC (Figure 6.2, Chapter 5). Any benefits of high FAC are unlikely to be associated with an increase in density or diversity of food resources, since sedentary grazers did not use filamentous algae as a major food source (Chapter 5), and the density of their likely preferred food source, diatoms, declined as FAC increased (Chapters 4, 5). It is possible that FAC conferred other advantages on this grazer group,

such as refugia from flow or predation (cf. Dodds & Biggs 2002, Warfe & Barmuta 2004). Sedentary grazers are by definition unable to rapidly enter the drift (Mackay 1992), for example to escape from invertebrate predators, and therefore it is possible that refugia provided by filamentous algae from such predators may be of particular importance to these animals.

Further work that could follow from this study could examine in more detail the utility of filamentous algae in providing refugia. For example, a study of the main predators of both sedentary and mobile grazers may prove of interest, particularly if it involves an investigation of their foraging efficiency in filamentous algae compared to that on bare cobbles. Studies by other authors on macrophytes may inform such studies (e.g. Crowder & Cooper 1982, Mattila 1992, Warfe & Barmuta 2004).

The high density of sedentary grazers at reaches with high GPP/FAC was associated with a general shift in community composition, since mobile grazer abundances peaked at a low to moderate level of GPP/FAC at this scale (as well as at the patch and cobble scales). The low density of mobile grazers at high GPP/FAC may reflect a response to lower availability of preferred food resources, since stable isotope analysis indicated that the major food source for mobile grazers is diatom-dominated biofilm (Chapter 5). Kohler (1984) demonstrated that *Baetis tricaudatus* maximised energy gains from their food source by spending more time in periphyton patches than in areas without periphyton, and other authors have showed that small-scale variation in periphyton abundance influences the distribution of baetids (e.g. Fuller *et al.* 1986, Richards & Minshall 1988, Álvarez & Peckarsky 2005). In Chapter 5 of this study it appeared that this kind of small scale movement (between cobbles) also allowed *Centroptilum* sp. to select cobbles with preferred algal communities, indicating that the animals can respond to algal community structure as well as to algal abundance or biomass.

The reach scale shift from mobile to sedentary grazers with high productivity was not found at intermediate scales, but was shown at small scales. At the patch scale, sedentary grazers displayed no strong relationships with algal variables, suggesting that heterogeneity at this scale is beyond the extent of their perception (Chapter 4; see Kotliar & Wiens 1990). At the cobble scale, where larvae are able to crawl between cobbles, data on sedentary grazers was conflicting, but in the better replicated experiment in Chapter 5, they were more abundant on cobbles with a dense filamentous algal cover than on cobbles with a diatom film and no filamentous algae, while mobile grazers displayed the opposite pattern.

6.2 Conclusions

This study found that small-scale relationships of productivity and consumer diversity in South-east Queensland streams tended to be hump-shaped, and that larger-scale relationships were positive and linear. This pattern has been found with some frequency in other habitats (Waide *et al.* 1999, Mittelbach *et al.* 2001, Chase & Leibold 2002), but the relationship has rarely been investigated in freshwater lotic systems.

The study also has emphasised that the relationship of diversity with variables such as primary productivity is not always simple, as it can be complicated by responses to related variables such as the species composition of producers. While this study showed that experimental manipulation by light and nutrients could not completely tease apart algal productivity and species composition, further experimental work provided a depth of information about the aspects of species composition that grazing consumers respond to and why, particularly concerning the role of filamentous algae in providing food and/or habitat.

Indeed, filamentous algal cover and productivity have been shown to be of importance in structuring grazer communities of these small streams of South-east Queensland, at least in the dry season when flows are low and stable. It would be of considerable interest to investigate how these relationships change during the wet season when disturbance may be more likely to structure communities; disturbance and productivity have been coupled as factors that may interact to explain species diversity (Hildrew & Townsend 1977, Huston 1979, Death & Winterbourn 1995, Pollock *et al.* 1998, Biggs & Smith 2002, Cardinale *et al.* 2005).

The study also emphasised that in attempting to understand the responses of organisms to productivity and species composition, it is important to consider their ability to perceive heterogeneity at the relevant scale. The division of grazers into sedentary and mobile sub-groups has provided a clearer picture of how important it is to investigate relationships at the correct scale, which is one relevant to the organism of study (cf. Addicott *et al.* 1987, Kotliar & Wiens 1990). A key example in this study is the lack of response of sedentary grazers at the scale of patches, discussed above.

In summary, then, this study has teased apart many of the important elements of the communities of producers and consumers that must be considered in a study of productivity: diversity relationships in streams. The study of such relationships between process and pattern are increasingly important. Catchment, and particularly riparian, clearing and the addition of nutrients through agricultural runoff can cause increasing biomass and productivity of algae, and increasing dominance by nuisance species such as filamentous algae. The effects of such changes need to be better understood to allow effective management of freshwater biodiversity, and the healthy functioning of stream ecosystems in general.

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Taxa accumulation curves for grazers for survey sites with a) low grazer abundance; and b) high grazer abundance.

a)

