FLOOD DISTURBANCE RESPONSES OF INVERTEBRATE ASSEMBLAGES IN TWO COBBLE-BOULDER BED RIVERS OF THE WESTERN CAPE

Report to the
Water Research Commission

by

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WRC Report No 1411/2/08
ISBN 978-1-77005-646-6
Set No 978-1-77005-644-2

JUNE 2008

Obtainable from:

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This report emanates from a research project entitled “Determination of Substrate Maintenance Flows in Cobble and Boulder Bed Rivers: Ecological and Hydraulic Considerations” (WRC Project No 5/1411).

This report forms part of a series of two reports. The other report in this series is “The Development of a Hydraulic Model for Determining Bed Disturbance due to Floods in Cobble and Boulder Bed Rivers” (WRC Report no 1411/1/08).

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LIST OF SYMBOLS AND ABBREVIATIONS

a, b, c : Constants
A : Cross sectional flow area
C_d : Drag coefficient
C_x : Large scale roughness coefficient
d : Particle diameter
d_x : Particle size for which x % is smaller
D : Flow depth
DC : DRIFT flood class
EFR : Ecological Flow Requirements
Fr : Froude number
*F** : Particle densimetric Froude Number
g : Gravitational acceleration
I : Intensity of movement
k : Absolute bed roughness
M : Movability number
PM : Probability of movement
Q : Discharge
r : Rate of increase of percentage of movement
Re : Reynolds' number
Re_* : Particle Reynolds' number
s : Energy slope
S_f : Energy gradient
S_0 : Bed slope
U : Mean velocity
V_{ss} : settling velocity
y : distance above bed
z : bed elevation above datum
α : descriptive reach parameter
κ : Von Karman "constant"
θ : Shield's parameter
θ_{crit} : Critical Shield's parameter
μ : Dynamic viscosity
v : Kinematic viscosity
ρ : Density of water
ρ_s : Particle density
τ_0 : Bed shear stress
τ_{crit} : Critical bed shear stress

ACKNOWLEDGEMENTS

The research team would like to acknowledge the WRC for funding this research project as well as the members of the Steering Committee for their advice and guidance. The members of the Steering Committee are as follows:

Dr SA Mitchell	Water Research Commission (Chairperson – Year 1 and Year 2)
Dr MS Liphadzi	Water Research Commission (Chairperson – Year 3)
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Dr A Birkhead	Streamflow Solutions
Dr CJ Kleynhans	DWAF / IWQS
Mr MK Reinecke	University of Cape Town
Dr JM King	University of Cape Town
Prof KH Rogers	University of the Witwatersrand

This project owes enormous gratitude to Candace Hill and Sandile Koni who undertook the laboratory processing of invertebrate data and together sorted, identified and measured thousands of individual animals. Liesl Phigeland is also thanked for processing of periphyton samples and invertebrate sample sorting, as is Katy Lannes and Imtiyaz Ishmael, both students assisting with laboratory work. In addition the authors would like to acknowledge the following for their assistance in the gathering of data, which involved many hours, much of it underwater, in a cold mountain stream in the middle of winter: Charlene April, Tamsin Byfield, (late) Bruce Davison, Belinda Day, Justine Ewart-Smith, Candace Hill, Sandile Koni, Meg Ledeboer, Malusi Mslathelwa, Luyanda Phillip, Andrea Plos, Kate Snaddon, Mpumzi Tofu and Eric Malatsi. Denise Schael is also thanked for assistance with processing of statistical data and compilation of graphs.

EXECUTIVE SUMMARY

Introduction

This is an Extended Executive Summary for two Reports that present the findings of WRC Research Project K5/1411 and titled: *Determination of Substrate Maintenance Flows in Cobble and Boulder Bed Rivers: Ecological and Hydraulic Considerations.* The two Reports, which can be obtained from the Water Research Commission of South Africa, are titled:

- *The Development of a Hydraulic Model for Determining Bed Disturbance Due to Floods in Cobble and Boulder Bed Rivers*
- *Flood Disturbance Responses of Invertebrate Assemblages in Two Cobble and Boulder Bed Rivers of the Western Cape*

The first of these Reports, referred to as the Hydraulics Report, outlines the development of a mathematical hydraulic model used to predict bed disturbance under particular flood events by way of a simple empirical model that relates the DRIFT flood class to the intensity of movement (i.e. the total percentage of cobbles that move), and a more detailed model that looks at the probability of movement of individual stones in cobble and boulder bed rivers based on a critical Movability Number that represents the ratio of applied power to required power. This Report also presents preliminary guidelines for the determination of substrate maintenance flow requirements for cobble and boulder bed rivers based on the findings of the aforementioned two Reports.

The second Report, referred to as the Ecological Disturbance Report, considers the relationship between bed disturbance due to flood events and the impact and response of invertebrate assemblages in the two observed cobble and boulder bed rivers in the Western Cape. This Report also analyses the distribution of invertebrates during winter base-flow conditions and relates this to stone size and various hydraulic variables.

Aims and Objectives

The overall objective of this research project is to lay the foundation for the development of guidelines for the determination of substrate maintenance flow requirements to ensure the sustainability of cobble and boulder bed river ecosystems. The specific aims required to attain this objective are addressed in terms of the following deliverables:

1. Develop a theoretically based hydraulic model that will address the relationship between discharge and substrate disturbance in cobble and boulder bed rivers.
2. Define and quantify ecologically significant substrate disturbance levels in cobble and boulder bed rivers.
3. Develop guidelines for the specification of substrate maintenance flow components in cobble and boulder bed rivers.

The above aims have been met through the collection and analysis of data from two flood seasons on two mountain streams in the Western Cape of South Africa. The results of these deliverables are presented and discussed in the two reports referred to earlier and are summarised in this extended executive summary.

Literature Review

A literature review was undertaken to synthesise current knowledge on existing hydraulic models for incipient motion in cobble and boulder bed rivers, and on stream ecosystem disturbance by floods. The latter topic included consideration of existing approaches to both the measurement of the disturbance event and the quantification of the disturbance response by stream invertebrates and periphyton as a major food source in open-canopied rivers.

Data Collection

The research was conducted in two relatively undisturbed mountain streams in the Western Cape, the Molenaars River and the Berg River. Close to 800 stones ranging in size from 25 mm to 1100 mm per median diameter were marked, 345 in the Molenaars and 435 in the Berg, just prior to the start of the flood season. The dimensions of each stone were recorded in terms of the three major axes and the base-flow hydraulic characteristics of depth and velocity were also recorded. In addition, samples were taken for the analysis of invertebrates and periphyton.

The movement or non-movement of the marked stones was recorded after each of thirteen flood events at both study sites. The floods ranged from small freshettes that resulted in negligible disturbance to bankfull floods. The largest observed flood resulted in the movement of 44% of the marked stones at one of the study sites. After each flood event, the marked stones were located and returned to their original position in preparation for the next event. In addition to recording the movement or non-movement of stones, pre- and post-flood sampling was done of the invertebrate and periphyton communities for a number of flood events to determine the level of disturbance due to the flood events.

Hydraulic model to predict movement of individual stones

A theoretical mathematical model was first developed based on the theory of applied power. This model defines incipient motion as the point at which a stone is more likely to move than to not move (i.e. the critical value is when the probability of movement is greater than 50%). The theory of unit stream power was used to develop a Movability Number that represents the ratio of applied power to required power in cobble and boulder beds with non-uniform bed material. The critical value was determined using the observed data as:

$$\frac{\sqrt{gDs}}{V_{ss}} \cdot \left(\frac{d}{k}\right)^{1/3} = 0.12$$

with D : flow depth, measured down to the top of the stone.

d : individual stone diameter measured on the second longest axis

s : energy slope

V_{ss} : Turbulent settling velocity ($V_{ss} = \sqrt{\frac{4(\rho_s - \rho)gd}{3\rho C_d}}$)

k : absolute bed roughness (k = minimum of d_{84} or D)

d_{84} : particle diameter for which 84% of particles are smaller

C_d : drag coefficient ($C_d = 0.4$)

ρ : density of water

ρ_s : density of particle

g : acceleration due to gravity (g = 9.81 m/s^2)

For uniform beds the absolute roughness can be represented by the average stone size (i.e. $k = d$). In this case the equation is equal to that found to represent the threshold of movement on uniform beds by Rooseboom (1998) as depicted in the Liu Diagram.

In addition to the initially marked and sampled stones, a number of additional stones were also sampled for invertebrates and periphyton after a series of flood events. The above model was used to determine whether these additional stones would have been likely to have moved under the previous flood events.

These stones were used to extend the analysis of the impact of flood disturbance on invertebrate assemblages and as a control for the impact of the initial sampling method.

It is important to note that this relationship was developed using data obtained from only thirteen flood events and from only two streams. The average bed slope of the Molenaars study reach was 0.018 m/m and for the Berg studies reach it was 0.015 m/m. The observed particles were all in the cobble to boulder range with a maximum stone size of just over 1 m in diameter. The d_{84} for the Molenaars study reach was 538 mm while the d_{84} for the Berg study reach was 372 mm. The d_{50} for the Molenaars study reach was 248 mm while the d_{50} for the Berg study reach was 205 mm.

It is unclear at this stage if this represents a universal finding for all rivers of non-uniform particle size distribution. To be able to answer this will require the model to be tested on other rivers. The results from the two rivers tested, however, where consistent despite being of different size and having different stone size distribution. Based on this observation it could be hypothesized that the above results will be universal at least in the case of cobble and boulder bed rivers.

Average Bed Disturbance in Relation to DRIFT Flood Class

A second empirical model was also developed that related the intensity of movement or stream competence to the DRIFT flood classification. This relationship was described by the equation:

$$I = \frac{e^{34.3.\alpha.DC}}{96.9.\alpha} \quad \text{with} \quad \alpha = S_0 \frac{d_{84}}{d_{50}}$$

where I = the intensity of movement as a percentage

DC = the DRIFT flood classification

S_0 = the average bed slope

d_{84} = the median stone diameter for which 84% are smaller

d_{50} = the median stone diameter for which 50% are smaller

It is important to note that this reach factor (α) is only provisional at this stage. The above relationship is based on a few samples in only two rivers in the Western Cape. The above equation is therefore a proposal for a possible form of universal relationship between the intensity of movement (I), the DRIFT flood class (DC) and the specific reach characteristics (α).

Further research and testing of this relationship on other rivers is important before the above relationship can be considered for use in environmental flow assessments and rehabilitation studies.

This relationship will enable scientists to get a first order estimate of the level of disturbance likely to be associated with a particular flood class for cobble and boulder bed rivers. This can then be used to set the required flood magnitude for the desired level of ecological disturbance. It will also enable the practitioner to make a more informed judgement on the impact of having more or less flood of a certain class in the managed flow regime as part of the DRIFT flood classification methodology.

Relationship between Invertebrate Fauna and Hydraulic Variable

A baseline survey of the invertebrate fauna of both rivers showed that invertebrate assemblages in the Molenaars River appeared to have stronger relationships than was the case in the Berg River, between their density distribution and hydraulic parameters such as point measurements of velocity, depth, or defined in terms of hydraulic biotopes. The most significant relationships identified through analysis of the baseline survey data, however was a negative linear correlation between invertebrate density and stone particle size for both the Berg and Molenaars Rivers, which indicates that some 25 - 31% of overall invertebrate density can be explained by particle size. The strength of this relationship

varied between taxa with only a few taxa exhibiting a positive association with particle size. More taxa were significantly correlated with stone particle size than any other variables.

Post Disturbance Recovery: The Molenaars River Study Site

Ecological data were only collected at the Molenaars site in 2003. This happened to be a very dry year and as a result the floods analysed with pre- and post-flood sampling were very small and resulted in less than 3% of bed disturbance. The study data were then best used to examine recovery processes after an initial disturbance - the initial denudation of stones during the pre-season sampling - emulating artificial disturbance studies prevalent in the scientific literature.

Recovery rates of the invertebrate taxa following initial disturbance were highly variable, and recovery was slower than that measured in other studies. Species-specific responses were identified and explained, in terms of mobility, population structure and initial population densities, as well as recovery rates of periphyton and food resource quality on disturbed substrata. Some findings indicating high levels of micro-habitat specificity and potential competitive interactions were also discussed.

The minor floods that occurred during the sampling period affected the recovery of invertebrates on denuded substrata to different degrees. In some of the taxa which had shown little initial recovery, the increased velocities associated with the floods were considered to have increased effective mobility and facilitated recolonisation.

Where recovery after initial sampling was rapid, the taxa exhibited various responses to the small flood events, ranging from apparent flood-induced emergence, or susceptibility of only large instars to floods, through various levels of susceptibility of the population to increased flows, including no measurable response to increased flows. In other words, there are large differences in the extent to which species perceive small floods as disturbance.

These species-specific responses to small flood flows are summarised in **Table 1**.

It should be noted that these data must be considered preliminary, since the patchiness of invertebrate distributions, especially when abundances were low, as well as the wide variance associated with estimates of population density precluded statistically significant results in most instances. Nevertheless, they do represent the first species-level data for flood-related responses on invertebrates in Western Cape rivers.

Table 1: Summarised species-specific responses to small early winter floods in the Molenaars River, 2003

SPECIES / TAXON	SUSCEPTIBILITY TO FLOODS	
	Description	**Change in density over flood period**
Species showing high resilience (good / full recovery after initial sampling, before floods)		
Afroptilum spp.	differential loss small instars	↓
Demoreptus capensis	recruitment of new instars	≈
Pseudocloeon sp.		↓↓
Euthraulus elegans		≈
Lithogloea harrisoni	recruitment of new instars	↑↑↑
Afronurus harrisoni	differential loss large instars or flood-mediated emergence	↓↓
Afronurus sp.		↓↓
Notonemouridae	recruitment of new instars	↑↑↑
Simulium spp.	recruitment of new instars	↑↑↑
Orthocladinae		≈
Tanypodinae		↓↓
Helodidae		≈
Hydrachnellae		↓
Species showing medium resilience (moderate recovery after initial sampling, before floods)		
Baetis spp.	may be associated with food quality	↓
Demoulinia spp.		↓
Lestagella penicillata		≈
Aprionyx spp.	Autumn emergence - small numbers depleted by floods	↓↓↓
Tanytarcini		≈
Chironomini		≈
Species showing low resilience (poor or no recovery after initial sampling, before floods)		
Cheumatopsyche afra		food-facilitated partial recovery
Chimarra sp.		flood-facilitated partial recovery
Agapetus agilis	recruitment of new instars	pattern not clear
Elporia spp.	recruitment of new instars	≈
Elmidae larvae		flood-facilitated partial recovery
Elmidae adults		↓

Note: The resilience of different taxa is indicated categorically as 'high', 'medium' or 'low', based on the extent of recovery observed in the month after initial baseline sampling, but prior to floods. Susceptibility to flow is also provided within categories of percentages, because of the low level of significance in the results. These categories are as follows: ≈- no change (± 24% increase or decrease); ↓ (25 - 69% decrease); ↓↓ (70 - 84% decrease); ↓↓↓ (85 - 100+% decrease). Arrows facing upwards indicate increases in density.

Invertebrate Responses to Large, Within-year Flood Events

In the Berg River in 2004 there were two large intra-annual floods during the study period that moved between 25 and 43% of the marked bed particles, and three minor spates (DRIFT Class I and II) that moved less than 3%. The larger floods represented a low and a high DRIFT Class IV flood, and moved all size categories of river bed materials (small cobble through to boulders), but to different degrees. These larger floods are more akin to descriptions of 'disturbance' used in the scientific literature, although the cumulative effect of small floods on population dynamics should not be ignored.

The floods in the Berg River were associated with some 58% decrease in total invertebrate density, cumulative for the two-month period. Nearly all individual invertebrate taxa declined significantly, whilst three mayfly taxa increased in densities on stones over the study period. The large floods on the Berg River appeared to exceed a disturbance threshold for other taxa that were not affected by the smaller floods on the Molenaars River, for example, species of Simuliidae.

The Berg River study allowed for the effects of stone movement or non-movement during floods to be described, in relation to the magnitude of the disturbance-response by invertebrates. The percentage decrease in total invertebrate density on stones that were unmoved over the whole study period, relative to those that moved in both large floods was 40% and 62% respectively, a difference of some 20%. This result indicates that, despite obvious flood-induced mortality, many taxa were still present in reasonable densities on moved stones - an unanticipated finding. These results also indicate a 'relative refugium' afforded to invertebrates on stable stones. Whilst this was only some 20 % for total invertebrates, it was shown to be more or less important for different taxa. It is noteworthy, however, that a number of taxa virtually only survived floods because of the relative refugium of unmoved stones - viz. Leptophlebiidae, most Trichoptera, and the mayfly *Afroptilum spp*. Similarly, *Lithogloea harrisoni*, which appears on the river bed at the start of winter, only increased in population density on unmoved stones.

The responses to floods on both unmoved stones vs. those moved in both large floods are summarised in **Table 2**, for invertebrate taxa, which were represented in sufficient densities in order to show patterns. The susceptibility to flow is a measure of the extent to which the series of floods reduced population densities.

Table 2: Summarised species-specific responses to winter floods in the Berg River, 2004, showing the relative refugium from flood mortality afforded by unmoved stones.

SPECIES / TAXON	UNMOVED STONES		STONES MOVED IN BOTH LARGE FLOODS	
	Repeat-sampled	Additional	Repeat-sampled	Additional
No relative refugium offered on unmoved stones				
Demoreptus capensis	↓↓↓	↓↓	↑↑↑	↑↑↑
Notonemouridae	↓	↓	≈	↑
Simulium spp.	↓	↓↓	≈	≈
Demoulinia spp.	↓↓↓	↓↓↓	↓↓↓	↓↓↓
Cheumatopsyche afra	↓↓↓	↓↓↓	Not present in Baseline	
Tanypodinae	↓↓↓	↓↓↓	↓↓↓	↓↓↓
Orthocladinae	↓	↓	↓	↓
Elmidae adults	↓↓	↓↓↓	↓↓↓	↓↓
Elmidae larvae	↓↓	↓↓	↓↓↓	↓↓
Low relative refugium offered on unmoved stones				
Cheumatopsyche maculata	↓↓↓	↓↓	↓↓↓	↓↓↓
Athripsodes bergensis	↓↓	↓↓↓	↓↓↓	↓↓↓
Afronurus sp.	↓↓↓	↓↓	↓↓↓	↓↓↓
Aprionyx spp.	↓↓	↓↓↓	↓↓↓	↓↓↓
Chironomini	≈	≈	≈	↓
Baetis spp.	↓	≈	↓	↓
Hydrachnellae	↓	↓	↓↓	↓
Euthraulus elegans	↓↓	↓↓	↓↓↓	↓↓↓
Chimarra sp.	↓↓↓	↓	↓↓↓	↓↓↓
Afronurus harrisoni	↓	↓↓↓	↓↓	↓↓↓
Tanytarcini	↓↓	↓	↓↓↓	↓↓
Moderate to high relative refugium offered on unmoved stones				
Lestagella penicillata	↓	↓	↓↓↓	↓↓↓
Helodidae	↓	↓	↓↓↓	↓↓↓
Afroptilum spp.	↑	↑	↓↓↓	↓↓↓
Lithogloea harrisoni	↑↑↑	↑↑↑	↓	≈

Note: Susceptibility to flow is based on percentage reduction in population density, and provided within categories of percentages. These categories are as follows: ≈- no change (± 24% increase or decrease), ↓ (25 - 69% decrease); ↓↓ (70 - 84% decrease); ↓↓↓ (85 - 100+% decrease). Arrows facing upwards indicate increases in density.

Summary of Flood Disturbance Response of Invertebrate Assemblages

The key findings of the analysis of flood disturbance responses of invertebrate assemblages in the two rivers studied are summarised below:

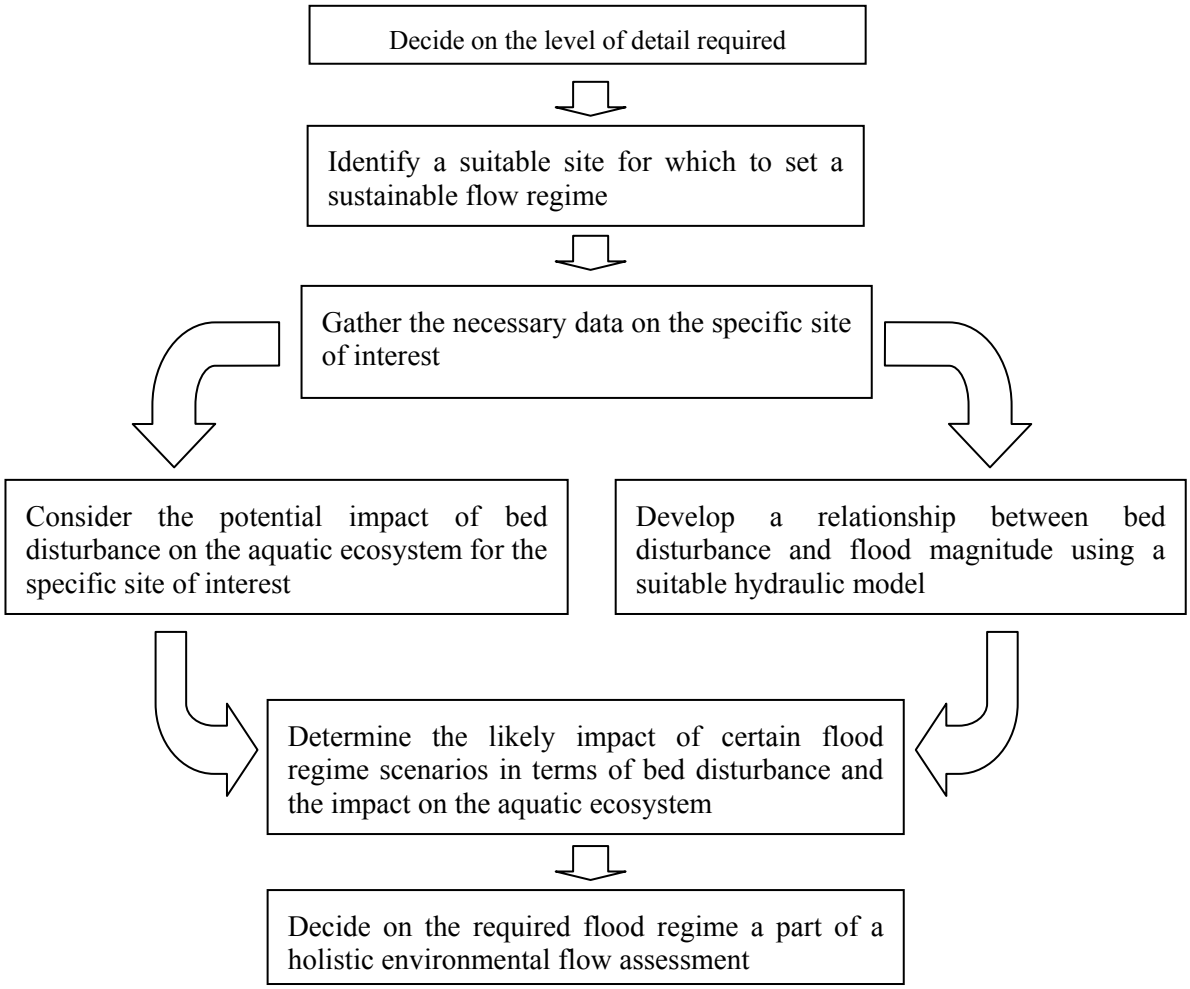
- Large, but regularly occurring, intra-annual floods are associated with higher levels of population reductions and affect all stream invertebrates.
- Movement of substratum particles is not a threshold for disturbance-responses, since almost all taxa were reduced on unmoved as well as moved substrata.
- There is a wide difference in the relative refugium afforded to different taxa, as a result of some substrata remaining stable over a flood.
- Resistance to floods at a reach level is considerable, indicated by a 58% overall reduction in invertebrate density (or 42% survival) as a result of two floods that moved between 25 and 43% of the river bed particles, in all size classes.
- Resistance to floods may be exaggerated by the immigration of new individuals of some species, in the form of new recruits of small instars from the hyporheos or upstream reaches, which would constitute a resilience response to floods in these taxa.
- No direct relationship was found between invertebrate densities after a flood and the distribution of maximum forces acting on bed particles during the flood, measured as unit applied stream power, possibly as a result of micro-scale movements of invertebrate within or on the same substratum particle.

These results add to the current understanding of how floods may affect ecological processes regarding species interactions, since they clearly demonstrate substantial differences in the disturbance-response between different and potentially competing species. The preliminary species-specific results may aid in setting flow requirements in rivers, particularly where there is evidence of species interactions, or where pest species (e.g. Chironomidae, Simuliidae) may proliferate under low disturbance regimes.

Guidelines for the Determination of Substrate Maintenance Flows

Proposed guidelines for the determination of substrate maintenance flows have been developed and are presented in the Hydraulics Report. The proposed guidelines are intended for use in the DRIFT method of defining environmental water requirements, but they can also be applied to any other method. The proposed guidelines are summarised in **Figure 1**.

Figure 1: Proposed Guidelines for the determination of substrate maintenance flows in cobble and boulder bed rivers



The proposed guidelines draw on the findings of this Study in terms of recommendations for a suitable hydraulic model for predicting either the average level of bed disturbance based on DRIFT flood class, which could be used for a simple intermediate level reserved determination study, or the more detailed model that predicts the movement of individual stones based on the critical ratio of applied power to required power, also known as the movability number. For a more detailed comprehensive reserve determination study, an understanding of the impact of particular floods on the movement of individual stones can be used in conjunction with an understanding of how stone movement impacts on the populations of particular key invertebrate species, to determine the suitability of a specific flood regime.

It is important to note that the proposed guidelines are only preliminary in that they need to be considered in the light of the broader requirements for determining environmental water requirements for rivers.

Recommendations for Further Study

It is important to note that the models and guidelines presented in this Report are based on a limited sample of thirteen flood events in two rivers in the Western Cape. It is important that the recommendations made in these Reports are tested on other rivers and for other flood events, before they can be fully developed. These and other research recommendations with regards to the hydraulic model are listed below:

- Further investigations into reduction in transport capacity due to the presence of bed forms in cobble and boulder bedded rivers in addition to the influence of non-uniform bed material.
- A study of the equilibrium distribution of stone sizes in cobble and boulder bedded rivers with particular reference to the presence of bed forms such as clusters of larger stones with smaller stones located inside.
- Developing a better understanding of the mechanisms for energy dissipation in sheltered areas of the bed through detailed field observations and possible laboratory experiments and the impact that this will have on the incipient motion of stones in these sheltered hollows.
- Investigate ways of determining absolute bed roughness (k) and energy slope (s) at particular points where stones are located on the bed of cobble and boulder bed rivers.
- Analysis of the structure of stable bed forms to determine if these can be identified and quantified in a study reach and the relevance that this will have on determining the bed roughness and the amount of refugia available for stream ecology.
- Further study is required to confirm the proposed empirical relationship between the intensity of movement and the DRIFT flood class. In particular the use of the reach characteristic term (α) needs to be tested on other rivers.

With regard to the investigation into the flood disturbance response of invertebrates in cobble and boulder bed rivers, it is important to note that the observational data on which this research was based, effectively represents only three replicates in what might be a highly variable set of responses to floods, dependent on not only the specifics of the flood hydrograph (peak and duration), but the timing with the season, initial population densities, and the like. Seasonal and inter-annual differences in responses are likely to be considerable, and these need to be investigated to substantiate these results.

The relatively successful outcome of the hydraulic model developed to describe incipient motion, in terms of its ability to indicate the movement status of previously unmarked river stones, raises the potential for simpler studies on flood responses to be undertaken in the future, free from the complicating error effects of repeat-sampled stones. This will enable large sample sizes to be processed, with more robust results.

1 INTRODUCTION

1.1 BACKGROUND

In cobble-bed rivers, many aquatic organisms are dependent on the channel bed for their survival. Depending on the species and life-cycle, the channel bed provides refuge from floods, shelter during droughts and from extreme temperatures, as well as interstitial spaces in which to lay eggs. Sufficient flow through the interstitial spaces allows the replenishment of nutrients and oxygen while metabolic wastes are continuously removed. Cobble- and boulder-beds are associated with complex periphyton – invertebrate dynamics; assist with the physical breakdown of organic detritus through the creation of turbulence in a heterogeneous bed; and provide a mechanism for entrainment of organic matter in the spaces between larger bed elements. Species differ in their substratum preferences and requirements. The suitability of substrata for colonisation by aquatic fauna and flora depends inter alia on the particle-size distribution, the size of interstitial spaces and the degree of embeddedness. The channel bed of cobble- and boulder-bed rivers is often referred to as a 'faunal reservoir', as it provides a source of individuals for recolonisation of a stream if invertebrate populations are depleted by adverse conditions.

To ensure a healthy and biodiverse ecosystem in cobble- and boulder-bed rivers, it is imperative that the channel bed is maintained in a condition that will allow for the habitat requirements and functions described above to be met. In pristine catchments this is achieved by the range of flows characteristic of the natural flow regime, which typically incorporates flows of different timing, duration and frequency. The construction of dams however, leads to a change in the flow regime, the flooding magnitude and frequency as well as the sediment-transport capacity in the river channel downstream. This has a definite, often negative, impact on the dynamics of substratum movement and maintenance, which in turn affects the biotic faunal and floral aquatic environment. The wise management of the flow regimes of regulated rivers thus requires that the environmental flow requirement for these rivers accommodates a 'substratum maintenance' flow component. The limited availability of water, the cost of water that is released and lost for storage and the financial implications associated with the installation of outlet structures at reservoirs, emphasise the need to specify substratum maintenance flows as accurately as possible.

However, the determination of a 'substratum maintenance' flow component is complicated by various factors. Firstly, there is very little scientifically-based data available regarding the impacts (both positive and negative) of different levels of substratum disturbance on the aquatic environment. Furthermore, it is necessary to contend with the complexity of flow and sediment transport processes in cobble- and boulder-bed rivers. This includes the effects of large-scale roughness, macro-scale bedforms, the heterogeneous nature of the substratum particles and the effects of hydraulic shielding on the critical flow conditions required to initiate sediment movement. In order to facilitate the specification of 'substratum maintenance flows' in cobble- and boulder-bed rivers, which can be incorporated into either an environmental flow requirement or river rehabilitation

programme, knowledge of the relationships between substratum disturbance, the aquatic environment and discharge is critical.

1.2 AIMS AND OBJECTIVES

The objective of this research project is to lay the foundation for the development of guidelines for the determination of substratum maintenance flow requirements to ensure the sustainability of cobble- and boulder-bed river ecosystems. The specific aims required to attain this objective are addressed in terms of the following deliverables:

1. Develop a theoretically-based hydraulic model that will address the relationship between discharge and substrate disturbance in cobble- and boulder-bed rivers
2. Define and quantify ecologically significant substratum disturbance levels in cobble- and boulder-bed rivers.
3. Develop guidelines for the specification of substrate maintenance flow components in cobble- and boulder-bed rivers.

Each of these objectives is addressed in a separate report, aimed at potentially different users. This report relates to the second of these three aims and describes the responses of aquatic invertebrates to floods of different magnitudes. The focus of the investigation was to link the level of disturbance of individual particles within the stream bed to the invertebrate response, using data collected on two rivers in the Western Cape over two winter flooding seasons in 2003 and 2004.

1.3 REPORT FORMAT

Chapter 2 of this report will present a literature review that looks at definitions and the current state of knowledge of what constitutes flood disturbance and how it affects stream fauna, in ecological stream disturbance studies. The focus of the review is on invertebrate fauna. The review includes a brief description of various approaches to measuring disturbance, both as a physical event and as an ecological response.

Chapter 3 is a description of the methodology employed for data collection and analysis, and a summary of the results from the hydraulic model development (the first objective outlined in section 1.2 above) is included in Chapter 4. This model was used to assign the disturbance level of one of the sets of data analysed in this invertebrate response study. Chapters 5 and 6 present the results of this study, followed by conclusions emanating from the project and recommendations for further work.

2 LITERATURE REVIEW

2.1 INTRODUCTION

Spatial patterns and patchiness of invertebrate distribution partly reflect the layering of temporal dynamics on environmental gradients (Ward, 1998). Ecologically meaningful temporal scales at which patterned change may be observed can range from days or weeks (e.g. colonisation of the stream-bed in intermittent streams) to geological events (Minshall, 1988). At an intermediate time scale, variability in physical conditions may have a pronounced effect on measures of community composition. For example, the increased faunal diversity in the mid-reaches of rivers versus headwaters or lower river zones has been ascribed in part to the more temporally variable temperature regimes in these mid-reaches (Minshall *et al.,,* 1985). Others have suggested that species richness should be higher with increases in annual temperature variation (Vinson & Hawkins, 1998), and with more physically complex substrata (Downes *et al.,* 1998b). As explanation of the underlying processes that give rise to such attributes, traditional equilibrium models assume a primacy of biotic interactions (e.g. competitive exclusion/resource partitioning) as determinants of community structure (Resh *et al.,* 1988; Townsend, 1989; Reice *et al.,* 1990; Wu & Loucks, 1995). Such processes take place within a constant environment, or one where species are adapted to a degree of variability. High species diversity is explained as the result of spatial or temporal heterogeneity. For example, spatial heterogeneity allows for niche differentiation, whilst temporal variation may permit even greater diversity if ecologically similar species can operate in different seasons - the concept of niche differentiation by means of temporal resource partitioning (Townsend, 1989). High species diversity is also ascribed to predator-mediated co-existence (Reice *et al.,* 1990). Such views are often invoked to explain the patterns of species richness described above (e.g. by Minshall *et al.,* 1985) and underpinning some of the tenets of the River Continuum Concept regarding species diversity (Vannote *et al.,* 1980).

More recently, the emphasis has shifted to attributing more importance to non-equilibrium and stochastic forces as agents of community structure (Townsend, 1989). Non-equilibrium studies focus on the behaviour of populations or communities over time in relation to non-equilibrium forces, rather than the properties of communities in equilibrium. Central to this field of investigation is the notion of disturbance as a major driver of communities, and the concept that, in fact, some communities may not ever reach an equilibrium state. At an extreme, such communities may be composed of species that are relatively independent of one another, and whose populations are limited by abiotic factors in a density-independent manner (Boulton *et al.,* 1992; Jacobsen & Encalada, 1998).

Lake (2000) describes three categories of disturbance. Floods represent the major form of natural ‘pulse’ disturbance in lotic ecosystems (Lake, 2000), whilst press disturbances refer to acute change that is maintained (e.g. sediment load change as a result of landslides; many anthropogenic impacts) and ramp disturbances are described as “creeping” change (e.g. drought, alien invasion). The following section is limited to

examining concepts and research findings relating to 'pulse disturbances' by flooding.

2.2 DISTURBANCE - A DEFINITION

Minshall (1988) defined disturbance as a "destructive, rapid (e.. spate) or prolonged (e.g. drought) change in the physical environment which exceeds the normal range of conditions experienced by a substantial number of organisms in a population, or the rate of their ability to adjust – resulting in their death and/or removal". Resh *et al.* (1988) included in their definition of disturbance only those events that are outside of a predictable range, given that organisms "are adapted to predictable seasonal fluctuations of discharge, temperature, dissolved oxygen etc." although they note that a precise definition of what is predictable is not easily reached. In contrast, Townsend (1989) did not make the definition of disturbance contingent on its predictability, and defined disturbance as "any relatively discrete event in time that opens up space which can be colonised by individuals of the same or different species". Similarly, Poff (1992) argued that a measure of predictability should apply only as an attribute of the disturbance regime, rather than as a defining criterion for disturbance per se. Poff (1992) argued that linking disturbance and predictability may result in using the magnitude of ecological response to define disturbance, rather than objective criteria related to the physical mechanism (e.g. bed turnover) of a disturbance. Furthermore, the assumption that organisms are adapted to predictable events (i.e. that disturbance by definition can only be unpredictable) does not give due cognisance to the wide variation in frequency and seasonal predictability of hydrological disturbance that "presumably…. creates noisy environmental selective forces that may not promote local adaptation" (Poff, 1992). Species traits (e.g. degree of 'weediness') or ecosystem attributes are likely to vary according to the heterogeneity of conditions, both predictable and unpredictable, that constitute the disturbance regime. According to Poff (1992), "evolutionary adjustments to hydrological disturbance may be reflected in biological attributes that confer differential survival and persistence in the face of that regime". Rather than an apriori assumption of adaptation, these provide the basis of testable hypotheses regarding the effects of inter alia the predictability of a disturbance regime of a stream on its biota.

Lake (2000) argued that most definitions confuse the biological response to a disturbance with the event itself, and proposed a narrower definition of disturbance as the application of "potentially damaging forces to habitat space occupied by a population, community or ecosystem ... [the magnitude of which] may be such that organisms may be killed or displaced, consumable resources may be depleted and habitat structure may be degraded or destroyed" (Lake 2000).

The critical difference in this definition is the identification of a <u>potential</u> impact as a result of the application of a force. A definition of disturbance that is contingent on the biota being adversely affected (for example, the "opening up of space" in the definitions of Resh *et al.* (1988) and Townsend (1989) explicitly implies mortality or displacement of biota) would preclude the possibility (at least hypothetically) that some biotas may be perfectly resistant to a disturbance, their populations remaining intact over the course of an event

characterised by "the application of a force", as per Lake's (2000) definition of disturbance (e.g. Lancaster, 1999; Lake, 2000). Lancaster (1999) described disturbance as a "response phenomenon", with responses being species specific, so that "whether a species perceives an environmental event as a disturbance will also be species specific". Her laboratory study (Lancaster, 1999) demonstrated variable responses by three taxa to increasing flow, these being either a) disturbance resistance (e.g. through physical attributes, such as clinging by hooks and claws) and b) changes in micro distribution (e.g. physical walking down a velocity gradient and / or accumulation in flow refugia). According to her definition of disturbance, species that show disturbance resistance through no net loss or movement of individuals will not have perceived the increase in flow forces as a disturbance. This description, whilst introducing a finer focus in the study of variable biological responses to disturbance, would require quantification of the response to environmental events before these may be pronounced 'disturbance events'. Further, the definition of disturbance will become increasingly complicated if it may be simultaneously classified as both a disturbance event and a non-disturbance. In addition, the concept of resistance defines species attributes, or resistance traits, in relation to the species' response to disturbance, rather than as a definition of disturbance.

Poff (1992) argued that a disturbance should be defined in terms of the physical event, but that the specification of a disturbance is scale dependent, and needs to be ecologically relevant to the question at hand. In other words, disturbance needs to be quantified both as a physical force and as a response event, where ecological response should be described at the same spatial or temporal scale as the force that is measured.

In relation to flood disturbance, to measure disturbance forces and the responses of biota at the same spatial scale would mean identifying the size of the patch most appropriate to the measure of both. A scale that measures magnitude of forces that act directly upon substratum particles and their biota may be a better basis for developing an understanding of the mechanism by which a 'disturbance event' elicits one or another biological response. Different thresholds in the magnitude of physical forces may represent different scales of disturbance, and may be accompanied by a variety of biological responses, including resistance, use of refugium and/or reductions in populations or biological fitness.

2.3 MEASURING HYDROLOGICAL DISTURBANCE BY FLOODS

Physical definitions of disturbance put forward by, for example, Resh *et al.* (1988) include hydrological indices representing events outside of a 'normal range' of flows, defined by them as 2x median monthly flow, but such approaches are criticised by Poff (1992) as arbitrary statistical measures that do not necessarily represent a known level of physical disturbance or constitute ecologically meaningful forces acting on biota. Debates on the definition of disturbance have led to increasing support in ecological studies for using the movement of substratum particles, as a function of discharge, as a criterion for defining and measuring disturbance (McElravy *et al.,* 1989; Cobb *et al.,* 1992; Lancaster & Hildrew, 1993b; Death & Winterbourn, 1994; Townsend *et al.,* 1997b; Downes *et al.,* 1998a; Biggs *et al.,* 1999; Bond & Downes, 2000; Gjerløv *et al.,* 2003; Riseng *et al.,* 2004). Two main

approaches have been used to determine bed movement - using theoretical relationships to calculate bed movement, and field-based measures, discussed in turn below.

2.3.1 Calculating bed movement using theoretical relationships

A common approach to estimating bed particle movement is the application of empirical relationships relating particle size to the forces required to move the particle. Incipient motion defines the beginning of sediment movement. In other words it encompasses all the factors involved at the threshold between non-movement and movement of a particle. A number of relationships have been proposed to link critical threshold parameters to the initial motion of a grain. The best known criteria are based on critical shear stress as originally developed by Shields (1936).

Most ecological studies have used equations defining critical shear stress to identify a particle size that would be at incipient motion at a given discharge, briefly described below (Downes *et al.,* 1997; Lorang & Hauer, 2003; Gordon, 2004). Shear stress represents momentum exchange across the planes and can be derived from the equivalency between forces acting in the various planes and momentum exchange. In open channels shear stress may be thought of as the frictional or drag force (per unit area) causing flow resistance along the channel boundary (Gordon *et al.,* 2004), described by:

$$\tau = \rho g R S \qquad [2.1]$$

where ρ is the density of water (= 1000kg m^{-3} at 20˚C), g is acceleration due to gravity, *R* is the hydraulic radius (or average flow depth, D (m) in wide or rectangular channels) and *S* is the energy (or bed) slope, expressed as a fraction.

The value for critical shear stress, also termed critical tractive force, is derived from the assumption that at incipient motion, the shear force acting to overturn a particle is balanced with the submerged weight of the particle, which thus holds it in place. The equation describing incipient motion is known as the Shield's equation, where critical shear stress (τ_c in N/m^2) is:

$$\tau_c = \theta_c g d (\rho_s - \rho) \qquad [2.2]$$

where θ_c is also called the dimensionless critical shear stress or dimensionless mobility factor, or Shield's parameter, d is a representative particle size (in m), g is acceleration due to gravity and ρ_s and ρ are particle and water densities, in kg/m^3 (Armitage & McGahey, 2003).

The onset of motion occurs when the shear stress along the bed (τ_0) exceeds some critical shear stress (τ_c) at which point the moment of the drag force (F_{drag}) about the pivot point of the relevant particle exceeds that of the immersed weight force of the particle (F_{iwt}) as shown in Figure 2.1.

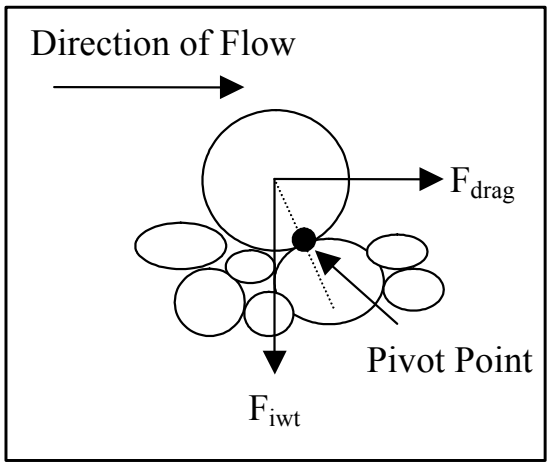


Figure 2.1 Schematic representing the hydraulic forces acting on a particle on the streambed by water flow.

The value of the constant, θ_c has been empirically defined as 0.04 - 0.06 for hydraulically rough conditions (Gordon, 2004), but is dependent on particle shape, bed packing and fluid properties. θ_c is higher under hydraulically smooth conditions, which are generally considered to represent special conditions in sand bed rivers, because grains in the upper layer are held together by a laminar flow envelope (Gordon, 2004).

This equation has been used to estimate disturbance intensity in streams in a number of ways. For a given flood size, the average depth is used in equation [1] to calculate reach-level shear stress, which is then substituted into equation [2] to predict the larges particle size to be moved under that discharge.

McElravy *et al.* (1989) used the discharge at which shear stress would be calculated to move the median size particle, as a threshold for defining disturbance in their inter-stream comparison (McElravy *et al.,* 1989). The basis for this is the controversial concept of equal mobility (see Gordon *et al.,* 2004, p190): based on the observation that in mixed alluvial channels, all particles may be moved at essentially the same average shear stress, and thus τ_c can be based on one grain diameter (the median) rather than computing individual values for each size fraction. A similar approach was used by Scarsbrook and Townsend (1993) who based their threshold shear stress equations on data gathered specifically in an upland gravel-bedded stream, in an attempt to improve the estimate of θ_c. This study compared stream stability on the basis of the theoretical shear stress required to effect movement of 50% of bed material at each site (Scarsbrook & Townsend, 1993).

Cobb *et al.* (1992) estimated the percentage of bed paving material at incipient motion (i.e. in motion) at low medium and high discharges, using the median diameter of a particle as an estimate of the critical tractive force, or critical shear stress, required for incipient motion, and relating this to a particle-size frequency distribution for each site. They used this percentage of bed in motion to define a discharge-related average shear stress for a range of sites, which was then related to biological attributes.