b)
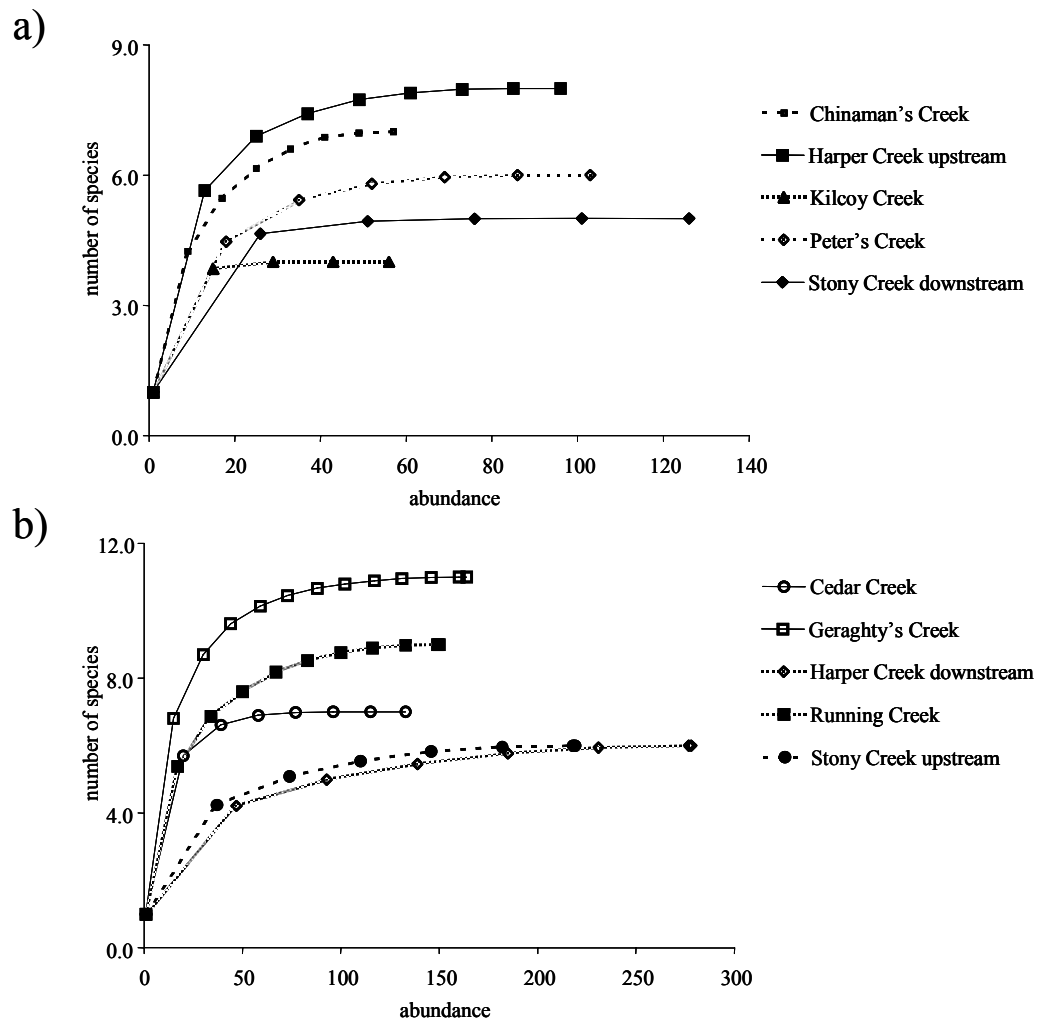
Appendix B

Classification of all taxa collected throughout the study, with authorities for species. All insect taxa are larvae unless indicated, (a) = adult.

Classification	Taxon		
Platyhelminthes			
	Turbellaria		
Nematoda			
Annelida			
	Oligochaeta		
Mollusca			
	Gastropoda	Ancylidae	*Ferrissia* sp.
		Corbiculidae	
		Hydrobiidae	
		Lymnaeidae	*Pseudosuccinea columella* Say 1817
		Planorbidae	*Gyraulus* sp.
		Thiaridae	*Thiara* sp.
Arthropoda			
	Hydracarina		
Crustacea			
	Decapoda	Atyidae	*Caridina indistincta* Calman, 1926
			Caridinides wilkinsi Calman, 1926
			Paratya australiensis Kemp 1917
		Palaemonidae	*Macrobrachium* sp.
Hexapoda			
	Coleoptera	Dytiscidae	*Barrethydrus* sp.
		Elmidae (a)	
		Elmidae	*Austrolimnius* sp.
			Kingolus tinctus Carter & Zeck, 1929
		Halipilidae (a)	
		Hydrophilidae	*Bersosus* sp.
		Hygrobiidae (a)	
		Psephenidae	Larval type B
			Sclerocyphon basicollis Lea 1895
			Sclerocyphon minimus Davis 1986
			Sclerocyphon sp. C1
			Larval type F
			Sclerocyphon striatus Lea 1895
		Psephenidae	*Sclerocyphon* larval type B
	Diptera	Ceratopogonidae	
		Chironomidae	Aphroteniinae
			Chironominae
			Orthocladinae
			Podonominae
			Tanypodinae
		Culicinae	
		Dixidae	
		Empididae	
		Ephydridae	
		Tipulidae	

Appendix B cont.

Arthropoda			
Hexapoda cont.			
	Ephemeroptera	Baetidae	*Baetidae G 2 sp MV1*
			Baetidae G 2 sp MV6
			Bungona sp.
			Cleon sp.
			Centroptilum sp.
		Caenidae	Caenid Genus C sp. B
			Caenid Genus C sp. C
			Tasmanocoenis arcuata Alba-Tercedor and Suter 1990
			Tasmanocoenis queenslandica Soldan 1968
			Wundacaenis dostini Suter 1993
		Leptophlebiidae	*Atalomicra bifasciata* Cambell and Peters 1993
			Atalomicra sp AV1
			Atalophlebia albiterminata Tillyard 1936
			Atalophlebia sp. AV12
			Austrophlebioides sp. AV11
			Austrophlebioides sp. AV12
			Austrophlebioides sp. AV6
			Jappa kutera Harker 1954
			Jappa sp AV2
			Jappa sp AV4
			Koorrnonga sp AV5
			Koorrnonga sp AV1
			Koorrnonga sp AV2
			Nousia sp. AV1
			Nousia sp. AV15
			Nousia sp. AV6
			Tillyardophlebia rufosa Dean 1997
			Tillyardophlebia sp AV6
			Ulmerophlebia sp. AV2
			Ulmerophlebia sp. AV3
	Hemiptera	Corixiidae	*Micronecta* sp.
	Lepidoptera	Pyralidae	Nymphulinae sp.18
			Nymphulinae sp.3
	Odonata		
	(Epiproctophora)	Gomphidae	*Hemigomphus gouldii* Selys 1854
		Hemicordulidae	
		Oxygastridae	*Hesperocordulia* sp.
		Synthemistidae	
	(Zygoptera)	Diphlebiidae	*Diphlebia coerulescens* Tillyard 1913
		Synlestidae	*Synlestes selysi* Tillyard 1917
			Synlestes weyersi Selys 1869
	Plecoptera	Gripopterygidae	
		Notonemouridae	*Austrocercella* sp.
	Trichoptera	Atriplectidae	
		Calamoceratidae	*Anisocentropus* sp.
		Calocidae	*Caenota* sp.
			Pliocaloca sp.

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Appendix B cont.

Arthropoda			
	Hexapoda cont.		
		Calocidae/	
	Trichoptera cont.	Helicophidae	Genus Cal/Hel A sp. AV1
		Ecnomidae	*Ecnomina batyle* Neboiss 1977
			Ecnomus cygnitus Neboiss 1982
			Ecnomus sp. C1
			Ecnomus turgidus Neboiss 1982
		Helicopsychidae	*Helicopsyche cochleaetesta* Korboot 1964
			Helicopsyche murrumba Mosely 1953
			Helicopsyche ptychopteryx Brauer 1865
			Helicopsyche tillyardi Mosely 1953
		Hydropsychidae	*Cheumatopsyche* sp. AV11
		Hydroptilidae	*Hellyethira eskensis* Mosely 1934
			Hellyethira ramosa Wells 1983
			Hellyethira simplex Mosely 1974
			Hellyethira sp. C1
			Hellyethira sp. C2
			Hydroptila scamandra Neboiss 1977
			Orthotrichia sp.
			Oxyethira sp.
		Leptoceridae	*Leptorussa* sp. C1
			Notalina sp. C1
			Oecetis sp.
			Triplectides altenogus Morse and Neboiss 1982
			Triplectides ciuskus ciuskus Mosely 1953
			Triplectides parvus Banks 1939
			Triplectides volda Mosely 1953
		Odontoceridae	*Marilia fusca* Kimmins 1953
		Polycentropodidae	*Paranyctiophylax* sp. AV5
			Plectrocnemia sp. AV1
		Tasimiidae	*Tasiagma ciliata* Neboiss 1977
			Tasimia sp. AV1

Appendix C

Equations for regression relationships from Chapter 3.

1. Regression equation from Pollock *et al.* (1998) $y = \beta_0 + \beta_1 * x * e^{(\beta_2 * x^{\beta_3})}$

2. Linear equation $y = \beta_1 x + \beta_0$

Reach scale

Independent variable	Dependent variable	Equation
$(GPP+0.5)^{\frac{1}{2}}$	$\log_{10}$(number of grazer taxa + 1)	1. $\beta_0=0.6752$, $\beta_1=0.0111$, $\beta_2=1.003$, $\beta_3=-0.9949$
	$\log_{10}$(grazer density + 1)	1. $\beta_0=9.776$, $\beta_1=-1.863$, $\beta_2=-0.1764$, $\beta_3=0.7454$
	(sedentary grazer density)$^{\frac{1}{2}}$	1. $\beta_0=-0.2234$, $\beta_1=1.591$, $\beta_2=116.6$, $\beta_3=-2.188$
	$\log_{10}$(mobile grazer density + 1)	1. $\beta_0=1.331$, $\beta_1=0.0419$, $\beta_2=0.0406$, $\beta_3=-0.2172$
	(mobile: sedentary ratio)$^{\frac{1}{4}}$	1. $\beta_0=0.9172$, $\beta_1=-0.0066$, $\beta_2=0.0751$ $\beta_3=-0.0623$
FAC	$\log_{10}$(number of grazer taxa + 1)	1. $\beta_0=0.8101$, $\beta_1=0.0004$, $\beta_2=3.139$, $\beta_3=-0.1783$
	$\log_{10}$(grazer density + 1)	not significant
	(sedentary grazer density)$^{\frac{1}{2}}$	1. $\beta_0=11.67$, $\beta_1=0.0749$, $\beta_2=-0.0826$, $\beta_3=-0.2114$
	$\log_{10}$(mobile grazer density + 1)	not significant
	(mobile: sedentary ratio)$^{\frac{1}{4}}$	1. $\beta_0=0.8679$, $\beta_1=-0.0214$, $\beta_2=-0.8218$, $\beta_3=0.2689$
	Beta diversity-1	1. $\beta_0=5.960$, $\beta_1=0.6296$, $\beta_2=-1.079$, $\beta_3=0.6170$
	Beta diversity-2	2. $\beta_0=1.098$, $\beta_1=0.07561$
(chlorophyll a)$^{\frac{1}{2}}$	$\log_{10}$(number of grazer taxa + 1)	1. $\beta_0=0.7294$, $\beta_1=1.0527$, $\beta_2=-4.021$, $\beta_3=-0.1024$
AFDM	$\log_{10}$(number of grazer taxa + 1)	1. $\beta_0=0.1550$, $\beta_1=0.1344$, $\beta_2=-0.0245$, $\beta_3=1.350$
depth	$\log_{10}$(number of grazer taxa + 1)	1. $\beta_0=0.7261$, $\beta_1=0.01787$, $\beta_2=-9.300*10^{-7}$, $\beta_3=4.260$
(velocity)$^{\frac{1}{2}}$	$\log_{10}$(number of grazer taxa + 1)	1. $\beta_0=0.-7.119$, $\beta_1=3.1077$, $\beta_2=0.9680$, $\beta_3=-0.8294$
turbidity	$\log_{10}$(number of grazer taxa + 1)	2. $\beta_0=1.038$, $\beta_1=-0.0384$

Appendix C cont.

Reach scale cont.

conductivity	$\log_{10}$(number of grazer taxa + 1)	not significant	
rock surface area	$\log_{10}$(number of grazer taxa + 1)	not significant	
temperature	$\log_{10}$(number of grazer taxa + 1)	not significant	