Jonker (2002) highlighted the fact that the Shield's equation describes sediment entrainment for uniform sediment sizes, rather than describing sediment transport in natural channels, and makes no allowance for shielding or armouring effects, when in actual fact the critical shear stress for a specified grain size increases in natural channels with increasing roughness. Death & Winterbourn (1994) demonstrated that the critical tractive force was not a good indication of the extent of bed disturbance. Similarly, Englund (1991a) found only a weak relationship between particle size, by category, and whether a stone was overturned or not. Other authors (Downes *et al.,* 1997; Townsend *et al.,* 1997b, c; Downes *et al.,* 1998a; Biggs *et al.,* 1999; Duncan *et al.,* 1999; Lorang & Hauer, 2003) agree that the assumption of a linear relationship between critical sheer stress and the movement of a given particle size is unlikely to hold up in all but the most uniform of channels.

Downes *et al.* (1997) found that the spatial variation in force required to move river bed stones, which they physically measured, depended highly on rock size, but also on bed packing (degree of embeddedness) and varied more between rivers than between stream orders or sites. They demonstrated that rocks in different size classes overlapped completely in the force required to move them, both between rivers and within sites, and concluded that methods of estimating disturbance using shear stress equations may be misleading given the sometimes order of magnitude difference in the force required to move two particles of the same size, but of different bed characteristics or particle embeddedness.

Similarly, in their field study measuring displacement of stones marked in situ (Downes *et al.,* 1998a), the disturbance of a stone was significantly related not only to its size category but also to its packing Bed packing in this case was defined qualitatively as loose-lying versus >50%embedded or wedged by surrounding rocks.

Thus, the same relative increase in discharge may result in considerable differences in applied forces and in actual bed movement within individual sites and between different streams, largely dependent on geomorphological features like channel size, bed particle sizes and packing, heterogeneity (roughness) and gradient. In this regard, disturbance may need to be quantified in a locally specific manner, for example as the proportion of bed particles that are mobilised by a given discharge.

Riseng *et al.* (2004) argued that although the Shield shear stress formula approach does not provide accurate predictions of sediment transport at a local scale, as it does not account for spatial variation in bed mobilisation nor streambed armouring and embeddedness, they nevertheless considered the utility of this approach for inter-stream comparisons of their "index of rock movement at bankful flow". They defined this index as the difference between a) the diameter of rock expected to move at bankful flow (D_{bf}, from the Shield's equation for critical shear stress, where θ_c was estimated for different stream sites "based on streambed packing" and b) the size of the D_{84} particle. The D_{84} was chosen on the observation that entrainment of this particle size was associated with large scale bed mobilisation.

However, Lake & Schreiber (1991) found that out of eight sites, spanning four stream orders, the site with the highest bankful average shear stress had the lowest movement of tracer stone particles recorded over a period of two years. They found no relationship between bankful shear stress and particle movement.

2.3.2 Field based measures of stone movement

Other approaches have used more intensive data collection techniques, rather than theoretically based equations for estimates of bed movement. Townsend *et al.* (1997a, b) and Gjerløv *et al.* (2003) used painted tracer particles of either the median or a defined percentile, placed randomly on the stream bed, to measure bed movement at high discharges. Stone movement was assessed at 2 to 4-month intervals. The percentage of moved stones in any period was either regressed against maximum discharge in the preceding period, in order to calculate the discharge required to move 50% of the particles as a threshold for disturbance (Gjerløv *et al.,* 2003), or the percentage of particles moved, averaged across sampling times, was used as a basis to define the intensity of disturbance for each of a number of compared sites (Townsend *et al.,* 1997a).

In a comparison of disturbance level and biological pattern across 27 rivers, Townsend *et al.* (1997b) defined three measures of disturbance: intensity (the average percentage of stones moved over the study period); frequency (the number of times over the study period when more than 40% of stones moved) and the maximum intensity of disturbance (the maximum percentage of the bed particles that moved in one event). They found a strong correlation between disturbance frequency and intensity, as per their definition, and a correlation between these and the percentage of small particles (diameter 8-32 mm) present at a site.

Downes *et al. (*1998a) criticised the method of placement of stones in river beds to assess movement. They compared movement of 40 randomly placed rocks with 60 marked in situ at six sites in three rivers, and found that stones placed randomly on the stream bed moved half as often as those marked in situ. Whilst it may seem counter-intuitive, in that a deliberately moved stone could be considered to be less snugly located within the bed and thus more, not less, likely to be subsequently dislodged by spates, Downes *et al.* (1998a) considered that the human-placed rocks might be placed in positions where they were sheltered from shear stresses that would lead to their mobilisation, given that there may be only a small number of locations with high enough ambient shear stress to move the sizes of rocks used in their study. In addressing this, Gjerløv *et al.* (2003) repositioned all stones on each sampling visit to ensure that any stone in a sheltered position was not maintained there.

Downes *et al.* (1998a) recorded 60% cumulative bed movement of particles in the size range 40 – 200 mm over a six month winter period during which at least nine flood events occurred, including three floods estimated to have a return period >3 years. Their study demonstrated that spatial scale at which physical disturbance of stream substrata occurs appears to be the scale of individual rocks, rather than whole sites, with as much variation in disturbance at the site level as between sites, even with large floods. Furthermore, this

movement was patchily distributed at a site level, with a generally clumped distribution of disturbed rocks, indicating that some parts of the stream bed were more prone to disturbance than others.

Whilst the studies of Downes *et al.* (1998a), Gjerløv *et al.* (2003) and Townsend *et al.* (1997a,b) measured stone movement at intervals during which numerous floods occurred, Matthaei *et al.* (1999a) recorded the fate of 400 stones, marked in situ, over the course of two individual flood events and two pairs of floods, in the cases where floods followed too closely upon one another to undertake fieldwork. Three reaches of different bedform characteristics were included in this study, in a catchment with high sediment supply. In this study, a flood of a return period of approximately six months, and thus not nearly approaching bankful, moved between 68 and 72% of particles at each of their three sites. The stable subset of unmoved stones was significantly larger and more embedded than those stones that were displaced. A larger flood with a return period of 2.8 years removed some 80 - 85% of the remaining marked stones. If one assumes that the particles moved by the small flood would also have been moved by the large flood, then the latter flood accounted for a 93 - 96% movement of the bed surface stones. Despite this, the authors found that the bed surface materials remaining after the floods were unchanged in size or embeddedness. Curiously, therefore, a third flood with a similar magnitude and return period to the first monitored flood was associated with only 32 - 42% particle movement. This high variability in stone movement of up to 40% difference in the total sediment mobilisation, during floods with approximately the same peak discharge and duration, was not explained by any of the variables measured.

2.3.3 Appropriate thresholds constituting disturbance

Although the movement of bed particles undoubtedly constitutes a physical disturbance, it may under-represent the disturbance forces acting during the discharge event. Flow forces acting on river bed materials increase with increasing discharge, and these may be as important as actual particle movement. This may be particularly true in heterogeneous cobble- and boulder-bed rivers, where substantial hydraulic forces may be present long before bed entrainment occurs. Furthermore, the use of a statistic such as 40% bed movement as a threshold for disturbance (e.g. Townsend *et al.,* 1997b; Gjerløv *et al.,* 2003) was acknowledged by these authors to be arbitrary.

Many studies reported are of rivers with relatively small bed material and hence generally low channel roughness compared to Western Cape rivers. In a study of the upper foothill and mountain stream reaches of the Western Cape Province (Jonker, 2002), median particle size was found to be between 200 and 300 mm, with the 70^{th} percentile between 300 and 400 mm, and the 90^{th} percentile ranging from 400 to 600mm. In contrast, Townsend *et al.* (1997b) considered large particles in their 27 rivers to be those with a diameter of >128 mm, with a maximum particle size, excluding bedrock, of some 250 mm diameter. Mean particle size in the study of Death & Winterbourne (1994) was 72-85 mm over their range of sites; and in the study of Lake *et al.* (1989) was 16 mm. The particle size range in the study of Matthaei *et al.* (1999a) was 2-64 mm. Only the studies of

Downes *et al.* (1998a), with small, medium and large rock categories in the order of 40 - 100, 101-200 and >200 mm respectively, and Death (2003), where boulders were defined as particles >300mm, have remotely comparable substratum categories.

The wider the range in bed material the more unpredictable is the relationship between discharge and movement of a particle of given size likely to be, because of the greater degree of roughness (Jonker, 2002). In addition, the concept that only a particle that moves represents some threshold constituting disturbance precludes, for example, the potentially destructive forces acting on large stable substratum particles caused by extremely high shear velocities, but which are not competent to move the particle because of its weight. Such bed particles may provide refugium for organisms that can withstand extreme shear forces, but create conditions for the erosion of more mobile or fragile taxa, or their retreat into other habitats (see section 2.5.4a). For example, some studies have measured increases in drift with elevated discharge where sediment entrainment did not occur (Mathooko & Mavuti, 1992; Imbert & Perry, 2000). Other sources of disturbance that do not relate to particle movement include abrasion by suspended particles in these fast-flowing areas during floods (Downes *et al.,* 1998a) and smothering by sediment deposition (Matthaei *et al.,* 1999b).

Death (2003) developed an index of flow force as the sum of the distances travelled over three months by five randomly placed stones in each of three size classes, multiplied by the mean weight of that size class. He argued that this described the relative magnitude of force acting on the substratum at different sites, rather than the proportion of substratum moved during a spate. This approach was intended to overcome the criticism that quantifying particle movement as the measure of disturbance underestimates the disturbance caused by high shear stress without substratum movement (Death, 2003), by incorporating the size (weight) of larger stones into the index. It is nevertheless still based on the measurement of particle displacement - particles that are too large to move, despite very high shear forces acting on them, will always contribute to a low flow force index.

Lancaster & Hildrew (1993b) regarded bottom shear stress as the most meaningful measure of flow forces with respect to invertebrates, because they considered it to reflect the shearing force of water, which has the potential to dislodge organisms. They advocated this approach for comparing the hydraulic differences between streams. They characterised whole-reach hydraulic habitat through the creation of frequency distributions of shear stress, measured with FST hemispheres (Statzner & Muller, 1989) from spot measurements at a site. They were able to repeat these measurements at the same point for a range of discharges to demonstrate how the distribution of shear stresses and the proportion of low and high shear stress areas changed with discharge at different sites and within different morphological units at a site (Lancaster & Hildrew, 1993b). This approach was also followed by Gjerløv *et al.* (2003) to quantify the proportion of hydraulic refugia likely to be present at high discharges. She modelled the 2-dimensional distribution of shear stress over the stream bed in her study streams using macro-channel measurements (Lamouroux & Statzner, 1992), and calibrated these results according to two field-based measurements of shear stress over the study sites - at a low and a

moderate discharge. This model was used to describe the distribution of areas of different shear stress at the same relative flood discharge in each of the study streams. Townsend *et al.* (1997c) used the percentage of points that were characterised by "low" shear stress as one of three criteria for differentiating the refugium potential of different streams. The shear stress values were measured during non-flood discharges, whilst the refugium potential is an attribute that has relevance during flood periods. Field-measurement of shear stress during floods is not possible, and the approach was based on the assumption that some fraction of the "low" shear stress locations would remain low even at an elevated discharge. This approach also assumes that the relative proportions of high and low shear stress points remain constant from stream to stream - that one stream with a greater proportion of low shear stress points than another stream, measured at low discharge, would still have the same relatively greater proportion of low shear stress point than the other stream at an elevated discharge.

The characterisation of stream refugia and their importance in determining the biological effects of floods is discussed further in section 2.4.4.

In relation to quantifying disturbance, it seems apparent that, whilst increased flow forces provide one type of disturbance for stream biota, a qualitatively different level of disturbance may occur with the actual displacement of a bed particle. The spatial distribution of hydraulic forces acting on the substratum is likely to be different from the distribution of dislodged bed particles, so that both may need to be mapped and quantified independently in studies of disturbance.

Furthermore, as Downes *et al.* (1997) concluded, if disturbance by rock movement is a significant source of variation in biotic patterns, then a disturbance event should be followed by an increased variability in species richness and composition from rock to rock, depending on the mobility of that rock - and perhaps also for stable rocks, on the level of hydraulic stress that pertained during the disturbance event. This has implications for the scale at which disturbance studies are executed. The use of reach-level averages may prevent patterns from becoming apparent, as they blur substantial and important variations in data, possibly resulting in poor estimations of both the magnitude / frequency, and the effects of, disturbance.

2.3.4 Stream power as an alternative theoretical approach

Duncan *et al.* (1999) reviewed the deficiencies of the range of substratum-based approaches to the measurement of disturbance, including problems with theoretical approaches, accuracy and, not least, the effort involved in marking and following bed particles. These issues emphasise the continued importance of finding general rules that describe the magnitude of particle movement and/or flow forces acting at a local (stone) scale during floods. Duncan *et al.* (1999) presented a modified version of the Shield's equation, accounting for heterogeneous particle sizes, the effects of slope and small relative depths and Lorang & Hauer (2003) discussed the considerations that need to be incorporated into an assessment of stream stability based on flow competence equations such as critical shear stress.

Armitage & McGahey (2003) reported that, although the shear stress is probably the most commonly used method of determining incipient motion, probably the most serious criticism of its use is that the rate of sediment transport is not uniquely determined by shear stress (Armitage & McGahey, 2003). In steep channels a large portion of the shear stress is manifested as turbulence around large objects, rather than frictional drag on bed particles. Equally, achieving localised threshold entrainment is more a function of the maximum instantaneous shear stress than the channel-averaged measures of shear stress used in incipient motion equations. Instantaneous shear stress values are affected by turbulence, which is considerable during high flows in channels with high roughness (Lorang & Hauer, 2003).

A number of researchers have preferred to use unit stream power as an indicator of sediment motion, although this application is not generally described in standard hydraulic introductory texts for ecologists (e.g. Gordon *et al.,* 2004). However, Armitage & McGahey (2003) argued that the quantity represented by unit stream power is more directly related to the entrainment threshold than is critical shear stress, because it can be computed at any point in the water column, and because turbulence is directly related to dissipation of energy.

The movement of bed particles (or water) requires expenditure of energy, which is provided in streams by the release of potential energy as water travels down a slope. The stream power model of incipient motion equates the power made available through the loss of potential energy in a flowing stream with the power required to maintain the movement along the bed (applied power), and compares this to the amount of power required to entrain particles (required power). Incipient motion occurs when the applied power at the bed equals or exceeds the required power to lift the particle.

The input unit stream power made available through the loss of potential energy in a flowing stream, or applied power per unit volume (in Watts / m^3) is described by the equation

$$AP = \int_{y=0}^{D} \rho g s v dy \qquad [2.3]$$

where ρ is the density of water (= 1000 kg m^{-3} at 20 ˚C), g is acceleration due to gravity, D is flow depth (m), *S* is the energy (or bed) slope, expressed as a fraction, and where v is the velocity at distance y above the bed, with y_0 = the distance above the bed where the velocity is mathematically zero (Jonker, 2002). The stream power dissipation per unit volume (the power required to maintain movement along the bed) is represented by

$$\int_{y=0}^{D} \tau \frac{dv}{dy} dy \qquad [2.4]$$

where τ is the shear stress at distance y above the bed. According to the law of conservation of power, these terms must be equal - i.e. the power input resulting from the release of potential energy [3] is equal to the power dissipated, or the power being applied

to maintain motion or deform the element [4] (Rooseboom, 1998).

The parameter ρgsv represents the amount of unit power made available by the flowing stream, whereas the parameter $\tau\frac{dv}{dy}$ represents the power applied per unit volume to maintain motion.

Stream power is defined as the rate of change of energy (energy dissipation). The manner in which this energy is dissipated will determine the sizes of eddies over a point and thus the potential for transport of bed material (Rooseboom, 1974; 1998).

The mechanism by which motion is maintained along the bed is different under laminar and turbulent conditions. Under laminar conditions energy dissipation occurs at the molecular level to overcome the forces resisting the relative movement of fluid particles. The amount of energy required to maintain motion is thus dependent on the viscosity of the fluid. Under turbulent conditions, however, energy dissipation occurs through the formation of turbulent eddies. The amount of energy required is thus dependent on the size of the turbulent eddies that form, and these are representative of the absolute roughness of the bed. As the power applied along the bed of a river varies depending on whether energy dissipation occurs under laminar or turbulent conditions, the critical condition for sediment movement also depends on whether energy dissipation occurs under laminar or turbulent conditions.

Where alternative modes of flow exist, that mode of flow which require the least amount of unit power will be followed and it therefore follows that fluid flowing over moveable material would only transport the material, if it will result in a decrease in the amount of unit power being applied (Rooseboom, 1974; 1998).

Under laminar or smooth turbulent conditions, Rooseboom (1974) showed that the unit stream power applied along the bed equals

$$\frac{(\rho gsD)^2}{\rho\nu} \qquad [2.5]$$

In this equation the kinematic viscosity, ν, is significant as under laminar flow conditions, energy dissipation occurs at the molecular level.

The applied power required per unit volume to entrain a particle with density ρ_s and settling velocity V_{ss} in a fluid with density ρ, equals:

$$(\rho_s - \rho)gV_{ss}$$

Stokes's law (Graf, 1971), defines the settling velocity of a particle with diameter d under viscous conditions as:

$$(V_{ss})_{LAM} \alpha \; d^2 g\frac{\rho - \rho_s}{\rho\nu}$$

The critical condition for the movement of sediment particles is reached when the power applied along the bed exceeds the power required to suspend the sediment particles. In laminar or smooth turbulent flow therefore, a relationship defining the threshold for sediment transport under viscous conditions can be defined from the above equations. This relationship, calibrated with data by Grass (1970) and Yang (1973), was found to be:

$$\frac{\sqrt{gDs}}{V_{ss}} = \frac{1.6}{\frac{\sqrt{gDs}}{\nu}\cdot d} \qquad [2.6]$$

for values of $\frac{\sqrt{gDs}\cdot d}{\nu} < 13$, i.e. with smooth turbulent or completely laminar flow over a smooth bed (Rooseboom, 1974, 1998).

Under conditions of rough, turbulent flow, Rooseboom (1974; 1998) showed that the unit applied power near the bed at (y_0), where $D\text{-}y_0 \approx D$, is

$$\tau\frac{dv}{dy} \approx \frac{30\rho gsD\sqrt{2\pi gsD}}{k} \qquad [2.7]$$

Under turbulent conditions energy dissipation occurs through the formation of turbulent eddies and not at the molecular level as is the case under laminar or smooth turbulent flow conditions. Viscosity is therefore not significant, but rather the size of the turbulent eddies that form. The size of these eddies represent the absolute roughness (k) of the bed. In the case of a bed with a uniform size distribution the size of the turbulent eddies that fit between the particles can be considered to be equal to the diameter of the bed particles (d) as shown in Figure 2.2 and hence d can be substituted for k in the above equation.

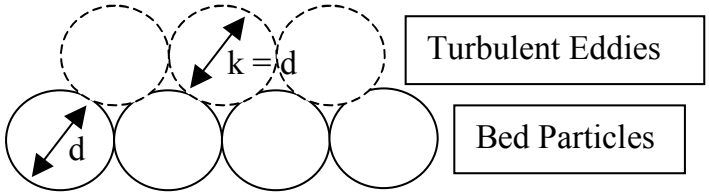


Figure 2.2 Schematic showing the relationship between k and d for a uniform bed.

Furthermore, under conditions of turbulent flow, the settling velocity as expressed by Graf (1971) equals:

$$(V_{ss})_{TURB} = \sqrt{\frac{4(\rho_s - \rho)gd}{3C_d}}$$

From the above equations, and by substituting k with d, Rooseboom (1974) showed that the critical condition for the movement of sediment along an even uniform bed in rough turbulent flow can thus be defined by:

$$\frac{\sqrt{gDs}}{V_{ss}} = \text{Constant} \qquad [2.8]$$

The stream power approach is considered to have advantages over other approaches to incipient motions advantages in that it involves scalar quantities (unlike the momentum-impulse law used in shear stress models which use vector quantities), its terms are directly time-dependent and they account for the roughness (k) of the bed directly (Armitage & McGahey, 2003; Rooseboom, 1998). Further, Rooseboom (1998) showed that the stream power equations give theoretical and numerical support to the empirically derived components of the Liu Diagram for incipient motion (Liu, 1957).

2.3.5 The Liu Diagram of Incipient Motion

Liu (1957) developed a diagram for incipient motion that is often used to describe the criteria affecting incipient motion. The Liu diagram was developed empirically in terms of shear stress, but Rooseboom (1974) was able to interpret the parameters in terms of applied unit power.

The parameter on the y-axis of the Liu diagram is $u.V_{ss}$ and is known as the mobility number. Interpreted in terms of applied unit power, this parameter is $\sqrt{gDs}/V_{ss}$ which represents the ratio of the power applied at the bed to the power necessary to entrain a particle.

The parameter on the x-axis, $(\sqrt{gDs} \cdot d/\nu)$ may be regarded as a type of particle Reynolds number (Re*), which indicates whether laminar or turbulent conditions prevail at the bed. A plot above the threshold line in Figure 2.3 therefore implies that the unit power applied along the bed is greater than the unit power required to suspend particles.

Under turbulent conditions (i.e. high Re* values) along an even bed the ratio of applied power to required power is considered to be constant. This was confirmed by Rooseboom (1974; 1998) who calibrated the Liu Diagram using data from Yang (1973) and found for Re*>13. $\sqrt{gDs}/V_{ss} = 0.12$

Critical conditions for the movement of sediment along an even bed in rough turbulent flow are thus defined by a straight horizontal line with a constant value of

$$(\sqrt{gDs}/V_{ss}) = 0.12$$

In laminar or smooth turbulent flow incipient motion becomes dependent on viscosity and the relationship defining the threshold for sediment transport is defined as $\sqrt{gDs}/V_{ss} = 1.6/(\sqrt{gDs} \cdot d)/\nu$.

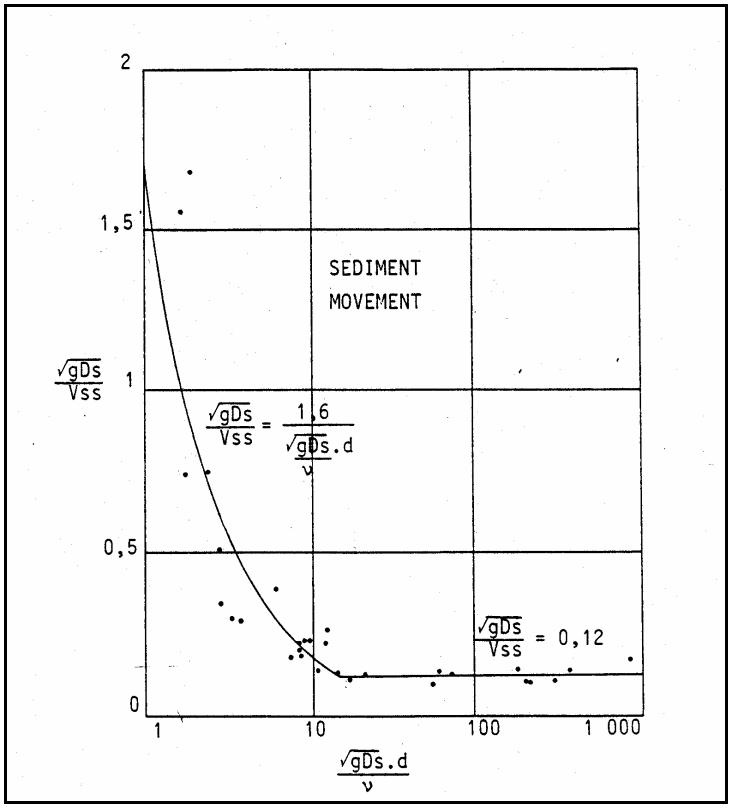


Figure 2.3 **The Liu diagram for critical conditions for incipient motion of cohesionless sediment, with axes re-interpreted in terms of unit applied stream power, after Rooseboom (1974).**

2.4 THE EFFECTS OF FLOODING ON STREAM BIOTA

2.4.1 Disturbance magnitude and frequency

Some field studies have related the magnitude of flood discharges, expressed as a multiple of baseflow discharge, to biological response. For example, in an ecological study of New Zealand rivers, Quinn & Hickey (1990) found that invertebrate density in a cobble-bed river after an autumn flood of ca. 60 times the median flow was 680 times lower than summer levels. Elevated flows that were less than 20 times the annual median flow had no discernible effects on invertebrate density, biomass and taxonomic richness (Quinn & Hickey, 1990). Robson (1996) recorded a 25% reduction in invertebrate numbers on bedrock riffles, but a slight increase in the cobble riffles, in response to a spate reaching peak daily discharge of 15.5 times the preceding baseflow, but where peak instantaneous discharge over 30 times the baseflow.

Grimm & Fisher (1989) found that during summer flash-flooding in an Arizonan, USA, desert stream, the percentage decrease in periphyton (as Chlorophyll a) was correlated with Qmax, but beyond a threshold flood size, the periphyton standing crop was essentially eliminated. Blue-green and filamentous algae were eliminated by floods ≈ 100 times summer baseflow, whilst the groups more resistant to flood scour (diatoms) were eliminated by floods ≈ 1000 times summer baseflow.

Periphyton reduction was not significantly different in cobble riffles and sand-gravel runs. Flows in the order of 500 x summer baseflow generally caused 80% reduction or more in invertebrate density.

Biggs & Close (1989) reported that flood flows exceeding median flows by 6-fold always reduced periphyton biomass significantly, whilst Quinn & Hickey (1990) found that sites recently affected by floods exceeding 20 times the annual median discharge had 7-fold lower periphyton densities.

In these descriptive studies, however, the physical forces acting on the biota that result from increased discharge or hydraulically-based measures of disturbance magnitude (e.g. velocity, shear stress, stream power, suspended sediments, bed movement) probably varied considerably depending on channel and bed properties. This means that the biological responses described are difficult to compare (for example in streams with suspected different hydrological or hydraulic properties). Useful comparisons of results can only be meaningfully undertaken when they are related to these sorts of physical forces.

A number of field experiments have examined the effects on invertebrates and periphyton of artificially disturbing stones, mimicking what might be the effects of floods. For example, in a study of invertebrate recovery after simulated flood disturbance, Boulton *et al.* (1988) overturned and acid-scoured forty and sixty-four rocks, respectively, from a riffle site in a fifth-order, 9 m wide Australian stream. The study indicated that reductions in invertebrate and epilithon densities were directly related to the magnitude of the disturbance: simply overturning stones (simulating the effects of small floods) had little effect on epilithon, except to re-orientate its position (to the under-side of the stone). Invertebrate numbers on overturned stones were significantly reduced by 10 – 100%, (but not consistently for all taxa), but recovered rapidly, within four days. With acid-scoured stones - simulating large flood disturbance - reduction in algae and invertebrate populations was total. Epilithon cover had not recovered to pre-disturbance levels after 32 days, whilst invertebrate species richness, but not densities, reached pre-disturbance levels in 32 days.

Lake *et al.* (1989) experimentally disturbed riffle biotopes to mimic a flood event, by kicking and raking 35 areas, each 1 m^2, distributed between two riffles in an Australian stream. The authors recognised the difficulty of relating experimental patch sizes to the size of areas disturbed by floods, and suggested that the experiment resembled more the sorts of disturbance that might occur with minor floods (although see Downes *et al.,* 1998a). Disturbance frequency was three times (each 10 days apart – 3XD) or only once (final day – 1XD) in a period of twenty days, following which invertebrate assemblages were monitored for a period of 70 days. There were marked decreases in the various parameters in the disturbed plots compared with control plots – reductions in the order of 54 - 72% for trapped organic material, 60% in invertebrate species richness, 80% in invertebrate numbers and 30% in invertebrate species diversity (H') were recorded in disturbed plots. Smaller decreases (5 - 9%) in the number of invertebrate species, numbers of individuals and species diversity (H') were recorded with the more frequently

disturbed (3xD) plots than with those disturbed only once (1xD), but only immediately following disturbance, on day 0 of the recovery process. This, and the fact that there were no differences in the composition of colonising fauna between treatments, led to the conclusion that disturbance frequency at this scale does not influence the rate of recolonisation or confer selective advantage or disadvantage on any species (Lake *et al.,* 1989). After 33 days, there were no significant differences in the above community measures between control and treatment plots, indicating the rapidity of recovery from small-scale disturbance. The study, however, was somewhat confounded by the effects of three spates that occurred during the recovery period, measuring between five and six times baseflow levels, but equally applied to both experiment and control treatments. Although no significant differences were detected over the study period in the mean number of species per sample in the control samples, the total number of individuals in these samples declined over the study period (Lake *et al.,* 1989). Indeed, the control sites themselves could arguably be said to have undergone natural, repeated, small scale disturbance, the consequences of which were not significant for species assemblage structure but included a significant reduction in overall invertebrate density.

One of the criticisms of artificial disturbance studies is that their relevance to real flood effects cannot be assessed. However, Matthaei *et al.* (1999a) and Downes *et al.* (1998a) concluded that since patchy stone movement at a site is probably the dominant effect of floods smaller than bankful, even in unstable beds, as evidenced by their own studies, small-scale experimental disturbance studies may simulate the effects of disturbance more effectively than previously thought.

Experimental disturbance studies have frequently been used to examine the effect of disturbance frequency on stream assemblages. For example, Robinson and Minshall (1986) overturned preconditioned bricks with different frequencies and compared relative densities of periphyton and invertebrates with disturbance frequencies of every three, nine, 27 and 54 days, with those on undisturbed artificial substrata effectively remaining in the stream for 108 days. Disturbance frequency was interpreted in relation to its effect of reducing the time available for recolonisation, and so their samples effectively represented different lengths of time since the last disturbance. Discharge was constant over the study period. The authors found significantly lower periphyton biomass on frequently disturbed substrata, although this effect was only significant in open-canopied streams. In both open-canopied and shaded streams, and in both summer and autumn, invertebrate densities and species density declined with increasing disturbance frequency, with the exception of one grazer taxon which showed a positive relationship with disturbance frequency during the summer experiment. However, they found no difference in the response of invertebrates to disturbance frequencies of 27 days or greater, which led to their conclusion that ‘equilibrium conditions’ may be established within 27 days of disturbance (Robinson & Minshall,1 986).

Gawne & Lake (1996) mimicked disturbance by overturning preconditioned bricks, at frequencies of once per month and once per week, in a heavily shaded New Zealand stream, in order to examine both biofilm and herbivore responses to disturbance. They

found a significant reduction in periphyton as a result of disturbance, even though their stream sites were shaded, but not in organic matter, bacterial abundance or densities of the grazer species that they sampled. No effects of disturbance frequency were observed. The differences between these results and those from the study of Robinson & Minshall (1986) may be ascribed to potential differences in periphyton resilience, as a result of lower temperatures and lower nutrient levels in the shaded sites (Gawne & Lake, 1996). If recovery of periphyton biomass was slower than the frequency of disturbance, then this could explain the lack of a disturbance frequency effect. Clearly issues such as productivity of a site need to be incorporated into disturbance studies if differences in results are to be explained adequately.

Death (2003) argued that covariance between disturbance and food availability may obscure direct effects of disturbance on stream invertebrates and his 1996 study showed that resource availability (periphyton, organic matter) was implicated along with disturbance frequency in determining invertebrate assemblage composition. Death (2003) found that in shaded streams with low periphyton biomass, periphyton reduction by floods that caused substratum disturbance, although significant, was far lower even in relative terms than that reported for studies on open-canopied streams. This result is consistent with those of Robinson & Minshall (1986). Differences in invertebrate assemblages in shaded streams were determined more by stream size and permanence than by disturbance regime, since the key effect of disturbance was the temporary loss of animals which are highly resilient. In contrast, in unshaded streams, where disturbance affected both the invertebrate fauna and its food base more significantly, Death (2003) concluded that invertebrate recovery may lag behind the recovery of stone surface biofilms.

Bond & Downes (2000) considered there to be a paucity of studies that provide direct evidence of how disturbance affects stream biota. For example, artificial disturbances may not measure natural responses as they would lack possible cues for refuge seeking behaviour that natural floods might provide as discharges increase (Bond & Downes, 2000). This has led to a growing preference for field studies that measure or estimate both the magnitude of physical disturbance and its associated biological response. Many of these take the form of inter-stream comparisons.

Cobb *et al.* (1992) related reductions in invertebrate densities to the percentage of bed pavement in motion, calculated using the equations for critical shear stress. Whilst they found a correlation between discharge and substratum movement, the latter accounted for more variation in benthic invertebrate density than did discharge. The authors developed a strong second-order polynomial regression between intensity of disturbance and invertebrate density - insect densities started to decline with a substratum displacement of about 10%. This effect was variable among taxa, with the strongest relationships between disturbance and Plecoptera, Ephemeroptera and Trichoptera, and less so in the case of Chironomidae, Simuliidae or beetles. At more stable sites, no significant relationships were found between substratum movement or discharge and these latter three groups (Cobb *et al.,* 1992). Interannual differences were also pronounced at physically unstable (disturbance-prone) sites, in relation to the frequency of disturbance events in any

year: comparing Ephemeroptera / Plecoptera / Trichoptera densities between two years with and without small summer-autumn spates, the authors found that in the dry year characterised by the absence of autumn spates, stable and unstable sites had similar, high summer invertebrate densities. Invertebrate densities at stable sites were little or un-affected by interannual variation in small spates, whilst there was nearly 400% difference in summer invertebrate densities between the two years at unstable sites, despite the fact that the wetter year was still below the average with regard to flood frequency. Other studies comparing streams of differing substratum stability, and hence physical bed disturbance during high flows, have also found that species richness and diversity were both higher in the more stable streams (Scarsbrook & Townsend, 1993; Death, 1996b).

Nislow *et al.* (2002) argued that determining the specific flood magnitudes necessary to effect measurable biological responses would be an important advance in disturbance studies. Of course, such information can be used in conjunction with long-term hydrological data to determine the frequency with which such a threshold disturbance will affect stream assemblages - and this may be a useful basis for comparing the fauna of different streams (see section 2.5 below). They calculated average shear stress and stream power during large (bankful and overbank) floods, for sites in adjoining catchments, as well as channel widths and mean particle size before and after the floods, to indicate scour and sedimentation respectively. They also examined changes in invertebrate and fish densities from before and after the floods. Their results indicated that ranking sites according to measures of bedload movement and sedimentation during these floods closely matched the ranking of sites according to the magnitude of biological response, whilst the average shear stress and stream power were not useful in this regard (Nislow *et al.,* 2002).

Bond & Downes (2003), however, cautioned against assuming that bed movement needs to occur to cause a measurable biological disturbance effect. In an experimental study (Bond & Downes, 2000) they found that the densities of caddisflies on small and large bricks, both tethered to the bed or left unfixed and thus allowed to be moved by a flood, were not significantly different after a flood. This suggests that increased hydraulic forces acting on even fixed substrata may play as great a role in disturbance as rock tumbling (Bond & Downes, 2000). This conclusion is reinforced by studies that demonstrate increases in drift with elevated discharge, where bed entrainment did not occur (e.g. Mathooko & Mavuti, 1992; Imbert & Perry, 2000; Bond & Downes, 2003).

2.4.2 Patchiness of disturbance effects

Perhaps one of the most profound consequences of small disturbances in streams, defined as within-year flood events, is the subdivision of the habitat into patches. Patch dynamics is a framework for examining the effects of disturbance over large landscapes, where disturbance acting on smaller-scale patches ultimately gives rise to a mosaic of patches, each at a different point of recovery from disturbance or biological succession, allowing for an overall increase in diversity, compared with a uniform landscape (Townsend, 1989). Processes of change, for example population growth, disturbance,

nutrient cycling, foraging, can create, maintain, modify or destroy the dynamics and types of patches, whilst the characteristics of patches such as longevity, size, and arrangement of patches will affect biotic and abiotic processes over a range of scales, and thus facilitate or constrain ecological processes (White & Pickett, 1985; Pringle *et al.,* 1988).

The concept of patch dynamics emphasises that changes in resource availability and community structure occur within patches as a result of competitive interactions. This has given rise to debate about the usefulness of the framework, or specific patch dynamics models of species coexistence, in freshwater studies, where the major fauna are highly mobile (e.g. Townsend, 1989; Downes, 1990; Hildrew & Giller, 1994; Barrat-Segretain & Amoros, 1996). Downes (1990) suggested that differential colonisation rates could be more significant than competition in determining species abundances where patches are available for short periods only. In cobble- or gravel-bed streams that are characterised by fauna with high mobility, patchiness in the effects of disturbance may therefore be only short-lived.

These arguments emphasise the need to understand scale in relation to the patchiness of disturbance as well as in terms of the response of the biota both across the streambed and over time. Downes *et al.* (1998a) demonstrated how the scale of disturbance is usually less than a whole reach or even a whole site, but pointed out rather that disturbance patch size was often equivalent to the spatial scale of individual rocks. They argued that measuring biological response at a large scale, for example by combining samples taken from a whole site as has been the general practice in ecological studies over the past few decades, with the exception of artificial stream experiments, makes estimates of disturbance less accurate, because a large amount of information on variability is collapsed into an average response (Downes *et al.,* 1998a). Bond & Downes (2000) examined the effect of rock size and movement on two caddisfly species during spates. They found a 10% reduction in density over a period characterised by high flows, including one flood of bankful discharge. Whilst the caddis densities were an order of magnitude higher on large rocks (>20 cm top width) than small (5-10 cm) before the flood, they were similarly low on both stone sizes after the flood, and highest on medium substrata (11-20 cm top width), suggesting that they either moved, or were removed from large substrata in particular.

Matthaei *et al.* (2000) examined invertebrate responses to a flood that caused patchy bed particle movement. By mapping individual stone positions, and through the strong relationship identified between stone size and embeddedness and stone movement, they were able to separate *apriori* stable (i.e. unlikely to have moved) from unstable stones, sampled before and after a small flood. Whilst stable and unstable stones prior to the flood were similar to each other in invertebrate species composition, invertebrate density and richness increased on stable stones after the flood and decreased on unstable stones, relative to their pre-flood condition. Stable and unstable stones returned to more similar states within 19 days. The results of this study suggest a) active use of refugia during floods and b) that the clumped distribution of invertebrates may in part be explained by the

disturbance history of the site, a potentially important parameter to include in comparative stream studies.

(Englund, 1991a) demonstrated that, in Swedish streams with patchy moss cover, the overturning of mossy stones created a more diverse habitat, created by decaying moss on undersides of overturned stones and because of upper stone surfaces having a cover of moss at various stages of recolonisation. He estimated recolonisation to be a process taking in excess of two years, whilst overturning of stones was estimated to occur naturally at a rate of less than 8% per annum. Different affinities of invertebrate taxa for moss cover resulted in a patchiness of associated invertebrate assemblage composition that remained 12 months after the initial disturbance. In addition, his study provided some evidence for disturbance mediating competition between the two moss species in these rivers. Matthaei & Townsend (2000) compared invertebrate densities in patches of stream bed that were differently affected by a flood, more than two months after the flood. Three patch types were defined according to their prior disturbance level, as scour, fill and stable patches. Their results indicated that the disturbance history of the patch had a significant effect on species assemblage, with different species, or different developmental stages of the same species, preferring different patch types as defined above, although not consistently across different sites. They speculated that disturbed patches may reflect an early stage of predictable successional changes. Thus they concluded that disturbance may result in an imprint on the invertebrate community that persists for relatively long periods after an event. The resulting successional mosaic will depend on the nature of the disturbance regime and on productivity levels. Using the same approach, Matthaei *et al.* (2003) found that periphyton assemblages sampled after flood events were also determined more by patch history (scour, fill or stable) than habitat parameters, with intriguing temporal differences in these patterns. In the immediate post-flood phase, periphyton densities were highest on stable patches, implicating a refugium function for these areas, especially since grazer densities were also higher in these patches than others; however, two weeks later, densities had become highest in scour patches; periphyton sampled three months after separate flood event was more than four times greater in fill patches than in scour or stable patches. The reasons for these temporal shifts were not yet clear, but point to important avenues for research, in relation particularly within a patch-dynamics framework, since patchy disturbance effects may have considerable longevity in stream ecosystems.

2.4.3 Disturbance - diversity models

Two models that invoke disturbance as agents of community structure and that have received some attention with regard to freshwater studies are Connell's (1978) Intermediate Disturbance Hypothesis (IDH) and Huston's Dynamic Equilibrium Model of community structure (Huston, 1979, 1994). Temporal variation can enhance co-existence and diversity by reducing the likelihood of competitive exclusion, but "this occurs through the medium of physical disturbance in a patchy habitat in which dispersal is a fundamental and large-scale process" (Townsend, 1989). (Townsend *et al.,* 1997c) found that the relationship between species richness and disturbance intensity and / or frequency

conformed to the predictions of the Intermediate Disturbance Hypothesis, which states that disturbance frequency affects the outcome of ecological processes such as succession. The IDH implies that, in a competitive hierarchy, intermediate levels of disturbance will prevent superior competitor species from eliminating inferior competitor species, because the latter will persist as colonisers in the disturbed areas (Connell, 1978). Clausen & Biggs (1997) attempted to define the relationship between periphyton and invertebrate density, richness and diversity, and hydrological variability, in 83 New Zealand rivers. They found that periphyton biomass was highest in streams a) which are smaller, or have a low mean discharge, because these have more stable substrata and b) which are less variable hydrologically. In contrast, their study showed that long-term average invertebrate density (but not diversity) was highest in streams of intermediate disturbance frequency. Periphyton species richness and diversity were strongly negatively related to the amount of flooding in a river relative to baseflow conditions, the average size of flood events, and flood frequency but invertebrate diversity bore no or only weak relationships to flow variables. They found no evidence to suggest that periphyton or invertebrate diversity followed the pattern predicted by the Intermediate Disturbance Hypothesis.

Wootton (1998) suggested that the IDH is supported in studies where species compete for space or a space-related resource, whilst counter examples come from studies of very mobile species, where mobility may swamp the local effects of disturbance: removed species are replaced rapidly, and thus competition is not alleviated. In contrast, (Townsend *et al.,* 1997c) found that both mobile and more sedentary species conformed to the expected patterns of the IDH, concluding that competition between mobile species may be more important than previously thought. Wooton (1998) further demonstrated, using theoretical models, that whilst the IDH considered only single trophic levels, the variable effects of disturbance on different parts of the food web affect the outcome of disturbance in multi-trophic systems. Although there are many examples of disturbance-mediated coexistence between competing species in freshwater ecosystems (e.g. McAuliffe, 1984; Hemphill & Cooper, 1986; Englund, 1991b; Kohler, 1992; Wootton *et al.,* 1996; Cardinale & Palmer, 2002), Reice (1985) suggested that the IDH did not apply to streams because of the lack of a general demonstration of competitive hierarchies in streams. In an experimental test of disturbance frequency effects, he found reduced densities of invertebrates with each additional disturbance of cobble baskets that were placed in a stream and allowed to become colonised over a period of five weeks, with disturbance treatments applied at the start of week 2 and 4. However, there was no evidence that disturbed and undisturbed treatments became more similar over the period following disturbance, as would be expected with recovery and the re-establishment of quasi-equilibrium. An explanation for this could be a low population growth rate, which would affect the onset of any potential competitive interactions. In this study, species richness and diversity varied little among treatment groups on a given date. In addition, although most taxa continued to increase over the study period in all treatments, there were some taxa that demonstrated initial increases followed by a decline in the control treatment.

Similarly, Death (1996b) found that periphyton and invertebrate densities and taxon

richness were reduced by disturbance frequency, measured as time since last disturbance, using the definition followed by Robinson & Minshall (1986). Stable sites showed less displacement in assemblage and were also quicker to recover. Death (1996b) concluded that there was little support for the existence of a group of rapidly colonising species that was eventually replaced by a slower but competitively superior species, as would be expected from theoretical perspectives like the patch dynamics concept, or the IDH. Rather, relative dominance at unstable sites declined only as other taxa became more abundant. The author did acknowledge, however, that the time scale of measurement of biological response may not have been long enough to measure competitive displacement. Indeed at the stable sites, the dominance of some groups increased with time since disturbance, with concomitant declines in the absolute abundances of at least some taxa (Death, 1996a). The same criticism could apply to the study of Reice (1985), particularly given the slow rate of recovery reported by this author.

McCabe & Gotelli (2000) considered Huston's Dynamic Equilibrium Model (Huston, 1979; 1994) to offer a broader range of predictions than the classic IDH. This model predicts that diversity is determined not so much by competitive ability as by the influence of the environment on the net outcome of species interactions. In other words, diversity is the result of an interplay between population growth rate, competitive exclusion, and population reductions that reduce the chances of competitive exclusion. Disturbance is major source of population reduction, and therefore plays a major role in community structure. In this model, at low rates of population growth and competitive displacement, maximum diversity will occur at low levels of disturbance (perhaps a scenario fitting Reice's (1985) study), and vice versa, whilst only at intermediate growth rates would the scenario of the IDH apply. It is noteworthy that the demonstration of competitive hierarchies is just as necessary in studies that invoke dynamic equilibrium.