Cobble scale

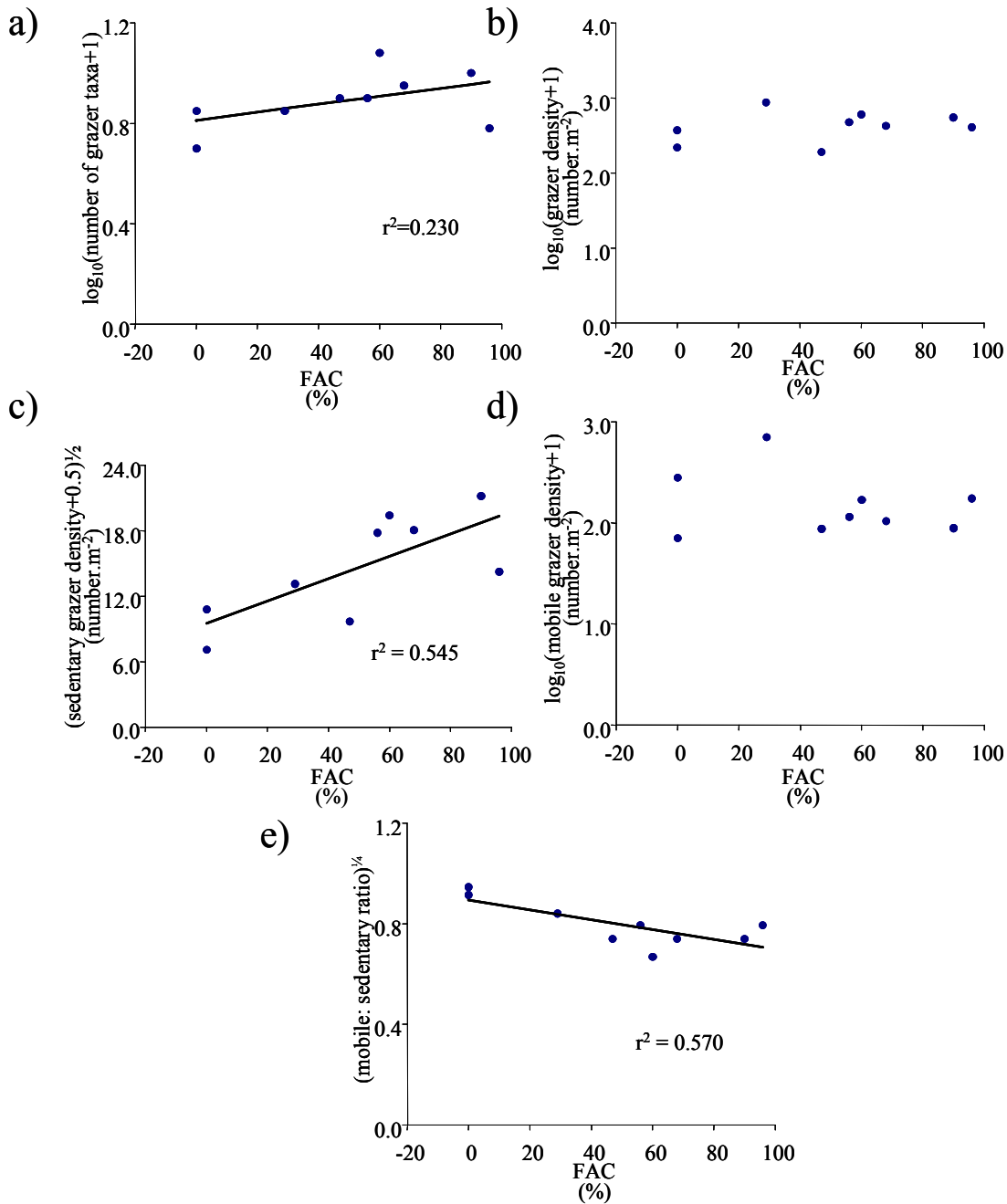| Independent variable	Dependent variable	Equation
GPP	$\log_{10}$(number of grazer taxa + 1)	not significant
	(grazer density+0.5)$^{\frac{1}{2}}$	not significant
	sedentary grazer density	not significant
	mobile grazer density	not significant
	mobile: sedentary ratio	not significant
FAC	$\log_{10}$(number of grazer taxa + 1)	β_0=0.8443, β_1=-0.0067, β_2=-0.1035, β_3=-0.1574
	(grazer density+0.5)$^{\frac{1}{2}}$	1. β_0=20.97, β_1=-0.1418, β_2=0.2226, β_3=-0.8319
	sedentary grazer density	1. β_0=372.7, β_1=-3.435, β_2=-5.981, β_3=-19.03
	mobile grazer density	not significant
	mobile: sedentary ratio	not significant
$\log_{10}$(chlorophyll a)+1	$\log_{10}$(number of grazer taxa + 1)	1. β_0=-5.313, β_1=9.2363389, β_2=0.4648, β_3=1.503
$\log_{10}$(AFDM+1)	$\log_{10}$(number of grazer taxa + 1)	1. β_0=-0.7173, β_1=59.90, β_2=-9.743, β_3=0.8175
depth	$\log_{10}$(number of grazer taxa + 1)	1. β_0=-0.5124, β_1=10.92, β_2=9.876, β_3=1.830
rock surface area	$\log_{10}$(number of grazer taxa + 1)	rock surface area

Relationships of grazer variables: a) number of grazer taxa, b) grazer density, c) sedentary grazer density, d) mobile grazer density and e) mobile : sedentary taxa ratio; with gross primary production at the reach scale. Downstream Harper Creek site excluded. Only significant regressions (p < 0.05) drawn. n = 10, p < 0.001.
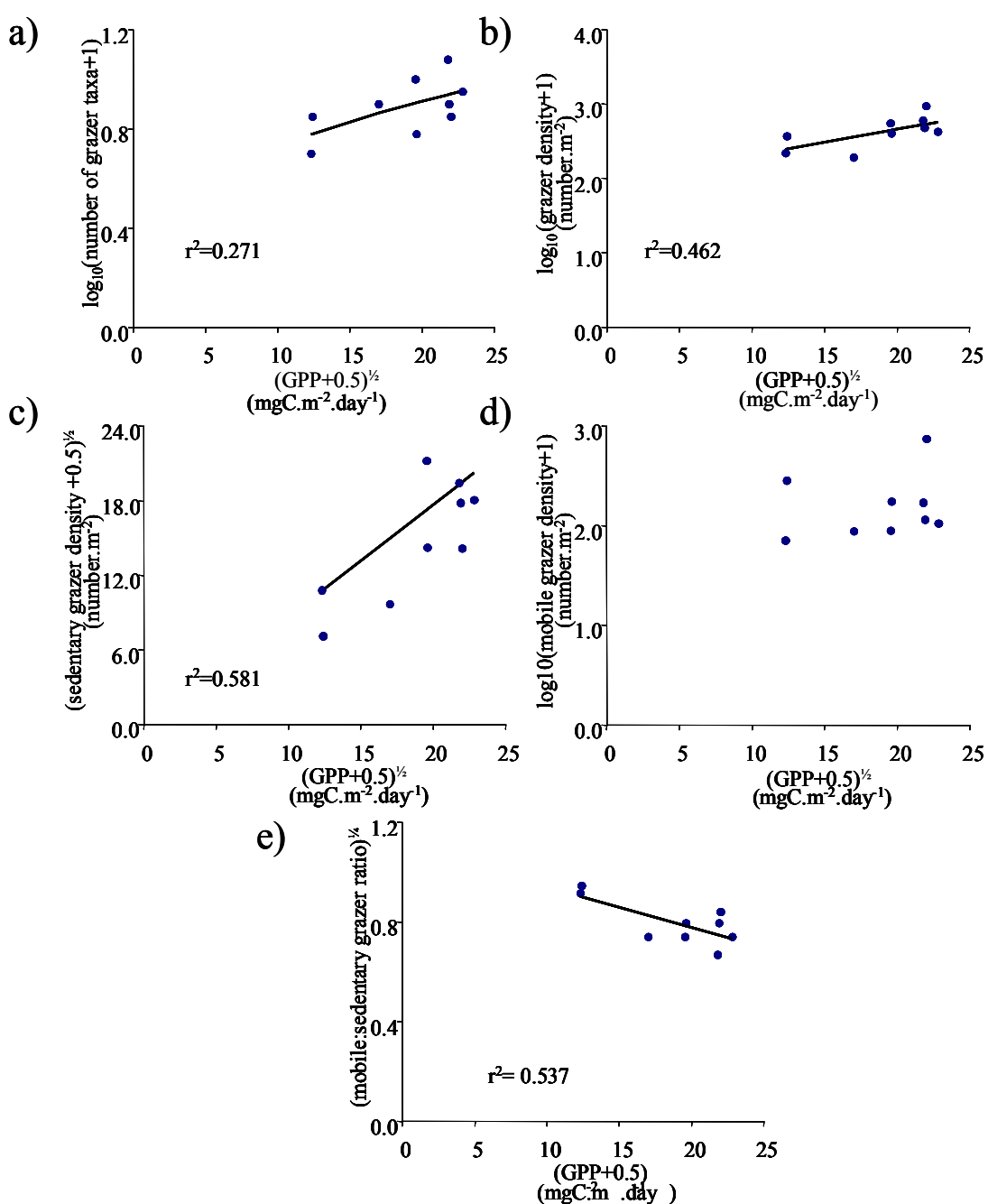
Appendix D cont.

Relationships of grazer variables: a) number of grazer taxa, b) grazer density, c) sedentary grazer density, d) mobile grazer density and e) mobile : sedentary taxa ratio; with filamentous algal cover at the reach scale. Downstream Harper Creek site excluded. Only significant regressions (p< 0.05) drawn. n = 10, p< 0.001.

Appendix D cont.

Regression equations from Chapter 3. Downstream Harpers Creek site excluded.

1. Regression equation from Pollock *et al.*(1998) $y = \beta_0 + \beta_1 * x * e^{(\beta_2 * x^{\beta_3})}$

2. Linear equation $y = \beta_1 x + \beta_0$

Reach scale

| Independent variable	Dependent variable	Equation
$(GPP+0.5)^{\frac{1}{2}}$	$\log_{10}$(number of grazer taxa + 1)	1. $\beta_0=0.4117$, $\beta_1=0.0635$, $\beta_2=-0.2589$, $\beta_3=0.4273$
	$\log_{10}$(grazer density + 1)	1. $\beta_0=1.970$, $\beta_1=0.0392$, $\beta_2=-0.1278$, $\beta_3=-0.0240$
	(sedentary grazer density)$^{\frac{1}{2}}$	1. $\beta_0=-0.2235$, $\beta_1=0.9733$, $\beta_2=-0.1254$, $\beta_3=-0.1330$
	$\log_{10}$(mobile grazer density + 1)	not significant
	(mobile:sedentary ratio)$^{\frac{1}{4}}$	2. $\beta_0=1.1012$, $\beta_1=-0.0161$
FAC	$\log_{10}$(number of grazer taxa + 1)	1. $\beta_0=0.8096$, $\beta_1=0.0019$, $\beta_2=-0.0881$, $\beta_3=0.1600$
	$\log_{10}$(grazer density + 1)	not significant
	(sedentary grazer density)$^{\frac{1}{2}}$	2. $\beta_0=0.8944$, $\beta_1=-0.0019$
	$\log_{10}$(mobile grazer density + 1)	not significant
	(mobile:sedentary ratio)$^{\frac{1}{4}}$	2. $\beta_0=9.5178$, $\beta_1=0.1026$

Appendix E

Plan maps of Chapter 4 experimental sites: a) Upper Brisbane, b) Lower Brisbane. CS= shaded; CUS = control; NPS = Nutrients, Shade; NPUS = Nutrients.
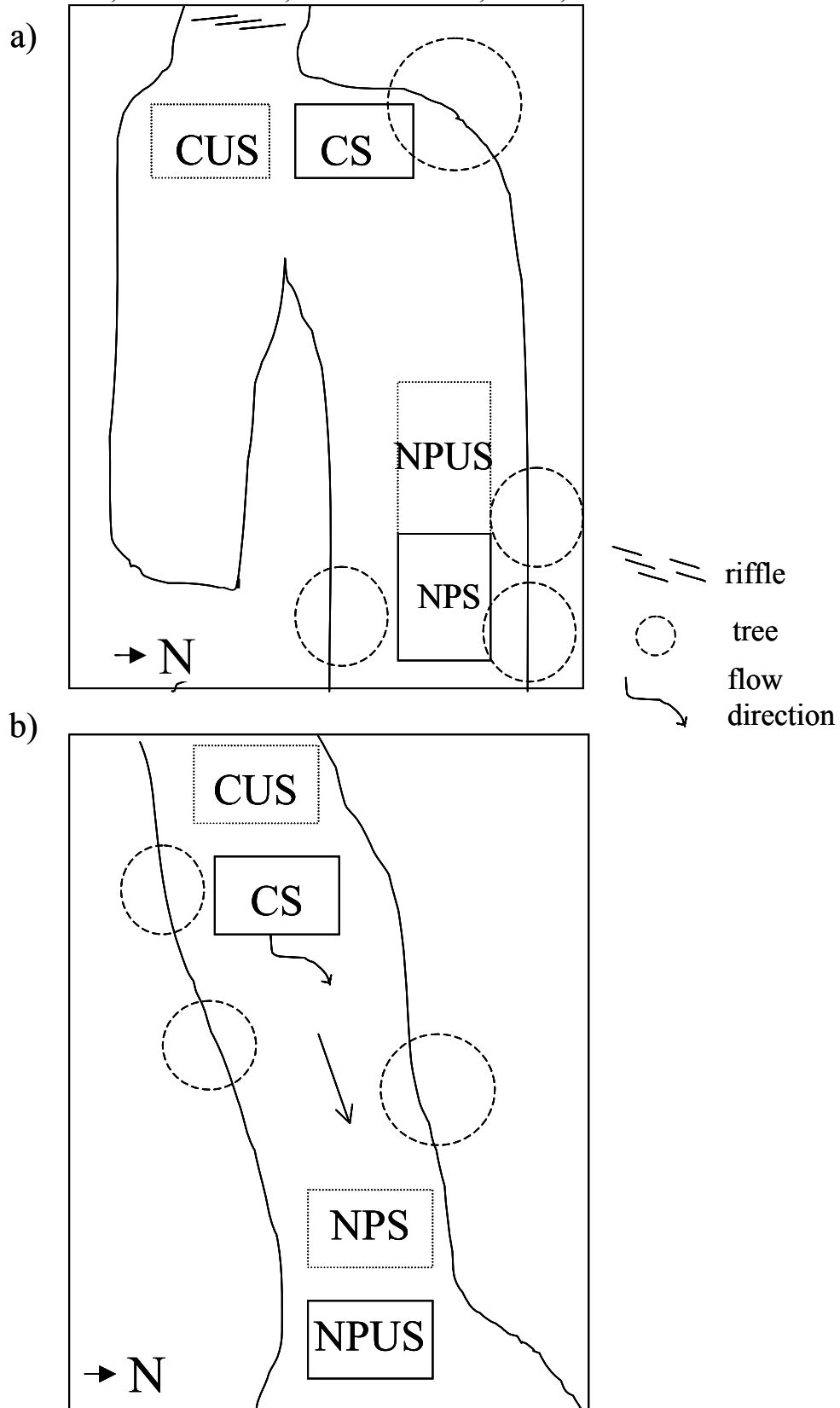
Plan maps of Chapter 4 experimental sites: c) Upper Coomera, d) Lower Coomera. CS= shaded; CUS = control; NPS = Nutrients, Shade; NPUS = Nutrients.