Significantly, McCabe & Gotelli (2000) argued that ecological studies should differentiate between species density, defined as the number of species per area, and species richness, defined as the number of species per number of individuals sampled, because the latter is strongly affected by sample size or total invertebrate abundance. In their study species richness was determined using a rarefaction technique that allows for comparison of species richness in samples of different sizes, by estimating the expected species richness for a given number of individuals drawn randomly from a sample (McCabe & Gotelli, 2000). They noted that most studies that report on species richness actually refer to species density, as defined by them. Vinson & Hawkins (1998) also concluded that most studies do not account for the natural increase in species richness with density, and that after rarefaction, many supposed increases or decreases in species richness may be found to be artefacts of this phenomenon.

McCabe & Gotelli (2000) examined the interplay of disturbance intensity, frequency and spatial extent on invertebrate indices in a third order, low gradient stream by disturbing preconditioned artificial substrata. Whilst invertebrate abundance and species density were reduced in proportion to the intensity and extent of disturbance of artificial stones, species richness estimated by their technique increased with increased

disturbance intensity, and was higher in disturbed than in control samples. McCabe & Gotelli (2000) attributed this to the reduction in competitive displacement afforded by high levels of disturbance, under conditions of high population growth (i.e. high mobility), in agreement with one of the scenarios predicted by Huston's Dynamic Equilibrium Model.

Death & Winterbourn (1995) found a strong positive linear relationship between species number and environmental stability (defined by variability in temperature, depth, velocity and substratum movement). However, the decline in species number with increased variability followed a similar decline in animal abundance, and rarefied species richness (i.e. independent of total density) may have yielded different results, a point acknowledged by the authors. Species evenness, however, peaked at sites of intermediate stability. These authors also concluded that their data may fit Huston's Dynamic Equilibrium Model, where community structure is a trade-off between the frequency of population reduction and the rate at which competitive exclusion proceeds: in this case, competitive displacement may occur at stable sites, but it proceeds slowly enough to preclude the exclusion of species, only species evenness being affected, thus maintaining similar richness levels at intermediate and stable sites. An alternative explanation is that the patchy nature of the stream environment promotes the maintenance of fugitive species through high mobility of the fauna. This explanation would still implicate at least low-intermediate levels of disturbance in the maintenance of patchiness.

2.4.4 Between-disturbance intervals, seasonality and succession

Working in perennial rivers, McElravy *et al.* (1989) as well as Feminella & Resh (1990) found that inter-annual variation in benthic macroinvertebrate densities in the immediate post-wet season were closely related to hydrological characteristics (e.g. total rainfall; maximum number of days between storms) of the preceding season, but found little relationship between wet season characteristics and the following late dry season invertebrate biota.

Feminella & Resh (1990) found densities of a mid-instar grazing caddis were substantially reduced by increased flood size and during wet years, when flood frequency was higher, and this resulted in lower competition between late instars and concomitant increased growth and fecundity. Despite this, however, these interannual differences did not affect the reproductive output of the population as a whole, because higher densities of late instars in drier years compensated for lower reproductive output. Nor did these interannual differences affect early-instar densities in the following dry season, when biotic interactions are strongest, because early-instar densities are related to overall reproductive output. Similarly, Hendricks *et al.* (1995) examined the possible long-term effects on population characteristics of two floods on a river characterised by bivoltine insect taxa, with peak densities of adult emergence and egg-laying in May (post-winter) and September (summer). The fauna maximised growth and reproduction over the relatively short, 4-month summer low-flow period, with a second generation per annum over the longer 8-month winter season which was characterised by frequent high flow events. The authors presented data to show how a population reduction of some 50%, caused by a

November flood with a 60-year return period at the start of an otherwise dry winter, was a seemingly short-lived effect. Insect densities the following summer had generally recovered to similar or higher densities than in previous summers. The authors attributed this to increased fecundity as a result of lowered intraspecific competition, reflecting a relatively constant summer carrying capacity, as in the study by Feminella & Resh (1990). However, a far smaller flood (7-year return period) occurring in the next winter season had as large an impact as the 60-year flood. Interestingly, Hendricks *et al.* (1995) speculated that the effect of the flood-mediated reduction in selective pressure during the first flood could be that it gave rise to a genetically unstable next generation, whose phenotypes were less able to withstand the physical stresses associated with the following wet season. The feedback effect of this genotypic weakness in the longer term is presently simply a matter of speculation.

Indeed, most studies of temporal pattern show a consistency in the seasonal signature of invertebrate assemblages that is only rarely overridden by the effects of wet season flooding (e.g. Meffe & Minckley, 1987; McElravy *et al.,* 1989; Giller *et al.,* 1991; Boulton & Lake, 1992; Boulton *et al.,* 1992; Cobb *et al.,* 1992; Robinson & Minshall, 1998).

Desert streams subject to intense floods that disturb the unstable substrata, are often viewed as extremes within the gradient of ecosystems driven by equilibrium or stochastic forces. Research on these systems has provided insights into the importance of and mechanisms for post- flood succession (e.g. Fisher *et al.,* 1982; Grimm & Fisher, 1989; Boulton *et al.,* 1992). These and other studies (Silva Filho & Maltchik, 2000) have shown the importance of flood magnitude and the length of the interval between floods and the drying phase, as well as nutrient availability, in determining succession sequences of periphyton and macroinvertebrates in intermittent streams. Flood magnitude may exert its influence at the level of biotic resistance to a flood, whilst flood frequency and seasonality of disturbance both dictate the time available for recovery, or impose the physical constraints to recovery (e.g. high baseflow discharge, temperature), and thus exert more influence on resilience of a system (Grimm & Fisher, 1989). Boulton *et al.* (1992) showed that inter-annual variation in assemblage composition was most stable in spring, a period when flash floods are rare and stream connectivity is high.

Flecker & Feifarek (1994) found that during periods of low flow not subject to spates (up to 3 months), overall invertebrate densities remained relatively stable, although population numbers for individual species fluctuated considerably more. They inferred from this that biotic interactions during the dry season in perennial rivers are most likely to replace disturbance in controlling community patterns of distribution and abundance. On the other hand, Jacobsen & Encalada (1998) found that the invertebrate assemblages of Ecuadorian highland streams were governed by stochastic flooding in the wet season, never reaching beyond the “early successional stage” during the short dry season of only three months. This may be related to the generally low temperatures recorded by these authors at these stream sites, which may impose the constraint of low growth rates on recovery, even during stable periods.

Even with intermittent streams, floods are often viewed as 'reset' events. Long periods of stability between floods, relative to the life span of stream organisms, have been shown to allow for the development of stronger biotic interactions such as competition or predation, which can directly influence community structure (Grimm & Fisher, 1989). Minshall *et al.* (1985) referred to two basic community types – opportunistic (stochastic) and equilibrium communities – and suggested a seasonal, or sometimes an aseasonal, basis to a shift from one type to the other, based on the change in disturbance forces acting on the stream environment. They further suggested that the conformance of species-abundance data to the log-normal distribution, indicated by the magnitude of the coefficient of determination, R^2, can be used as a relative measure of equilibrium state across seasons within the same stream. Assuming equilibrium conditions are necessary for density-dependent factors to operate, Minshall *et al.* (1985) concluded that the dynamic nature of streams may only periodically allow for such forces to be expressed, and that the alteration between the 'opportunistic' and 'equilibrium' status of a community may or may not be on a seasonal basis, depending on the disturbance regime. (Death,1996b) related a habitat stability index, describing different levels of environmental stability, to four models of species distribution, viz. geometric series, log and log normal series, and the broken stick series. He concluded that communities in unstable streams and in the most stable streams conformed best to the log series distribution, with a single very dominant species and large numbers of relatively rare ones, whilst streams of intermediate stability were modelled best by the log normal distribution, with more uniform species distributions. He also found that seasonal changes in the model of best fit were associated with seasonal changes in stability at their sites – i.e. there is a seasonal basis to patterns of 'equilibrium-type' communities and those that are less structured by biotic interactions, sensu Minshall *et al.* (1985).

2.4.5 Predictability of disturbance

It is now widely recognised that most stream ecosystems exhibit a combination of deterministic and stochastic behaviour (Palmer & Poff, 1997), where flow disturbances (floods and droughts) are among the most important of these stochastic forces affecting community attributes. Based on information theory, Colwell (1974) derived a measure of predictability, and its components, constancy and contingency, to describe periodic phenomena where at least two states over time or space may be described.

Cobb *et al.* (1992) developed an index of predictability (from definitions in Colwell, 1974) based on the percentage of days each month that produced flows great enough to move at least 10% of the substratum (the threshold for decreases in invertebrate abundances), and compared this with an index of predictability based on the discharge. They found that predictability based on the flow regime differed little between sites, but using the predictability of substratum movement, substantial differences between sites were apparent. Variation in the timing of substratum movement (the contingency aspect of predictability) was the greater contributor to unpredictability than constancy of conditions (the amplitude of changes). Predictability was not determined by substratum instability (defined as percentage of bed material in motion at bankful discharge) per se - no

linear correlation existed between substratum stability and predictability - but nonetheless, their least predictable site was also the one with by far the highest percentage of bed material in motion at high discharges.

Townsend & Hildrew (1994) argued that disturbance that is unpredictable is more likely to elicit a strong biological response than the same magnitude event that is predictable, because these may act as evolutionary drivers determining species adaptations and ultimately population characteristics.

Five aspects of the flow regime are regarded as important regulators of ecological processes in river ecosystems: the magnitude, frequency, duration, the timing (or predictability), and rate of change (flashiness) of high and low flows (Poff *et al.,* 1997). The first three of these are thought to determine the extent of disturbance and time available for recovery or the significance of periods of harsh or benign conditions; the last two may determine species life cycle and behavioural adaptations that promote persistence and ultimately the characteristics of lotic communities (Poff *et al.,* 1997).

Poff & Ward (1989) classified streams across the USA into nine streams types, which were assessed using criteria such as the degree of intermittency, flow variability, and flood regime. They regarded this as a major axis of the habitat templet (sensu Southwood, 1977) of lotic organisms (see section 2.5) and suggested that "the position of a stream in flow space [based on flow statistics] should provide some *apriori* basis for expectations of biotic attributes". This is because the historical flow regime in any one stream should act as an evolutionary force, determining the success of species life-history attributes and, ultimately, of species populations. Their stream types were defined as 'harsh intermittent'; 'intermittent flashy'; 'intermittent runoff'; 'perennial flashy'; 'perennial runoff'; 'snowmelt'; 'snow + rain'; 'winter rain'; and 'mesic groundwater'(Poff & Ward, 1989).

Gasith & Resh (1999), in developing hypotheses about the attributes of stream communities in Mediterranean climates (the 'winter rain' stream type of Poff & Ward, 1989), suggested that the seasonal predictability of disturbance in these systems should result in assemblages that exhibit life history adaptations that maximise growth and reproduction during stable and mild periods. Also, the sequence of flooding and drying should select for life-history features (species traits) that favour resistance to dislodgement and allow rapid recolonisation responses.

2.5 DISTURBANCE AS A DRIVER OF COMMUNITY AND SPECIES ATTRIBUTES

2.5.1 Community persistence and stability

Stability of natural populations or communities refers to the extent to which there is constancy in the numbers of organisms (Connell & Sousa, 1983). On the other hand, where the system under consideration is "profoundly affected by changes external to it" and confronted with unpredictable forces, then the degree of constancy becomes less important than the persistence of relationships between populations over time (Connell & Sousa, 1983). Thus the degree to which communities persist may contribute much to the understanding of the forces behind their structure, and the relative importance of

deterministic versus stochastic drivers (Townsend *et al.,* 1987).

Connell & Sousa (1983) argued that for a system to be considered stable, there must be one or more equilibrium points at which a system remains, or returns to following a disturbance. In their opinion, persistence is less concerned with the existence of equilibria but on how populations are buffered against extinction in the face of disturbance. Persistence of a population according to their definition indicates that a population or species either did not become locally extinct over a given time period, or if it did, then it was able to recolonise the area within a time span of one generation (Connell & Sousa, 1983).

Townsend *et al.* (1987) defined persistence as the extent to which the species complement of an assemblage remains unchanged over a time period encompassing at least one complete population turnover. Others (e.g. Reice, 1985) have referred to a coefficient of community as the degree of overlap of a species complement over a given time period. Stability has also been defined as the relative constancy of species densities (i.e. their ranked abundance relative to other species in an assemblage) over time (Meffe & Minckley, 1987).

Few studies worldwide have dealt with the persistence of locally defined communities. Woodward *et al.* (2002) examined the effects of three decades of progressive increases in pH on community structure. Townsend *et al.* (1987) found that persistence of stream communities over a 7-year time interval was highest at sites of low annual maximum temperature and temperature range. From local studies in the Western Cape, there is some evidence that spatial patterns in invertebrate assemblages may be predictable and repeatable. For example invertebrates in the undisturbed reaches of the Berg River, sampled at an interval of some 40 years were compared by Dallas & Day (1992), with comparable patterns in community structure, something that implies a measure of persistence in community structure in the face of environmental fluctuations.

Death & Winterbourn (1994) found that species composition was highly persistent across seasons in stable but not in unstable streams, whilst rank abundances of common taxa showed no significant differences across seasons (i.e. the community was stable according to the definitions of Meffe & Minckley, 1987), and concluded that rare species are most affected where physical conditions are more variable.

Trajectory studies of persistence as described by Hildrew & Giller (1994), i.e. that measure persistence at one or a few sites, sampled repeatedly over a period of years (Meffe & Minckley, 1987; McElravy *et al.,* 1989; Giller *et al.,* 1991; Bradt *et al.,* 1999; Scarsbrook, 2002), indicate that in the medium term, communities tend to be generally persistent, albeit unstable with regard to absolute invertebrate abundance. In these studies, increased temporal variability, and reduced habitat stability are associated with lower persistence.

2.5.2 Resistance and resilience of aquatic biota

Community persistence is a product of either resistance or resilience. Resistance may be defined as the capacity to avoid change (Connell & Sousa, 1983), whilst resilience is the

capacity of reduced or impacted populations or communities to recover after a disturbance (Hildrew & Giller, 1994). Resistance involves the persistence, unharmed, of a population or species assemblage through a disturbance event, implying some attribute on the part of the species that affords it tolerance of the disturbance.

Biggs & Thomsen (1995) attributed variability in the effects of flood disturbance on algal assemblages to two types of resistance properties of communities: 'inherent', which relate to the physical attributes of the dominant species in an assemblage, such as tensile strength, shape, and 'conditional' properties, which are more within-assemblage explanations for variability in the effects of similarly sized flood. These include the age and successional state, acclimation to a given velocity or shear stress. From laboratory experiments on the differences in community resistance to increases in shear stress arising from increased flow, these authors demonstrated the higher resistance of diatom species to floods than filamentous species. Biomass loss in filamentous algae was asymptotic with 50% removed with the first incremental increases in shear stress (less than 6-fold increases). In contrast diatom dominated communities lost under 50% biomass at shear stress increases in excess of 40x the incubation shear stress, with a more linear relationship between biomass removal with increasing shear stress. Even after exposure to shear stresses of up to 90 N m^{-2}, the biomass persisting on the substrata in diatom dominated communities was between 20 and 30 mg m^{-2}. The authors concluded this value may approximate minimum values for biomass that could be expected following non-bed-moving spates (Biggs & Thomsen, 1995), and concluded that consideration of community type, not just the physical magnitude of the change in flow, is essential in studies that evaluate disturbance effects.

Most studies of disturbance indicate that aquatic communities are not resistant to disturbance at the small scale (Niemi *et al.,* 1990), but generally show high levels of resilience to disturbance. Even in the case of major discharge disturbances where a large proportion of the biota is lost, recovery is still rapid (Gray, 1981; Townsend, 1989; Flecker & Feifarek, 1994). For example, without access to hydrological data, Flecker & Feifarek (1994) were able to use rainfall data to show a positive correlation between invertebrate density and the number of days since a heavy rainstorm, observed to be linked to rearrangement of bed material, in neotropical streams, demonstrating that insect reductions were quickly ameliorated following spates. Gray (1981) studied recolonisation of a desert stream subject to flash flooding, showing that aerial recolonisation was the dominant mode of recolonisation, rather than adaptations for resistance or recolonisation from undisturbed patches. Grimm & Fisher (1989), also working in a desert stream, found macroinvertebrates whose densities had been reduced by some 80% by large floods took 13 – 52 days to reach pre-flood levels. In their study, successional change in invertebrate assemblage structure was inhibited in cases where post-disturbance (post-flood) sequences of recovery were short because of the onset of the next flood, but that for sequences longer than 40 days without new floods, there were complex natural patterns of succession in invertebrate assemblages that were not related to flood disturbance. These were considered to be rather mediated by biotic interactions.

Niemi *et al.* (1990) reviewed recovery processes in more than 100 freshwater systems subject to disturbance, concluding that the resilience is related to a) the scale of disturbance, which includes the temporal extent of changes to ecosystem properties, spatial magnitude and distance to potential recolonising sources; b) the timing of a disturbance; c) the presence of refugia, and d) the life-history traits of species within the system, for example generation time and propensity for dispersal. One of the important aspects of impact and recovery, or resistance and resilience, studies, however, is that they need to recognise the extent to which conditions fluctuate temporally - aquatic populations after a disturbance seldom return to pre-disturbance densities precisely because of temporal heterogeneity that imposes new gradients on the biotic and abiotic template that governs species population dynamics. An example of such a gradient could be changes in productivity mediated by seasonal temperature variability. For this reason, temporal trajectories are more useful in recognising resilience than static comparisons of abundance.

The basis for resilience lies both in the characteristics of the organisms (in particular their mobility) and in the heterogeneity of the physical environment (Hildrew & Giller, 1994). The latter have received considerable attention in attempting to explain the great variability in flood effects on biota, through the development and testing of hypotheses regarding refugia in streams. The former are the subject of attempts to link the species traits of biota inhabiting streams to particular regime characteristics - or habitat templates (sensu Southwood, 1977; Townsend & Hildrew, 1994). Indeed the terms resistance and resilience can be used to describe either morphological or physiological adaptations, or pre-adaptations (sensu Edmunds & McCafferty, 1988), where resistance traits describe adaptations to withstand the physical stresses of disturbance, and resilience traits describe adaptations to escape these stresses temporarily (Townsend & Hildrew, 1994; Lancaster & Belyea, 1997).

Many studies have investigated the relationship between disturbance and the set of adaptations of the fauna inhabiting different rivers. (Townsend *et al.,* 1997a) found strong positive relationships between the intensity of disturbance and the proportion of the invertebrate community displaying resistance traits, for example streamlined or flattened body shape, or resilience traits, such as high adult mobility.

2.5.3 Refugia

Refugia - habitats or environmental factors that reduce disturbance effects or provide mechanisms for persistence of biota in disturbed environments - may occur at a range of scales (e.g. Sedell *et al.,* 1990).

At a local scale, benthic assemblages recover from disturbance as a result of spates in time spans generally shorter than one generation time, an observation that suggests that there may be considerable flow refugia in or associated with stream channels (Lancaster & Hildrew, 1993b) or ‘within -habitat refugia’, using the categorisation used by Lancaster & Beylea (1997). Indeed, since many recent studies indicate that disturbance, especially in smaller floods (within-year return period) occurs at the scale of individual stones (e.g.

Downes *et al.,* 1998a; Matthaei *et al.,* 1999a), recolonisation of denuded substrata may occur simply via the redistribution of fauna, rather than colonisation from a distant source (Matthaei *et al.,* 1999b). An important caveat is the recognition that disturbance effects may be highly variable between rivers or sites, depending on the hydraulic characteristics of the site.

In this context, I define two fundamentally different types of instream flow refugia. The first may be defined as localised areas where hydraulic forces acting on the substratum remain low during a flood event, such as hydraulic dead zones, which prevent density-independent loss of animals and provide a source of colonists for recovery in denuded areas (Lancaster, 1990; Lancaster & Hildrew, 1993a, b; Rempel *et al.,* 1999; Lancaster, 2000). In this regard, Matthaei *et al.* (2003) also found scour, fill and stable patches in a stream bed that were not related to particle size, or in other words must have been related to the presence of patches where hydraulic forces remained low over the course of a flood. Most taxa utilising such refugia do so through active or passive movement with the onset of a disturbance event. At the scale of individual rocks facing high flow forces, these taxa cannot be considered to be resistant, but rather resilient, since they do not survive through a disturbance on that stone, but rather collect in refugia from where they can recolonise denuded patches of the stream bed after the disturbance.

The second type of instream refugium might be that of large stable particles (e.g. Townsend *et al.,* 1997b; Francoeur *et al.,* 1998). Very large particles may indeed be subject to considerable hydraulic stress during a flood, but for an organism that is well-adapted to resist such stresses, they may be preferable refugia to 'hydraulic dead zones' which could provide for other dangers, such as increased encounters with predators in these flow refugia (e.g. Thomson *et al.,* 2002). Such refugia, by virtue of the fact that they do not move allow for taxa using them to resist disturbance at even a local stone scale.

Other instream refugia include 'microform bed clusters' (MBCs), which are defined as bedform micro-units consisting of several stones that are particularly resistant to entrainment during high flow (Biggs *et al.,* 1997; Francoeur *et al.,* 1998), but see Matthaei *et al.* (2000). The hydraulic character of MBCs are uncertain, as they comprise centrally an anchoring 'stoss' and large 'clast' stone which give these formations their stability. However, it may be that within the stable stone complex, hydraulic refugia in the form of low shear stress spots could exist.

Other classes of refugia (i.e. not in-stream refugia) identified by Lancaster & Beylea (1997) include temporal refugia through complex life cycles (e.g. different phases occupy different habitat types), changes in habitude (where different life stages use different microhabitat types, such as hyporheic eggs), and, over wider catchment scales, between habitat refugia.

Hydraulic dead zones have been posited as a novel approach to examining the flow refugium potential of stream reaches (Lancaster & Hildrew, 1993b), and have been addressed in theoretical models (Bond *et al.,* 2000).

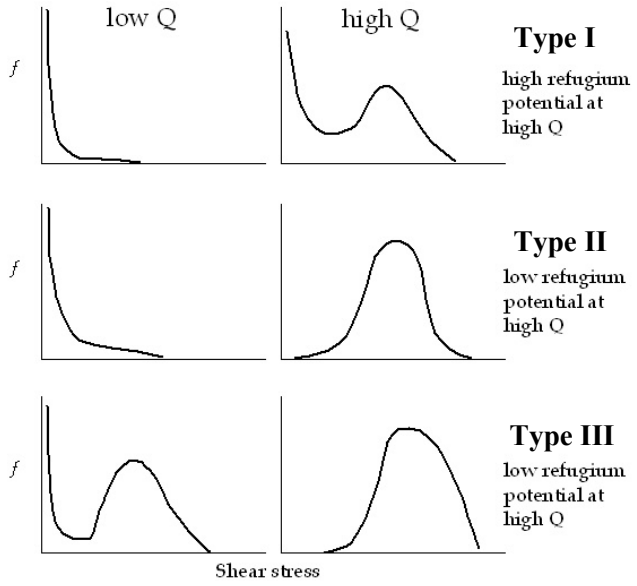


Figure 2.4 Characterisation of in-stream flow refugium potential in streams with different shear stress distributions at low and high flows (after Lancaster & Hildrew 1993b).
***f* = frequency of occurrence.**

The availability of in-stream flow refugia will be related to the heterogeneity of channel and bed morphology, where roughness elements create resistance to flow. For example, Lancaster & Hildrew (1993b) identified different stream types according to 1) the proportion of streambed occupied by hydraulic dead zones (non-flowing areas of transient storage within the water column, for example, in turbulent eddies, channel margins, wakes around larger bed elements, reverse flows within pools and on bends) and 2) changes in the frequency distributions of shear stress with increasing discharge (see section 2.3.2c).

These stream types are illustrated in Figure 2.4. More retentive streams (their 'Type I' streams) were characterised by a skewed unimodal distribution with a majority of low shear stress spots at base flow, shifting to a bimodal distribution at high discharge, with a greater proportion of higher shear stress spots but still a prevalence of low shear stress spots (potential refugia) even at elevated discharge. At the other end of the spectrum were ('Type III') streams which exhibited a bimodal distribution of shear stress at low discharge, with many low stress spots, but a large proportion of high stress areas, shifting to a unimodal, bell shaped distribution with few or no areas of low shear stress Lancaster & Hildrew (1993a). The proportion of streambed occupied by hydraulic dead zones was greatest with Type I streams, but, interestingly, this proportion did not increase consistently with the stream exhibiting lower refugium potential, based on shear stress distributions (Lancaster & Hildrew, 1993b).

2.5.3.i Use of refugia

Experimental studies (e.g. Winterbottom *et al.,* 1997a; Winterbottom *et al.,* 1997b; Lancaster, 2000) as well as field studies (e.g. Lancaster & Hildrew, 1993b; Francoeur *et al.,* 1998; Rempel *et al.,* 1999; Matthaei *et al.,* 2003) have reported on biota using within-habitat (instream) refugia during spates, where densities in these areas were higher immediately post-spate than prior.

Gjerløv *et al.* (2003) found a stronger relationship between recolonisation rates of invertebrates post-floods and the availability of refugia than with the frequency of disturbance. Rate of recolonisation was strongly correlated with the extent of refugium availability, but only in streams exhibiting low refugium availability at high flow.

Mobility is important for two reasons – as a resilience trait it will determine the speed of recovery of populations on denuded substrata; but also, if active selection of refugia does occur, mobility may confer greater survival rates for more mobile taxa – i.e. more mobile species should accumulate differentially in refugia and demonstrate higher resilience to disturbance. On the other hand, low mobility should go hand in hand with resistance traits combined with the selection of other forms of refugia, such as stable substrata.

If stone movement is determined by its size and/or its embeddedness (e.g. Downes *et al.,* 1998b) then the distribution of less mobile or sessile organisms may be correlated with either large size or embeddedness of a stone, as a result of species selection for refugia. For example, (Englund, 1991a) found a strong relationship between the occurrence of moss and the embeddedness of small stones, but not of larger stones. Largest stones also had proportionally more moss than medium and small stones.

One of the implications following from a) the well documented effects of floods in reducing invertebrate abundances and b) the importance of refugia in mitigating this effect, is that, barring recruitment of new individuals (e.g. from upstream reaches / smaller instars from the hyporheos) invertebrate densities on the streambed at a site scale should decline gradually over a period of repeated disturbance such as a flood season. The relative proportion of refugium patches in a stream should thus determine the overall magnitude of population losses during a spate of a particular threshold intensity, and thus the rate or trajectory of this decline in abundance over successive disturbances.

2.6 SYNTHESIS OF ISSUES ADDRESSED IN THIS STUDY

Some of the key questions that arise from a review of current literature, and which form the focus of work in this study include the following:

Flood disturbance may be characterised as the application of hydraulic force, resulting in a biological response, which may vary between taxa, from ‘perfect resistance’ to total mortality, followed by variable recovery (resilience). Evidence suggests that the scale at which disturbance acts, and thus should be measured, is individual substratum particles, particularly in the case of within-year floods.

While inter-stream comparisons of stability / disturbance level linked to properties of the biota are important, it is proposed that additional fundamental work is required in explaining the mechanism of disturbance and the honing of tools that assist with its measurement at the appropriate spatial scales. The use of stream power theory may have much to offer in this regard, and does not appear to have been used in ecological disturbance studies to date.

The most appropriate way in which to conduct ecological studies of disturbance within an ecosystem may indeed be to attempt to understand what happens to fauna on disturbed patches, in this case moved stones, versus undisturbed ones. The large scale roughness of cobble- and boulder-bed rivers of the Western Cape results in substantial hydraulic sheltering, and thus in a range of disturbance effects associated with floods, both in terms of flow forces acting on bed particles and of particle movement. Whilst this provides a useful basis for the study of flood effects, it also necessitates completion of the difficult task of approximating what the magnitude of flow forces are that act on individual bed particles during a flood, as well as the consequence of these forces in terms of whether or not the stone moved.

Linking invertebrate response to disturbance of individual particles is fraught with difficulties, not least because of the heterogeneity in species assemblages typically found from one patch to another in the stream. To what does one compare the biological composition of a 'disturbed stone', if not an average species composition from before the disturbance occurred? In this study an attempt has been made to repeat-sample marked stones before and after disturbances (allowing time for reconditioning of sampled stones). The advantage of this approach is that it allows a direct comparison between physically identical patches (stones) before and after a disturbance, which can then be linked to an estimate of the hydraulic forces brought to bear upon the stones during the disturbance.

3 METHODS

3.1 STUDY SITES

Both study sites are located in the Western Cape of South Africa. Both rivers have their origin in the same mountain range and the two study sites are located within 50 km of each other, but in different catchments (Figure 3.1). This area of the country is characterised by winter rainfall with heavy rain (over 1000 mm per annum) in the mountain catchments.

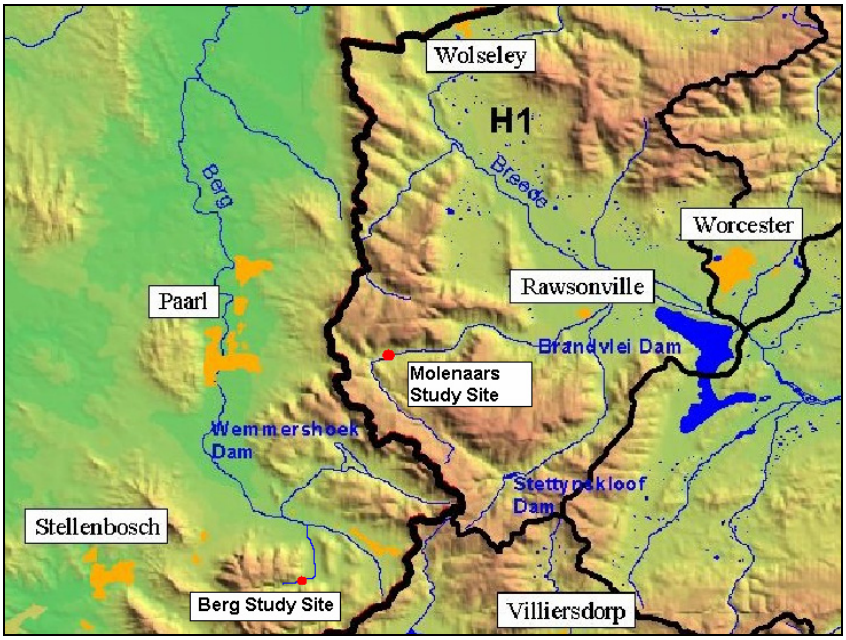


Figure 3.1 Location of Study Sites

Both sites were located in the headwater rivers of the Cape Fold Mountains and are thus characterised by short, but intense flood events, relatively steep gradients, and bed particles predominantly derived from the Table Mountain group sandstones in the cobble to boulder bed range as defined by the Wentworth scale in Table 3.1.

Table 3.1 Classification of bed particle sizes (adapted from Brakensiek *et al.,* 1979).

Class (Wentworth)	Diameter (mm)
Boulder	>256
Cobble	64 to 256
Gravel	2 to 64
Sand	0.0625 to 2
Silt	0.0039 to 0.0625
Clay	< 0.0039

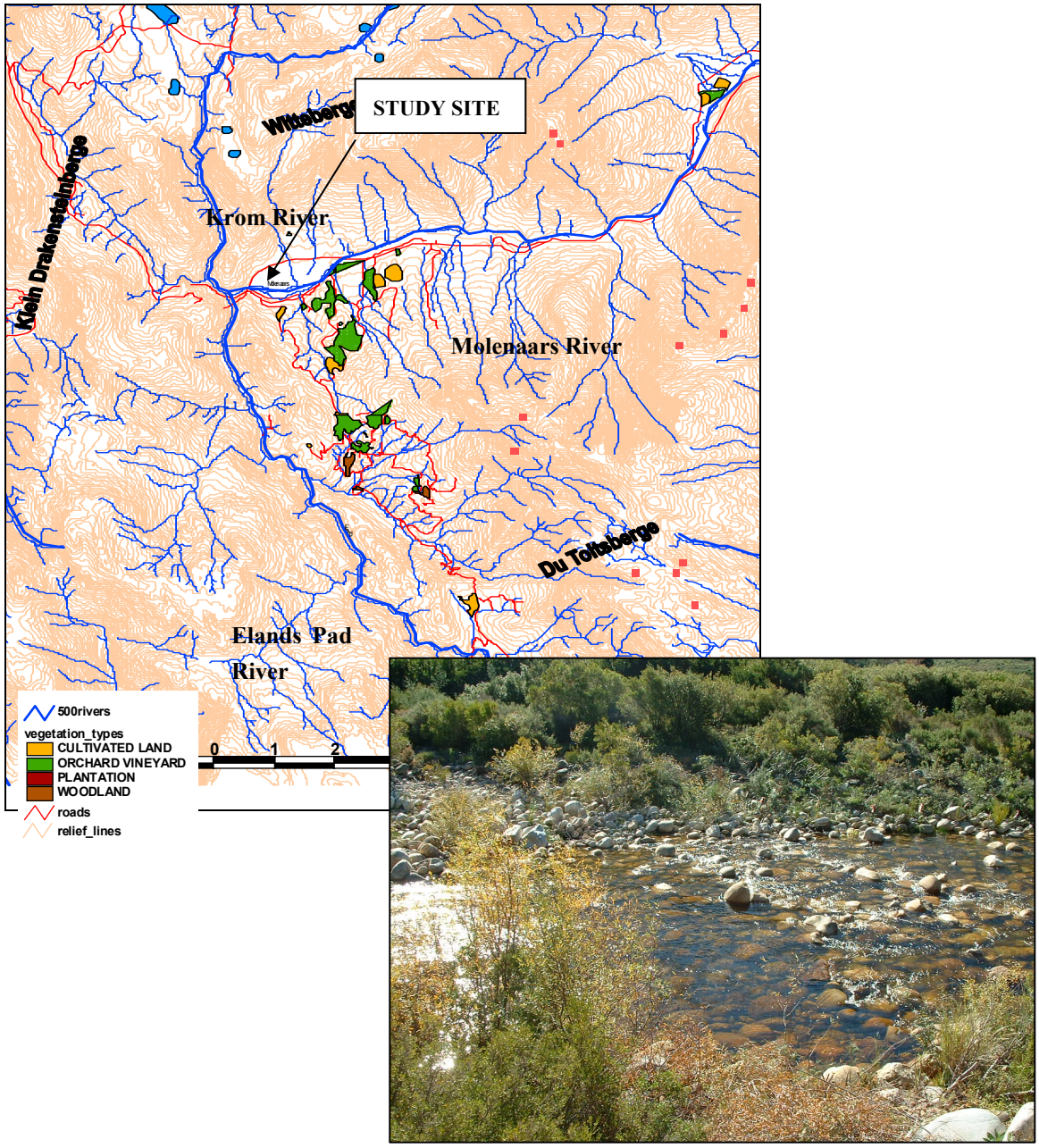


Figure 3.2 Detail of the Molenaars River, showing the study site and (inset) looking across the study site from high up on the right bank.

The first study site was located on the Molenaars River (Figure 3.2). This river is one of the main tributaries of the Breede River, which is the largest river in the Western Cape and flows into the Indian Ocean. The study reach has relatively well defined banks on both sides and consists primarily of a riffle and rapid section ending in a large pool.

The second study site was located in the headwaters of the Berg River (Figures 3.3 and 3.4), which is the second largest River in the Western Cape and flows into the Atlantic Ocean. The study site was located on a slight bend in the river and has a steep bank on the outside (left hand) bank and a lateral bar of deposited cobbles on the inside bank. A small rapid section dominated the upstream half of the site, leading to a shallow run in the downstream half of the reach.

The planform of the Molenaars and Berg River study sites as well as the thalweg profile, a selection of cross-sections, stone particle-size distribution plots and field notes are provided in appendices in the Volume 1 report for this project. (1411/1/07)

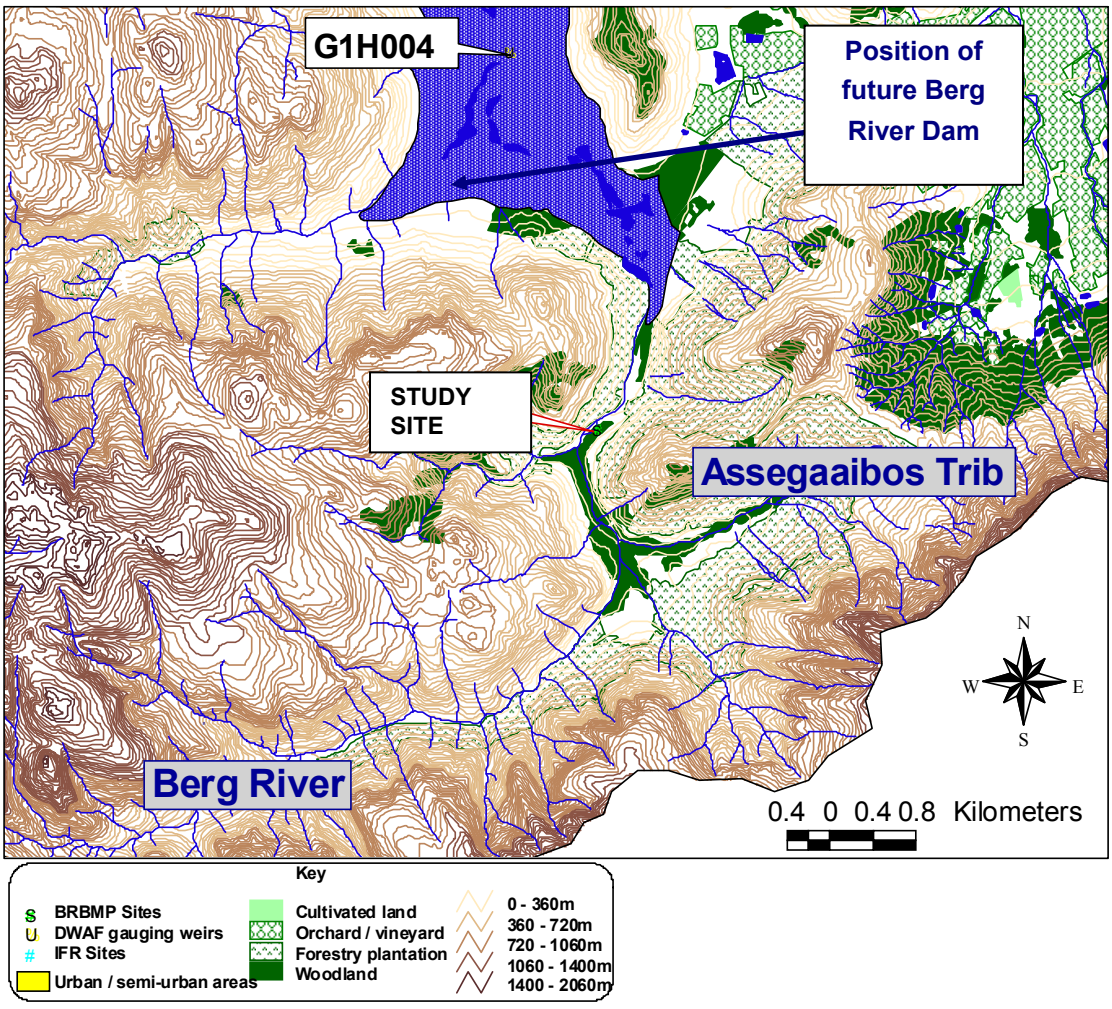


Figure 3.3 Detail of the Berg River, showing the study site.

Figure 3.4 The Berg River Study Site at summer low flow (baseline) and at winter baseflow (post-flood sampling).

3.2 HYDRAULIC AND STONE MOVEMENT DATA

3.2.1 Sampling strategy

The approach to collecting data on the movement of stones, linked to flood events, had to satisfy the requirements of both of the main objectives of the overall project viz. provide data for the calibration of a theoretically-based hydraulic model, and simultaneously allow for biological data to be collected from the stones. This required on the one hand a) a large enough sample of stones to be representative of the full range of hydraulic conditions likely to prevail during a flood; b) a systematic selection of stones to provide a random sample for particle size distribution analysis and c) the positioning of all stones along fixed cross-sections, to allow for the calculation of hydraulic indices from surveyed bed heights and water levels, and to facilitate finding the marked stones after each flood event. In addition, since many of the stones on a systematic grid, covering lateral bars and channel margins would be exposed and therefore not unavailable at times for biological sampling, the sample size had to be sufficient to include at least 200 stones from which biological data could be collected on any one occasion.

3.2.2 Baseline (pre-flood) hydraulic data

A detailed survey of both study sites was performed prior to initial sampling of the individual stones for hydraulic and biological data. Thirty cross-sections were established at each selected study site, placed at 2m intervals, and the bed level was surveyed at 1 m intervals along each cross-section. In addition a detailed digital terrain model of the Molenaars study site was developed using aerial photogrammetric survey of the study area prior to the initial baseline data collection and this was deemed to be accurate within 0.10 m. The thirty cross-sections were marked by steel pegs on each bank of the river and the stones to be studied were selected by stringing a tape between the pegs and selecting stones at 1.0 or 1.5 m intervals across each cross-section. In total, 345 and 435 stones were selected at the Molenaars and Berg River study site respectively. In the case of the Molenaars River, the site was re-surveyed at the start of the 2004 data collection period, because the late floods of 2003 caused bed movement and a re-survey was needed to ensure accuracy in the hydraulic data calculated from these bed levels. Similarly, following a large flood in 2004 (the second flood monitored during the 2004 study period) both sites were re-surveyed again to ensure accuracy in the hydraulic data calculated thereafter.

A tape measure was stretched across each cross-section, between two permanent stake markers, and stones were randomly selected at either 1 m or 1.5 m intervals. These were sampled for invertebrates and, for the Berg River, periphyton (see section 3.3.2) and then measured, marked with an individual number and replaced. Lead-weighted fish markers were used to pinpoint the exact position of stones whilst they were being sampled and measured (Figure 3.5). The selected stones were marked and numbered with paint and waterproof pen. Both the top and the bottom of the stones were marked to make it possible to determine if the stone had been turned over during a flood event. Submerged stones that could not be lifted were marked with putty into which an identity number was scratched. Initially small magnets were attached to the stones as it was felt that this

would allow for easier location of stones after floods.

It was found, however, that there was too much natural magnetism in the rocks to make this a reliable method for locating stones after a flood and it was thus abandoned. If possible, the stones were measured in terms of their three main axes. Embedded stones that could not be lifted were measured according to their second longest axis (dy).

After sampling, the stones were returned to their original positions, and water depth and average velocity (at 0.6 depth from the water surface) were recorded above each of the marked stones, as was the flow type - a visual categorisation of the nature of the water flow used in hydraulic biotope studies (Rowntree, 2001). Flow velocity and depth were recorded using a Scientific Instruments Inc. Model 1205 Mini Meter Current Meter. Measurements for flow were taken in revolutions per 45 seconds and converted to velocity with the equation:

$$\text{Velocity (metres per second)} = ((\text{Rev/Time} \times 0.977) + 0.028) \times 0.3048$$

(Scientific Instruments Inc. 1980)

Table 3.2 Definition of different hydraulic biotopes (Rowntree, 2001; King & Schael, 2001). Flow type acronyms are defined in Table 3.2.

Hydraulic Biotope	General description	Flow type
Backwater	A morphologically defined area alongside but physically separated from the channel, connected to it at its downstream end; occurs over any substratum type	BPF or NF
Slackwater	An area of no perceptible flow within but hydraulically detached from the main channel; occurs over any substratum type	BPF or NF
Pool	Has direct hydraulic contact with upstream and downstream water; occurs over any substratum type	BPF
Trickle run	Cobble and boulder substratum; few bed elements submerged	TR
Run	Any substratum type apart from silt; relative roughness low; often in transitions zones between riffles and the downstream pool	RSF or SF
Glide	Occurs over any substratum type, where depth is sufficient to minimise relative roughness. Glides exhibit uniform flow with no convergence or divergence	SBT
Chute	Typically in boulder or bedrock channels where flow is funnelled between large bed elements. Chutes are generally short and exhibit flow acceleration, often due to flow convergence	SBT with acceleration
Riffle	Occur over coarse alluvial substrata from gravel to cobble; relative bed roughness is high	FRF or BSW
Rapid	Occur over more or less fixed substrata, such as bedrock or boulders	USW or BSW
Cascade	Occur over bedrock or boulder substrata; small cascades may occur in cobble where the bed has a stepped structure due to cobble accumulations	FFF

Figure 3.5 Example of a fish-marker marking the position of a stone and of a numbered stone repositioned on the stream bed.

Figure 3.6 Plastic stage pipe used to measure flood levels.

Figure 3.7 The Molenaars (left) and Berg (right) Rivers in flood. Iron stakes marking cross-sections across the Molenaars River are visible on the left of the photograph with yellow plastic caps.

River biologists have long recognised that different patches of stream may generally be associated with specific groups of invertebrate fauna. The concept of the hydraulic biotope was introduced to provide some consistency in the description and naming of these categories of physical habitat, whilst concentrating on the flow-related aspects that define an organism's living space (Rowntree & Wadeson, 1996). Hydraulic biotopes are defined according to the combination of flow types and substratum (Tables 3.2 and 3.3). floods at both the Molenaars and Berg study sites.

Considerable effort has been put into an examination of the biological distinctness of hydraulic biotopes (e.g. King & Schael, 2001), whilst attempts have also been made to define the hydraulic character of biotopes, in order to allow for the development of a relationship between discharge and biotope availability (e.g. Schael, 2005). One of the outcomes of these studies has been the recommendation that the RSF flow type used to identify run biotope may not adequately discriminate between units that are biologically different (Schael, 2005). Thus, in this study run biotope with RSF flow types were sub-divided where information was available. In the Berg River work the flow type on its own was used, as defined in Table 3.3. For the Molenaars River, the more detailed descriptions of each stone sampled allowed runs to be split into fast, medium or slow run.

Table 3.3 Definitions of flow types used in Table 3.1 (from Rowntree, 2001)

Acronym	Flow type	Definition
NF	No flow	No water movement
BPF	Barely perceptible flow	Smooth surface, flow only perceptible through the motion of suspended objects
SBT	Smooth boundary turbulent flow	Water surface smooth; streaming flow takes place throughout the water profile; turbulence can be seen as the upward movement of fine suspended particles, or as boils on the surface in stronger flow
TR	Trickle	Shallow flow between bed elements with few submerged bed particles.
RSF	Rippled surface flow	The water surface has regular disturbances which form low transverse ripples across the direction of flow
FRF	Fast riffle flow	Shallow broken water flowing over cobbles
SF	Surging flow	Undular waves form on the surface, but they move downstream, breaking up
USW	Undular standing wave	Standing waves form at the surface, but there is no broken water
BSW	Broken standing wave	Standing waves present which break at the crest (i.e. white water)
FFF	Free-falling flow	Water falls vertically, without obstruction

The offset from the survey pegs was recorded and used to determine the co-ordinates of each stone in a local co-ordinate system. The bed level of each stone could then be determined according to the detailed survey. The following hydraulic measurements were measured or calculated to describe the base flow conditions: stone size, depth, velocity,

and the measures derived from these using local slope, viz. Froude number, Reynolds number, input stream power and bed shear stress. Reynolds number represents the ratio of turbulent to laminar flow, defined as:

$$\mathrm{Re} = \frac{VD}{\nu}$$

where D is the depth, V is velocity and ν is the kinematic viscosity. Froude number, the ratio of inertial to gravitational forces acting on stream flow, is defined as:

$$Fr = \frac{V}{\sqrt{gD}}$$

where V is velocity at each point, *g* = acceleration due to gravity and D the depth at each point. Froude number reflects the interaction of flow depth and velocity at a given point, related to the effects of bedform whereas Reynolds number is a better measure of conditions within the mass of water flowing over a point (Gordon, 2004). The third hydraulic parameter computed for each point in these analyses was input stream power. This index is defined as the rate of potential energy expenditure over a unit stream length:

$$W = \rho g V S$$

where ρ is water density, V is velocity, *g* =acceleration due to gravity and *S* is the energy slope over each point. For these analyses, slope was taken as the average water surface slope between three consecutive cross-sections. There will be local fluctuations in the energy slope that are lost by using the average water slope, but using the average water slope is a good first estimate of the average energy slope. For calculating Stream Power during floods, the average water slope for the full reach was used. This assumed that the flow was more-or-less uniform along the reach at high flows.

Finally, shear stress is defined as the frictional force causing flow resistance at the bed. Shear stress (τ) is calculated according to the following formula:

$$\tau = \rho g(D - y)s$$

where D is the distance from the water level, s is the energy slope, and y the distance from the bed.

Eight clear plastic pipes, 2 m long, were placed at intervals along either bank of the study reach to be used to measure the water level during a flood (Figure 3.6). The pipes were attached to metal y-sections that were concreted into the ground. The plastic pipes had holes drilled in the bottom and the top to let water in and air out. Sawdust, cork flakes or finely cut dry grass were placed in each pipe. These materials floated on the water surface inside the pipe, rising with the increasing water level. After a flood the level of the ring of sawdust / cork residue adhering to the inside of the pipe was measured as the highest water level reached under the relevant flood. The inside of the pipe was then washed clean and the cork flakes replaced ready for the next flood.

3.2.3 Flood measurement and stone-movement data

The first set of flood-event data was collected at the Molenaars study site during the winter of 2003. Six flood events were recorded during this period. During the winter of 2004 flood event data was collected for five

After each flood event the study sites were revisited. Cross-sections were searched from downstream to upstream. Searches were carried out as soon as it was safe to enter the river, for two reasons. The first was to ensure that a full search could be carried out before the arrival of the next flood (which can be almost immediate in the western Cape) and the second was because invertebrate sampling, for the floods that were sampled, needed to be carried out as close to the flood as possible, to measure its effect on invertebrate distribution.

Searches for stones were thus carried out underwater using goggles in shallow - medium depth water that was nevertheless still fairly turbulent. Marked stones were located wherever possible. The movement of a particular stone was noted either in terms of whether it had simply turned over or had moved out of position. In the latter case the distance that it had moved was recorded, if the stone was located. Sweep searches of the river bed up to 30 m downstream of the site were undertaken simultaneously to locate stones that had moved some distance. Stones that had been turned over or moved were replaced in their original locations ready for the next flood event. Where marked stones could not be located, they were assumed to have been washed out of the study site reach, were recorded as moved, and were replaced by the stone occupying the same location along the cross-section, with its new individual number. The dimensions of any new stones were recorded and used for the analysis of subsequent flood events.

The resulting data set, comprising field notes and measurements for the initial site Baseline survey and details of individual stone movement from each of the post-flood visits are provided in detail in the first report (Hydraulic Model) for this project.

The maximum water level for each flood event was recorded by measuring the height of the cork or sawdust ring left on the inside of the plastic pipes. By comparing this to the surveyed heights of the pipes it was possible to calculate an average water level profile for the study reach. This was used to measure the water slope during the flood as well as the depth above each sampled stone, for the calculation of various hydraulic parameters relating to that flood.

3.2.4 Flood analysis

In one of the recent holistic environmental flow assessment methods used in South Africa, DRIFT (King *et al.,* 2003), flood flows are classified into eight flood classes based on analysis of the long- term average daily flow hydrological record. Classes 5 to 8 represent the inter-annual flood events with a return period of between two and fifty years. Classes 1 to 4 represent the spectrum of intra-annual flood events and the level of these floods is obtained simply by halving the two-year return period flood to obtain the Class 4 flood which is halved again to obtain the Class 3 flood, and so on.

The eight flood classes for the two gauges immediately downstream of the study sites were determined by Howard (2004) for G1H004 on the Berg River and King *et al*. (2004) for H1H018 on the Molenaars River and these are shown in Table 3.4. Howard (2004) noted that there was some concern about the reliability of the flow record for G1H004 prior to 1980. For this reason he determined flood classifications based on both the full record and a shorter record after 1980. For the purpose of classifying the floods studied during this project, the classification based on the shorter record was used. This was based on the greater level of accuracy of the flow record after 1980, but introduces a higher level of uncertainty, particularly with regards to the longer return period floods.

The maximum flow experienced at the study reach within each flood event was estimated by reducing the instantaneous flood peak observed at the downstream gauge by the ratio of the catchment area upstream of the study site to the catchment area upstream of the gauge. The estimated maximum flow rate, average daily flow rate, flood volume (including base flow) and class of flood as determined from the average daily flow rate at the downstream gauge for all the observed flood events during the invertebrate study periods are given in Tables 3.5 and 3.6.

Table 3.4 DRIFT Classification based on average daily flows for H1H018 and G1H004 (m^3s^{-1})

Class	Recurrence Interval	H1H018 (Molenaars)	G1H004 (Berg) (Short Record)	G1H004 (Berg) (Long Record)
I	Intra annual floods	5.0	3.6	4.3
II		16.0	7.2	9.5
III		31.0	14.5	19.1
IV		61.0	29.0	38.2
V	1 : 2 years	93.7	58.7	76.3
VI	1 : 5 years	146.0	75.3	118.0
VII	1 : 10 years	181.0	78.8	154.6
VIII	1 : 20 years	187.0	85.6	178.0

Table 3.5 Flood events observed at the Molenaars Study Site.

Year	Event Number	Date	Duration (hours)	Max Flow (m^3s^{-1})	Avg. Daily Flow (m^3s^{-1})	Volume (Mm^3)	DRIFT Class
2003	1	10th July	33	5.56	3.72	0.41	I
	2	18th July	21	15.23	5.41	0.49	I
	3	25th July	14	8.60	4.20	0.28	I
	4	1st August	26	28.76	7.98	0.95	I
	5	8th August	26	36.46	14.45	1.74	II
	6	18th August	32	140.80	30.29	4.15	III

Table 3.6 Flood events observed at the Berg Study Site.

Year	Event Number	Date	Duration (hours)	Max Flow (m^3s^{-1})	Avg. Daily Flow (m^3s^{-1})	Volume (Mm^3)	DRIFT Class
2004	1	5th June	28	7.27	2.08	0.40	I
	2	14th June	44	84.51	32.58	3.48	IV
	3	26th June	27	4.82	2.62	0.29	I
	4	3rd July	24	11.74	5.68	0.44	II
	5	23rd July	20	60.98	17.70	1.66	IV

3.3 ECOLOGICAL DATA

3.3.1 Sampling design

3.3.1.i Molenaars River

The sampling design for the investigation of invertebrate response to floods was the collection of two data-sets from each of 200 stones, i.e. the invertebrate fauna was collected from each stone on two occasions. Invertebrate collections from all stones were made at the start of the study (the Baseline survey) and the stones then returned to their precise location, following which recolonisation with stream fauna was possible. The timing of the Baseline study was aimed at minimising possible temporal differences in invertebrate assemblages that might not be due to flood disturbance, but also allowing the initially sampled stones sufficient time in the river to become 'reconditioned' before the onset of floods in the river. A criterion of 30 days after initial sampling was considered to represent the time required for re-establishment of the baseline condition.

The validity of this approach is based on the assumption a) that the sets of stones being compared were representative of the invertebrate assemblage in the river and b) that recovery of the invertebrate fauna had occurred prior to the first flood that was to be examined. These assumptions were tested by examining the extent to which sub-sets of the baseline stones that were repeat-sampled at different dates, and compared for differences between the two time intervals, were indeed representative of the whole

community at the start of the study period. Secondly, the sampling of a subset of 50 of the baseline stones before each the two floods allowed for the establishment of a control for those sampled after the flood in the event that recovery from initial sampling was not complete.

In the Molenaars River, therefore, 200 stones were initially sampled in June 2003, marked and returned to their original location, and then sub-sets (n = 50) of these same stones were repeat-sampled on one more occasion, either immediately prior to and immediately after flood events in mid and late July 2003 (Figure 3.8).

Not all stones marked for the stone-movement monitoring and hydraulic model calibration were used for the invertebrate study, partly because many of the systematically selected stones were immovable and / or emergent boulders. Whilst the majority of samples were taken from whole (i.e. movable) stones, some samples were taken from the upper surfaces of large submerged boulders (i.e. immovable stones), as some taxa tend to dominate on these kinds of surfaces and their fate during a flood was also of interest. Each set of fifty stones repeat-sampled before or after a flood was selected at random from within these two main categories of 'whole' and 'immovable' stones.

For the Molenaars River study, 200 out of the 345 marked stones were sampled for invertebrate fauna in May 2003, the Baseline survey. This sample size allowed for two floods to be sampled for invertebrate responses, within the repeat-sampling, pre-and-post flood approach described above. The first flood of the season was a small flood which occurred on 10 July, one month following baseline sampling (Figure 3.9), in what was regarded as an unusually dry winter season.

The second flood used to measure invertebrate responses was in fact the fourth of the winter season, as the forecasted rainfall for the second and third floods was not high and it was wished to obtain data for both a small and a larger flood event in the river. Despite this, the fourth flood was also not substantial, with larger floods occurring only late into winter. By late winter, however, the Baseline stones had all been sampled either before or after Flood 1 or Flood 4, and no further data were collected. Biological data were collected from the Molenaars River only in 2003, whilst stone movement data were collected in 2003 and 2004.

Due to the limitations of the scope of the project, only 30 stones from each set of 50 sampled stones were actually processed and analysed. Seventy of the 200 baseline stones were processed, corresponding to the stone numbers that were repeat-sampled before and after the first flood, and some of those sampled before the second flood. Of each subset of 30 stones processed, between three and seven stones were representative of 'stone tops' only, with the remainder being 'whole stone' samples.

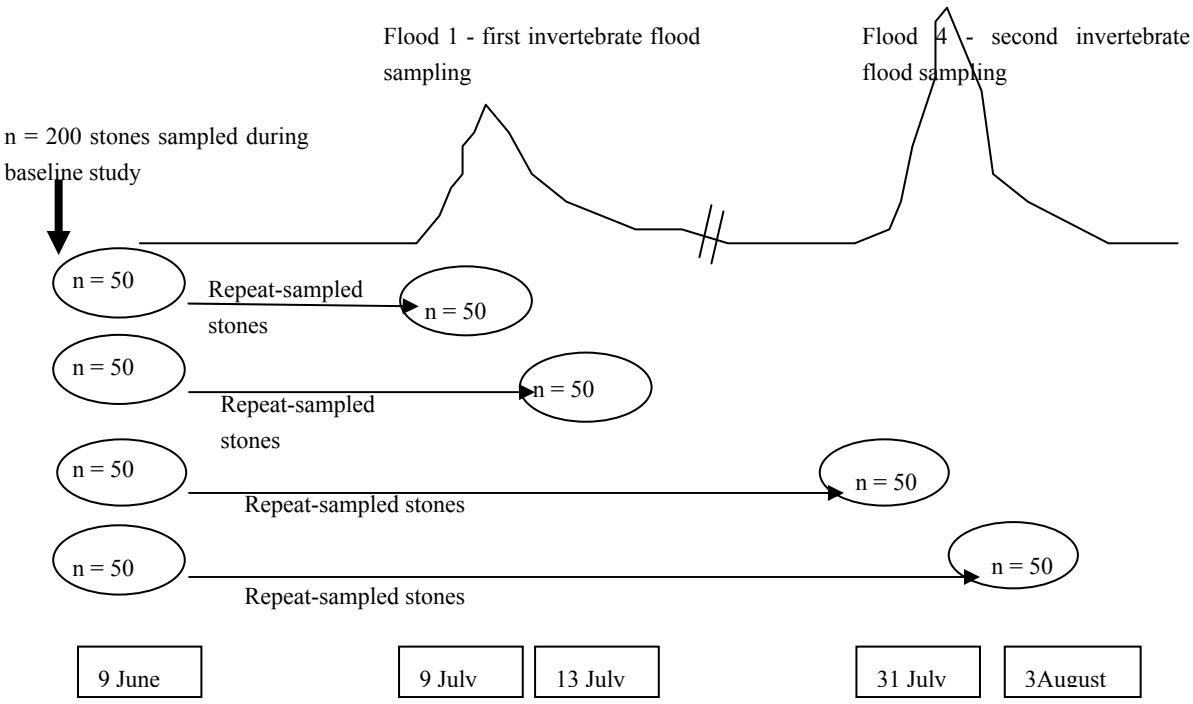


Figure 3.8 Sampling approach for the Molenaars River study in 2003.

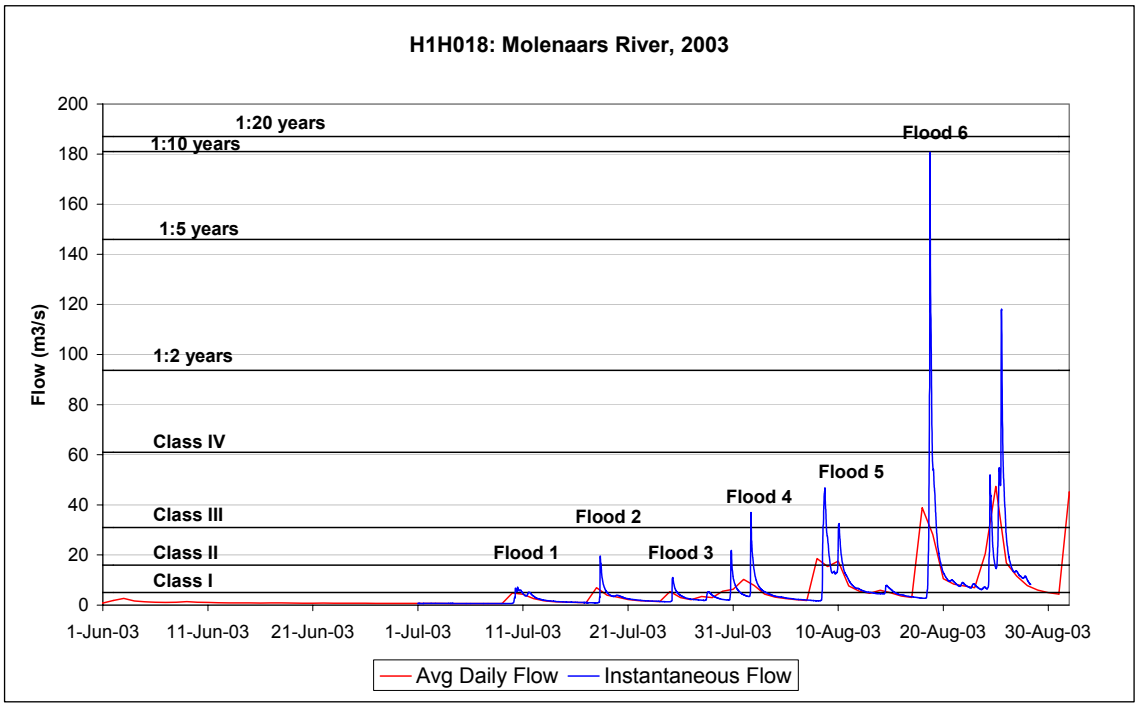


Figure 3.9 Flood Events Observed on the Molenaars River (H1H018) in 2003. Stone movement data were collected after all six floods, whilst invertebrate sampling was undertaken before and after Flood 1 and Flood 4. The equivalent DRIFT flood classes are indicated.

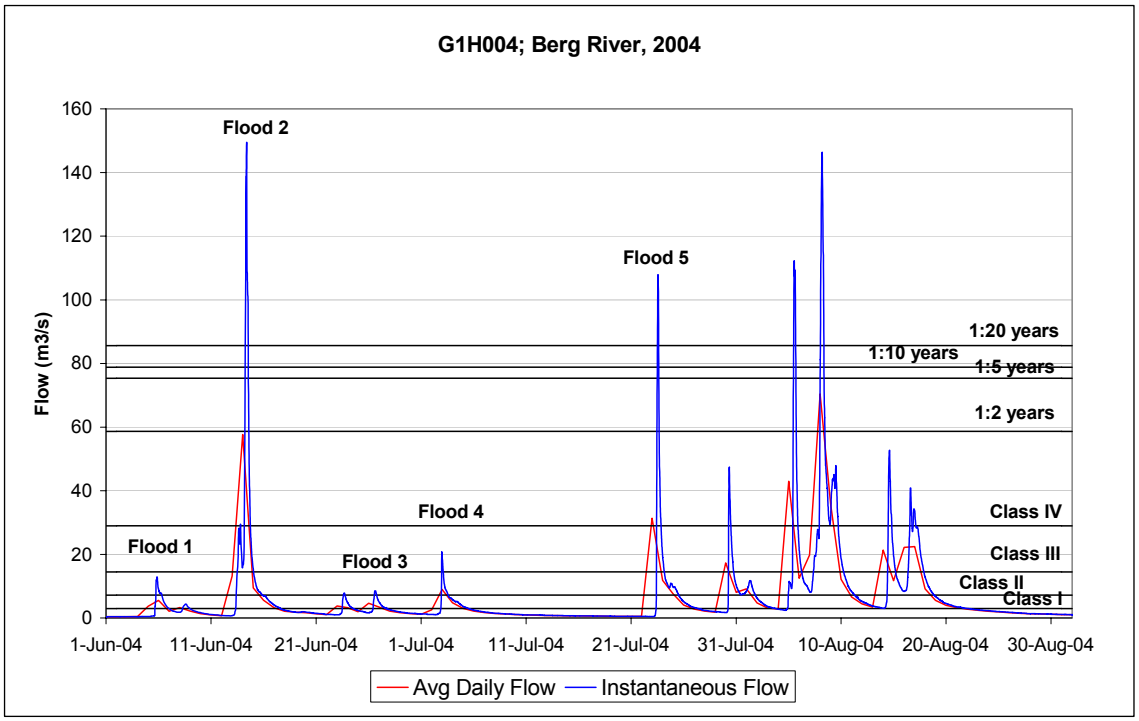


Figure 3.10 Flood events observed on the Berg River (G1H004) in 2004. Stone movement data were collected after all five floods, whilst invertebrate sampling was undertaken in May and again only after Flood 5. The equivalent DRIFT flood classes are indicated (see section 3.5).

3.3.1.ii Berg River

For the Berg River invertebrate study in 2004, a different design was necessitated, because of difficulties with field conditions. The initial Baseline sampling was conducted from 17 - 22 May 2004, earlier than that undertaken for the Molenaars River the previous year, which was performed in early June. This was in an attempt to allow sufficient time for reconditioning of the sampled stones, but nevertheless minimising possible temporal differences in invertebrate assemblages. Sampling in the Berg River also included whole stones and the upper surfaces of immovable stones, as in the Molenaars River. In addition, periphyton data were also collected from all whole stones.

Unfortunately, a small flood occurred in early June 2004, followed immediately by a large one (DRIFT Class 4) on 14 June (Figure 3.10). This was judged as far too soon after the Baseline survey to allow for meaningful sampling to be conducted, as the effects of the initial denudation of stones would override or confound any flood-disturbance effects. A large proportion of stones were also washed away, thus reducing the biological dataset from 220 to fewer than 100 stones, only 61 of which were whole stone samples.

Post-flood invertebrate sampling was therefore only conducted immediately following the fifth flood of the season (July 2004), two months - and five floods - after the Baseline survey. The final data set, therefore, comprised repeat-sampled stones with different disturbance histories, depending on whether or not they were moved by the floods.

With few exceptions, which were excluded for the data analysis stones either remained stationary, moved in the second flood (the largest for the study period), or moved in both the second and fifth floods.

An additional data set of invertebrate and periphyton samples from unmarked stones was also collected during the Post flood survey, with some 58 of these being whole stone samples and 20 representing stone top surfaces from immovable stones. This data set was intended to act as a control for the possible sampling effects associated with repeat-sampling the Baseline set of stones. This control set was necessary because the Pre-flood control data as collected in the Molenaars River study could not be collected from the Berg River, as explained above.

In addition to being a control data set, the additional stones were used to test the predictions of the hydraulic model of incipient motion (see summary in section 4). The hydraulic model can be used to provide an estimate of the likelihood of a stone with a particular dimension being moved or unmoved by a flood of known magnitude, based on knowing the applied stream power at the stone location on the bed. To this end the dimensions of the additional stones and their position along each cross-section were recorded, as well as point depth and velocity at 0.6 m at each stone position, so that the likely disturbance history of the stone could be determined based on the hydraulic model. Thus, the additional stones were identified as ‘probably unmoved’, ‘probably moved in Flood 2 only’ and ‘probably moved in Flood 2 and 5’, the three categories of stone movement identified for the Repeat-sampled stones. In addition, some of the additional stones fell into the ‘immovable stone tops’ category. Table 3.7 summarises the

different stone categories identified for analysis.

3.3.2 Field methods

Invertebrates only, and both invertebrates and periphyton were collected from individual stone samples. A hand net (mesh size 125 μm), with aperture area of 300 X 300 mm was held downstream of the stone, close to the stream bed. The stone was then lifted free of the bed, and held in the mouth of the net, whilst the area upon which the stone had rested was gently brushed to collect invertebrates associated with the sampled stone that might have retreated to the stream bed as the stone was lifted. Brushing was done carefully to cause as little disturbance the surrounding substratum particles as possible, to avoid over-sampling the area upon which the stone had rested. A lead-weighted fish marker with a numbered floating cork was used to demarcate the position of the stone. Thereafter the net and stone were raised close to the water surface to prevent accidental sampling of any other animals dislodged from the bed. Invertebrates were removed from the stone as gently as possible by hand and with a toothbrush and / or forceps to minimise the amount of periphyton dislodged in the process (Figure 3.11).

Table 3.7 Categories of stones sampled in the Berg River in 2004.

Stone category	Description of sampling frequency and nature of disturbance to stones	Number in category
Whole stones sampled		
1	Sampled in May Baseline survey; unmoved in all floods; re-sampled in July after 5th flood	26
2	Sampled in May Baseline survey; moved in Flood 2 but not thereafter; unmoved in 5th flood; re-sampled in July after 5th flood.	14
3	Sampled in May Baseline survey; moved in Flood 2 and subsequent floods, also moved in Flood 5; re-sampled in July after 5th flood.	21
4	Additional stones sampled for the first time after 5th flood - movement status derived from hydraulic model as unmoved	26
5	Additional stones sampled for the first time after 5th flood - movement status derived from hydraulic model as moved in Flood 2 but not thereafter	14
6	Additional stones sampled for the first time after 5th flood - movement status derived from hydraulic model as moved in Flood 2 and subsequent floods, also moved in Flood 5	18
Top surfaces of stones sampled (too large / embedded to sample fully)		
7	Paired stones, sampled in May Baseline survey; unmoved in all floods; re-sampled in July after 5th flood	24
8	Additional stones sampled for the first time after 5th flood - movement status in 5th flood derived from hydraulic model as probably unmoved	20

Sampling of medium and large stones required two people. All stones on the Molenaars and on the Berg River respectively were sampled by the same person to minimise potential error associated with sampling effort. Notes were also made of the orientation and degree of packing around the stone, and every effort was made to replicate these conditions when the processed stone was returned to the stream bed.

After removal of invertebrates, the stones were placed on large white plastic trays, scrubbed with a toothbrush and rinsed with river water (Figure 3.11), in order to remove periphyton growth attached to the stone.

The standard 2 minutes scrubbing time recommended for cobble sizes by Biggs & Kilroy (2000) was modified to take into account the large range in stone particle size at the site. Scrubbing time was thus scaled from 1 minute for small cobble (60 - 90 mm x-axis) to 18 minutes for small boulder (400+ mm x-axis). In all cases however, rocks were observed to be cleaned until no change in the colour of rinsing water was evident. The rinsing water and periphyton slurry (usually approximately 200 ml) was stored in labelled plastic collecting jars, on ice in the field and transferred to a freezer within 12 hours of collection. Periphyton samples were only taken from whole stones, not from the tops of immovable boulders.

The dimensions of each stone were measured as the longest axis (x), the longest horizontal axis perpendicular to x (y) and the longest vertical axis of the stone (z). The surface area of each stone was then calculated using the regression equation for stone area derived from a regression (r^2 = 0.93) between the measured dimensions of a stone and its surface area:

$$\text{Stone area (in cm}^2\text{)} = 0.014x + 33.819$$

where x = the sum of the multiples of measured axes, xy+xz+yz (in mm^2). Sixty river stones from the Berg River were used to establish this relationship. For these stones, both x, y, and z dimensions and the surface area was measured, the latter by covering them precisely with metal foil, which was then weighed. The foil area was calculated from the known weight per unit area of foil. The values obtained for surface area in cm^2 were converted to m^2.

3.3.3 Laboratory methods

The invertebrate samples were preserved in 4% buffered formalin in the field. Upon return to the laboratory the samples were strained through a 250 µm sieve and transferred into 70% alcohol for preservation. Invertebrates were separated from the debris collected at the same time, and identified to a range of taxonomic levels, in part based on available expertise and on a presumption of the likelihood of different species-specific flood responses. Thus Trichoptera were identified to species or morpho-species, based on the best taxonomic keys available. Ephemeroptera were identified to genus (for the Baetidae) or species (other Families). Simuliidae and Blephariceridae (Diptera) were comprised each of only one genus. Chironomidae were identified to sub-Family or Tribe, since these correspond generally with differences in size and feeding guild. Other Families, including

Notonemouridae (Plecoptera) and all the Coleoptera, were identified to Family level only, based on morphological similarities between species and / or the difficulty of separating young instars.

Invertebrate identifications were performed using Nikon SMZ 1500 and SMZ 1B dissecting microscopes, an Olympus compound microscope and numerous field guides and taxonomic keys (Davies, 1998; De Moor, 2002; Barber-James & Lugo-Ortiz, 2003; De Moor & Scott, 2003; Mansell, 2003; Samways & Wilmott, 2003). All animals were measured with a calibrated graticle inserted into the microscope eye-piece. The head width was used as the unit of measurement, as it is most often regarded as the most stable measure correlated with specimen age.

Each periphyton sample was divided into two equal portions, in order to determine two different measures of periphyton, the ash free dry weight (AFDW) of the periphyton on a rock, and the concentration of Chlorophyll *a*, both expressed as a density in mg m^{-2} of stone surface.

To obtain AFDW, the periphyton slurry of each half-sample was filtered onto Whatmann GFF 4 glassfibre paper, dried to a constant weight at 60°C and then ashed in an oven at 400°C for 4 hours. The difference between the ashed and dry weights represents the total organic content of the periphyton of each sample.

Figure 3.11 Removing invertebrates (left) and periphyton (right) from cobbles.

The eukaryotic photosynthetic component of periphyton is indicated by chlorophyll a mass (Biggs & Kilroy, 2000). For each sample, chlorophyll was extracted with methanol, boiled at 70°C for 3 minutes to increase extraction efficiency and to fix the chlorophyll by destroying the enzymes (Biggs & Kilroy, 2000). Absorbance was measured at a wavelength of 665nm with a spectrophotometer. Background absorbance was measured at 750nm.

Finally, after invertebrates had been removed from the preserved samples in the laboratory for identification and enumeration, the remaining debris

associated with each sample was dried to a constant weight at 60°C and then ashed in an oven at 400°C for 4 hours, this time to determine the total content of organic and inorganic matter associated with each sample point. This was divided by half the stone surface area to approximate an amount of matter per m^2 of the river bed associated with each stone.

3.4 DATA ANALYSIS

3.4.1 Overview

Initial analysis of the data was aimed at identifying patterns in the Baseline (pre-flood) data, and quantifying relationships between invertebrate assemblages and community indices on one hand, and periphyton and physical parameters on the other hand. The extent to which these relationships and community attributes were maintained or altered by floods was one of the key objectives of this analysis.

This was achieved using a combination of uni- and multi-variate statistical methods. All multivariate statistics were produced using PRIMER Version 6. for Windows and the univariate statistics were produced using STATISTICA Version 7.

In addition, a test was done to assess potential difference between sub-sets of the baseline samples from the Molenaars River, to establish the representativeness of a sample size of approximately 23 - 28 stones, which represented the size of each subset of the whole stones sampled during the repeat-sampled on one of four future pre- or post-flood occasions. Also, recovery of initially sampled stones, prior to flooding, was measured by comparing baseline stones (9 June) with those taken during the first pre-flood sampling session (9 July).

The movement of stones during a flood was expected to constitute a higher level of disturbance than non-movement with increased applied stream power. This hypothesis was tested by examining the change in invertebrate composition on moved versus unmoved stones, relative to the Baseline or Pre-flood condition. Statistical methods for this analysis included correlation analysis, analysis of variance and multi-variate cluster analysis.

A second hypothesis was that the magnitude of force acting on individual bed particles would be related to the loss or otherwise of invertebrates, such that areas experiencing lower applied power might act as refugia, and accumulate individuals eroded from areas experiencing high hydraulic forces during a flood. To explore this, a correlation was sought between the densities, or the change in densities, of invertebrate taxa on each stone after a flood and the applied stream power acting on that stone during the flood. It was further hoped that this might indicate various thresholds of applied forces at which different taxa become disturbed.

Finally, changes in population structure were investigated by comparing pre- and post-flood size frequency distribution data for selected individual taxa.

3.4.2 Multivariate statistics

A group of computer-based programs specifically developed for multivariate and statistical analyses of multispecies data was used to investigate the relationships between samples at each sample time, and between samples taken before and after floods. These programs collectively form the software package PRIMER (Plymouth Routines in Multivariate Ecological Research) Version 6, developed at the Plymouth Marine Laboratory, United Kingdom (Clarke & Warwick, 1994). Multivariate analysis has an advantage over univariate methods (e.g. ANOVA) of maintaining much of the complexity of community-based biological data, as the comparisons of samples are based on the extent to which they have particular taxa in common and at the same levels of abundance. PRIMER is particularly useful as a tool to display the relationships between biological samples when the taxa-by-samples arrays are large, and thus patterns in community data not readily apparent (Clarke & Warwick, 1994).

The PRIMER routines follow an initial computation of similarity coefficients between each pair of samples to produce a triangular similarity matrix. A 4^{th}-root transformation of invertebrate data is recommended for comparison of samples from different sites or treatments, in order to dampen the effect of the most dominant taxa on the similarity matrix, whilst also being invariant to scale change (Field *et al.,* 1982). For this study, the benthic invertebrate data were square-root transformed, because density differences were considered as important as species differences in before- and after-flood comparisons. The Bray Curtis coefficient of similarity does not take account of joint absences when computing similarity between pairs of samples, and, because many of the taxa recorded during this study were absent from many of the samples (e.g. as a result of seasonality in occurrence or because they occur only rarely in the benthos), this measure was chosen for the analysis (see Field *et al.* (1982) and Clarke & Warwick (1994) for a discussion on the relative merits of similarity coefficients).

A number of routines in the PRIMER package were used to test for significant differences between groups of samples identified *a priori* (ANOSIM), to represent relationships between samples/times (CLUSTER analysis and MDS ordination), to identify taxa contributing to these differences (SIMPER), and to examine the relationship between groups of invertebrates sampled and the environmental variables measured as they were collected (BIOENV). These are described briefly.

3.4.2.i Analysis of Similarities

ANOSIM is a multivariate approach to the analysis of similarities between of groups of samples that are defined *a priori*, which compares the average similarity of all pairs of samples within a group to the average similarity of pairs of samples corresponding to replicates from different groups. The resulting test statistic, R ranges from -1 to 1, but usually falls between 0 and 1, since a negative R-value denotes that samples within the designated group are less similar to each other than to samples from other groups, which would be unlikely (Clarke & Warwick, 1994). The closer to 1 the R-value, the greater the

difference between groups, whilst an R = 0 denotes no difference between groups.

The probability of the R-value being significantly different from zero is computed by comparing the results computed with those generated from randomly defined combination of the chosen groups. Clarke & Warwick (1994) caution against falsely rejecting the null hypothesis of no difference between groups in multiple tests (i.e. pairwise comparisons in ANOSIM), suggesting a conservative probability, or p-value be used to avoid potential Type 1 errors associated with multiple comparisons. In these analyses therefore, a p-value, of 0.01 is used as a threshold for significance, implying a 1% risk of false conclusion.

ANOSIM is a useful tool for testing the relevance of groupings assigned to the samples prior to any classification techniques such as CLUSTER or MDS. Examples from this study would be the testing of whether pre-flood and post-flood samples are significantly different, whether samples in different flow types represent distinct invertebrate assemblages, or whether assemblages on stones that have been physically disturbed are different from those on stones that have not. However, care should be taken when interpreting the biological relevance of very low R values, even should these be statistically significant, as they imply that the factor being tested (e.g. flood effect) is only a weak discriminator of these groups.

3.4.2.ii Cluster analysis

Hierarchical cluster analysis fuses samples that have the highest similarities into distinct groupings, and then joins groups into larger clusters at progressively lower levels of similarity, to produce a plot of the natural similarities between groups of samples, irrespective of any group-identification assigned to them apriori. The results are represented in a dendrogram, with the x-axis representing the samples and the y-axis the level of similarity at which successive groupings are formed. Of the various hierarchical sorting strategies available, group-average sorting was used because it joins two groups of samples together at the average level of similarity between all members of one group and all members of the other, and so considers natural variability between samples (Clarke & Warwick, 1994).

Although dendrograms have the advantage of clustering samples into distinct groups, the cut-off levels for the groupings are arbitrary and there are some disadvantages to this approach, for example, cluster analysis attempts to group samples into discrete clusters and may hereby tend to over-emphasize discontinuities, forcing a continuum or graded series into discrete classes. This makes it advisable to employ an additional method of presentation of the group relationships, e.g. ordination, which displays group inter-relationships on a continuous scale (Clarke & Warwick, 1994).

3.4.2.iii Ordination

The non-metric multidimensional scaling method of ordination (non-metric MDS) was performed, using the PRIMER program MDS (Clarke & Gorley, 2001). The purpose of

non-metric MDS is to construct an ordination of the sites or samples, in a small number of dimensions, in this instance 2-d for ease of display, by interpreting some function of the similarity/dissimilarity measure between each pair of sites as Euclidean distance. It is an iterative procedure (nine iterations were used) where a starting map of the sites is constructed in the required number of dimensions, and the configuration is perturbed in a direction which decreases the stress to an acceptable minimum. A coefficient of stress provides an indication of the distortion involved in compressing the data: a stress coefficient < 0.05 gives an excellent representation of the data, with no prospect of misinterpretation; a stress value <0.1 indicates a good ordination; stress <0.2 gives a potentially useful 2-dimensional plot, although interpretation of the data should be complemented by an alternative technique. A stress coefficient >0.2 indicates an unreliable representation of the relationships among samples.

3.4.2.iv Determining discriminating taxa

The SIMPER (Similarity Percentage) routine in PRIMER was used to identify the taxa most responsible for the groupings of samples defined through the cluster and ordination techniques, or where ANOSIM identified significantly different groupings that were considered to be biologically relevant. SIMPER is computed on the initial triangular similarity matrix in PRIMER. This analysis produces a breakdown of average s*imilarity within* groups (i.e. representative taxa of each group), as well as a breakdown of average *dissimilarity between* groups, into differential contributions from the various taxa, ordered in decreasing contribution. Thus the n taxa contributing the first 50% of dissimilarity between 2 groups could, for example, be identified in this way. The SIMPER results also include a term indicating, for each discriminating taxon, the ratio between the average dissimilarity of that taxon between the two groups, and the standard deviation of that dissimilarity. In other words, a taxon with a high ratio of average / standard deviation would indicate that it is consistently dissimilar (across all the samples within a group) and thus a good discriminating species between the two groups.

3.4.2.v Linking environmental and biological data

The BIOENV routine in PRIMER was used to identify the variable or combination of variables that is able to discriminate between samples in the same manner as was achieved using invertebrate data. The input files to this analysis consist of a set of environmental (e.g. physical or chemical) data, as well as the invertebrate similarity matrix with which the environmental variables are to be matched.

3.4.3 Univariate statistics

A number of basic comparative statistics were calculated to describe attributes of invertebrate assemblages, both before and after floods. Because invertebrate data were collected from stones of differing sizes, actual counts - total numbers of invertebrates or total number of species - were expressed as densities per unit area of stone surface, to take into account differences in available surface area.

In the case of species counts (total actual number of taxa on each stone) two

comparative measures were calculated, to account for *either* the area of the stone (species density per unit stone area) or the total abundance on a stone (rarefied species richness, or number of species per 100 individuals). The concept of rarefied species richness is recommended by McCabe & Gotelli (2001) as a better measure of true species richness than simple species density, since the greater the size of the sample the more chance there is of finding additional taxa.

The difference in invertebrate attributes (for example density, richness) between categories of samples - biotope grouping or movement status during a flood - was tested for statistical significance using the non-parametric Kruskal-Wallis ANOVA by ranks. This test was chosen because the data did not meet one or both of the assumptions of normality (Kolmogorov-Smirnov test) or equal variances (Levene's test) that were required for the use of parametric statistical testing. Statistical significance was shown by a p-value ≤ 0.05. Non-parametric ANOVA tests for differences among groups or treatments, based on the ranking of pooled data between and across groups.

Where Kruskal-Wallis tests were significant, pair-wise differences between groups were explored using Dunn's Pairwise multiple comparison procedure.

Pearson correlation as well as regression analysis was used to assess relationships among variables. The former measures the strength of the linear relationship between two variables, and is compared with the null hypothesis that no linear relationship exists between them (correlation coefficient, r, is zero). The regression coefficient of determination (R^2) is a measure of how much the dependent (y) variable may be explained in terms of the independent (x) variable.

Correlation analysis requires that the assumptions of independence between variables as well as normality in distribution are met. In order to normalise data, 4^{th}-root transformation (invertebrate data) and log transformation (periphyton and organic matter) of data was performed. Other physical data were not transformed, unless explicitly indicated.

Finally, population structure was investigated by comparing frequency distributions of individuals within invertebrate head width size classes. All individuals of each species or taxon were measured and included in the analysis. Population structure changes in the pre- and post- flood surveys were investigated, as well as potential differences in the size distribution of members of a species that remained on moved vs. unmoved stones after a flood. These size-frequency distributions were visually interrogated to interpret population characteristics - for example, to investigate whether floods might affect one portion of a population of a given species more than another. Statistical differences between data sets were examined using a Kolmogorov-Smirnov test for significant differences between frequency distributions.

4 SUMMARY OF THE HYDRAULIC MODEL OF INCIPIENT MOTION

4.1 INTRODUCTION

This summary represents a synthesis of the major aspects of the hydraulic model developed as part of the WRC project, which is described in detail in a separate report (Cullis et al., 2006).

Two hydraulic models for incipient motion were developed. The first model was concerned with the threshold of movement for individual stones. This was developed in order to gain a better understanding of the forces experienced by a particular stone during a flood event and is of particular relevance to the ecological component of this project. It was decided that this model would be based on the Liu Diagram (see Section 2.3.5), as this is an incipient motion diagram that is familiar to most people interested in stream hydraulics. Furthermore it was decided to interpret the results in terms of the conservation of stream power.

The second model was developed in order to investigate the relationship, if any, between the DRIFT flood classification system and the level of bed disturbance. Such a model was deemed to be potentially useful in determining the impact that the reduction in the number of a certain class of flood under a managed flood regime would have on the disturbance of the bed particles and hence on the maintenance of benthic habitat. Because the model outputs would be described in terms of DRIFT flood size classes, it would be easy to incorporate into the currently widely used and most sophisticated system for determining environmental flow requirements in South Africa. A simple empirical model was selected for this purpose and this was calibrated with the data collected during the thirteen flood events experienced at the two study sites.

4.2 RESULTS

The data from all the floods were plotted in the Liu Diagram, which was introduced in Section 2.3.5, and which shows the critical conditions for sediment movement in uniform stream channels. The flow regimes in cobble- and boulder-bed rivers are dominated by turbulent flow. As the parameter on the x-axis, may be regarded as a type of particle Reynolds number (Re*), which indicates whether laminar or turbulent conditions prevail at the bed. As such, it was expected that the data points should plot well to the right along the x-axis of the Liu diagram - the part representing turbulent conditions, and where the critical conditions for movement are characterised by a constant value for $\sqrt{gDs}/V_{ss}$ (the y-axis in the Liu diagram). This constant represents the point where the applied power along the bed equals the power required to move a particular stone, the threshold of movement.

The results of this study, however, indicated that the threshold of movement for the smaller stones did not conform to the constant value expected in the Liu diagram for fully turbulent flow (Figure 4.1, shown for the Berg River, although all data sets conformed to the same

pattern). In Figure 4.1, the threshold of movement (TOM) for moved stones is less reliable than that for unmoved stones, because the former might have moved at a discharge, and hence applied power that was less than that represented by the flood peak. Even looking only at unmoved stones, however, the threshold of movement is not the constant value predicted by theoretical equations. Many of the smaller stones are not moved at the expected threshold where AP=RP, as calculated theoretically, but in fact require a higher ratio of applied to required power (y-axis value) in order to become entrained.

Three possible explanations for why the smaller stones required relatively greater applied power to move them than predicted were investigated:

- Some of the stones were embedded.
- The observed rivers had bed material with a non-uniform size distribution.
- Laminar conditions may have played a role in the entrainment process of the stones.

It was concluded that the primary reason that could account for the deviation from the expected constant value of the threshold of movement in the Liu diagram was the fact the original modified Liu diagram was derived for uniform particle-size beds whereas the data of the Molenaars and Berg Rivers represented non-uniform particle-size beds. When the derivation for the y-axis in the Liu diagram was modified to provide for non-uniform bed particle sizes, an extra factor was obtained and the function on the y-axis changed to:

$$\frac{\sqrt{gDs}}{V_{ss}} \cdot \left(\frac{d}{k}\right)^{1/3} = \text{Constant} \qquad (4.1)$$

In a uniform bed, the absolute roughness (k) is equal to the particle size, but this changes with non-uniform conditions. Charlton *et al*. (1978) and Jonker *et a*l. (2002) showed that the average absolute roughness (k) of a non-uniform bed is reasonably well related directly to d_{84}. This is due to the fact that the bigger stones in the bed (d50 to d100) play the dominant role in determining the eddy size. To account for the fact, that the depth of water above certain particles during some of the flood events was less than d_{84}, and hence the average eddy size would not be able to develop to this size, the absolute roughness above individual stones was taken as the minimum of the maximum flow depth (D) and d_{84}.