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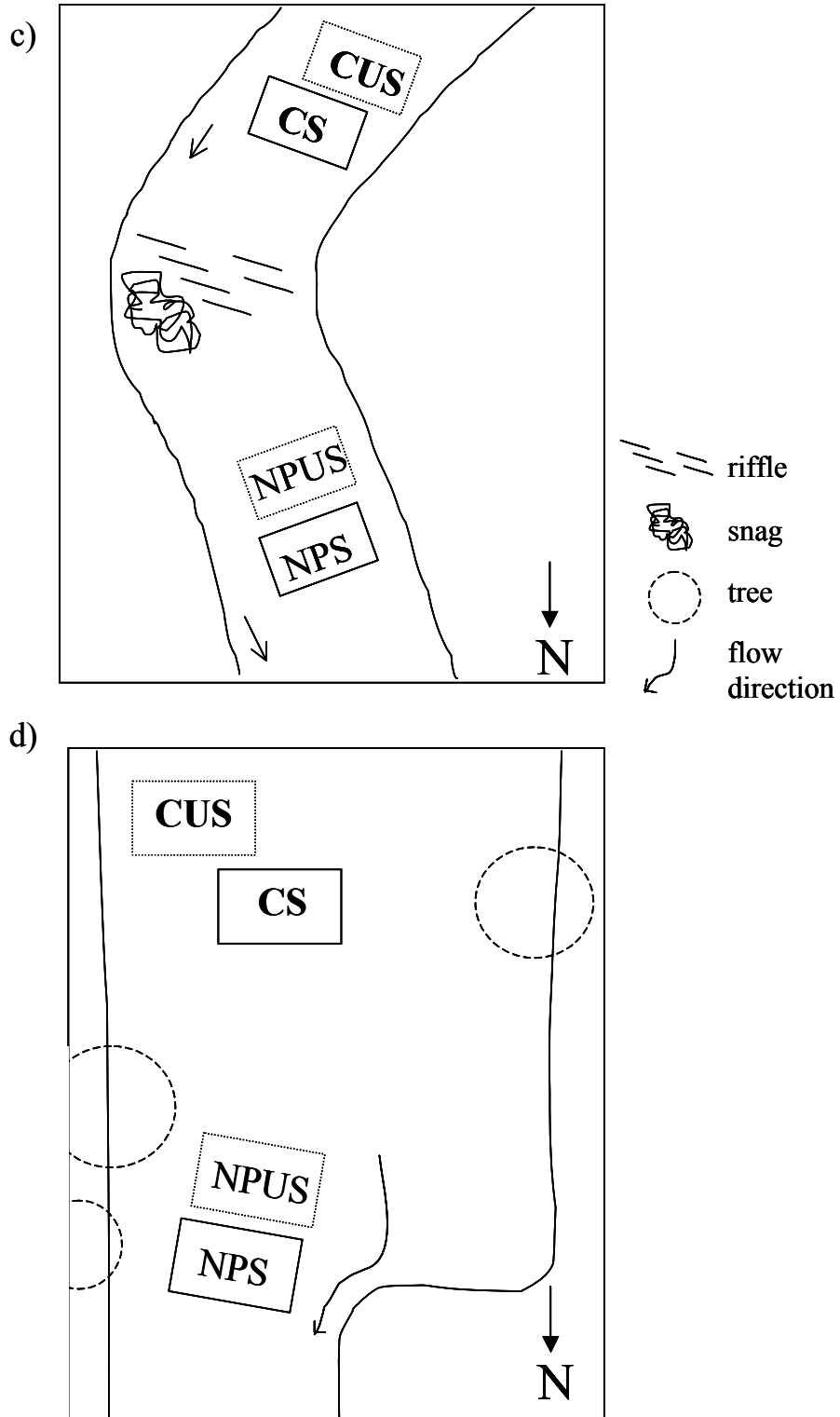
Appendix F

Calculations of algal cell density (see 4.3.3)

For each sample:

- 100 μl of sub-sample were extracted using a micropipette and evenly spread on a slide with a 22 x 50 mm cover slip.
- Each cover slip was divided into a grid of 10 x 5 mm and 10 randomly chosen points were selected for each slide.

Therefore the full calculations were as follows:

- The total area of a cover slip is 22 mm x 50 mm= 1100 mm^2
- The diameter of the field of vision is 325 μm.
- The area sampled per point is πr^2 = 82946 μm^2 = 0.082946 mm^2
- The total area sampled per slide 0.082946 x 10 = 0.82946 mm^2
- The ratio (0.82946/1100) x100= 0.075% of slide was sampled.
- Volume sampled per slide 0.00075 x 100 = 0.075 μl sampled per slide
- 2 slides per sample were examined, then 0.15 μl were observed per sample.
- Thus the results are expressed in number of filaments, colonies and cell / 0.15 μl of solution.

Example: If there are 300 cells of *Ulothrix*, then in numbers of cells/ volume there are 300 / 0.15 = 2000 cells/ μl or 2000000 cells/ ml.

One ml of sample represents a proportion of the total sample. This proportion represents the proportion of surface area from which that millilitre was sampled.

For example, if the sample represents 0.002 of the total volume, and the total volume was taken from 40 mm^2, then the sample was effectively taken from 0.002 * 40 = 0.80 mm^2.

Finally the number of cells/ml was divided by this surface area to get cells/mm^2.