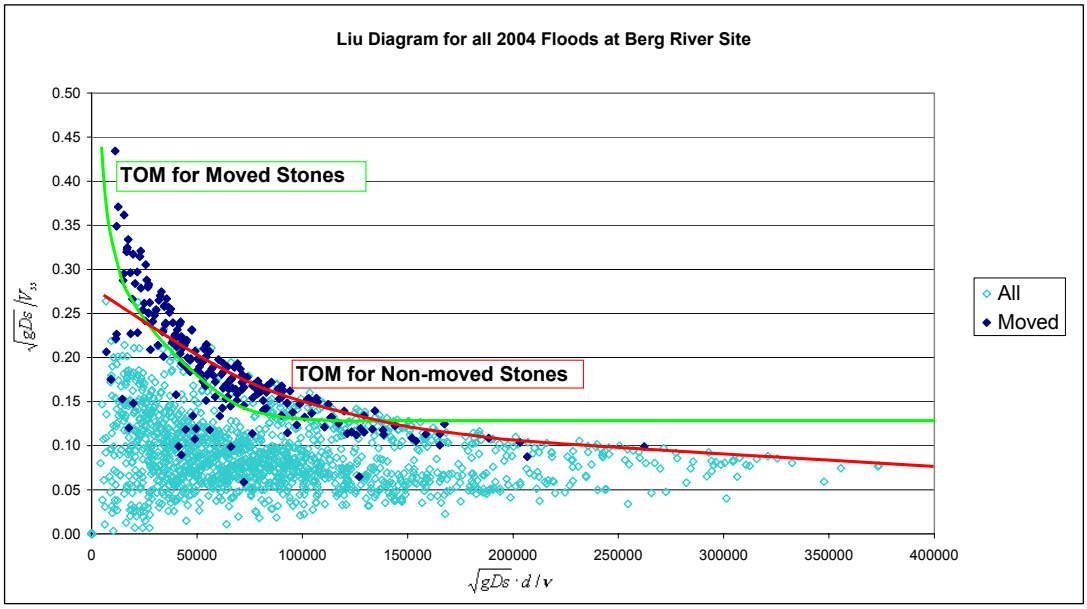


Figure 4.1 Stone movement data from all Berg River floods in 2004, plotted in a Liu diagram, to indicate the threshold of movement for moved and unmoved stones.

The parameter on the y-axis of the Liu diagram represents the ratio of the power applied at the bed to the power necessary to entrain a particle. (AP/RP), whilst the x-axis represents a particle Reynolds number and indicates whether laminar or turbulent conditions prevail at the bed. TOM = threshold of movement.

The development of eddies, on any bed, is a three-dimensional process. The bed configuration (in all directions) in the vicinity of a stone in the bed will determine the local eddy size. In the case of a bed with uniform size particles the eddy size would be of the same order as the particle diameter. The reason for this is that on a uniform particle size bed the bed shape will generate eddies similar in size as the particles. For this reason k can be substituted for d on a uniform bed (Figure 4.2).

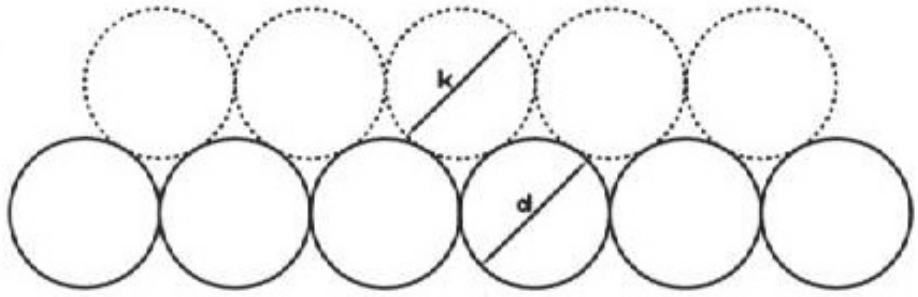


Figure 4.2 Eddy formation in a uniform particle size bed.

It is, however, not possible to accurately predict the exact size of the eddies that will form in a non-uniform particle size bed due to the complexity and variability of such a bed configuration. In a non-uniform particle size bed it can however be assumed that the average bed roughness will be largely determined by the larger stones in the bed. Because flow resistance across the bed is not a localized phenomenon it may be

assumed that the applied power and hence the eddy size across a non-uniform bed will tend towards uniformity, with the average eddy size of the same order as that of the larger stones that dominate in determining the average absolute roughness of the bed. Figure 4.3 depicts a two-dimensional representation of the eddy formation process in a non-uniform particle size bed.

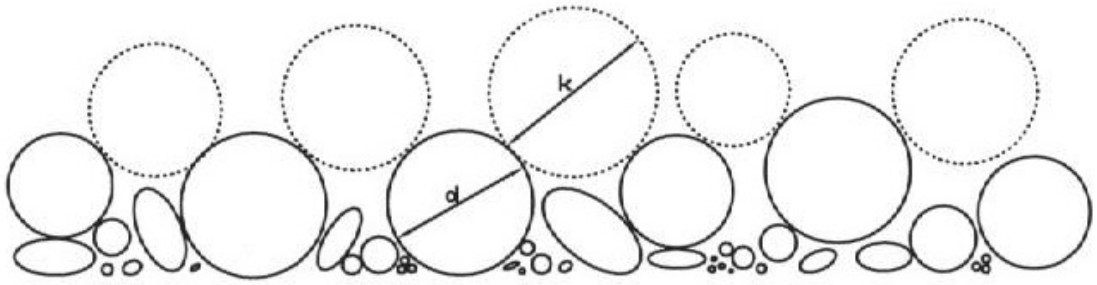


Figure 4.3 Eddy formation in a non-uniform particle size bed.

It is clear from the above figure that the bigger particles will play a dominant role in the eddy formation process in a non-uniform particle size bed. This figure not only depicts a two-dimensional representation of the eddy formation process in a non-uniform particle size bed but also the relative positions of different size stones. In a non-uniform particle size bed, smaller particles will generally be found in lower positions i.e. in the sheltered hollows between the larger stones.

As indicated in Figure 4.3, in a non-uniform particle size bed the average roughness and hence the average eddy size is largely determined by the larger stones in the bed. The smaller a stone the smaller the $(d/k)^{1/3}$ value will be for that stone since the general eddy size (k) will be of the same order of magnitude as the size of the larger stones in the bed. As the stone size increases the value of the term $(d/k)^{1/3}$ will increase accordingly as the size difference between a stone and the average eddy diminishes.

The above observation helps to explain, mathematically, why a deviation is noticed in the plot of the Molenaars and Berg River data from the anticipated constant threshold of movement line when plotted in the modified Liu diagram. In the Liu diagram a uniform bed was assumed (i.e. k could be made equal to d for every stone). It is thus apparent that if k is set equal to d it underestimates the size of the average eddy forming over the smaller stones. This underestimation of eddy size increases as the stone size becomes smaller. Thus the eddies over smaller stones are in general in actual fact larger (with a concomitant reduction in applied power) than is predicted in the Liu diagram for uniform conditions, which explains the apparent deviation.

Alternatively the bigger the stone size the more accurate the assumption that k equals d due to the fact that the average eddy size, which is being formed by the biggest stones, is much closer to the size of the bigger stones. This explains why the bigger stones on the graphs (i.e. furthest from the y-axis) plot close to the theoretical constant value (0.12) on

the y-axis.

Thus the upward deviation in the apparent threshold of movement line for smaller stones (i.e. those closest to the y-axis in Figure 4.1) can be explained in terms of the function that represents the y-axis of the Liu diagram, i.e. the ratio of applied power to required power along the bed.

For non-uniform beds, this function is given by: $\frac{\sqrt{gDs}\cdot\left(\frac{d}{k}\right)^{1/3}}{V_{ss}}$ rather than by: $\frac{\sqrt{gDs}}{V_{ss}}$ as for uniform beds.

Re-plotting the stone movement data, but using the modified equation representing non-uniform beds (Figure 4.4), and setting d = d_{84}, it is clear that the data deviate much less from the theoretical constant value, in particular the unmoved stone data, although there are still small but definite deviations noticeable. These small deviations can be attributed to the fact that even though provision has been made in terms of the average k value of the bed being used, transition effects interstitial spaces between small and large bed particles were not modelled. These transition effects are highly complex and are thus impossible to model.

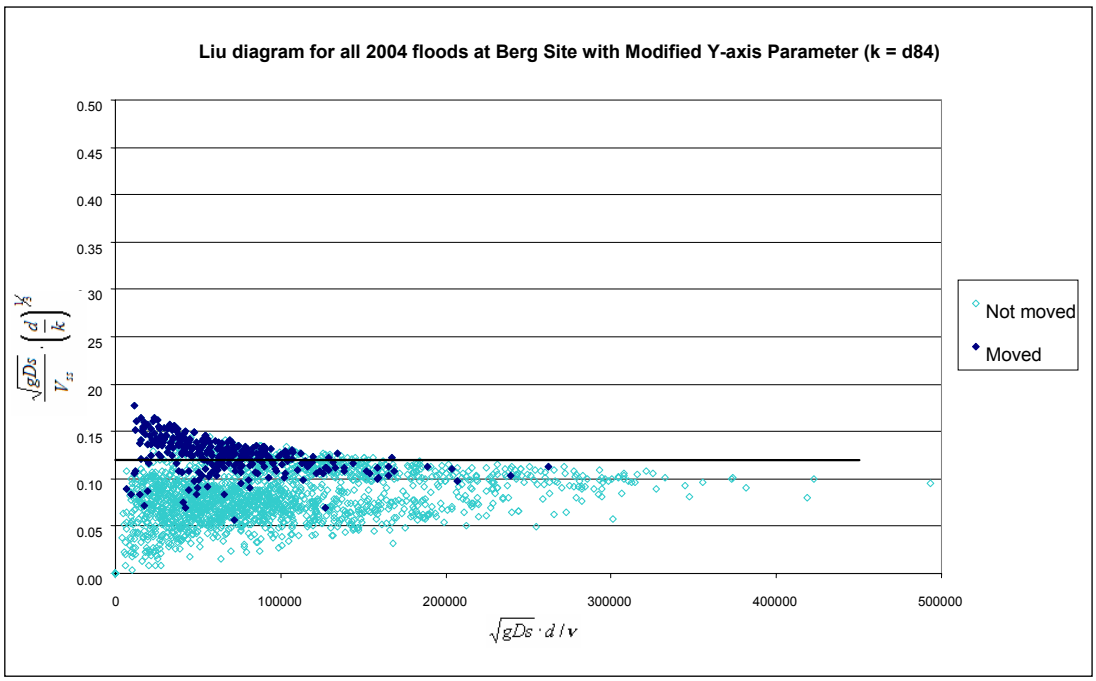


Figure 4.4 Stone movement data from all Berg River floods in 2004, plotted in a Liu diagram, but adapted for non-uniformity. The parameter on the y-axis of the Liu diagram represents the modified equation for incipient motion, as in Figure 4.1, but modified for non-uniform beds, where k=d_{84}. The parameter on the x-axis represents a particle Reynolds number and indicates whether laminar or turbulent conditions prevail at the bed.

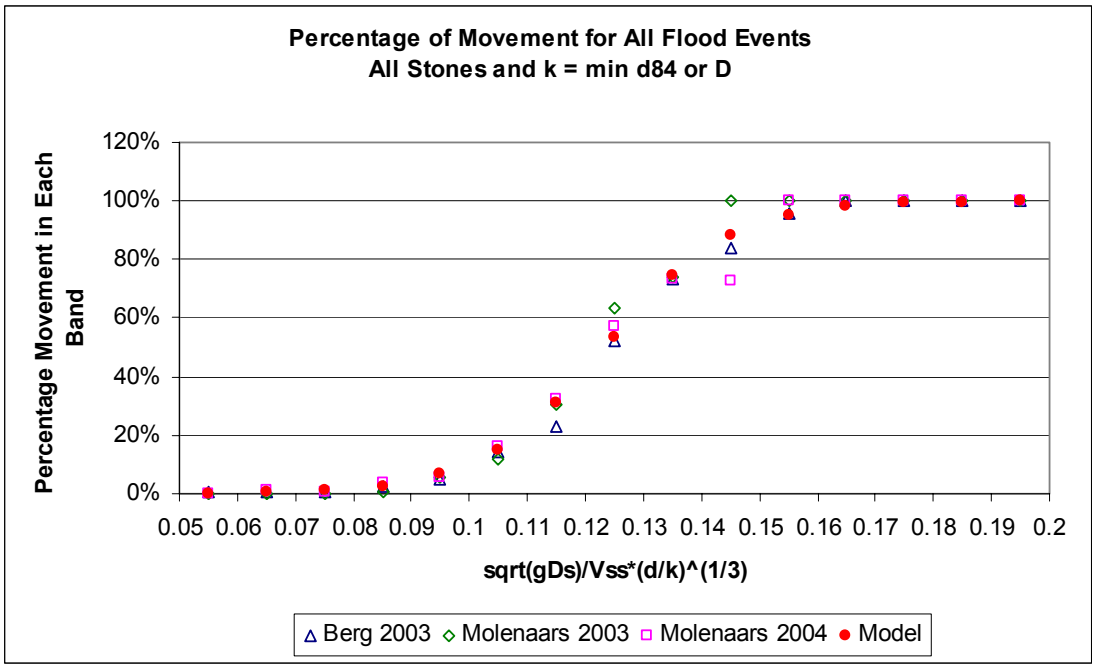


Figure 4.5 Percentage of stones that move plotted against the ratio of applied power to required power (the y-axis in Figure 4.4): all stones for all flood events.

From the above graph it appears that there is clearly defined line between movement and non-movement at a constant value of approximately 0.12. This is confirmed when the percentage of stones that move are determined for each constant band of the y-axis in Figure 4.4. This is plotted in Figure 4.5 for all data from both rivers for all floods.

From Figure 4.5 it is clear that the data from the two rivers plot very closely together which implies that they can be considered to be hydraulically similar and would imply that the results could be applied to other cobble- and boulder-bed rivers. There are many variable factors defining the point of incipient motion, but if it is considered to be the point at which a stone is more likely to move than to not move (i.e. its probability of movement is 50%) then the above figure shows that this corresponds to a constant value of 0.12.

Based on this observation it was concluded that incipient motion in cobble- and boulder-bed rivers could be defined by:

$$\frac{\sqrt{gDs}}{V_{ss}} \cdot \left(\frac{d}{k}\right)^{1/3} = 0.12$$

This relationship was used to determine whether or not previously unmarked stones would have moved under a particular flood event. It is also recommended that this relationship be used to determine the number of bed particles that will move, for studies examining the impact of a particular flood event or lack of flood event.

4.3 DISTURBANCE AND FLOOD SIZE

The study also sought to develop a better understanding of the relationship between the DRIFT flood classification system and the level of substratum disturbance. This was met through the development of an empirical model that related the intensity of movement (I, as percentage) under a particular flood event to the DRIFT flood classification (DC) of that event. The relationship between I and DC was best described by a log-linear plot as shown in Figure 4.6.

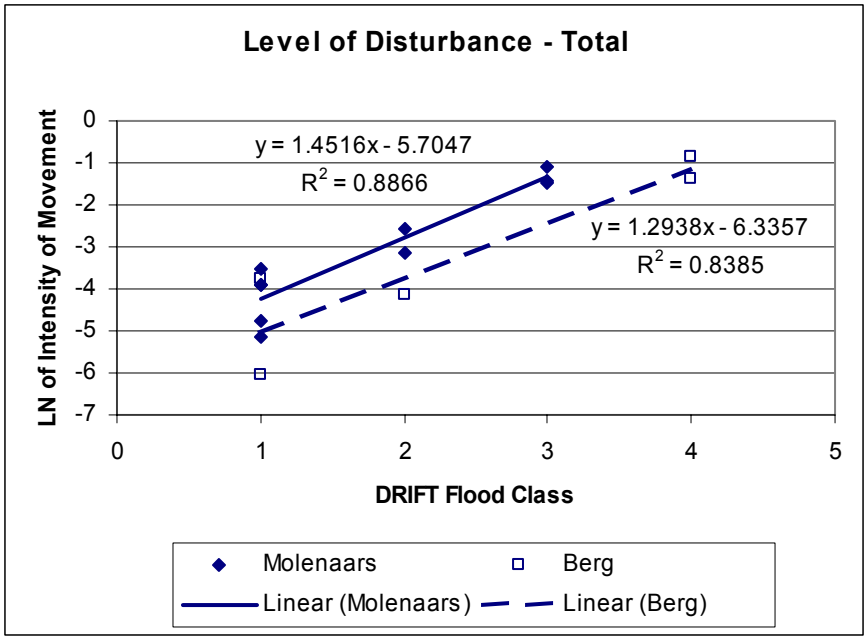


Figure 4.6 The relationship between DRIFT Flood Class and the level of disturbance, as represented by the intensity of stone movement. Intensity of movement is defined as the percentage bed movement in a flood

A single relationship was found that represented the situation in both rivers if an additional constant term (α) was incorporated to account for the difference in the stone size distribution (d_{50} and d_{84}) and the average bed slope (S_0).

$$I = \frac{e^{34.3.\alpha.DC}}{96.9.\alpha} \qquad \text{where} \qquad \alpha = S_0 \frac{d_{84}}{d_{50}}$$

As with the theoretical model developed for the movement of individual stones, it is unclear at this stage if this represents a universal finding for all rivers of non-uniform particle size distribution. The results from the two rivers tested, however, were consistent despite being of different size and having different stone size distributions. Based on this observation it could be hypothesized that the above results will be universal at least in the case of cobble- and boulder-bed rivers.

4.4 SIGNIFICANCE FOR STREAM ECOLOGY

The observation of a reduction in stream power due to non-uniform bed material is very significant for understanding ecological processes in streams. It provides evidence that, for the same size of bed particle, areas of relative shelter are provided in non-uniform beds as a result of the mixed nature of the bed. These may act as refugia for lotic organisms during flood events. These sheltered stones are shown in the Liu Diagram (Figure 4.7) as the stones that plot between the observed threshold of movement (TOM), which represents the line of equality for incipient motion in the presence of heterogeneous bedforms, and the line of equality for incipient motion under uniform bed conditions as described by:

$$\frac{\sqrt{gDs}}{V_{ss}} = 0.12$$

These sheltered stones, highlighted in Figure 4.7, occur where the applied power actually experienced by the stones (AP*) is less under conditions where heterogeneous bedforms are present than would be the case under conditions of a uniform bed (AP).

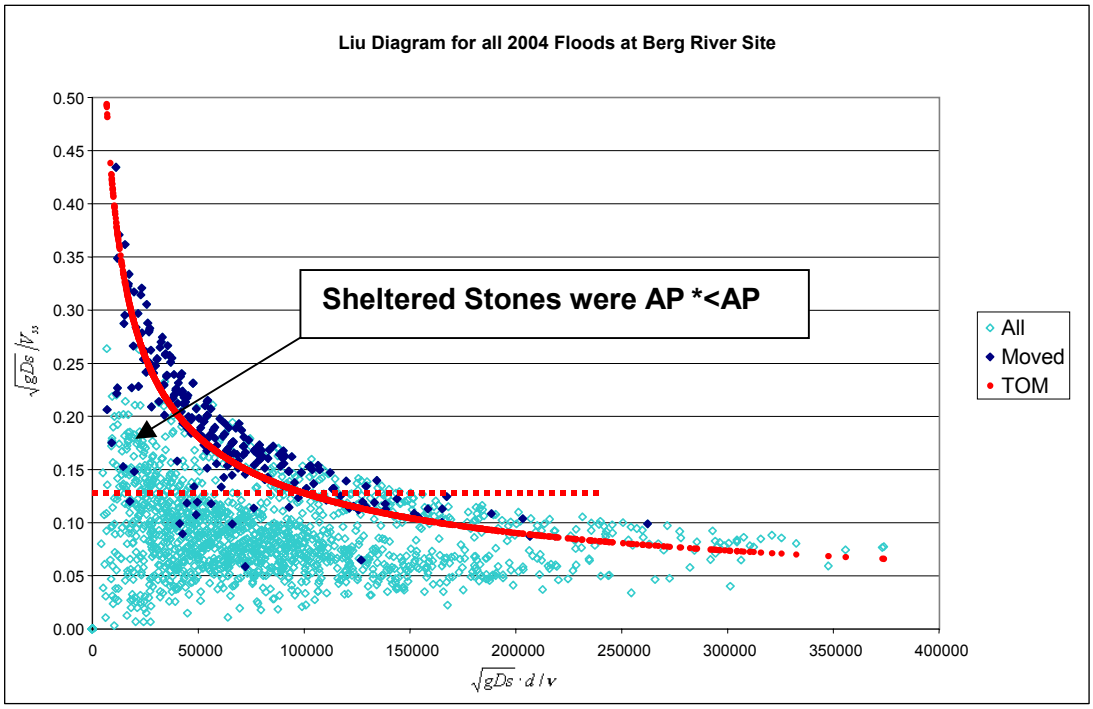


Figure 4.7 The presence of relatively sheltered stones in a naturally sorted bed. The x- and y-axes are as for Figure 4.4.

In conclusion, the two hydraulic relationships developed by this study provide the researcher with the tools to either make a first order estimate of the average level of substratum disturbance based on DRIFT class, or alternatively, to develop a more detailed measure of disturbance by considering the movement of individual stones during a particular flood event.

5 RESULTS OF THE BASELINE INVERTEBRATE STUDY

5.1 SUBSTRATUM CHARACTERISTICS

Bed particles were generally somewhat larger in the Molenaars River (mean stone dy = 319 mm, median = 265 mm, n = 344) than in the Berg River (mean stone dy = 275 mm, median = 228mm, n = 432). The Berg River had more gravel and small cobble than the Molenaars River (Tables 5.1 and 5.2), whilst the latter had a greater proportion of large boulders.

Table 5.1 Bed particle characteristics in the Molenaars River, baseline survey 2003. G = gravel, SC = small cobble, LC = large cobble, SB = small boulder; LB = large boulder.

Stone Size Classification	Total	G	SC	LC	SB	LB
Max size in class (mm)		64	161	256	514	1000
Total Number of Stones	344	4 (1%)	91 (26.5%)	73 (21%)	111 (32.5%)	65 (19%)

Table 5.2 Bed particle characteristics in the Berg River, baseline survey 2004.

Stone Size Classification	Total	G	SC	LC	SB	LB
Max size in class (mm)		64	161	256	514	1000
Total Number of Stones (%)	432	27 (6%)	120 (28%)	92 (21%)	139 (32%)	54 (13%)

5.2 INVERTEBRATE ASSEMBLAGES

5.2.1 Comparison of the Molenaars and Berg River invertebrate samples

Of the subset of whole stones that were fully sampled for invertebrates, the range of sizes in the two rivers was very similar, the Berg River sample set containing slightly larger stones (Table 5.3). Immovable boulders whose tops were sampled for invertebrates, however, were on average a little larger in the Molenaars River than in the Berg River (Table 5.3). Depth and velocity measured on each sampled stone were variable, but the Molenaars River was associated with clearly higher velocities on both whole and immovable stones.

The amount of organic matter associated with sampled stones in the Molenaars River was less than half that in the Berg River, although variability was very high, an indication of the patchy distribution of this food resource. In the case of immovable boulder tops, this measure of associated organic matter reflects a density of organics associated with the upper surface area of the stone and not particulate matter trapped underneath the stone or in interstitial spaces as is the case with whole stones.

A range of invertebrate community measures is presented in Table 5.4. The mean invertebrate count per stone in the Molenaars River was double that in the Berg River. This measure does not take into account differences in available surface area, but since stone sizes in the two rivers were approximately the same, total invertebrate **density** (number of individuals per unit stone area) was also significantly higher (Mann-Whitney test, $p<<0.0001$) and on average more than double in the Molenaars River than in the Berg River (Figure 5.1a): trout farms in the headwaters of the Molenaars River have been implicated in low-level chronic nutrient enrichment of its waters (Brown, 1996), whilst the Berg River reflects the natural oligotrophic state of Western Cape rivers. In addition, the invertebrate density on the top surface of immovable stones was considerably higher in the Molenaars than the Berg River (Table 5.4).

Table 5.3 Means (standard deviation) of physical characteristics and availability of organic matter and periphyton, associated with sampled stones in the Molenaars and Berg River baseline surveys.

Attribute	Molenaars River		Berg River	
	Whole stones	Immovable (tops only)	Whole stones	Immovable (tops only)
Particle size (dy, in mm)	186.0 (96.0)	502.2 (182.2)	252.0 (90.5)	411.8 (140.1)
Water depth (mm)	0.21 (0.15)	0.06 (0.03)	0.09 (0.09)	0.14 (0.08)
Average water column velocity (m s^{-1})	0.24 (0.20)	0.35 (0.23)	0.16 (0.17)	0.16 (0.11)
Associated organic matter (g AFDW m^{-2})	4.08 (7.04)	0.12 (0.15)	10.32 (11.98)	0.92 (0.99)
Periphyton AFDW (g m^{-2} stone surface)	not sampled		0.47 (0.39)	not sampled
Periphyton as Chla (mg m^{-2} stone surface)	not sampled		1.96 (1.38)	not sampled

Despite this probable nutrient enrichment, the species count (total actual number of taxa on each stone) averaged approximately 18 in both rivers (Table 5.4), with somewhat higher species density in the Molenaars River (Figure 5.1b). Species density on the top surfaces of stones was similar in both rivers and, expectedly, lower than that on whole stones, reflecting the fact that many benthic invertebrate taxa are only associated with the lower and under surfaces of river stones.

Rarefied species richness (species count per 100 individuals) was significantly higher in the Berg River than the Molenaars River (Mann-Whitney test, $p<<0.0001$; Figure 5.1c). This indicates that even though animal densities in the Molenaars River could be expected to be double those in the Berg River, the chance of inter-specific encounters would be greater in the case of the Berg River.

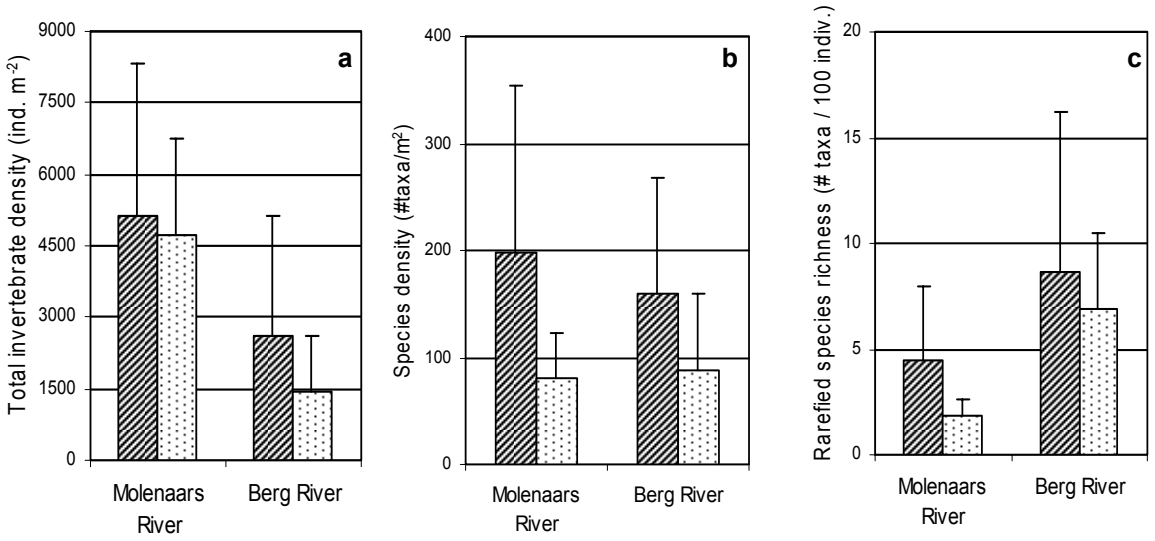


Figure 5.1 Invertebrate community measures on whole stones (hatched bars) and stone tops (stippled bars) in the Molenaars and Berg Rivers during their baseline surveys in June 2003 and May 2004 respectively. a) total invertebrate density per m^2 stone surface area, b) species density (no. taxa per m^2 stone surface area), and c) rarefied species richness.

Table 5.4 Means (standard deviation) of invertebrate community measures on whole stones and immovable boulder tops in the Berg and Molenaars Rivers during their respective Baseline surveys.

Attribute	Molenaars River		Berg River	
	Whole stones	Immovable (tops only)	Whole stones	Immovable (tops only)
Invertebrate abundance (average count per stone)	653.5 (489.5)	664.2 (642.0)	350.2 (248.2)	112.3 (71.5)
Invertebrate density (no. ind. m^{-2} stone surface)	5119.5 (3209.1)	4734.1 (2032.2)	2625.2 (2502.9)	1425.1 (1201.3)
Species count (# taxa per stone)	18.2 (5.6)	9.0 (5.3)	18.3 (4.8)	6.5 (3.6)
Species density (# taxa m^{-2} stone surface)	199.1 (154.2)	81.1 (42.1)	158.9 (109.7)	88.6 (70.1)
Rarefied species richness (# taxa per 100 ind.)	4.4 (3.5)	1.8 (0.8)	8.7 (7.6)	6.9 (3.6)

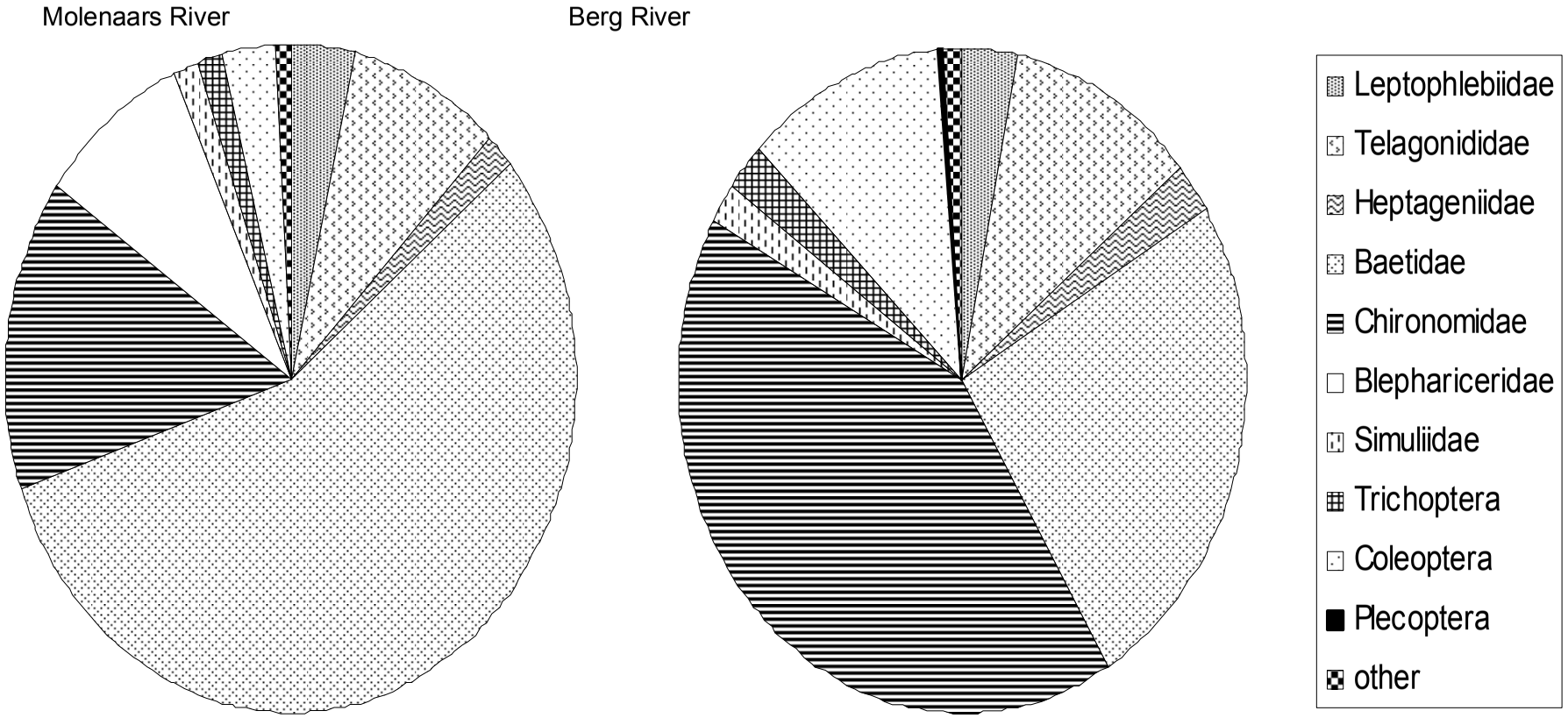


Figure 5.2 Proportions by density of major insect Families and Orders in the Molenaars and Berg Rivers during the baseline surveys.

In terms of their faunal composition, the most striking difference between the Molenaars and Berg Rivers from the baseline survey was the dominance of Baetidae in the former and of Chironomidae in the latter (Figure 5.2). Collectively, these two families comprised about 75% of the invertebrate density in each river. Other differences were the virtual absence of Blephariceridae in the Berg River (which situation persisted throughout the study period), and the greater proportion of Coleoptera (mainly Elmidae) in the Berg River than the Molenaars River. The high invertebrate density on the tops of immovable boulders in the Molenaars River was in part a reflection of these taxonomic differences, since tops of immovable boulders were dominated by Baetidae and *Elporia* spp. in that river.

5.2.2 Relationship between invertebrate assemblages and physical variables

Invertebrate assemblages in the Molenaars River at the start of the flood season, in June 2003, were fairly well differentiated by hydraulic biotopes (Figure 5.3), with a gradation of assemblage structure from the slower-flowing pool, through shallow backwaters and slow runs, to fast runs and riffles. The single pool biotope sample was most dissimilar from the remaining samples, separating from these at 30% similarity (Figure 5.3a). The moderate stress level (0.15) on the MDS plot suggests that it is a reasonable representation of the relationship between samples. Nevertheless, the groupings identified from the hierarchical cluster analysis (Figure 5.5a) are superimposed upon the MDS plot (Figure 5.3b). The various categories of run biotope, usually described in terms of rippled surface flow, were subjectively determined according to their visual characteristics (how marked the ripples were) and differences between these sub-categories were most ambiguous, with the exception of fast run which grouped well with riffle biotope.

ANOSIM performed on the groupings of invertebrate samples grouped according to their *apriori* assigned biotope indicated strong pairwise differences, particularly between backwaters and riffle / fast run biotopes (Table 5.5, italics), but less so between categories of run. Pairwise differences between biotopes represented by single samples were not examined (i.e. pool, vegetated run and vegetated backwater).

Based on the cluster analysis and MDS, four main biotope clusters were identified, indicated by dashed lines in Figure 5.3b, and subjected to SIMPER analysis in order to identify those taxa most characteristic of each biotope cluster, as well as those which best discriminated between biotope clusters. The species differences between the biotope clusters are presented in Table 5.6, both as the taxa most characteristic of each biotope cluster as well as those most consistently responsible for the dissimilarity between these clusters. The Dissimilarity / Standard deviation ratio in Table 5.6 indicates the consistency with which various taxa discriminate between biotopes (see section 3.4.2 iv).

Table 5.5 Results of a 1-way ANOSIM testing for differences in invertebrate assemblages between *apriori*-defined hydraulic biotopes in the Molenaars River, June 2003 (baseline survey). Only significant pairwise comparisons are presented.

Groups	R Statistic	p-Value
GLOBAL SAMPLE STATISTIC	0.42	0.001
backwater - riffle	*0.941*	*0.001*
backwater - fast run	*0.669*	*0.001*
backwater - run	0.477	0.001
slow run - riffle	*0.747*	*0.001*
slow run - fast run	0.397	0.001
run - riffle	0.437	0.002
riffle - fast run	0.086	0.05

Biotope clusters had between 54 and 66% within-group similarity, with the best differentiated group comprising fast run and riffle samples (Figure 5.3, Table 5.6). Pairwise comparisons between biotope clusters showed overall low average dissimilarities, emphasising that hydraulic change, and associated invertebrate assemblages, is represented by a gradation over two (and three) dimensional space. Differences between biotopes were represented by changes in species composition in some cases, but more often by differences in density of taxa over the range of biotopes. Biotope preferences for a number of species may be inferred from these results, for example, *Afroptilum* sp (Baetidae, Ephemeroptera), *Aprionyx* spp. and *Euthraulus* sp. (Leptophlebiidae, Ephemeroptera) were largely restricted to backwaters and Run cluster 1, and poorly represented in fast runs / riffles; *Elporia* spp. (Blephariceridae, Diptera) and *Demoreptus capensis* (Baetidae, Ephemeroptera) dominated in fast runs / riffles. No taxa were exclusive to only one cluster, and only a few taxa were unrepresented in one or more biotopes. Examples of the latter are *Caenis* spp. (Baetidae, Ephemeroptera) absent from the fast run / riffle; and Simuliidae (Diptera), *Chimarra* sp., and *Athripsodes bergensis* complex (Philopotamidae and Leptoceridae, respectively, both Trichoptera) absent from backwaters.

Comparing the similarity between samples generated by the invertebrate data with that generated using seven continuous-data hydraulic variables calculated from field measurements (the Primer BIOENV routine), revealed a fairly weak correlation, with the most relevant hydraulic variables being mean water column velocity, particle size (dy), shear stress and applied stream power (Table 5.7). The hydraulic variables used were depth, mean water column velocity (V), particle size (dy), shear stress (Sh), Froude number (Fr), Reynolds number (Re) and applied stream power (AP).

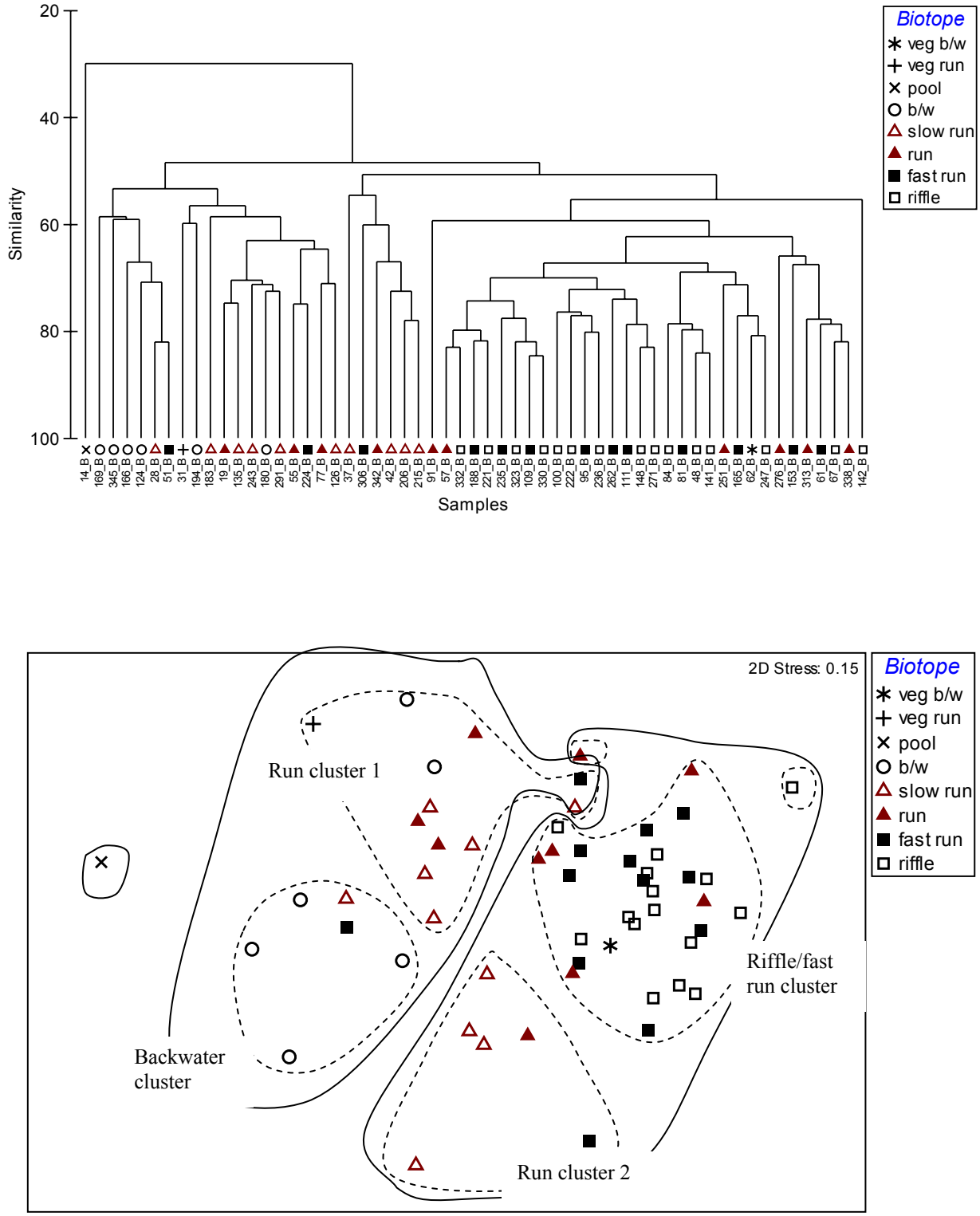


Figure 5.3 Molenaars River June 2003 invertebrate samples, represented as, square-root transformed densities;

a) hierarchical cluster dendrogram, based on Bray Curtis similarity coefficients,
b) 2-d MDS plot with the main groupings defined by cluster analysis delineated by ellipses. Sample numbers in figure 5.3a refer to actual numbers of individually marked and numbered stones.

Table 5.6 Condensed SIMPER results for each biotope cluster from the cluster analysis and MDS of Molenaars River samples in June 2003.

The taxa contributing to 60% of within-group similarity are shown, as well as the taxa that were best discriminators between biotope groupings (high Diss / SD ratio). In the pairwise comparisons, the average density of discriminator taxa is provided in turn for each biotope cluster in the order in which it is listed. The pool biotope is not included in the analysis since it was represented by only one sample.

Biotope cluster from MDS (average % similarity within biotope)	Taxa contributing to 60% of within-cluster similarity	Pairwise comparisons (average % dissimilarity between biotope-clusters)	Top discriminator taxa between pairs of biotope-clusters	Average density in each biotope cluster (Sq. root # m^{-2})	Diss / SD ratio
Backwater (53.5%)	*Afroptilum* sp. Orthocladiinae *L. penicillata* *Euthralus* sp.	Backwater vs. Run 1 (49.15)	*Afroptilum* sp. *Aprionyx* spp Tanypodinae *Afronurus* sp.	45.16 / 10.82 5.83 / 0.00 5.78 / 2.84 7.49 / 5.72	2.03 2.07 1.90 1.70
		Backwater vs. Run 2 (46.66)	Orthocladiinae *Aprionyx* spp. *L. penicillata* Tanytarsini	14.77 / 39.87 5.83 / 1.00 14.33 / 25.95 2.24 / 8.18	1.75 1.72 1.63 1.58
Run 1 (62.48%)	*Baetis* spp. *L. penicillata* *Afroptilum* sp. Orthocladiinae *Euthralus* sp.	Backwater vs. Riffle/fast run (58.11)	*D. capensis* *Afroptilum* sp. *Elporia* spp. *Baetis* spp. *Aprionyx* spp. Tanypodinae	1.21 / 18.39 45.16 / 6.12 1.89 / 25.73 13.23 / 45.11 5.83 / 0.98 8.87 / 4.41	2.56 2.31 1.89 1.86 1.83 1.61
Run 2 (62.05%)	*Baetis* spp Orthocladiinae *Afroptilum* sp. *L. penicillata*	Run 1 vs. Run 2 (52.80)	Athericidae Orthocladiinae Tanytarsini Tanypodinae *L. penicillata* *Afronurus* sp.	2.89 / 1.75 8.38 / 39.87 0.64 / 8.18 2.84 / 8.06 13.61 / 25.95 5.72 / 6.31	2.39 1.95 1.91 1.69 1.62 1.61
Riffle / fast run (66.32%)	*Baetis* spp. *Elporia* spp. *D. capensis* *L. penicillata*	Run 1 vs. Riffle/fast run (49.31)	*D. capensis* *Elporia* spp. Athericidae Tanytarsini *Baetis* spp.	3.65 / 18.39 4.98 / 25.73 2.89 / 2.50 0.64 / 6.46 21.32 / 45.11	2.26 1.84 1.68 1.61 1.56
		Run 2 vs Riffle/fast run (48.26)	*D. capensis* *Elporia* spp. Orthocladiinae	4.83 / 18.39 5.32 / 25.73 39.87 / 17.55	1.81 1.68 1.57

Table 5.7 BIOENV results to examine which environmental variables best explain the MDS and cluster patterns based on invertebrate assemblages in the Molenaars River in June 2003.