Taxa accumulation curves from nutrient and shading experiment for grazers for a) treatments with low grazer abundance; b) treatments with moderate grazer abundance; and c) treatments with high grazer abundance. U=Upper, L=Lower, B=Brisbane and C=Coomera.
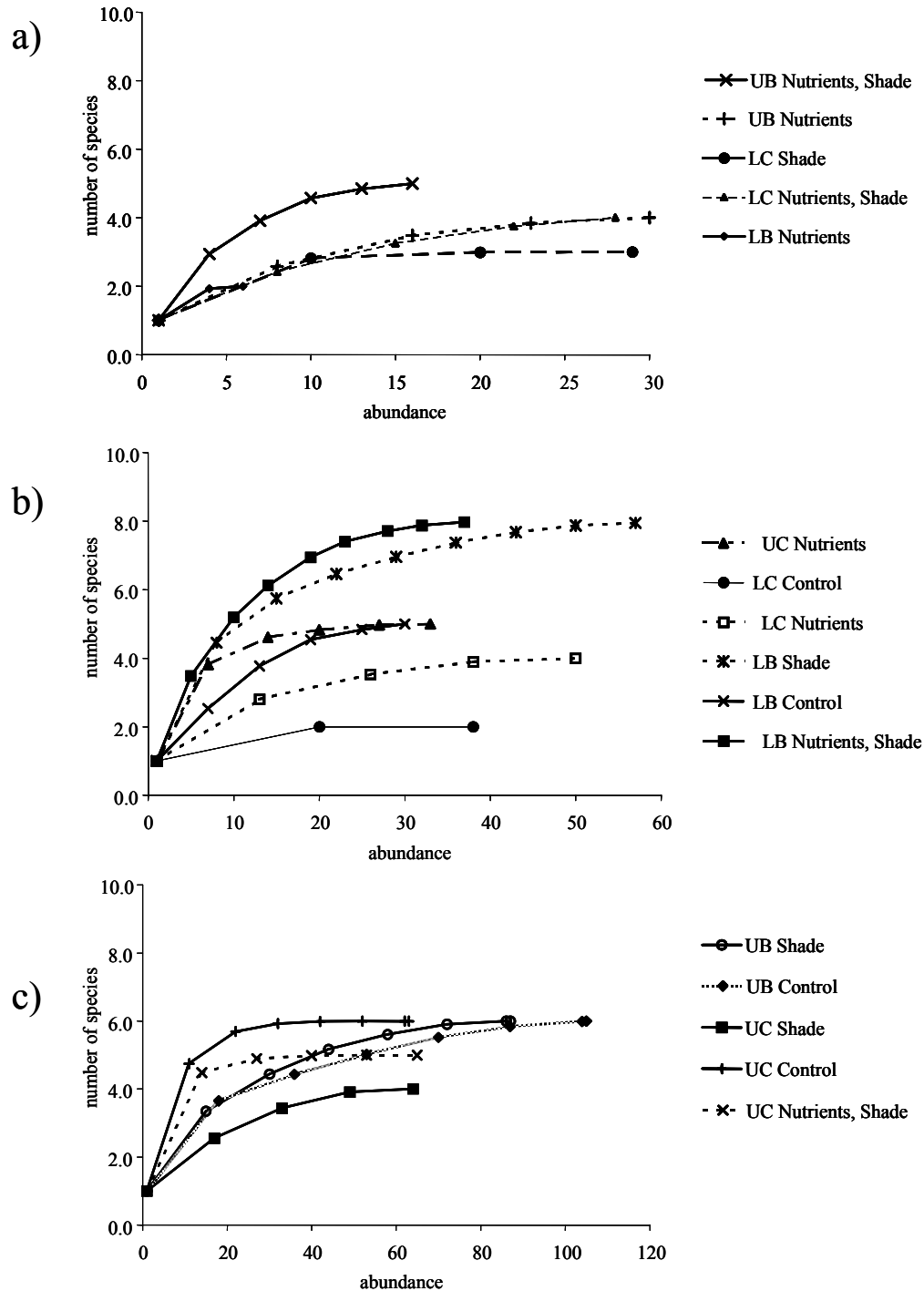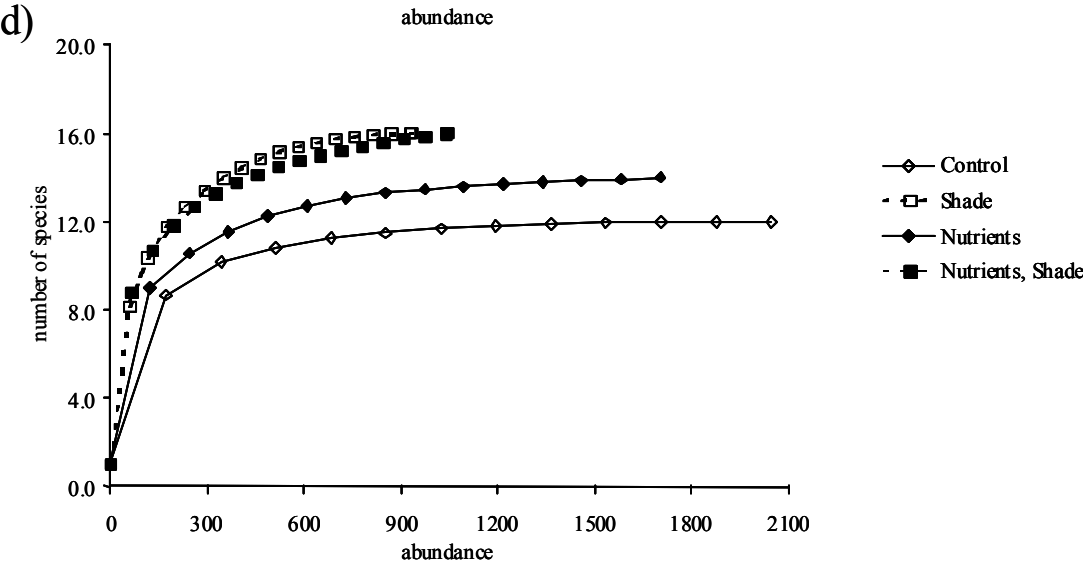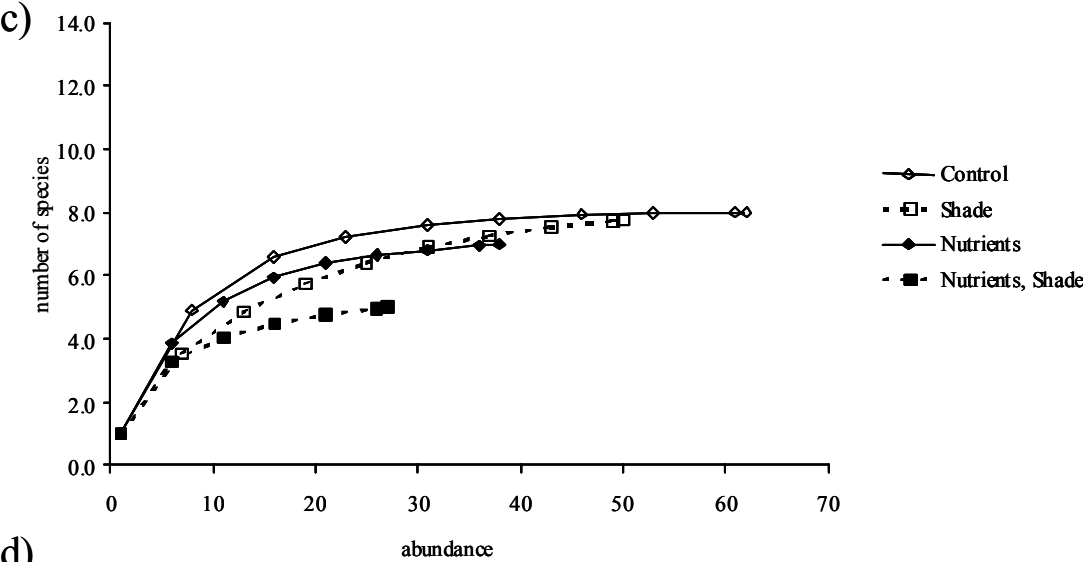
Taxa accumulation curves from nutrient and shading experiment for algae for a) Upper Brisbane and b) Lower Brisbane.
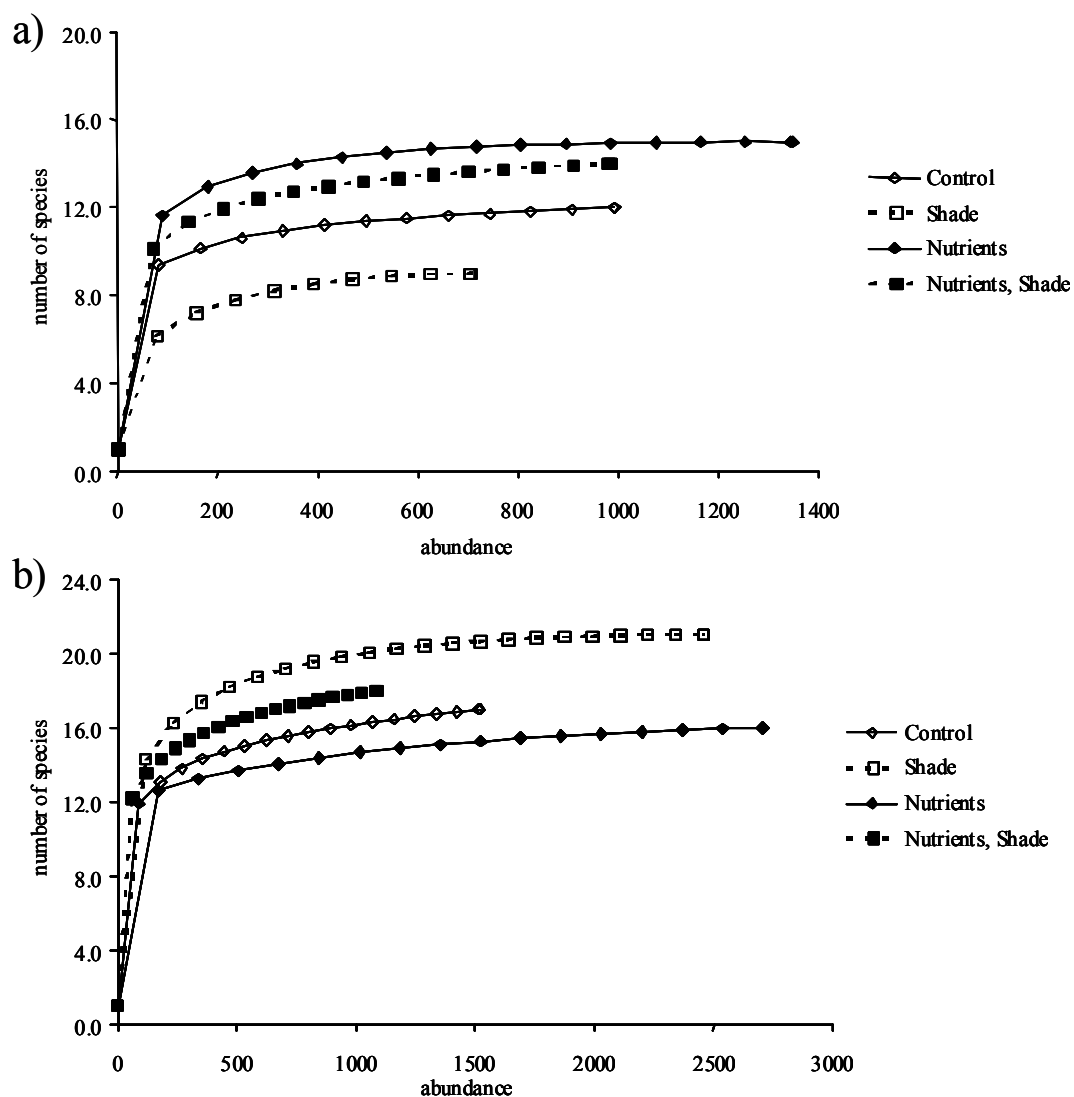
Taxa accumulation curves from nutrient and shading experiment for algae for c) Upper Coomera and d) Lower Coomera.