V = mean water column velocity, d(y) = particle size (length of the second longest axis), Sh = shear stress, AP = applied stream power. The combinations of variables that resulted in the highest ρ_w values are highlighted in bold text.

Combinations of 2, 3 and 4 variables	Correlation coefficient ρ_w
d(y), V	0.263
d(y), AP	0.263
d(y), V, AP	**0.274**
d(y), V, Sh	**0.274**
d(y), V, AP, Sh	0.269

In the Berg River in May of 2004, the most obvious trend associated with invertebrate patterns was that of a gradual shift in assemblage composition across hydraulic biotopes (here represented by flow type only; Figure 5.4), although this was not as clear as in the Molenaars River in June 2003. No distinct biotope groupings were suggested by the scatter plot, and although an ANOSIM to test for significant differences in assemblages between flow types was significant (Global R = 0.32, p = 0.001), few pairwise differences were strong (low R-statistic, Table 5.8) or significant below a p-value of 0.01 (see section 3.4.2i for conservative p-values required for pairwise tests in ANOSIM).

Table 5.8 Results of a 1-way ANOSIM testing for differences in invertebrate assemblages between *a priori*-defined hydraulic biotopes in the Berg River, May 2004 (baseline survey). Only significant (p<0.01) pairwise comparisons are presented.

Groups	R Statistic	p-Value
GLOBAL SAMPLE STATISTIC	0.32	0.001
NF - RSF	*0.525*	*0.001*
NF - FRF	0.366	0.008
BPF - FRF	*0.692*	*0.001*

The moderate stress level (0.15) on the MDS plot (Figure 5.4) suggests that it is a reasonable representation of the relationship between samples. Given the spread of samples, and the lack of strong clustering within the data, only two groups, identified as strong clusters from the cluster analysis dendrogram, defined at the 65% similarity level, are superimposed upon the MDS plot (Figure 5.4), and the dendrogram is thus not shown. These two groups represent a mixed RSF / FRF grouping (i.e. fast run / riffle equivalent to the Molenaars River cluster) and a mixed RSF / BPF grouping (i.e. run / slow run equivalent to the Molenaars River cluster).

A SIMPER analysis was run to examine species differences between these two defined groupings. The results (Table 5.9) show some similarities with the findings on the Molenaars River, although only two biotope clusters were compared in this latter instance. The discriminator taxa for the Berg River clusters were not strong, the relatively low Diss / SD ratios indicating that differences between biotopes were not highly consistent across samples. *Baetis* spp. (Baetidae, Ephemeroptera) and Orthocladiinae (Chironomidae, Diptera), the most numerous of the taxa in the Berg River, were simultaneously major representatives of both biotope clusters, although the orthoclads occurred in higher densities in the RSF / FRF cluster (Table 5.9).

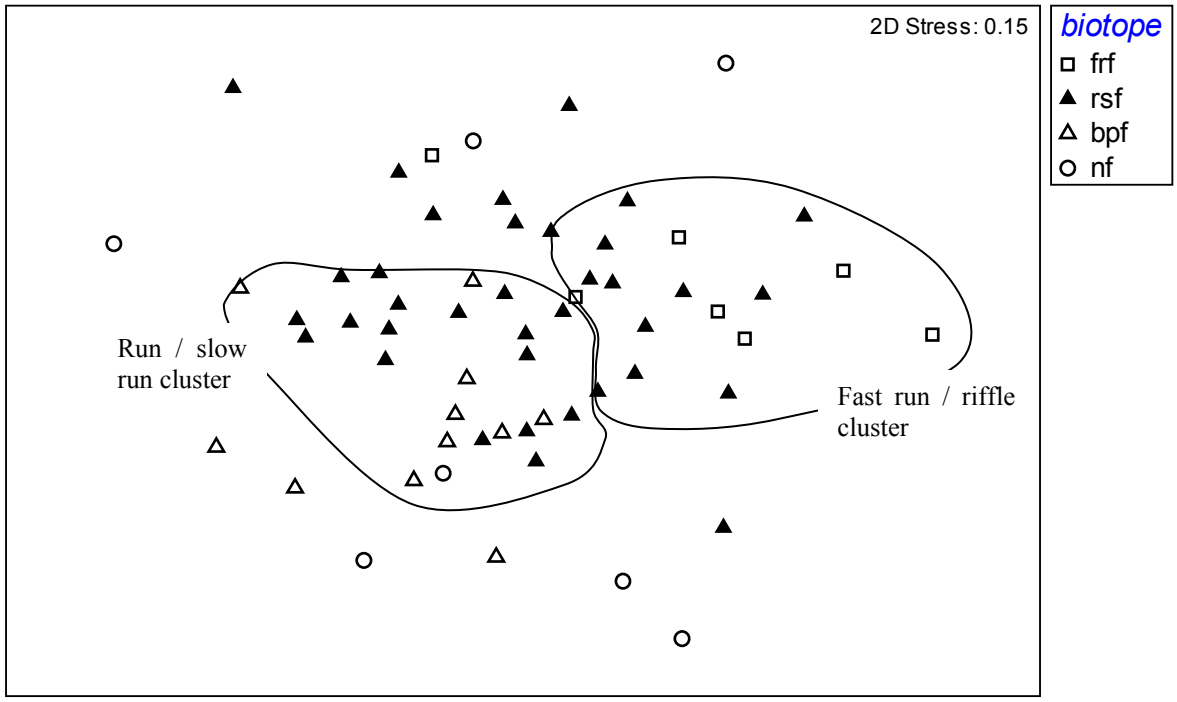


Figure 5.4 Berg River May 2004 invertebrate densities, square root transformed, 2-d MDS plot with the main groupings defined by cluster analysis delineated by ellipses.

Simuliidae (Diptera) were largely restricted to the fast run / riffle cluster, and a useful discriminator between the two groups, whilst the predator group Tanypodinae (Chironomidae) and *Adenophlebia* sp. were discriminator taxa dominant in slow run / run biotopes. *Elporia* spp. were absent from the Berg River samples, and *D. capensis* (Baetidae, Ephemeroptera) was present in very low numbers, unlike in the Molenaars River. Nonetheless, *D. capensis* and three Trichoptera taxa were between three and five times more numerous (if patchily so) in fast run / riffle biotopes than in slow runs (Table 5.9). As in the case of the Molenaars River, Leptophlebiidae (*Castanophlebia* sp., *Adenophlebia* sp. *Aprionyx* spp.) indicated a strong preference for slower-flowing biotopes (Table 5.9).

The environmental variables used for BIOENV analysis of the Berg River May 2004 data

included Chlorophyll a (Chla) and periphyton ash-free dry weights (AFDW), alongside the suite of hydraulic variables of depth, mean water column velocity, particle size (dy), shear stress, Froude number, Reynolds number and applied stream power. These variables individually and in combination were poorly correlated with the invertebrate assemblages: the best correlation from the BIOENV analysis was ρ_w = 0.168, using a combination of mean water column velocity, particle size, Chla and AFDW. Thus whilst the multivariate analysis identified a gradation of change in invertebrate species assemblages across visually-defined biotope groupings, there was a poor correlation (BIOENV) between these assemblages and hydraulic measurements associated with each sample.

Table 5.9 Condensed SIMPER results for each biotope cluster from the cluster analysis and MDS of Berg River samples of May 2004.

The taxa contributing to 60% of within-group similarity are shown, as well as the taxa that were best discriminators between biotope groupings (high Diss / SD ratio). Additionally, taxa that were numerically dominant in one or the other biotope cluster are listed.

Biotope cluster from MDS (average % similarity within cluster)	Taxa contributing to 60% of within-cluster similarity	Pairwise comparisons (average % dissimilarity between biotope-clusters)	Top discriminator taxa between pairs of biotope-clusters	Average density in each biotope cluster (Sq. root #/m^2)	Diss / SD ratio
BPF / RSF cluster (64.9%)	*Baetis* spp. Orthocladiinae Elmidae *L. penicillata* Tanypodinae	BPF / RSF vs. RSF / FRF (46.2)	Simuliidae Tanypodinae *Adenophlebia* spp Orthocladiinae.	1.12 / 9.38 9.29 / 4.44 5.04 / 0.56 15.20 / 44.20	1.69 1.64 1.58 1.42
		Taxa with 25 - 100x higher densities in BPF / RSF cluster	*Afroptilum* sp. *Aprionyx* spp. *Demoulinia* spp. *Castanophlebia* sp.		
RSF / FRF cluster (64.9%)	Orthocladiinae *Baetis* spp. *L. penicillata*	Taxa with 25 - 100x higher densities in RSF / FRF cluster	*D. capensis* *Chimarra* sp. *Cheumatopsyche afra* *Cheumatopsyche maculata*		

5.2.2.i Univariate relationships between hydraulic biotopes and invertebrate assemblages

Hydraulic variables (depth, velocity, Froude and Reynolds numbers, shear stress and applied stream power), taken individually, did differentiate between some pairs of biotopes (Kruskal-Wallis analysis of variance), but they did not do so consistently. For example, significant differences between riffle/ run and run biotopes were identified on the basis of

applied power and of Froude number, but these variables did not discriminate run biotopes from backwaters. Using shear stress, however, run and riffle/run biotopes were significantly different from backwaters, but not from each other. This inconsistency between the biotope groupings that are identified using calculated or measured hydraulic variables has also been the finding of other research into physical correlates with visually-defined biotopes (Schael, 2005).

The association between invertebrate density and species richness, and the various biotopes or flow types, as defined in the Molenaars and Berg River studies respectively (see section 3.2.2), was explored using non-parametric Kruskal-Wallis analysis of variance. Mean abundance of invertebrates per stone was higher in riffle and run biotopes and FRF flow types in the Molenaars and Berg Rivers respectively, than in other biotopes or flow types (Table 5.10). However, the total abundance per stone does not take into account differences in available surface area. When this is accounted for, total invertebrate **density** (number of individuals per unit stone area) was not significantly different across biotopes.

Similarly, the total species (or taxon) count per stone was not significantly different across biotopes. This measure does not take into account either the area of the stone (species density per unit stone area) or the total abundance on a stone (rarefied species richness). Species density also did not differ between biotopes. However, the rarefied species richness was significantly higher in slow runs than riffle biotopes in the Molenaars River in June 2003, and higher in BPF and NF flow types than in FRF in the Berg River in 2004. This indicates that, although the total number of individuals on a stone was higher in riffle or FRF biotopes in both rivers, the chances of an individual of one species on a stone encountering an individual from another species was greater in slow run biotopes. Total invertebrate density, species density and rarefied species richness differences across biotope clusters or flow types are shown in Figure 5.5 for the Molenaars and Berg Rivers.

Table 5.10 Kruskall-Wallis analysis of variance of various invertebrate community attributes to detect differences based on biotopes or flow types, in the Molenaars and Berg River baseline surveys.

H = test statistic, which is given only where significant differences were found among biotopes. Significant post-hoc multiple comparisons are also indicated, in order of the biotope with the higher densities of that taxon. n.s. = not significant. ind. = individuals.

Density / richness measure	H	P value	Significantly different densities per biotope cluster or flow type (post-hoc comparison)
MOLENAARS RIVER, 2003			
Abundance (#ind. individuals on stone)	10.0	0.04	Riffles and runs had higher means but n.s.
Total density (#ind. m^{-2} stone surface)		n.s.	
Species count (# taxa per stone)		n.s.	
Species density (#taxa m^{-2} stone surface)		n.s.	
Rarefied species richness (# taxa per 100 ind.),	12.9	0.010	Slow run > riffle (p = 0.020)
BERG RIVER, 2004			
Abundance (# individuals on stone)	9.77	0.020	FRF > BPF (p = 0.043) FRF > NF (p = 0.035)
Total density (#ind. m^{-2} stone surface)		n.s.	
Species count (# taxa per stone)		n.s.	
Species density (#taxa m^{-2} stone surface)		n.s.	
Rarefied species richness (# taxa per 100 ind.),	13.62	0.004	BPF > FRF (p = 0.006) NF > FRF (p = 0.020)

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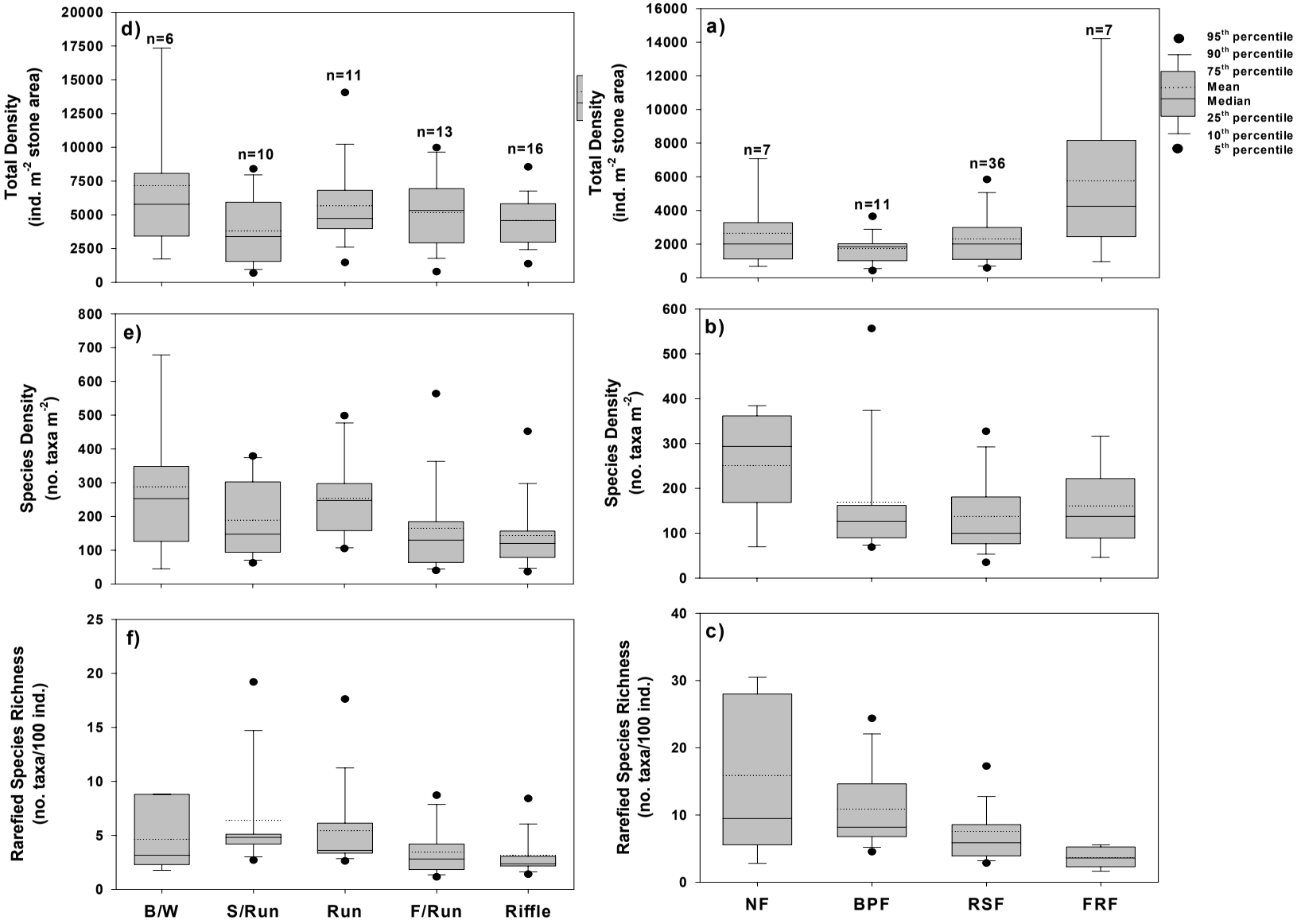
Figure 5.5 Box plots of a)Total invertebrate density (number of individuals per m^2 of stone surface), b) species density (number of taxa per m^2 of stone surface) and c) rarefied species richness (number of taxa per 100 individuals) in biotope clusters or flow types, in the Molenaars and similarly d, e, f) for the Berg River Baseline surveys.


d)
n=6
n=10
n=11
n=13
n=16
Total Density (ind. m-2 stone area)
a)
n=7
n=11
n=36
n=7
95th percentile
90th percentile
75th percentile
Mean
Median
25th percentile
10th percentile
5th percentile
e)
Species Density (no. taxa m-2)
b)
f)
Rarefied Species Richness (no. taxa/100 ind.)
c)
B/W
S/Run
Run
F/Run
Riffle
NF
BPF
RSF
FRF

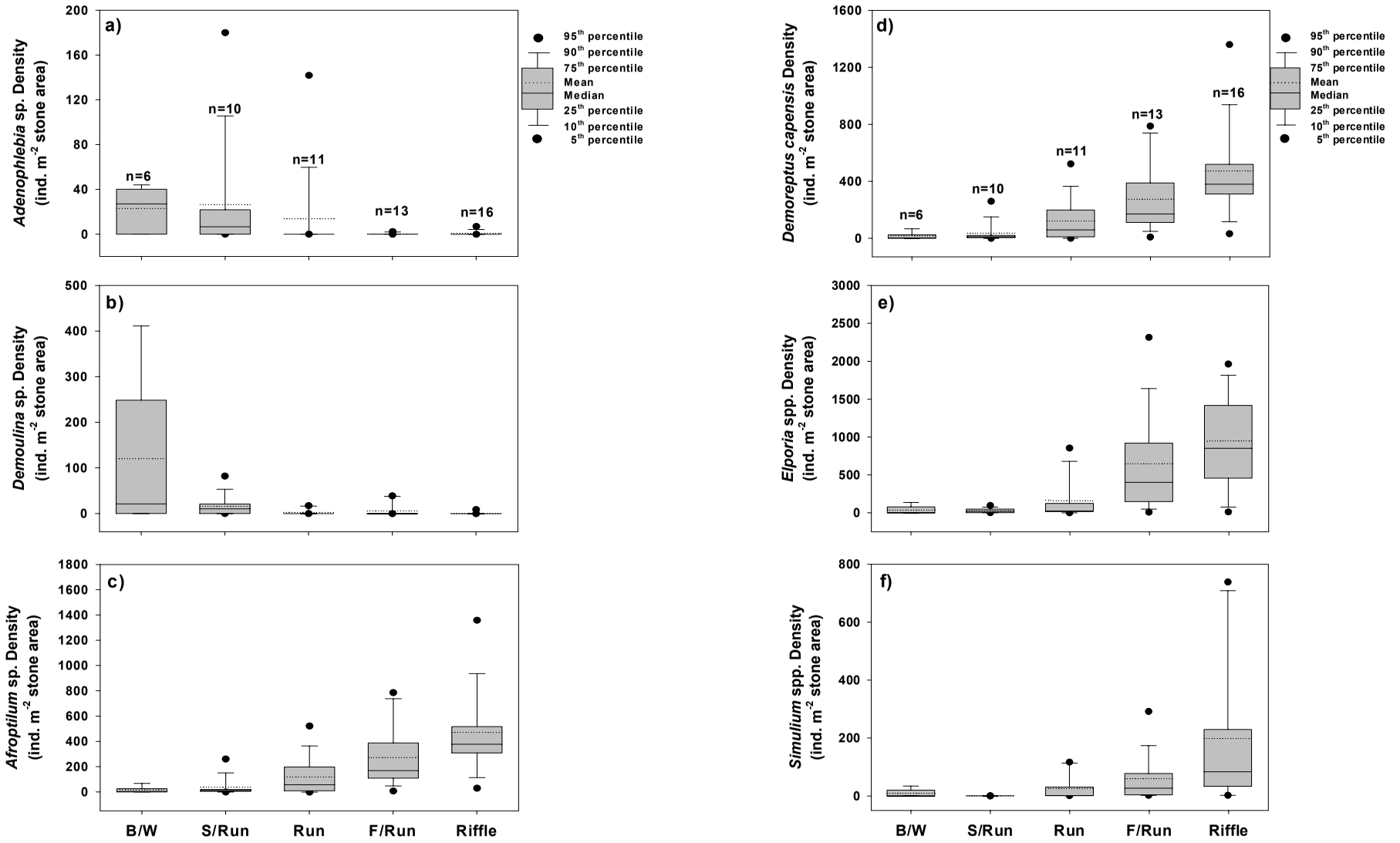


Figure 5.6 Box plots showing the mean, median and range of densities (number of individuals per m^2 of stone surface) per biotope for selected taxa in the Molenaars River, at the Baseline survey in June 2003.

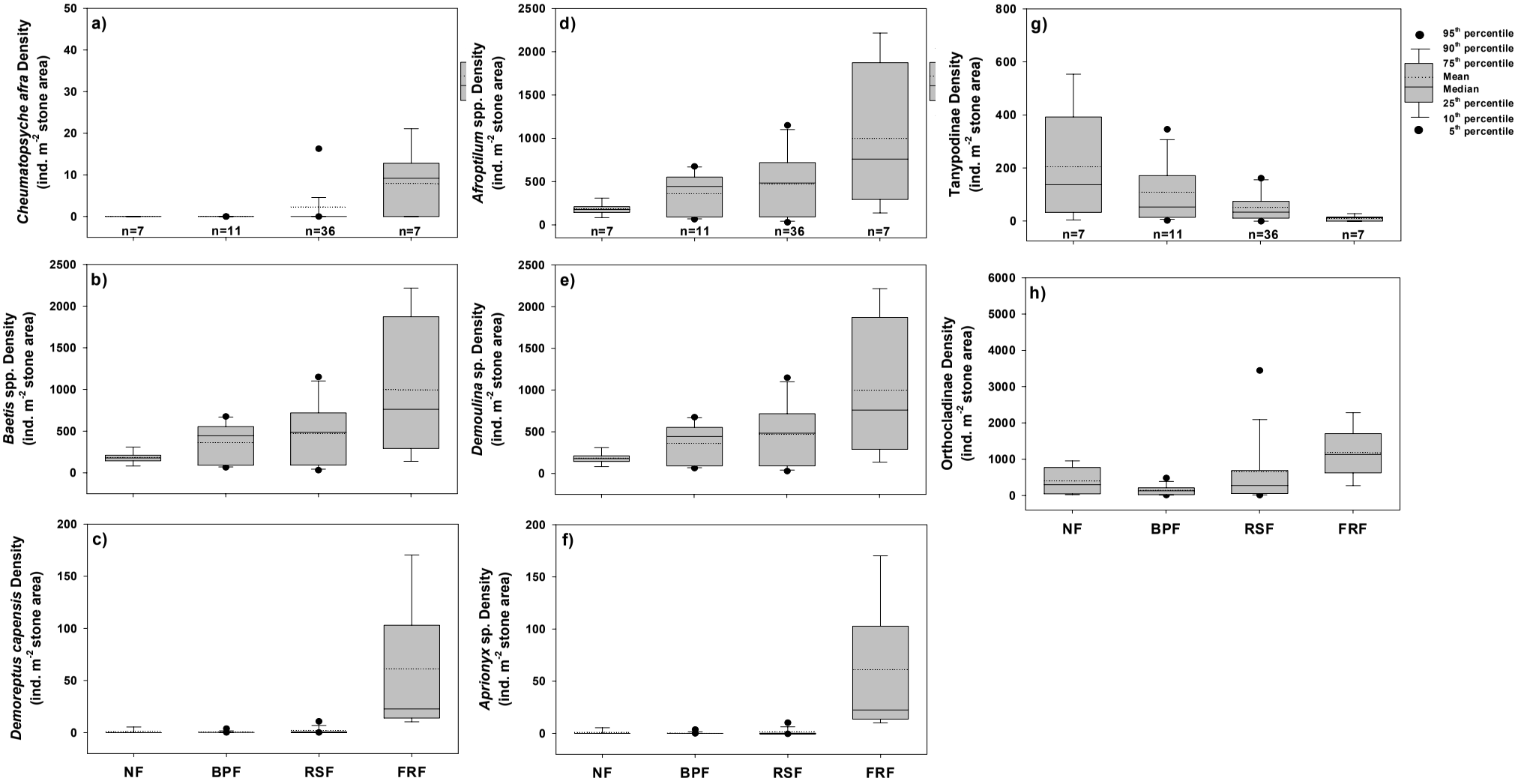


Figure 5.7 Box plots showing the mean, median and range of densities (number of individuals per m^2 of stone surface) per biotope for selected taxa in the Berg River, at the Baseline survey in May 2004.

At the level of individual taxa, a number of taxa occurred in significantly higher densities in one biotope or flow type than others (Kruskall Wallis analysis of variance and post-hoc pairwise comparisons; Tables 5.11 and 5.12; Figures 5.6 and 5.7). As with the multivariate analysis (SIMPER results, Table 5.8 and 5.9), discriminating taxa for slow biotopes included *Afroptilum* sp., *Demoulinia* sp., Tanypodinae and a number of Leptophlebiidae (*Aprionyx* sp., *Adenophlebia* sp.), whilst *Demoreptus capensis*, *Baetis* spp., *Cheumatopsyche afra*, Orthocladiinae, and *Elporia* spp. showed preferences for fast runs and riffles in either or both the Berg and Molenaars Rivers (Figures 5.6 and 5.7). Even these, however, were distributed in gradually increasing or decreasing densities from slow to fast biotopes. For the majority of taxa, however, the overlap in densities across biotopes obscured any preferences.

Finally, periphyton density and organic matter associated with a sample point are also potentially important factors determining the distribution of invertebrates. Periphyton did not differ among biotopes in the Berg River (no collection was made in the Molenaars River). However, there were significant differences in the relative amount of organic matter among flow types (Figure 5.8) in the Berg River (Kruskal-Wallis H = 12.11, p=0.007), with the slower flowing biotopes having the greatest amount of organic matter. Only pair-wise comparisons between RSF flow and NF were significant (p = 0.03). A similar pattern was evident in the Molenaars River, despite the much lower overall availability or organic matter, although differences between biotopes were not significant, because of the high level of patchiness in distribution of organic matter, even within biotopes.

Table 5.11 Kruskal-Wallis analysis of variance of density (ind. per m^2 stone surface area) to detect differences based on biotopes or flow types, for selected invertebrate taxa in the Molenaars and Berg River baseline survey.

Only significant results are shown. H = test statistic, which is given only where significant differences were found among biotopes. Significant post-hoc multiple comparisons are also indicated, in order of the biotope with the higher densities of that taxon. n.s. = not significant; ind. = individuals; b/w = backwater; sl. run = slow run.

Density (ind. per m^2 stone surface area)	H	P value	Significantly different densities per biotope (post-hoc comparison)
MOLENAARS RIVER 2003			
Aprionyx sp.	13.0	0.011	n.s. (highest mean in b/w)
Choroterpes sp.	10.8	0.029	n.s. (highest mean in b/w)
Adenophlebia sp.	13.2	0.010	n.s. (highest mean in sl. run + b/w)
Afroptilum sp.	28.1	0.000	b/w > fast run; riffle (p < 0.002) sl. run > fast run; riffle (p < 0.016)
Demoulinia sp.	11.7	0.020	n.s. (highest mean in b/w)
Demoreptus capensis	27.0	0.000	riffle > b/w; sl. run; run (p < 0.020)
Pseudopannota maculosa	10.8	0.029	n.s. (highest mean in fast run)
Chimarra sp.	16.2	0.003	n.s. (highest mean in riffle)
Elporia spp.	26.8	0.000	riffle > b/w; sl. run; run (p < 0.020) fast run > sl. run (p < 0.030)
Simuliidae	22.0	0.00	riffle > sl. run (p < 0.001)
BERG RIVER 2004			
Afroptilum sp.	19.3	0.000	BPF > RSF (p = 0.009) BPF > FRF (p = 0.026)
Baetis spp.	12.1	0.007	FRF > NF (p = 0.010
Demoreptus capensis	25.9	0.000	FRF > RSF (p = 0.001) FRF > BPF (p = 0.001) FRF > NF (p = 0.012)
Demoulinia spp.	21.4	0.000	BPF > RSF (p = 0.000) BPF > FRF (p = 0.003)
Aprionyx sp.	16.3	0.001	BPF > RSF (p = 0.007) BPF > FRF (p = 0.004)
Lithogloea harrisoni	14.8	0.002	BPF > RSF (p = 0.012) BPF > FRF (p = 0.014)
Cheumatopsyche afra	13.0	0.005	n.s.
Cheumatopsyche maculata	17.1	0.001	FRF > RSF (p = 0.018) FRF > BPF (p = 0.022)
Simuliidae	16.0	0.012	FRF > RSF (p = 0.045) FRF > BPF (p = 0.001)
Tanypodinae	15.6	0.001	BPF > FRF (p = 0.008) NF > FRF (p = 0.003)
Orthocladiinae	14.3	0.003	FRF > BPF (p = 0.012)

Table 5.12 Pearson's correlation coefficients of 4th root transformed invertebrate densities and abiotic variables, for taxa in the Molenaars River (M) in June 2003 and the Berg River (B) in May 2004. Only significant relationships are presented. Results are given as the Pearson's r-value. p-value is indicated as follows: * p <0.05; **p< 0.01; § p<0.001; † p< 0.000. Organic matter data were log-transformed to achieve normality. Other abiotic variables not transformed.

Responses to depth		Responses to velocity or hydraulic indices derived from velocity		Responses to organic matter		Responses to inorganic matter	
M	**B**	**M**	**B**	**M**	**B**	**M**	**B**
Tanytarsini 0.32 *		Chironomini -0.34 *	Orthocladiinae 0.47†	Tanypodinae 0.81 †	Tanypodinae 0.47 §	Tanypodinae 0.85 **	Tanypodinae 0.36 **
A. harrisoni - 0.43 **		Tanypodinae -0.32 *	Tanypodinae -0.30*	Chironomini 0.78 §	Chironomini 0.40 **	Tanytarsini 0.34 *	Elmidae 0.39 **
Aeshnidae 0.78 **		*Choroterpes* sp. -0.54 *	*Adenophlebia* sp. -0.38*	*Choroterpes* sp. 0.85 †	*Adenophlebia* sp. 0.39 *	*Choroterpes* sp. 0.72 **	Helodidae 0.41*
Hydroptilidae 0.56 *		*A. (bergensis)* sp. -0.47 *	*Aprionyx* sp. -0.4 *	*Aprionyx* sp. 0.90 *	*Aprionyx* sp. 0.55 §	*A. (bergensis)* sp.	Athericidae 0.40 *
Hydraenidae -0.61 *		*Afroptilum* sp. -0.56 †		*A. (bergensis)* sp. 0.93 †	Athericidae 0.58 †	0.62 *	
		Pseudocloeon sp. -0.37 *		*Afroptilum* sp. 0.76 †		*D. capensis* -0.49 *	
		D. capensis 0.65†		*Pseudocloeon* sp. 0.77 §		*Baetis* spp. -0.51 *	
		Baetis spp. 0.31 *		*A. harrisoni* - 0.67 *			
		Elporia spp. 0.51†		*A. agilis* -0.69**			
				Elporia spp. -0.50*			

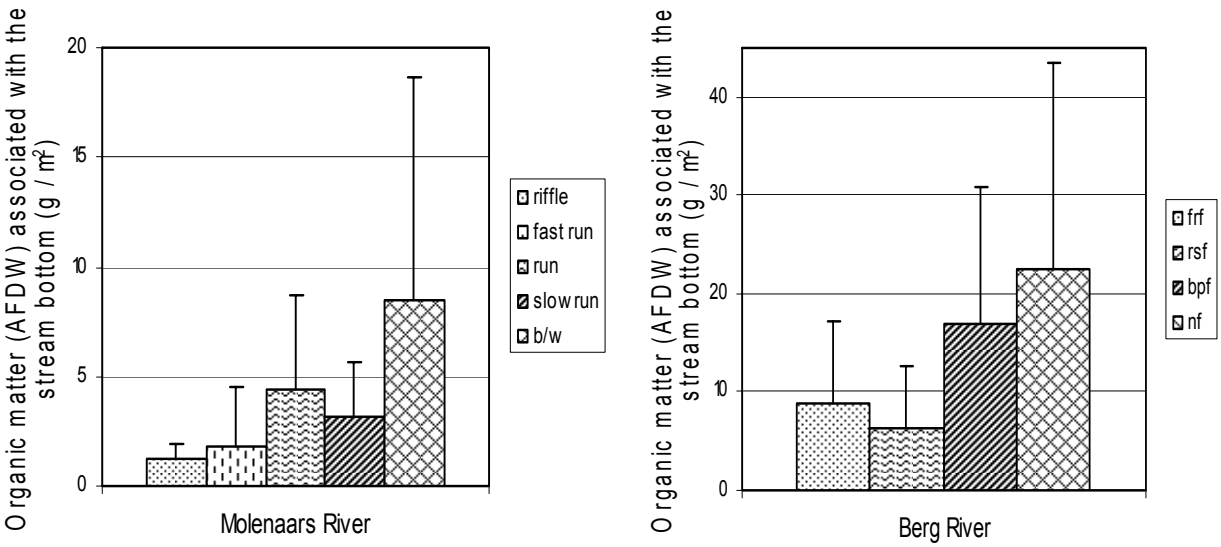


Figure 5.8 Mean (standard deviation) organic matter associated with sampled stones (AFDW in g m^{-2} of river bed), in biotopes or flow types, in the Molenaars and Berg River baseline surveys. Note scale differences between the Molenaars and Berg River plots.

5.2.2.ii Univariate relationships between hydraulic variables and invertebrate assemblages

Total invertebrate density was not correlated with either of the measures of periphyton density (Chla and AFDW, Berg River only), or with the amount of organic or inorganic matter associated with a stones, or indeed with any of the hydraulic variables related to flow and depth measured during the baseline surveys in each river in 2003 and 2004 (Pearson's Product Moment correlation on transformed normal data, all -p > 0.05).

However, different taxa might be expected to have different density patterns, in response to one or more sometimes opposite driving forces. Each taxon was thus examined separately in order to attempt to identify sets of relationships that might exist prior too flood disturbance, and which might then be used to measure a biological consequence (disturbance effect) of each flood.

In the Molenaars River in June 2003, a number of taxa demonstrated density differences in response to velocity, both negative and positive. A second set of responses implicated depth, although among fewer taxa. Finally, the AFDW or organic material associated with stones was highly correlated with distribution differences among many taxa preferring slower flowing waters. In the Berg River survey, a great deal fewer relationships between invertebrate density and abiotic variables were significant than in the Molenaars River, particularly those implicating velocity and depth in affecting invertebrate density distribution.

Summary data reflecting the three main relationships typical of the fauna are indicated in Table 5.12 and Figure 5.9, for both the Molenaars and Berg Rivers. In general, densities of the Leptophlebiidae (*Choroterpes* sp., *Aprionyx* sp., *Adenophlebia* sp.) were negatively correlated with velocity or velocity-based hydraulic indices, and positively correlated with

the amount of organic matter associated with the bed, in both rivers, whilst a similar relationship held for some Baetidae (*Afroptilum* sp., *Pseudocloeon* sp.) in the Molenaars River. Most chironomid groups were positively associated with organic matter availability and negatively associated with velocity, with the exception of Orthocladiinae in the Berg River which showed a significant positive relationship with velocity. Many taxa that are known to occur on the upper surfaces of stones (i.e. *Demoreptus capensis*, *Baetis* spp., *Elporia* spp., *Agapetus agilis*, Orthocladiinae) displayed either or both: a positive correlation with velocity; a negative correlation with organic or inorganic matter associated with a stone (Table 5.12).

Some taxa (e.g. Tanypodinae) displayed consistent relationships with the abiotic variables across both rivers, but others did not. Orthocladiinae density in the Berg River, for example, was significantly correlated with velocity in the Berg River but not in the Molenaars River, despite the similar range in velocities on the stones on which they occurred. For many taxa, inadequate representation in one of the rivers precluded the identification of relationships (e.g. Blephariceridae in the Berg River).

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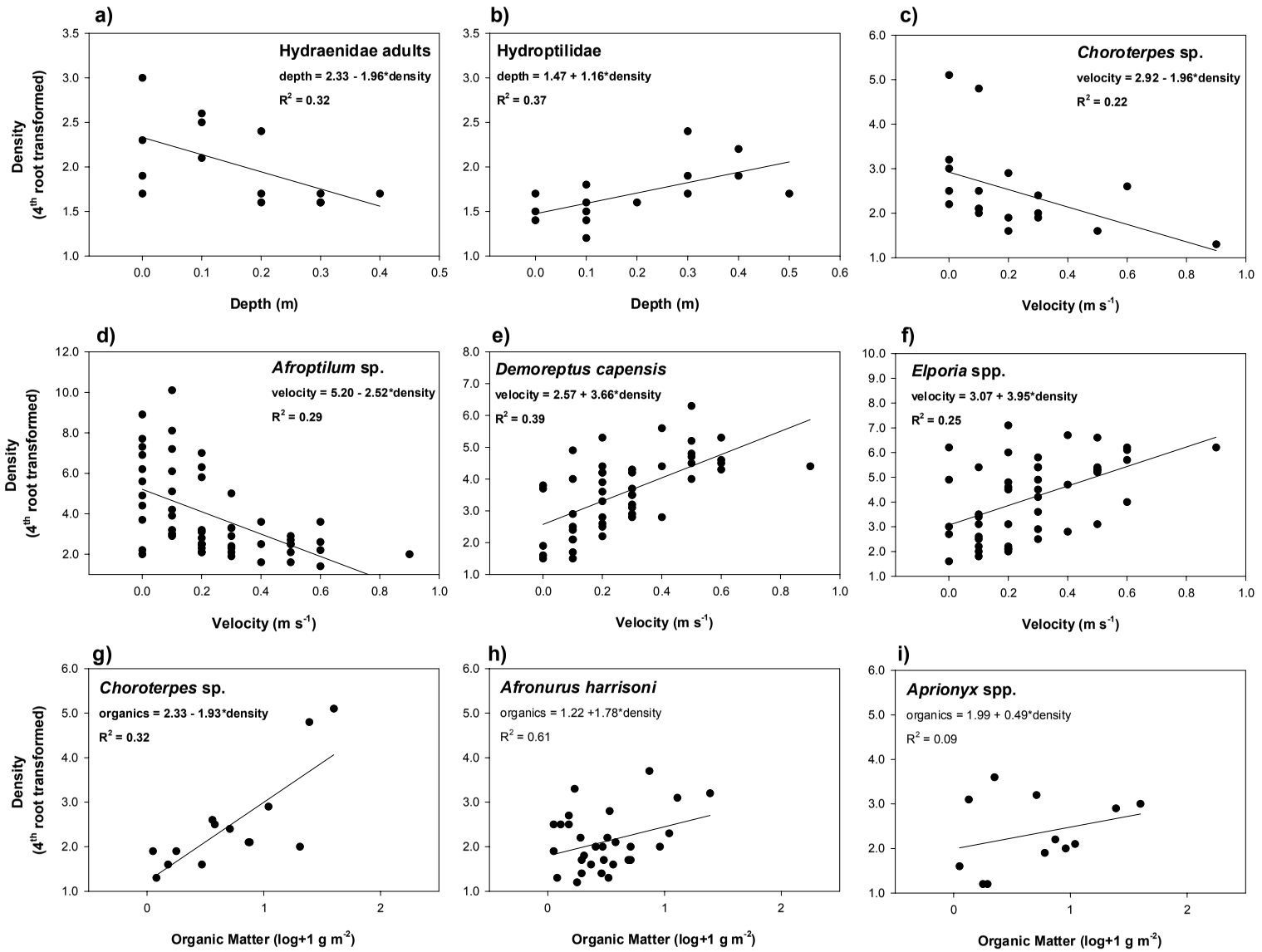
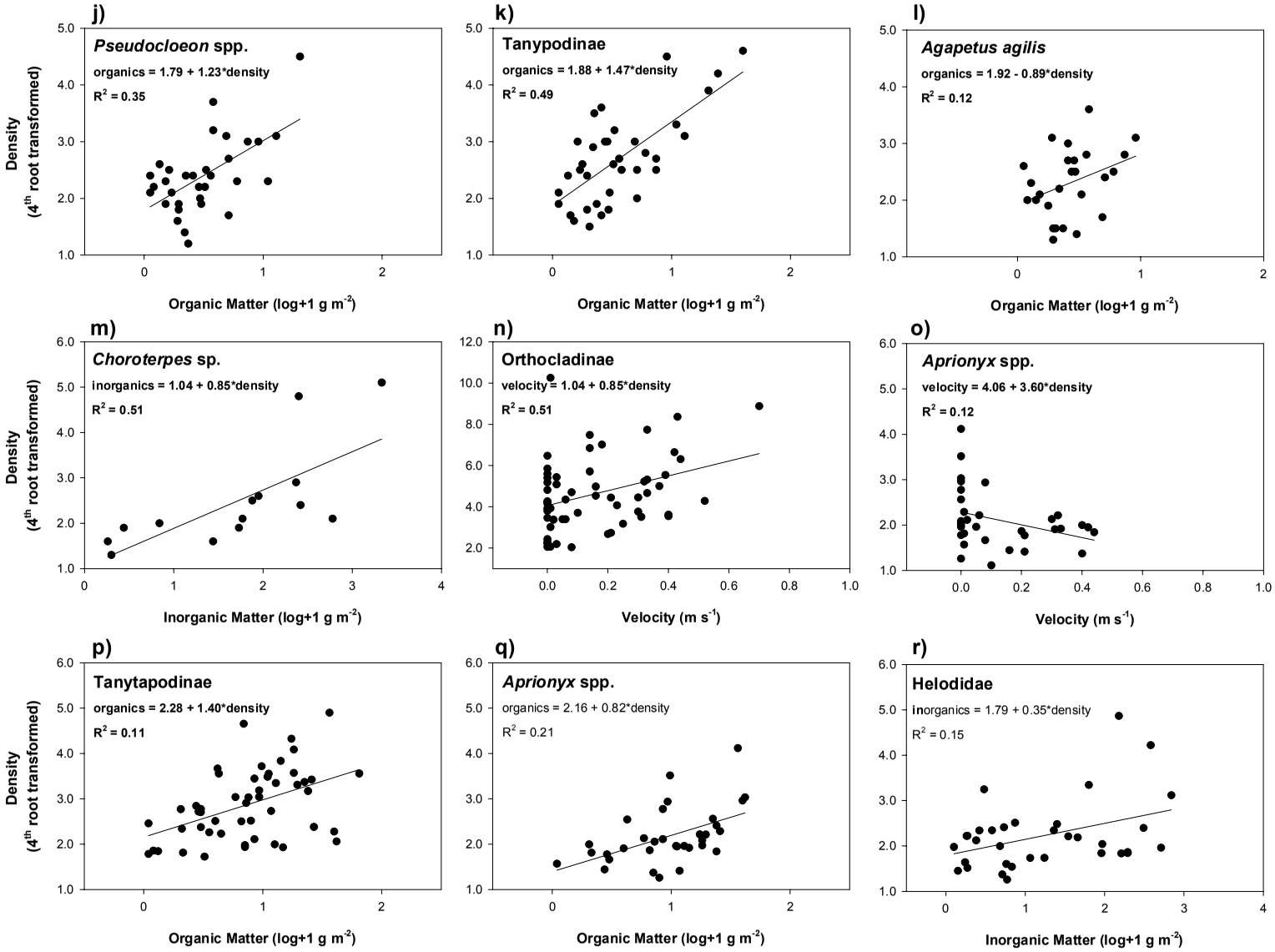
Figure 5.9

Correlation and linear regression of invertebrate density and four abiotic measures: depth, velocity, and the amount of organic and inorganic matter associated with the sample location. Plots a-m are for the Molenaars River in June 2003. Plots n-r are for the Berg River in May 2004 Transformations to obtain normality are as indicated on the graph axes. Statistical significance and correlation coefficients are provided in Table 5.12**.**

Figure 5.9 Continued

Correlation and linear regression of invertebrate density and four abiotic measures: depth, velocity, and the amount of organic and inorganic matter associated with the sample location. Plots a-m are for the Molenaars River in June 2003. Plots n-r for the Berg River in May 2004 Transformations to obtain normality are as indicated on the graph axes. Statistical significance and correlation coefficients are provided in Table 5.12**.**


a)
Hydraenidae adults
depth = 2.33 - 1.96*density
R2 = 0.32
Density (4th root transformed)
Depth (m)
b)
Hydroptilidae
depth = 1.47 + 1.16*density
R2 = 0.37
Depth (m)
c)
Choroterpes sp.
velocity = 2.92 - 1.96*density
R2 = 0.22
Velocity (m s-1)
d)
Afroptilum sp.
velocity = 5.20 - 2.52*density
R2 = 0.29
Density (4th root transformed)
Velocity (m s-1)
e)
Demoreptus capensis
velocity = 2.57 + 3.66*density
R2 = 0.39
Velocity (m s-1)
f)
Elporia spp.
velocity = 3.07 + 3.95*density
R2 = 0.25
Velocity (m s-1)
g)
Choroterpes sp.
organics = 2.33 - 1.93*density
R2 = 0.32
Density (4th root transformed)
Organic Matter (log+1 g m-2)
h)
Afronurus harrisoni
organics = 1.22 +1.78*density
R2 = 0.61
Organic Matter (log+1 g m-2)
i)
Aprionyx spp.
organics = 1.99 + 0.49*density
R2 = 0.09
Organic Matter (log+1 g m-2)


j)
Pseudocloeon spp.
organics = 1.79 + 1.23*density
R^2 = 0.35
k)
Tanypodinae
organics = 1.88 + 1.47*density
R^2 = 0.49
l)
Agapetus agilis
organics = 1.92 - 0.89*density
R^2 = 0.12
m)
Choroterpes sp.
inorganics = 1.04 + 0.85*density
R^2 = 0.51
n)
Orthocladinae
velocity = 1.04 + 0.85*density
R^2 = 0.51
o)
Aprionyx spp.
velocity = 4.06 + 3.60*density
R^2 = 0.12
p)
Tanytapodinae
organics = 2.28 + 1.40*density
R^2 = 0.11
q)
Aprionyx spp.
organics = 2.16 + 0.82*density
R^2 = 0.21
r)
Helodidae
inorganics = 1.79 + 0.35*density
R^2 = 0.15
Density (4th root transformed)
Organic Matter (log+1 g m-2)
Inorganic Matter (log+1 g m-2)
Velocity (m s-1)

Interestingly, few of the densities of individual taxa were correlated with either of the measures of periphyton density (Chla and AFDW). One or both of these measures were, however, correlated with both species density, as well as the densities of the mayfly *Lithogloea* sp., elmid adults, and most chironomid grazers (Table 5.13), although the taxon-specific correlations were weak, with r values generally around 0.3. It is note-worthy that the Leptophlebiidae, which displayed a relationship toward organic matter in the Berg River (Table 5.12), did not do so in the case of periphyton density. This periphyton measure incorporates all organic matter attached and growing on stone surfaces (for example including both algal cells and bacteria), whilst the organic matter associated with the stream bed reflects, in the main, particulate organic matter such as leaf fragments and decaying plant debris.