Appendix I

Equations for all regression relationships from Chapter 4.

1. Regression equation from Pollock *et al.* (1998) $y = \beta_0 + \beta_1 * x * e^{(\beta_2 * x^{\beta_3})}$

2. Linear equation $y = \beta_1 x + \beta_0$

Independent variable	Dependent variable	Equation
relativised GPP	relativised algal diversity	1. $\beta_0=0.3715$, $\beta_1=2.011$, $\beta_2=-1.100$, $\beta_3=2.001$
	relativised number of grazer taxa	1. $\beta_0=0.8184$, $\beta_1=1.010$, $\beta_2=1.716$, $\beta_3=142.7$
	relativised grazer density	1. $\beta_0=0.9063$, $\beta_1=0.4964$, $\beta_2=-0.4440$, $\beta_3=334.8$
	relativised sedentary grazer density	not significant
	mobile grazer density	1. $\beta_0=-1.237$, $\beta_1=18.54$, $\beta_2=2.296$, $\beta_3=0.7478$
	mobile: sedentary ratio	not significant
relativised FAC	relativised GPP	2. $\beta_0=0.3167$, $\beta_1=0.7185x$
	relativised algal diversity	1. $\beta_0=0.7372$, $\beta_1=1.054$, $\beta_2=-1.505$ $\beta_3=3.070$
	relativised number of grazer taxa	1. $\beta_0=0.9331$, $\beta_1=1.8159$, $\beta_2=23.203712$, $\beta_3=5.085$
	relativised grazer density	not significant
	relativised sedentary grazer density	1. $\beta_0=1.331$, $\beta_1=0.0419$, $\beta_2=0.0406$, $\beta_3=-0.2172$
	relativised mobile grazer density	1. $\beta_0=7.138$, $\beta_1=-116702$, $\beta_2=9.848$, $\beta_3=0.1152$
	relativised mobile: sedentary ratio	not significant
relativised number of algal taxa	relativised number of grazer taxa	1. $\beta_0=1.001$, $\beta_1=3.732$, $\beta_2=-4.087$, $\beta_3=-2.352$
	relativised grazer density	not significant

relativised sedentary grazer density	not significant
relativised mobile grazer density	1. β_0=-1.041, β_1=2.394, β_2=0.1850, β_3=5.176
relativised mobile: sedentary ratio	1. β_0=-0.5161, β_1=1.3298, β_2=0.5137, β_3=1.633