Table 5.13 Pearson's correlation between invertebrate densities (per taxon), invertebrate species density, and periphyton density as Chlorophyll-*a* and as ash-free dry weight (AFDW). Density data were 4^{th} root transformed; periphyton data were log+1 transformed. indiv. = individuals

	Correlation coefficient (r)	**Coefficient of determination (r^2)**	**p-Value**	**n**
Chlorophyll-*a* (mg m^{-2} stone surface)				
Species density (#taxa m^{-2} stone surface)	0.533	0.280	0.000	52
Lithogloea sp. (indiv. m^{-2} stone surface)	0.413	0.170	0.026	29
Elmidae adults (indiv. m^{-2} stone surface)	0.364	0.132	0.048	30
Orthocladiinae (indiv. m^{-2} stone surface)	0.351	0.123	0.011	52
Chironomini (indiv. m^{-2} stone surface)	0.338	0.114	0.047	35
Tanytarsini (indiv. m^{-2} stone surface)	0.314	0.099	0.036	45
Periphyton AFDW (mg m^{-2} stone surface)				
Species density (#taxa m^{-2} stone surface)	0.495	0.274	0.009	24
Chironomini (indiv./\ m^{-2} stone surface)	0.406	0.165	0.015	35
Tanytarsini (indiv. m^{-2} stone surface)	0.333	0.111	0.025	45

An important abiotic variable, from the perspective of a study examining particle movement by floods, is that of the substratum particle size. Thus the relationship between particle size and invertebrate assemblages is dealt with separately in section 5.2.3.

5.2.3 Possible pre-flood selection of stable stones by invertebrates

Stable bed particles have been hypothesised to act as refugia for invertebrates during flood disturbance (e.g. Townsend *et al.,* 1997c; Francoer *et al.,* 1998). Since the baseline samples were taken from stones whose subsequent stability (or movement) during floods was recorded, it provided an opportunity to test whether invertebrates or specific taxa might congregate on stable bed particles in the immediate pre-flood period, thereby avoiding dislodgement as a result of bed particle movement.

Molenaars River 2003 baseline survey **Berg River 2004 baseline survey**

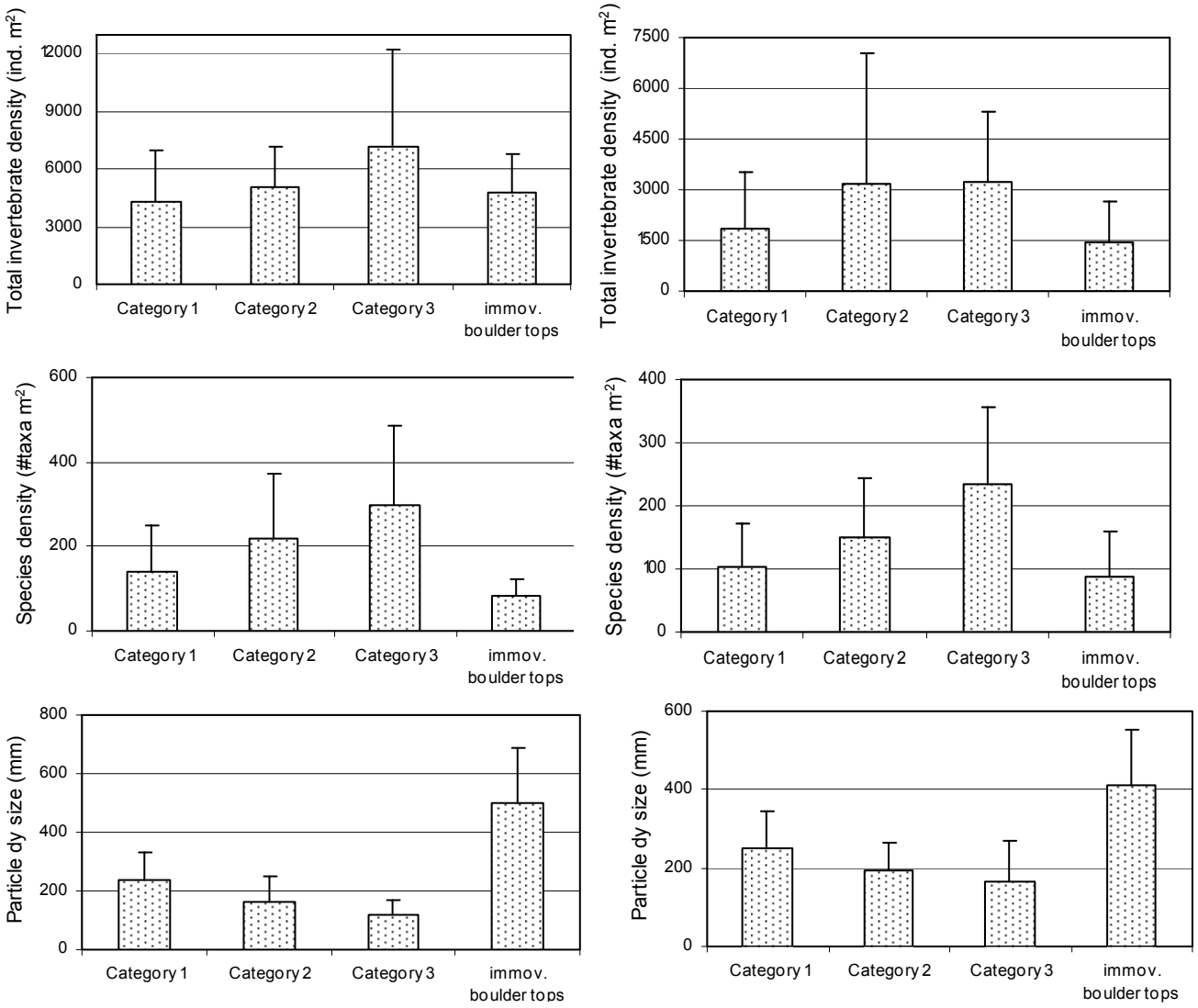


Figure 5.10 Average (standard deviation) values for a) total invertebrate densities per unit stone area, b) species density per unit stone area and c) particle size dy, for the baseline condition in the Molenaars and Berg Rivers, and comparing four categories of stones.

Three categories of stones were identified for each river, based on the degree to which stones sampled during the baseline survey then subsequently moved during floods. In both rivers, stones either remained stable (Category 1), or moved once, in the largest flood of that year (Category 2), or else they moved twice - in the largest and second largest floods (Category 3). Kruskal-Wallis analysis of variance was used to test whether, in the period immediately before the flood season, differences in invertebrate densities on these categories of stones might suggest that they were selecting stable stone particles.

In the Molenaars River in 2003, average total invertebrate density on unmoved stones was 4283 indiv. m^{-2}, lower than the density on the most mobile stones where densities averaged 7171 indiv. m^{-2} (Figure 5.10,), although this was not statistically significant (Table 5.14). In the Berg River, the difference between invertebrate densities on the Category 1-3 rocks was significant (Table 5.14) and substantial, with some 3250 indiv. m^{-2} on Category 3 (moved in two floods) stones, as opposed to 1833 indiv. m^{-2} on Category 1, unmoving stones (Figure 5.10). A similar pattern emerged comparing the species density (taxa m^{-2} stone surface), where Category 3 stones had a higher per unit richness than the larger stones of Category 1 (Figure 5.10) in both the Molenaars and Berg Rivers.

The tops of immovable boulders had average densities of even less than this - some 1400 indiv. m^{-2}, although this density represents only that of invertebrates occurring on the upper surfaces of the stones and is not comparable with whole stone samples.

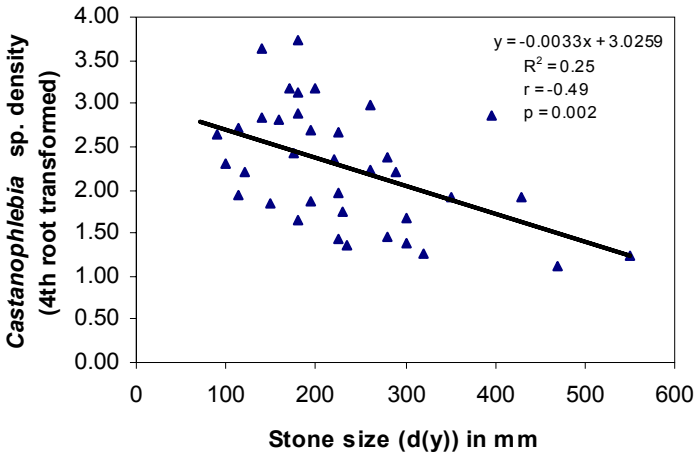
Table 5.14 Kruskal-Wallis analysis of variance between total invertebrate density, species density and particle size, and stone movement category. H = test statistic. Significant Post-hoc multiple comparisons are also presented.

	H	P value	Significantly different groups
MOLENAARS RIVER 2003			
Total density (# m^{-2})		n.s.	
Species density (# taxa/ m^{-2})	11.8	0.003	Category 1 vs Category 3 (p = 0.004)
Stone d(y) (mm)	15.2	0.001	Category 1 vs Category 3 (p = 0.027) Category 1 vs Category 2 (p = 0.001)
BERG RIVER 2004			
Total density (# m^{-2})	8.0	0.018	Category 1 vs Category 3 (p = 0.0001)
Species density (# taxa/ m^{-2})	17.0	0.002	Category 1 vs Category 3 (p = 0.0001)
Stone d(y) (mm)	14.5	0.001	Category 1 vs Category 3 (p = 0.0005)

Category 3 stones represent those that would move during the winter period in each river. These were significantly smaller than Category 1 stones (Table 5.14), a large part of the

reason that they were moved. Category 2 stones were not significantly different from either of the other stones groups, but nevertheless moved only during the largest flood of the season in each river. This apparent preference of invertebrates for stones that were in essence more mobile is probably to a large extent a consequence of the fact that invertebrate densities were shown to decrease with increasing stone size and that larger stones generally corresponded to Category 1, unmoving stones. Figure 5.11, depicts the significant negative correlation between invertebrate density and stone particle size, a reasonably strong relationship with r-values of between -0.50 and -0.55. At the level of individual taxa, the majority of taxa in both the Berg and Molenaars Rivers followed this pattern of higher densities (per unit area) on smaller stones (Table 5.15). Figures 5.12 and 5.13 show this relationship for selected taxa.

Non-significant correlations were returned especially where individual taxa were not represented on many stones. The strength of this relationship varied among individual taxa, from a weak negative r value to a very strong relationship of (r values between -0.60 and -0.98, Table 5.15). The more abundant taxa were, interestingly, not the main drivers of this pattern, for example in the Berg samples, with weak correlations between stone particle size and both orthoclad midges and the most numerous of all the taxa, *Baetis* spp. (Table 5.15).



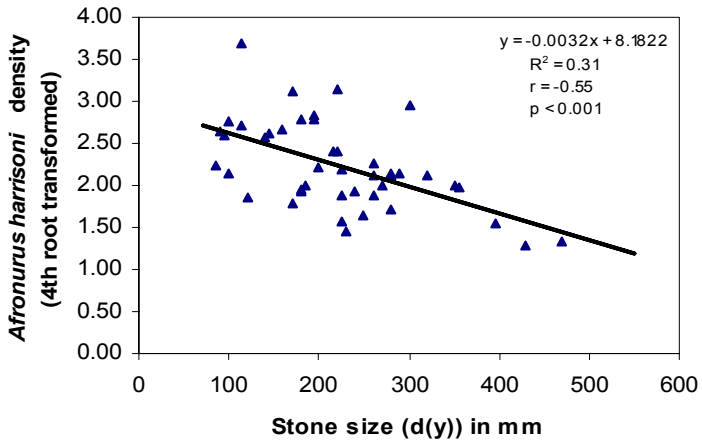


Table 5.15 Results of correlation and linear regression of 4th root transformed invertebrate densities and particle diameter (dy), for most taxa in the Molenaars River in June 2003 and the Berg River in May 2004. Taxa are ordered by highest R^2 values for the Molenaars River. Particle size was log-transformed for the Molenaars River data to obtain normal distributions. P-values in bold font indicate a significant correlation.

	Molenaars River June 2003				Berg River May 2004			
Taxon	**n**	**r**	**R^2**	**p**	**n**	**r**	**R^2**	**p**
Aeshnidae	10	-0.98	0.97	**0.000**	sample size too small			
Parecnomina	10	-0.80	0.64	**0.006**	20	-0.67	0.45	**0.001**
Afronurus	41	-0.78	0.60	**0.000**	44	-0.55	0.30	**0.000**
Notonemouridae	13	-0.77	0.59	**0.002**	31	-0.53	0.28	**0.002**
Hydroptilidae	15	-0.76	0.58	**0.001**	sample size too small			
Athripsodes	23	-0.71	0.50	**0.000**	42	-0.37	0.14	**0.017**
Cheumatopsyche	16	-0.69	0.48	**0.003**	sample size too small			
Castanophlebia	13	-0.65	0.42	**0.016**	37	-0.49	0.24	**0.002**
Chironomini	36	-0.62	0.39	**0.000**	43	-0.38	0.15	**0.011**
Tanytarsini	48	-0.61	0.37	**0.000**	54	-0.41	0.17	**0.002**
Lestagella	57	-0.61	0.37	**0.000**	61	-0.51	0.26	**0.000**
Choroterpes sp.	19	-0.60	0.36	**0.007**	not present			
TOTAL	59	-0.56	0.31	**0.000**	61	-0.50	0.25	**0.000**
Lithogloea sp.	sample size too small				36	-0.53	0.28	**0.000**
Pseudocloeon	39	-0.54	0.29	**0.000**	sample size too small			
Acarina	19	-0.52	0.27	**0.022**	26	-0.44	0.19	**0.026**
Aprionyx sp.	16	-0.51	0.26	**0.042**	36	-0.41	0.17	**0.013**
Helodidae	20	-0.49	0.24	**0.028**	36	-0.32	0.10	0.060
Afronurus sp.	51	-0.48	0.23	**0.000**	51	-0.44	0.19	**0.001**
Orthocladiinae	58	-0.47	0.22	**0.000**	61	-0.28	0.08	**0.028**
Tanypodinae	48	-0.45	0.20	**0.002**	53	-0.34	0.12	**0.012**
Elmidae	53	-0.42	0.18	**0.002**	55	-0.36	0.13	**0.007**
Baetis spp.	57	-0.38	0.14	**0.004**	61	-0.30	0.09	**0.019**
Afroptilum sp.	55	-0.36	0.13	**0.007**	18	-0.35	0.12	0.148
Athericidae	34	-0.34	0.12	**0.049**	38	-0.37	0.14	**0.023**
Adenophlebia sp.	15	-0.46	0.21	0.087	32	-0.28	0.08	0.127
Chimarra sp.	15	-0.45	0.20	0.096	18	-0.39	0.15	0.106
Elmidae adults	16	-0.29	0.08	0.285	36	-0.32	0.10	0.060
Agapetus agilis	34	-0.27	0.07	0.128	sample size too small			
Elporia spp.	48	0.26	0.07	0.078	sample size too small			
Euthraulus	55	-0.23	0.05	0.086	36	-0.37	0.14	**0.030**
Simuliidae	28	-0.15	0.02	0.450	36	-0.32	0.10	0.061
Hydraenidae	14	-0.06	0.00	0.842	12	-0.52	0.27	0.082
Demoreptus	48	0.05	0.00	0.760	18	-0.43	0.18	0.075
Cheumatopsyche	not present				16	-0.41	0.17	0.200

A number of taxa often observed to be prevalent on the upper surfaces of stones (e.g. *D. capensis*, *Elporia* spp., *Simulium* spp.) demonstrated a non-significant relationship with particle size (Table 5.15). Stronger relationships were generally found in the Molenaars than in the Berg River, but this may in part be a reflection of the higher densities of all invertebrates in the former, making relationships easier to demonstrate.

Another significant relationship was that between stone particle size and the density of periphyton covering the stones surfaces in the Berg River ($r = -0.66$, $p < 0.0001$; $r = -0.59$ $p < 0.0001$ for Chla and AFDW respectively; Figure 5.14). This relationship appeared for the most part to be operating independently of invertebrate density, since non-significant correlations were returned between invertebrate total density, as a whole, and for most taxa, and either Chla or AFDW, with the exceptions of, *inter alia, Lithogloea* sp. and the grazer chironomids (Orthocladiinae, Chironomini and Tanytarsini) as described in section 5.2.2*ii*. Even where a relationship between a taxon and periphyton density was established as significant, it was weak (Table 5.13).

Stone particle size was negatively correlated with the amount of organic matter associated with each stone, only in the Molenaars River, and then weakly so ($r = -0.32$, $p = 0.0.29$).

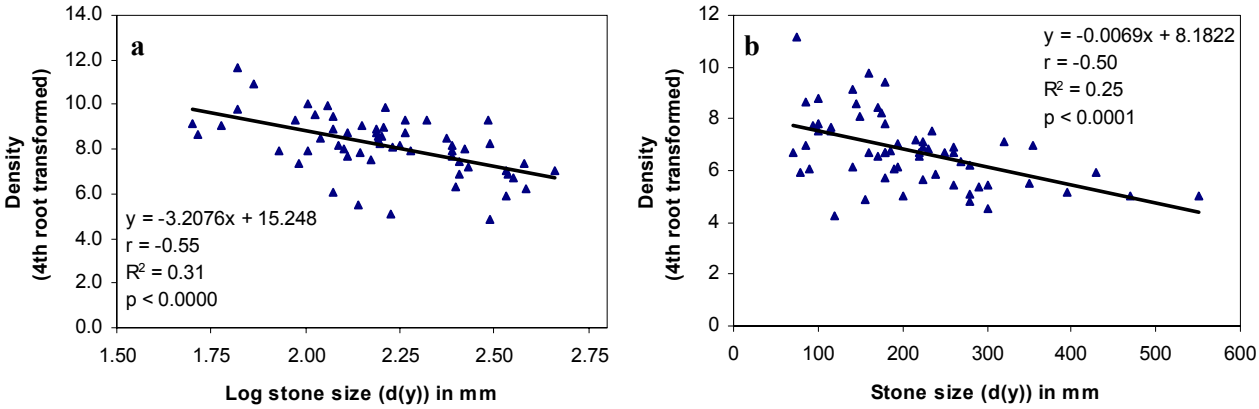


Figure 5.11 Correlation and linear regression of total invertebrate density and particle diameter a) in the Molenaars River in June 2003 and b) in the Berg River in May 2004, based on whole stone samples only. Transformations to obtain normality are as indicated on the graph axes.

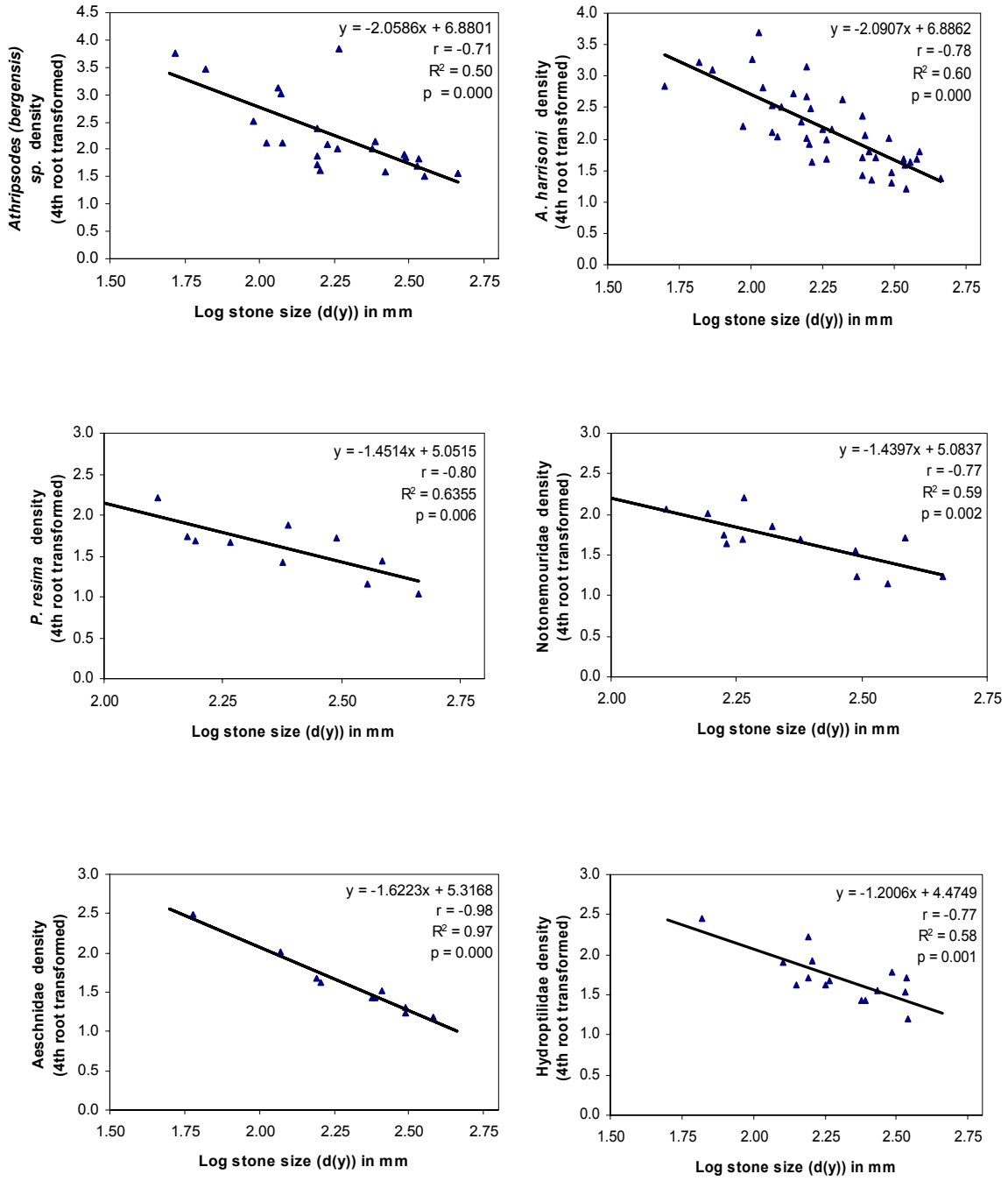


Figure 5.12. Correlation and linear regression of selected invertebrate taxon density and particle diameter in the Molenaars River in May 2004.

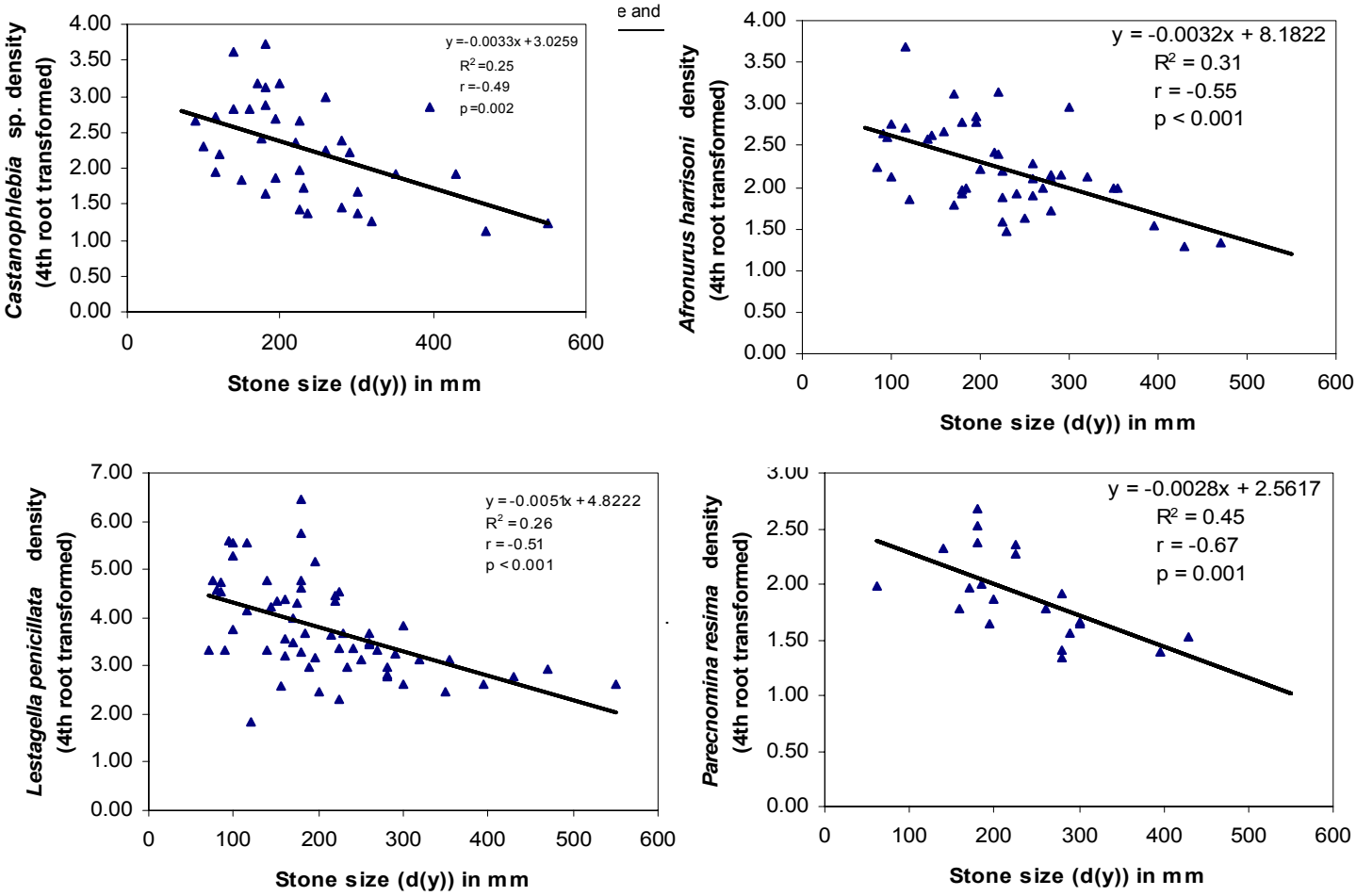


Figure 5.13 Correlation and linear regression of selected invertebrate taxon density and particle diameter in the Berg River in May 2004.

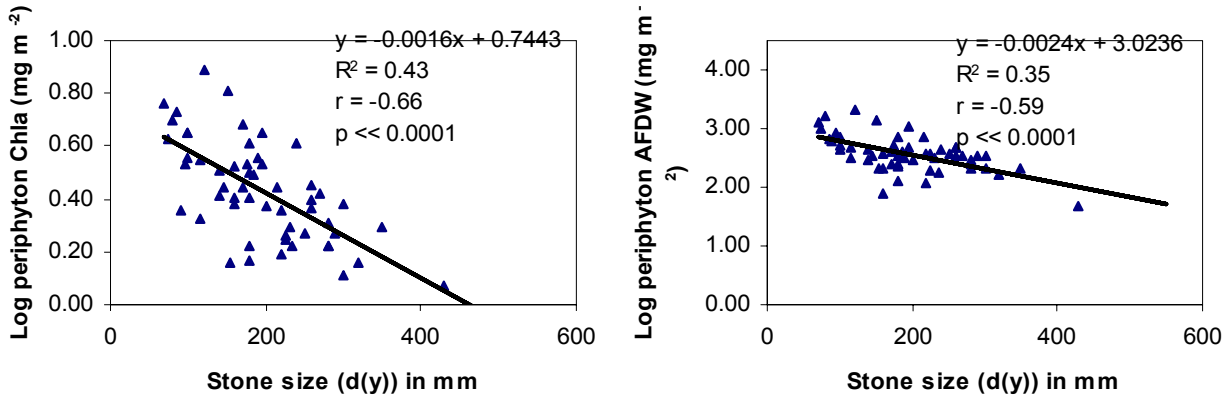


Figure 5.14 Correlation and linear regression of Chlorophyll a / periphyton ash-free dry weight (AFDW) and particle diameter (y-axis) in the Berg River in May 2004.

Finally, particle size did not differ among four biotope clusters in the Molenaars River (Kruskal-Wallis analysis of variance, p= 0.07) or among the four main flow types in the Berg River (p= 0.41). In other words, the relationship between stone particle size and invertebrate density appeared to act independently of any invertebrate preferences for, or assemblage differences across, biotope groupings, as described in section 5.2.1.

5.3 DISCUSSION

The late autumn / early winter invertebrate assemblages in the Molenaars and Berg Rivers, representing baseline conditions prior to floods, showed some interesting similarities as well as differences. Particle size differences were slight, the range of flow velocities, depths and other hydraulic variables were not dissimilar and the taxonomic overlap between the two rivers was very high - only a small number of taxa were well-represented in the Molenaars River but virtually absent from the Berg River, *Agapetus agilis* and *Elporia* spp. being the only two examples. On the other hand, the Berg River site was inhabited by more Hydropsychidae species than the Molenaars. The extremely low densities of *A. agilis* and *Elporia* spp. in the Berg River was not simply an artefact of possible inter-annual variation, but has been observed in other studies on this system. Both these species are grazers, are not widely mobile across the stream bed, and tend to colonise larger substratum particles in the Molenaars River (personal observation). This observation is reinforced by the finding that both taxa were among the few in either the Berg or Molenaars River whose densities did not increase with decreasing particle size (Table 5.15).

The most obvious and striking difference between the two rivers, however, was the substantially greater secondary productivity of the Molenaars River, as evidenced by invertebrate densities in the Molenaars River three or more times those in the Berg River, particularly of the mayfly group, Baetidae. Baetidae made up over 50% of the overall invertebrate density in the Molenaars River, but just under a quarter in the Berg River, which had highest densities of Chironomidae. Furthermore, Baetidae on the tops of immovable boulders in the Molenaars River were the main reason that densities on these stones and on whole stones were similar. In contrast, densities on immovable boulder tops in the Berg River were only half of that recorded on whole stones. These differences may be related to the combination of nutrient enrichment and the suspected relaxation of predation pressure on particularly baetid mayflies in the Molenaars River: Evidence is beginning to emerge that links elevated baetid densities to the absence of indigenous minnows in many mountain streams of the Western Cape, a common feature of these rivers following invasion by alien trout and / or bass. A study by Lowe *et al.* (2005) in the Witte River, a catchment immediately adjacent to the Molenaars, investigated changes in top-down predator effects on invertebrate assemblages and periphyton production, up- and down-stream of a natural barrier to alien fish invasion, comprising sites with and without indigenous minnows respectively. They found not only larger densities of Baetidae in the sites without indigenous fish than with them, but also different behaviour, where baetids at the former sites congregated on upper surfaces of rive stones, whereas in

the presence of indigenous fish, almost no top-dwelling baetids were observed (Lowe *et al.,* 2005). Algal densities were substantially greater in the presence of indigenous minnows than where these were replaced by bass. In the case of the Molenaars and Berg Rivers, the former has lost its complement of indigenous fish species, whilst the latter still supports populations of the Berg River redfin, *Pseudobarbus burgi* and the Cape kurper, *Sandelia capensis*. Reference has already been made to the fact that the Molenaars River receives enriched effluent from two trout farms in its headwater tributaries (Brown, 1996). Thus the combined effects of increased productivity from effluents entering the Molenaars River and the possible relaxation of predation pressure on mobile grazers may account for much of the difference in faunal characteristics between the Molenaars and Berg Rivers as indicated by their Baseline invertebrate surveys. At present the evidence is fairly circumstantial, and more investigation of the energetic requirements of top predators in both systems would be required to illuminate these possible trophic cascades (Biggs *et al.,* 2000).

Invertebrate assemblages in the Molenaars River appeared to have stronger relationships between their density distribution and hydraulic parameters than was the case in the Berg River, whether this be measured in terms of actual point measurements of velocity, depth and so on, or defined in terms of hydraulic biotopes (King & Schael, 2001; Schael, 2005). The taxa whose density was correlated with higher velocities, Froude number or Stream Power in the Molenaars River in June 2003 (e.g. *Baetis* spp., *D. capensis*, *Elporia* spp.) were also the most consistent discriminator species distinguishing between riffle / fast run and slower-flowing biotopes, as indicated by multivariate SIMPER analysis and Kruskal-Wallis analysis of variance (Tables 5.6 and Figure 5.8). *D. capensis* showed no density changes in response to velocity increases, or any other variables, in the Berg River in 2004, despite being a good discriminator between biotopes (multivariate SIMPER analysis and Kruskal-Wallis analysis: Tables 5.7 and Figure 5.9). This might reflect the fact that, at very low discharges, the average water column velocity may not adequately capture what aspect of the flow is 'felt' by an organism. Discharge in the Berg River in May 2004 reflected both the fact that the catchment is at its driest in late summer / autumn, prior to the onset of rains, and also that in 2004 in particular this dryness was exacerbated by the failure of rains the previous year which would have affected groundwater recharge and thus river baseflow.

The amount of organic matter associated with a stone location proved to be important for many taxa, especially chironomid and leptophlebiid taxa. On the other hand, slow biotopes and / or low velocities were also correlated with increased availability of organic matter.

These results agree with other studies on habitat relationships. For example Whole *et al.* (1995) found differences in distribution of organic matter and invertebrate taxonomic and functional groups between depositional, bedrock and cobble-riffle biotopes (Wohl *et al.,* 1995). Because species preferences overlap, and because each species range of tolerances for one or another hydraulic variable will differ, invertebrate assemblages should not be expected to be represented as distinct entities.

Probably one of the most pertinent relationships identified through analysis of the Baseline survey data was the significant linear correlation between invertebrate density and stone particle size (Figure 5.13, Table 5.15). The fairly high R^2 value for this relationship, for data from both the Berg and Molenaars Rivers indicates that some 25 - 31% of overall invertebrate density, respectively, can be explained by particle size, whilst individual taxa had individually stronger or weaker associations with particle size. More taxa were significantly correlated with stone particle size than any other variables. The importance of substratum size was hinted at by King & Schael (2001) in their evaluation of invertebrate communities within hydraulic biotopes, but could not be quantitatively demonstrated because their particle size range was restricted to small boulder and large cobble, and was defined categorically, not measured individually. Quinn & Hickey (1990) found that density and richness of collector-browsers were greatest on small cobble-boulder substrata, whilst filterers and facultative shredders had a strong preference for large cobbles and boulders. In this present study, over a particle size range, measured as the second longest stone axis, of between 80 and 550 mm, most taxa were found in higher densities on small particles. Important exceptions to this included the filter-feeding *Simulium* spp., and other taxa that are more strongly associated with the top surfaces of larger boulders in faster flow, for example *D. capensis* and *Elporia* spp.

Periphyton biomass was also strongly negatively related to stone particle size. Similar results were found between algal biomass and particle size in the study of Cattaneo *et al.* (1997). In that study, cobbles supported a greater biomass per unit area than boulders, whilst coarse and fine gravel supported increasingly lower densities of algae (Cattaneo *et al.,* 1997). In this present study, particle size ranges were somewhat higher than in the study of Cattaneo *et al.* (1997), with minimum particle sizes of around 80 mm excluding the gravel and sand categories, but with boulder sizes far in excess of those measured by Cattaneo *et al.* (1997). These authors attribute these results in part to the greater stability and better exposure of larger particles to flow and hence nutrient renewal, a relationship that was not found in the present study.

An independent relationship was demonstrated between periphyton and stone particle size: there was no co-correlation between the increased density of most invertebrate taxa on small stones and the increased availability of periphyton on small stones. The relationship between periphyton and invertebrate biomass was not clear, except for a correlation between the latter and the Chironomidae, elmid adults and *Lithogloea harrisoni*, and an increase in invertebrate species density periphyton on stones with greater periphyton biomass. However, the periphyton assemblage composition and particularly differences in life-form could account for greater invertebrate biomass, at least of grazers. In their study, Cattaneo *et al.* (1997) found strong differences in the proportion of loosely attached (removed by brushing or agitation) and firmly attached (not readily removable) life forms. They found that small substrata supported mainly the loosely attached algae, whilst the tightly attached forms increased in abundance with increasing particle size. The former life form was dominated by colonial cyanophytes, bacterial masses and motile diatoms, whilst the latter life form was dominated by adnate and filamentous algae.

According to Steinman (1996) collector-gatherers such as mayflies tend to feed on the outer layers or loosely attached portions of the periphyton mat, comprising stalked or short filamentous algae plus their epiphytes. Preference for particular life forms is less a result of an ability to discriminate different algal taxa, but rather a consequence of the restrictions on feeding placed by each species' mouthpart morphology (Steinman, 1996).

In relation to the study of flood effects, large stable particles have been suggested as potential refugia for invertebrates, from the effects of floods (Townsend *et al.,* 1997c; Francoer *et al.,* 1998). The findings of this study suggest that small particle size confers a relative advantage, perhaps associated with increased availability, better condition or type of food, or easier collection of food resources from within interstitial spaces, or perhaps associated with shelter from predation or hydraulic effects. The findings demonstrate clearly, though, that invertebrates are not selecting for large stable particles - at least not at the start of the flood season. What might occur during floods, however, is the subject of the following chapter.

6 INVERTEBRATE RESPONSES TO FLOODS

6.1 REPEAT-SAMPLED STONES: VALIDITY OF APPROACH AND RECOVERY FOLLOWING INITIAL SAMPLING

6.1.1 Sample size and representativeness

The approach to evaluating flood effects in the Molenaars River (section 3.3.1*i*, Figure 3.8) was based on repeat-sampling river stones on two occasions: the baseline conditions, where all stones were sampled and then, either immediately prior to or immediately after flood events in mid and late July 2003, where ¼ of the baseline stones were repeat-sampled on each occasion. The validity of this approach is firstly based on the assumption that the sample size of stones being compared was large enough to be representative of the invertebrate assemblage in the river. This was tested, using only the whole stone data for the baseline survey sample set, divided into four groups that corresponded with the four groups of stones repeat sampled before and after floods, with between 23 and 27 stones in each group.

Since only 70 of the invertebrate samples from Baseline stones were processed, a Mann-Whitney U non parametric T-test was conducted on two of the sub-groups of stones from this Baseline survey set. No significant differences were found between these groups, neither in the total invertebrate densities, nor in the densities of all but two of the 50 taxa taken individually. Those which were significantly different were Elmidae adults ($p = 0.009$) and *Choroterpes* sp ($p = 0.005$). The results suggest that a sample size of 23 or more is probably large enough to be considered representative of the overall invertebrate assemblage characteristics, with recognition of the caution required in interpreting comparison data for the two taxa which showed significant differences across subsets of the baseline samples. In the same vein, each pre- or post- flood sample set was also considered to be representative of the invertebrate population at the site, allowing statistical comparison between each pre- or post- flood sample set with the overall baseline dataset.

6.1.2 Recovery following initial denudation of repeat-sampled stones

A second requirement for comparing the Baseline survey data with post-flood surveys was a demonstration of adequate recovery of the invertebrate fauna after initial sampling, but prior to the first flood that was to be examined. This was evaluated by comparing Baseline data with the Pre-Flood 1 subset of samples.

Figure 6.1 shows the results of PRIMER cluster and MDS analysis of all Baseline and pre-Flood 1 samples collected on 9 June and 9 July respectively. The dendrogram groupings (Figure 6.1a) do not differentiate stones sampled on the two dates, but the major groupings (at 40 - 50% similarity) rather reflect the same sets of biotope clusters as were present during the baseline survey (refer to Figure 5.3). The scatter plot from MDS analysis (Figure 6.1b) confirms that this pattern of a gradual shift between biotopes, a feature of the baseline survey, was regained within a month after initial sampling. Indeed,

a two-way ANOSIM (using date of sampling and flow type as factors) indicated no significant difference between assemblages between sampling date, but significant differences between flow types (ANOSIM Global R = 0.43, p=0.001).

In Figure 6.1b, repeat-sampled stones are indicated by the stone number, with suffixes representing baseline (B) or pre-Flood 1 (F1pr). The distance between the points in the plot indicates the extent to which the assemblage on each stone returned to its initial condition between the Baseline and pre-Flood 1 sampling dates, i.e. a representation of its similarity.

The actual similarity coefficients between each pair of repeat-sampled stones were extracted from the similarity matrix. The average Bray Curtis similarity of the community on each stone on 9 June vs. 9 July (i.e. each re-sampled comparison) was 66.8% (n=22), which was higher than within biotope similarity levels (Figure 6.1b).

Mann-Whitney U was used to test for differences in mean total invertebrate / per taxon densities between the Baseline survey and the Pre-Flood 1 periods. In only five out of 50 taxa were there significant decreases in densities at the latter time ($p>0.05$), indicating a failure for full recovery to have occurred on repeat-sampled stones for these taxa (Figure 6.2). However, a number of other taxa show substantial decreases between these two surveys, but which were nevertheless not significant because of the high variance associated with patchily distributed populations. Examples include *Cheumatopsyche afra, Chimarra* spp and *Elporia* spp. Total invertebrate density was also lower after the initial sampling, albeit not significantly so. Other taxa recovered fully, or, in some instances (e.g. Simuliidae, *Afronurus* sp.) even increased in density, although these were again not significant.

Thus the community signature of samples taken during the Baseline survey was re-established a month later, on the same set of stones, as indicated by the restoration of biotopes assemblages in the Molenaars River over the time interval between the two sampling dates (PRIMER analysis). However, some species did not recover to full Baseline densities on the repeat-sampled stones. Recovery may have been affected by the population structure and life-history characteristics of individual species which determines the availability of colonists, and this is examined in more detail in section 6.4 on species-specific responses to floods. These results suggest that, in terms of using repeat-sampled stones to measure possible flood effects on invertebrates, cognisance should be taken of the species differences in recovery following the Baseline denudation of stones (i.e. the sampling effect). In the light of these results, the Pre-Flood 1 data set was considered an alternative or additional baseline condition against which to compare the effects of the subsequent floods.

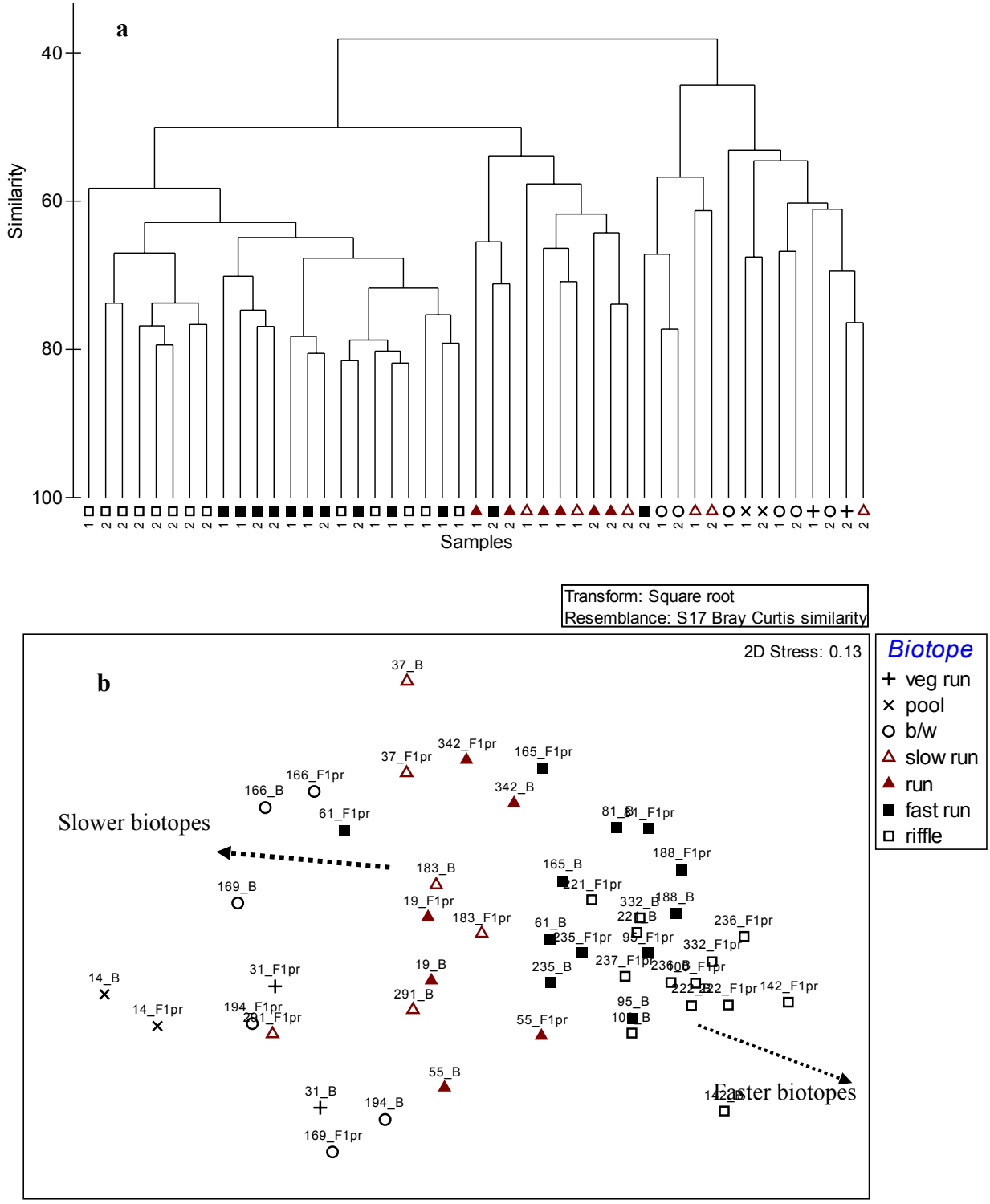


Figure 6.1 Molenaars River Baseline and pre-Flood 1 invertebrate assemblages from June and July 2003, 4th root transformed, a) hierarchical cluster dendrogram, based on Bray Curtis similarities; b), a 2-d MDS plot with the biotope at each sample location indicated by symbols.

Codes: 1 = Baseline and 2 = Pre-Flood 1 sampling in (a); biotope symbols as indicated in the key; individual sample numbers in MDS plot are suffixed with a B (baseline survey) or F1pr (pre-Flood 1 sampling).

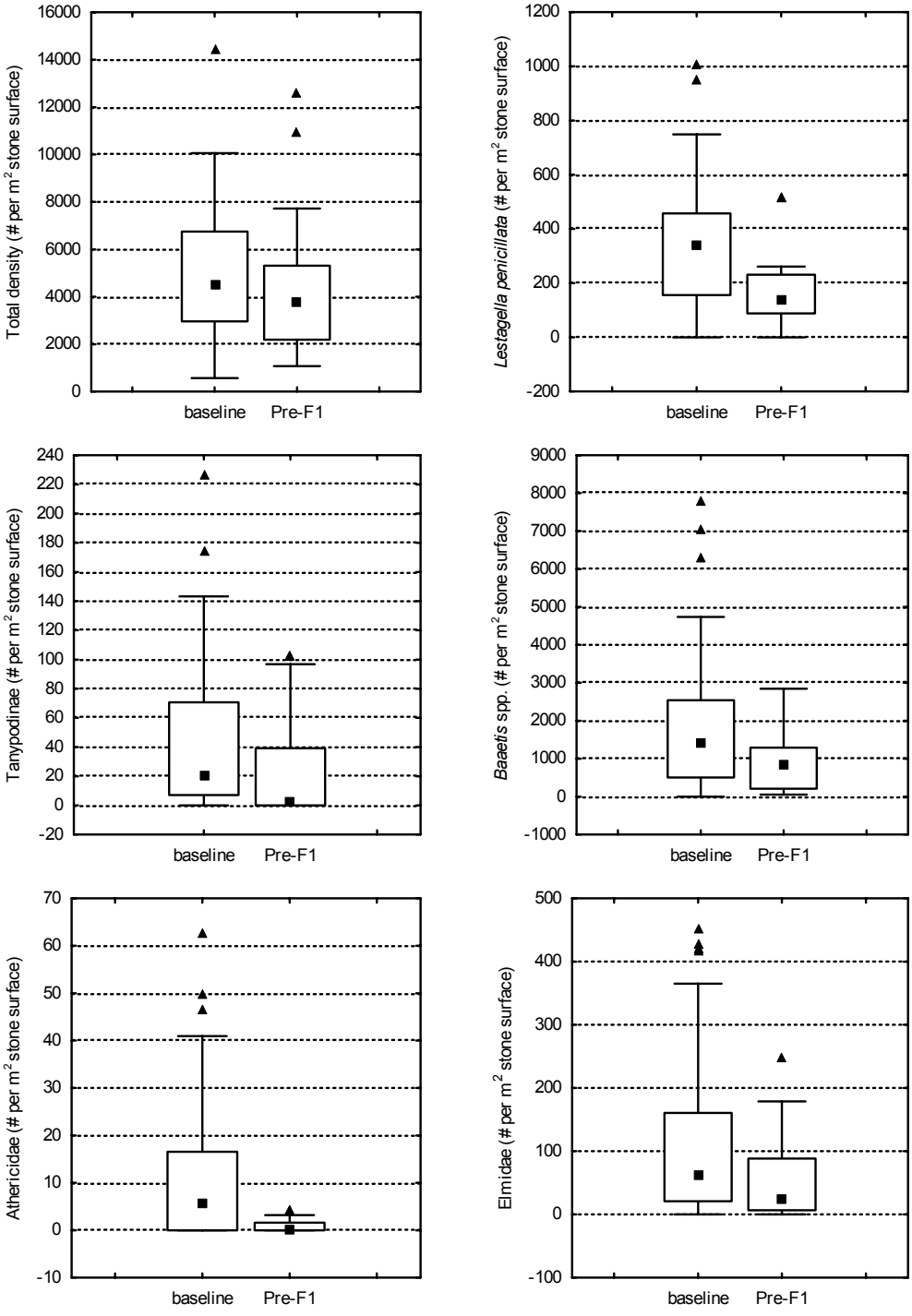


Figure 6.2 Box plots showing untransformed total invertebrate densities, and densities of selected taxa demonstrating a significant (Mann-Whitney U Test on 4th-root transformed data) decrease in density per m^2 stone surface area on repeat-sampled stones, from the Baseline to the Pre-Flood 1 sampling surveys.

Key: ■ = Median; ▯ = 25% -75%; ⊤ = Non-outlier range; ▲ = Outlier.

6.2 SUBSTRATUM MOVEMENT DURING FLOODS

The extent of particle movement, during floods in the Molenaars River in 2003 and the Berg River in 2004, is given in Table 6.1 and Figure 6.3 and in Table 6.2 and Figure 6.4 respectively.

The first and fourth floods in the Molenaars River in 2003, that is, those for which invertebrate response data were collected, were associated with no stone movement and with 2.9% overall stone movement respectively, roughly equally divided between small and large cobble (Table 6.1). The second and third floods were also associated with negligible bed movement (2 and 0.6% respectively). All four early winter floods were DRIFT Class I floods, with larger floods occurring only late in the winter season as shown in Figure 3.9, which depicts the daily and instantaneous flow record over the study period. These later floods were Flood 5, DRIFT Class II in early August, with 7.6% bed movement; and Flood 6, DRIFT Class III in late August, with 33.4% bed movement, including 40% of large cobble and nearly 15% of small boulders (Table 6.1).

In the Berg River in 2004 a large flood occurred at the start of the winter season in early June (Flood 2, a large flood within DRIFT Class IV, with 43.3% bed movement). This was followed by a period of small spates with negligible bed movement, and then five DRIFT Class III and IV floods in July and August. The first of these (Flood 5, just above the threshold defining a DRIFT Class IV, with 25.7% bed movement) was the final flood monitored during the study period, after which no further stone movement data were collected. Figure 3.10 depicts the daily and instantaneous flow record over the study period.

Class IV floods in the Berg River in 2004 also moved between 25 and 50% of large cobble and around 15% of small boulders, similar to the case of the Molenaars River in 2003. The same category event also occurred in the Molenaars River, with similar bed movement, although invertebrate data were not collected from that river in 2004.

Table 6.1 Stone Movements in the Molenaars River during 2003 flood events. Stone movement was defined as such even if a stone only turned over. G = gravel, SC = small cobble, LC = large cobble, SB = small boulder; LB = large boulder, as defined in Table 3.1.

Stone Size Classification		Total	G	SC	LC	SB	LB
Max size in class (mm)			64	161	256	514	1000
Total Number of Stones		344	4 (1%)	91 (26.5%)	73 (21%)	111 (32.5%)	65 (19%)
Flood 1	Moved Stones	0	0	0	0	0	0
	Movement %	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Flood 2	Moved Stones	7	0	7	0	0	0
	Movement %	2.0%	0.0%	7.7%	0.0%	0.0%	0.0%
Flood 3	Moved Stones	2	0	1	1	0	0
	Movement %	0.6%	0.0%	1.1%	1.4%	0.0%	0.0%
Flood 4	Moved Stones	10	0	6	4	0	0
	Movement %	2.9%	0.0%	6.6%	5.5%	0.0%	0.0%
Flood 5	Moved Stones	26	1	18	4	3	0
	Movement %	7.6%	25.0%	19.8%	5.5%	2.7%	0.0%
Flood 6	Moved Stones	115	4	65	29	16	1
	Movement %	33.4%	100.0%	71.4%	39.7%	14.4%	1.5%

Table 6.2 Stone movement in the Berg River during 2004 flood events. Stone movement was defined as such even if a stone only turned over. G = gravel, SC = small cobble, LC = large cobble, SB = small boulder; LB = large boulder, as defined in Table 3.1.

Stone Size Classification		Total	G	SC	LC	SB	LB
Max size in class (mm)			64	161	256	514	1000
Total Number of Stones (%)		432	27 (6%)	120 (28%)	92 (21%)	139 (32%)	54 (13%)
Flood 1	Moved Stones	1	1	0	0	0	0
	Movement %	0.2%	3.7%	0.0%	0.0%	0.0%	0.0%
Flood 2	Moved Stones	187	26	92	44	24	1
	Movement %	43.3%	96.3%	76.7%	47.8%	17.3%	1.9%
Flood 3	Moved Stones	10	2	3	3	2	0
	Movement %	2.3%	7.4%	2.5%	3.3%	1.4%	0.0%
Flood 4	Moved Stones	7	1	4	2	0	0
	Movement %	1.6%	3.7%	3.3%	2.2%	0.0%	0.0%
Flood 5	Moved Stones	111	10	58	28	14	1
	Movement %	25.7%	37.0%	48.3%	30.4%	10.1%	1.9%

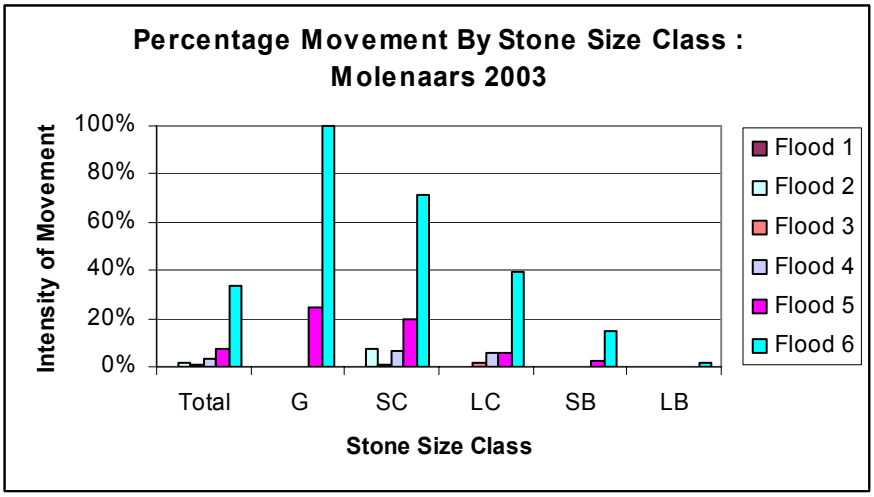


Figure 6.3 Particle size distribution and stone movement in the Molenaars River during 2003 floods, by substratum size class.

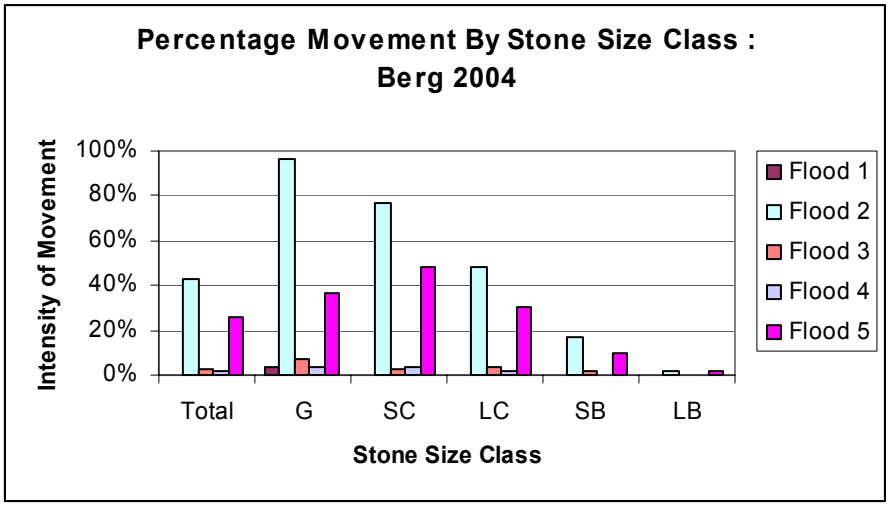


Figure 6.4 Particle size distribution and stone movement in the Berg River during 2004 floods, by substratum size class.

6.3 EFFECTS OF FLOODS ON MACRO-INVERTEBRATE ASSEMBLAGES

6.3.1 Community patterns in the Molenaars River

For Flood 1, the average Bray Curtis similarity for repeat-sampled stones from 9 June - 9 July was 66.8% (n=22), as indicated in section 6.1 as reflecting the extent of recovery of stones prior to the floods. The average Bray Curtis coefficient of similarity from 9 June - 13 July, i.e. from Baseline to post Flood 1, was 64.6% (n=27). This indicates that the change in community structure, from the Baseline to either before or after Flood 1, was not substantially different. A Mann-Whitney U test comparing the Bray Curtis similarities of repeat-sampled stones for the two periods (Baseline – Pre-flood and Baseline - Post-flood) returned a p value of >0.68, suggesting that the flood had no significant effect on invertebrate assemblage similarities.

Cluster and MDS analysis of flood assemblages for all five sampling periods - Baseline and pre- and post- Flood 1 and Flood 4 - showed a substantial overlap in sampling periods, with no discreet groupings evident (Figure 6.5a and b). Most samples fell into a similarity range of between 50 and 85% (Figure 6.5a). However, the MDS plot of all samples (Figure 6.5b) shows a gradient of change, with the Baseline samples on the opposite end of this gradient from most of the Post-Flood 4 samples.

An ANOSIM routine was used to test for differences by period. The Global R = 0.12, (p = 0.001), indicated that a significant difference was observable by period. Pairwise tests showed that the only significant difference in assemblage similarities was between the Baseline condition and the Post-Flood 4 survey (R=0.246, p = 0.001).

SIMPER analysis indicated an average dissimilarity of 53% between samples from Periods 1 and 5, representing Baseline and Post Flood 4 surveys respectively, as indicated in Figure 6.5. No taxa were very consistent discriminators of the two assemblages, as indicted by low (<1.5) ratios of the average dissimilarity / standard deviation (Diss/SD) in the species comparisons between the two groups. The top five discriminator taxa are indicated in Table 6.3.

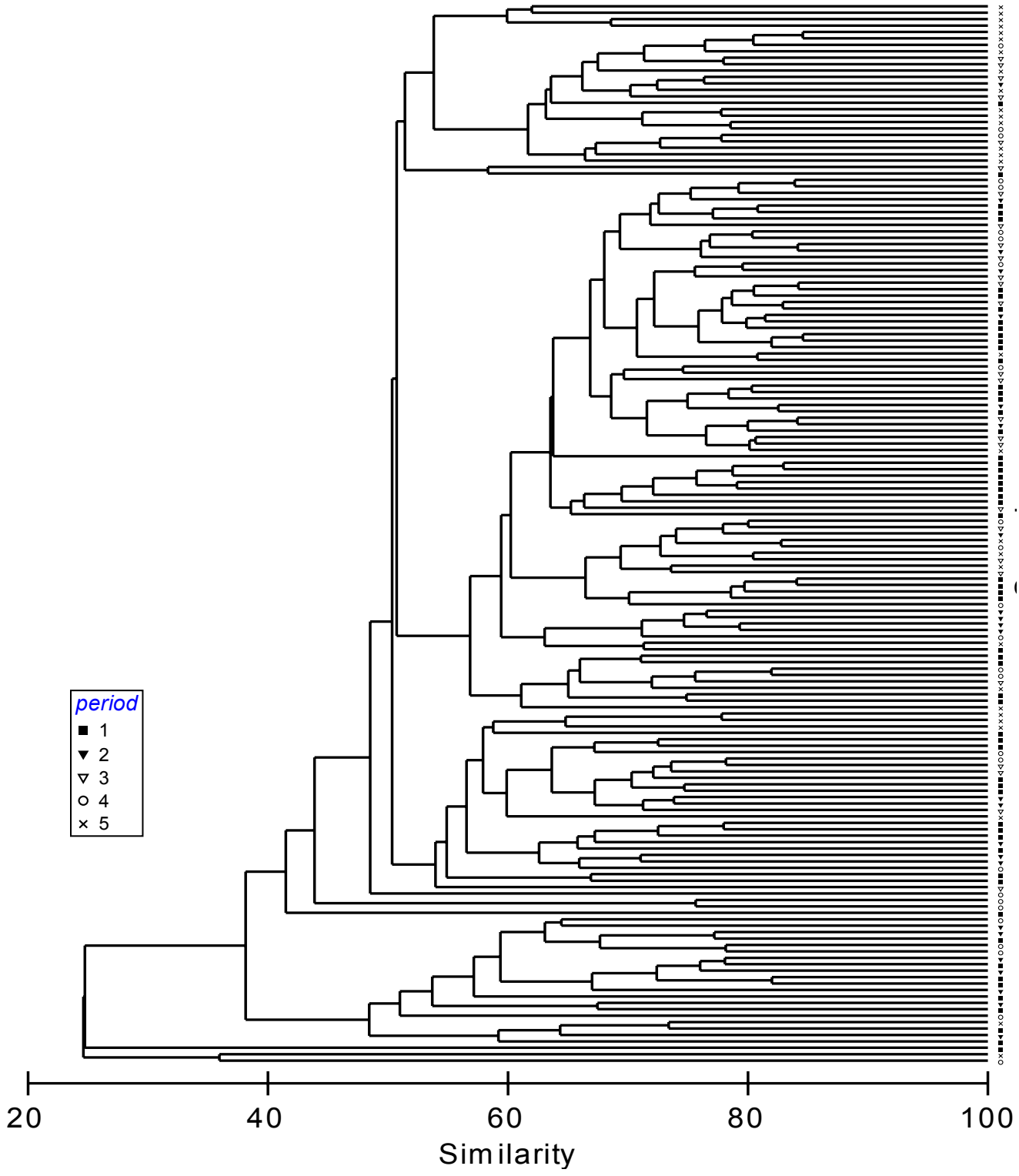


Figure 6.5a Molenaars River hierarchical cluster dendrogram of invertebrate assemblage changes over the five sampling intervals, based on Bray Curtis similarity coefficients. Samples are reflected on the y-axis by symbols, numbered by date of sampling as follows: 1 = Baseline survey, 2 = Pre-Flood 1 survey, 3 = Post-Flood 1 survey, 4 = Pre-Flood 4 survey, 5 = Post-Flood 4 survey.

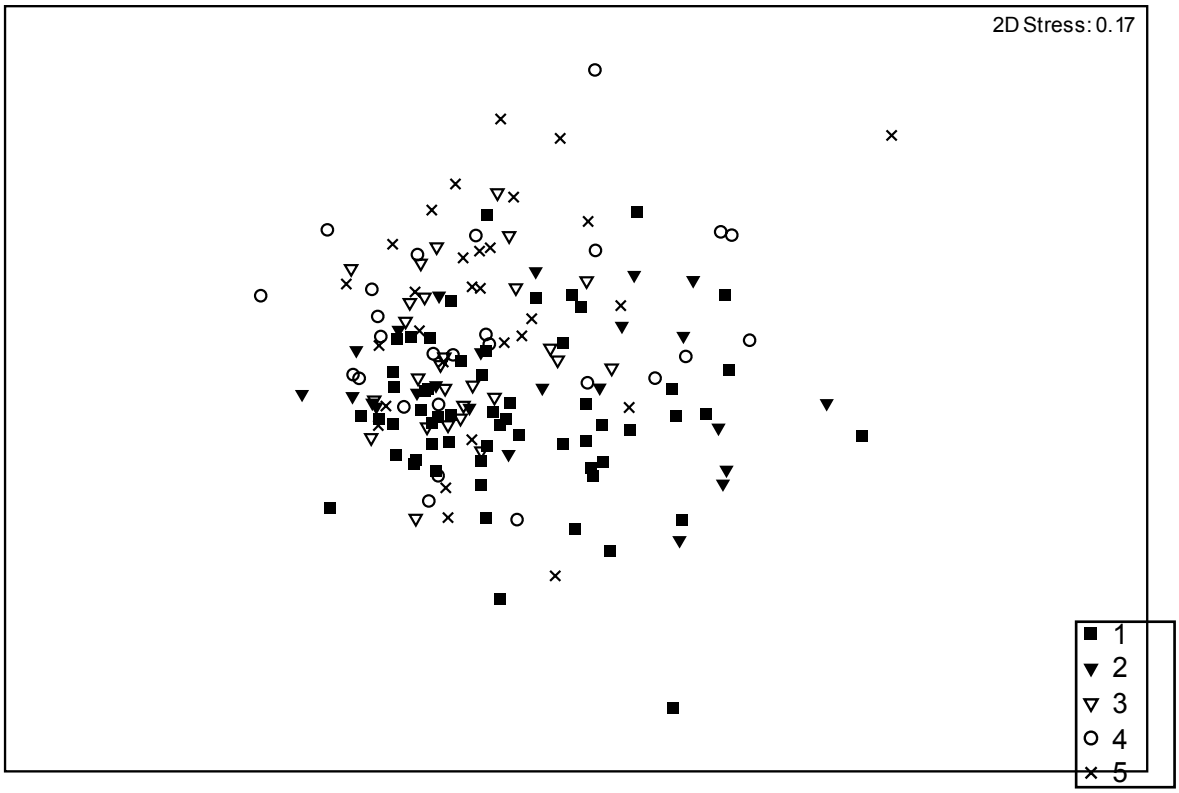


Figure 6.5b Molenaars River MDS plot of invertebrate assemblage changes over the five sampling intervals, based on Bray Curtis similarity coefficients.

Samples are reflected on by symbols, numbered by date of sampling as follows:
1 = Baseline survey, 2 = Pre-Flood 1 survey, 3 = Post-Flood 1 survey,
4 = Pre-Flood 4 survey, 5 = Post-Flood 4 survey.

Almost all the Pairwise comparisons in the SIMPER analysis indicated reductions in density between the Baseline survey and the final, Post-Flood 4 survey (Table 6.3). However, four taxa were either unchanged (*Demoreptus capensis*, Orthocladiinae) or increased significantly (*Simulium* spp., *Lithogloea harrisoni*) in density over this period. These and other species-specific responses to floods are examined in detail in Section 6.3.2.

Overlaying a bubble plot of total invertebrate density onto the MDS plot from sample similarities (Figure 6.6) shows a general, although inconsistent, decline in density over time since the Baseline survey, but without marked shifts in density before and after individual flood events.

Table 6.3 Discriminator taxa in a SIMPER analysis comparing the dissimilarities between invertebrate assemblages from the Baseline and Post-Flood 4 surveys in the Molenaars River in 2003. Taxa that cumulatively made up 75% of the dissimilarity between groups are listed, in order of their individual contribution (%) to dissimilarity. Those with the highest Diss / SD ratio were the more consistent discriminator taxa.

Discriminator taxa	Average abundance (sq. root)		Average dissimilarity	Diss/SD	Contrib %	Cumul. %
	Baseline survey	Post Flood 4 survey				
Baetis spp.	37.51	25.23	6.69	1.33	12.64	12.64
Afroptilum sp.	17.99	10.19	4.62	0.85	8.73	21.37
Elporia spp.	15.74	8.83	4.36	1.16	8.24	29.61
Orthocladiinae	20.40	20.07	4.06	1.20	7.66	37.27
Demoreptus capensis	11.59	11.81	3.26	1.31	6.17	43.44
Lestagella penicillata	18.64	12.58	3.09	1.00	5.84	49.28
Elmidae	9.30	6.76	2.27	1.15	4.29	53.57
Euthraulus elegans	9.87	7.32	2.27	1.30	4.28	57.85
Simulium spp.	4.86	6.75	2.13	1.06	4.02	61.87
Afronurus sp.	6.53	1.47	1.82	1.36	3.45	65.32
Tanypodinae	5.80	1.70	1.65	1.15	3.13	68.44
Tanytarsini	5.56	3.86	1.38	1.31	2.61	71.05
Pseudocloeon spp.	3.84	0.97	1.13	1.04	2.13	73.18
Lithogloea harrisoni	0.31	4.01	1.10	0.75	2.08	75.26

Kruskal-Wallis analysis of variance of total invertebrate density changes over the five sampling periods showed that the Baseline survey densities were not significantly different from the Pre-Flood 1 survey, but were significantly higher than all the following surveys (Figure 6.7a, Kruskal-Wallis analysis of variance, H= 28.40, p = 0.000, Dunn's Pairwise test significant for Baseline and F1-Pre surveys vs F4-Po, $P<0.05$). It should be noted here that the Pre-Flood 4 survey also reflects conditions in the river after the first three floods. Total density declined by 44% from the Baseline survey to the end of the study, post Flood 4. A comparison using the Pre-Flood 1 data with the post Flood 4 sample set, to account for potential sampling effects, indicated a 34% decline in total invertebrate density, over the two month period associated with four DRIFT Class 1 floods (Figure 6.7a).The amount or organic matter associated with each stone recovered fully after initial sampling, but showed a non-significant decrease from before to after each flood.

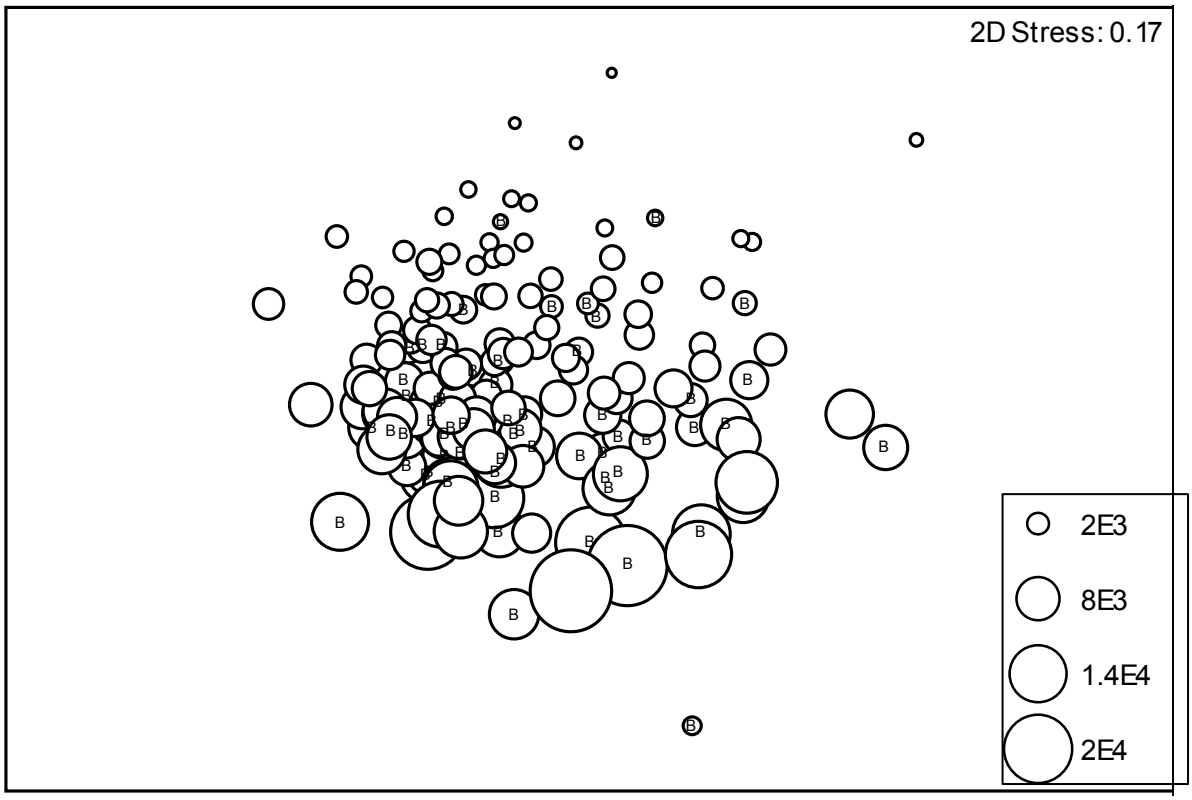


Figure 6.6 Molenaars River bubble plot of total invertebrate density per unit stone area, overlaid onto the MDS plot of invertebrate assemblages as in Figure 6.5b. Baseline samples are indicated with a B.

Invertebrate densities on immovable stones whose tops only were sampled were approximately as high as densities on whole stones, although the species complement was different and comprised largely of Baetidae and *Elporia* spp.. This total density declined by 70% over the study period (Figure 6.7b), although the pre- and post-Flood 4 surveys were represented by only four samples each.

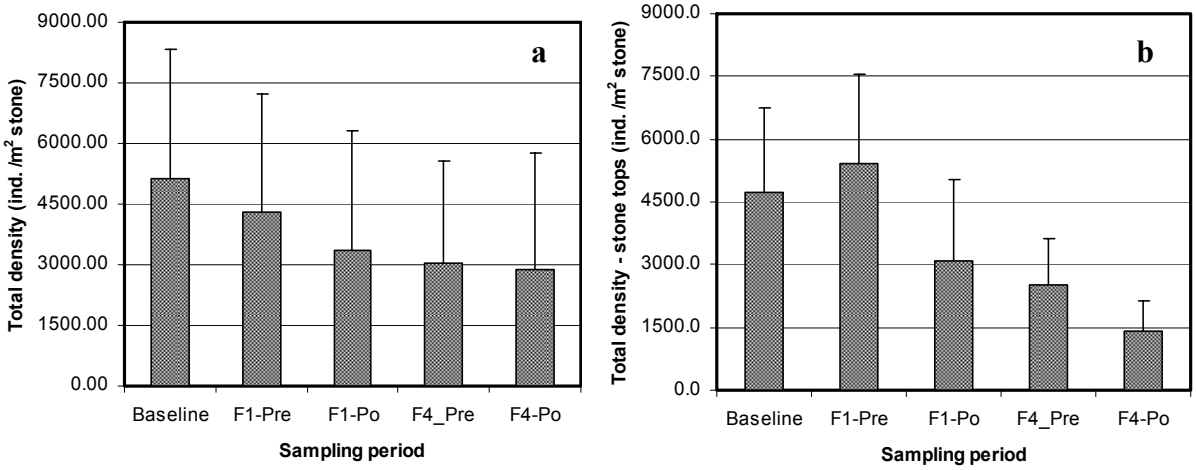


Figure 6.7 Mean total invertebrate densities in the Molenaars River in 2003 a) on whole stones and b) on the tops of immovable boulders, by sampling period. F1, F4 = Floods 1 and 4 monitored over the season; Pre, Po = pre- or post-flood sampling survey.

6.3.2 Community patterns in the Berg River

In contrast to the Molenaars River, invertebrate assemblages in the Berg River in 2004 were substantially different before and after the series of five floods that separated the Baseline and Post-flood surveys. As indicated in Figure 3.10 and Table 3.5, these floods comprised two DRIFT Class 1 floods, one Class II and two Class IV intra-annual floods, the largest being on the 14th June and the second largest on the 23rd July, some four days before the Post-flood survey.

The results of multivariate analysis of Baseline and post-flood samples are indicated in Figure 6.8. The 2-dimensional stress level associated with the MDS plot was 0.15, which makes the plot an adequate representation of the relationship between samples. The samples are spread fairly widely, but with a reasonably distinct separation between Baseline samples collected in May and the Post-flood samples collected in July. The Baseline samples nevertheless were only 56% similar, whilst the Post-flood samples were more dispersed, with a 53% similarity. However, the stones which were repeat-sampled were very similar in composition to the additional set of stones sampled during the Post-flood survey, as is shown by the large overlap in their distribution within Figure 6.8. This additional data set was collected to act as a control for the potential 'sampling effect' associated with repeat-sampling the Baseline set of stones (see section 3.3.1*ii*), and the MDS results suggest that the sampling effect was not significant.

To test this further, a 1-way ANOSIM was performed, based on the three sets of data - Baseline, Post-floods Repeat-sampled stones, and Post-floods Additional stones. The Global R-statistic = 0.234 ($p = 0.001$) indicating differences within the three groupings. Pairwise differences were assessed using a higher threshold for significance (a cut-off of $p< 0.01$), to avoid a Type 1 error. The results indicated that both post-flood data sets were significantly different from the Baseline data (Baseline - Repeat sampled stones: $R = 0.34$, $p = 0.001$; Baseline - Additional stones: $R = 0.37$, $p = 0.001$), but not from each other ($R = 0.02$, $p = 0.045$). This result reinforces the conclusion that sampling effects on the repeat-sample stones were not significant in comparison to the other effects - either the effects of floods or simply the shifts in seasonal signal over the two-month study.

SIMPER analysis was undertaken to identify the taxonomic differences between the Baseline survey data and Post-flood data. For the latter, both Repeat-sampled stones and Additional stones were combined, since the ANOSIM indicated they were not significantly different. There was a fairly low average dissimilarity of 54% between the two periods, which was similar to the magnitude of change measured in the Molenaars River over the two-month period for that study, even though the flood magnitudes were different. This is a reflection of the fact that changes in species composition were not to any large extent based on loss or gain of species, but more on shifts in the densities of invertebrate taxa over the study period.

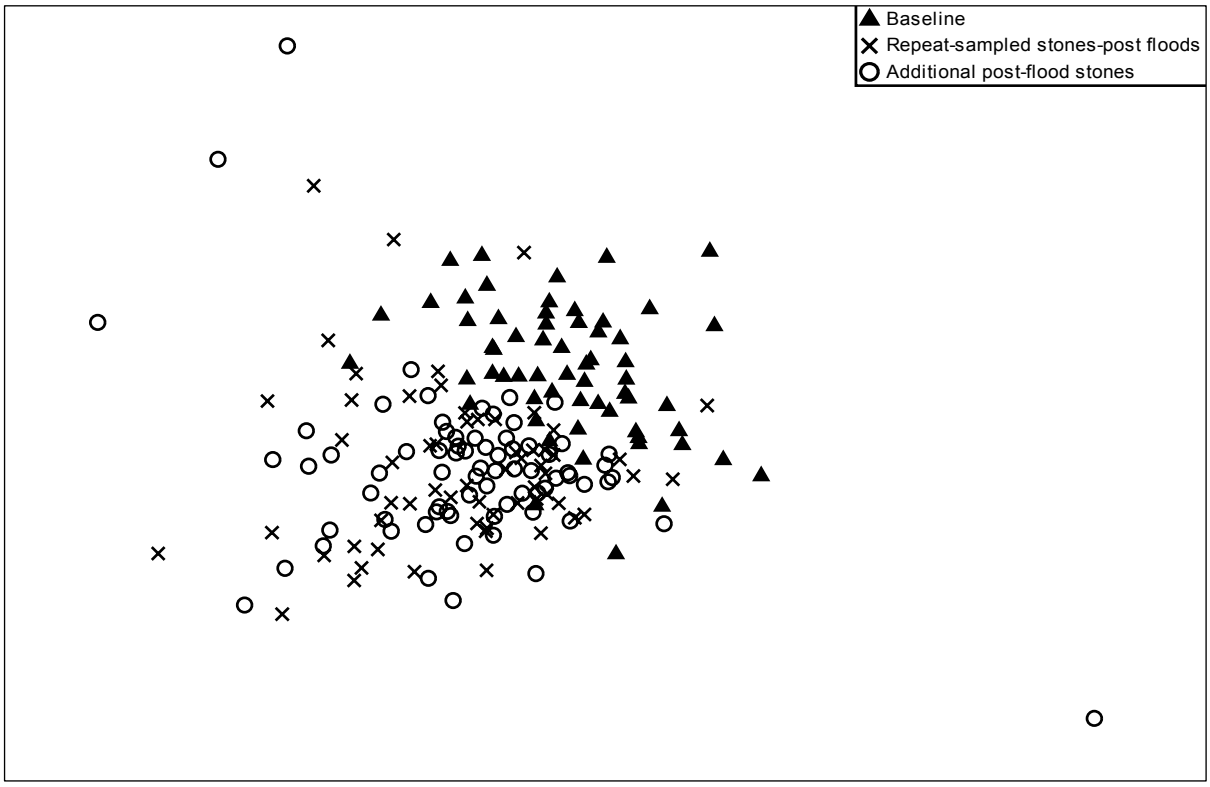


Figure 6.8 Berg River MDS plot of invertebrate assemblage changes over the pre- to post-flood period, based on Bray Curtis similarity coefficients. Both repeat-sampled and additional stones (control) samples for the post-flood period were included in the analysis.

As with the Molenaars River study, no taxa were consistent discriminators of the two assemblages, indicted by generally low (<1.5) ratios of average dissimilarity / standard deviation (Diss/SD) in Table 6.4. However, all taxa with the exception of *Lithogloea harrisoni* declined from the Baseline to the Post-flood sampling period.

A bubble plot of total invertebrate density superimposed onto the MDS plot from sample similarities showed a marked decline in total invertebrate density from the May Baseline samples to the Post-flood data set.

The amount of Chlorophyll *a* per unit stone area, as well as the amount of organic matter associated with stones (per m^2 river bed) declined significantly in the Berg River from the pre- to post-flood sample (Mann-Whitney U test, all $p < 0.001$). However, periphyton AFDW was not significantly different in the Post-flood period. Mean invertebrate density on whole stone surfaces declined from 2628 m^{-2} in the May Baseline sampling to some 1113 m^{-2} on Additional stones and to 1150 m^{-2} on Repeat-sampled stones (Figure 6.10a, Table 6.5), a decrease of 56 and 58% respectively.

This decrease was also substantially greater than the 34% decrease recorded in the Molenaars River over a similar period, but with smaller floods. Table 6.5 presents the percentage reduction by taxon from the Baseline to the Post-flood period, but separately for Repeat-sampled and Additional stones. Only taxa whose Baseline and / or Post-flood densities were greater than 1 indiv. m^{-2} are represented.

Table 6.4 Discriminator taxa in a SIMPER analysis comparing the dissimilarities between invertebrate assemblages from the Baseline and Post-Flood surveys in the Berg River in 2004. Repeat-sampled and Additional stones were pooled for the Post-flood data. Taxa that cumulatively made up 75% of the dissimilarity between groups are listed, in order of their individual contribution (%) to dissimilarity. Those with the highest Diss / SD ratio were the more consistent discriminator taxa.

Discriminator taxa	Average abundance (sq. root)		Average dissimilarity	Diss/SD	Contrib %	Cumul. %
	Baseline survey	Post Flood survey				
Orthocladiinae	23.97	17.74	6.61	1.09	12.30	12.30
Baetis spp.	22.75	18.71	4.79	1.26	8.91	21.21
Elmidae larvae	12.82	4.80	4.04	1.56	7.52	28.73
Lestagella penicillata	14.47	6.64	3.91	1.32	7.27	36.00
Tanypodinae	7.64	1.16	3.14	1.47	5.84	41.84
Afronurus sp.	5.58	1.33	2.17	1.45	4.03	45.88
Simulium spp.	4.26	3.17	2.05	1.02	3.82	49.70
Tanytarsini	5.92	2.45	2.03	1.35	3.78	53.48
Lithogloea harrisoni	2.66	4.16	1.73	1.13	3.22	56.70
Elmidae adults	3.72	1.22	1.63	0.99	3.03	59.73
Afronurus harrisoni	3.76	1.39	1.60	1.16	2.98	62.71
Athripsodes bergensis	3.61	0.93	1.51	1.12	2.81	65.52
Chironomini	3.77	2.54	1.50	1.18	2.80	68.32
Demoulinia spp.	3.32	0.27	1.49	0.85	2.77	71.09
Castanophlebia spp.	3.15	0.93	1.44	0.98	2.67	73.77
Helodidae	3.20	1.50	1.42	1.04	2.64	76.41

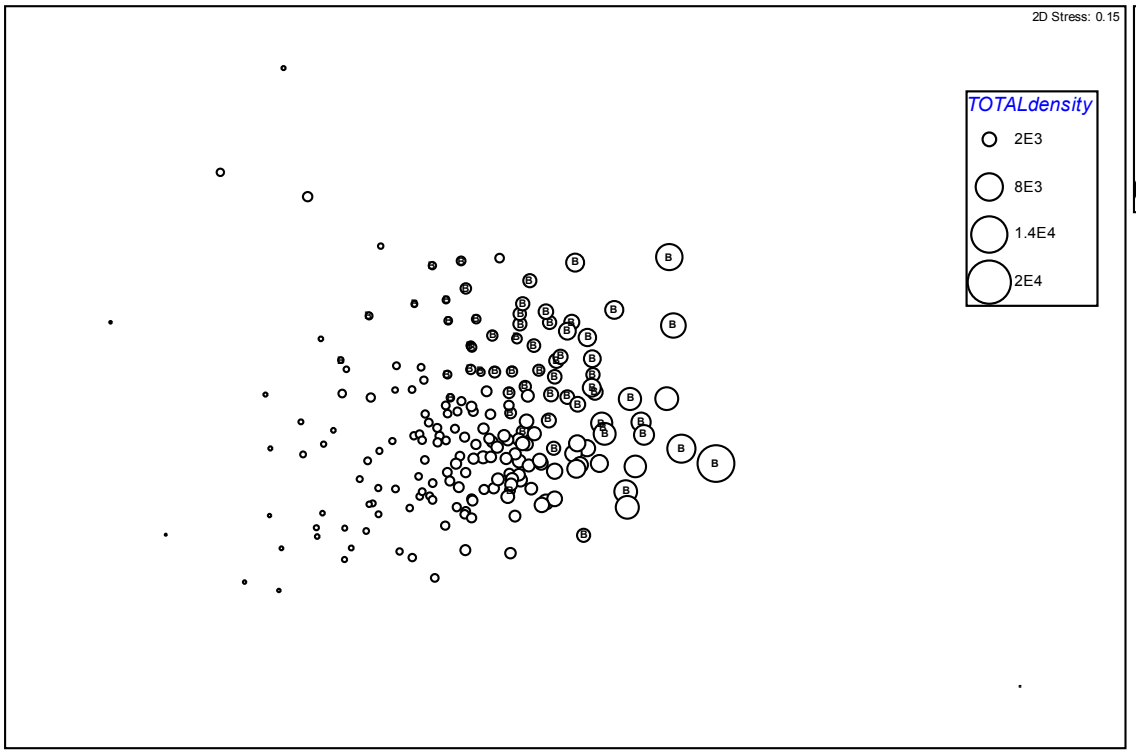


Figure 6.9 Molenaars River bubble plot of total invertebrate density per unit stone area, overlaid onto the MDS plot of invertebrate assemblages as in Figure 6.8. Baseline samples are indicated with a B.

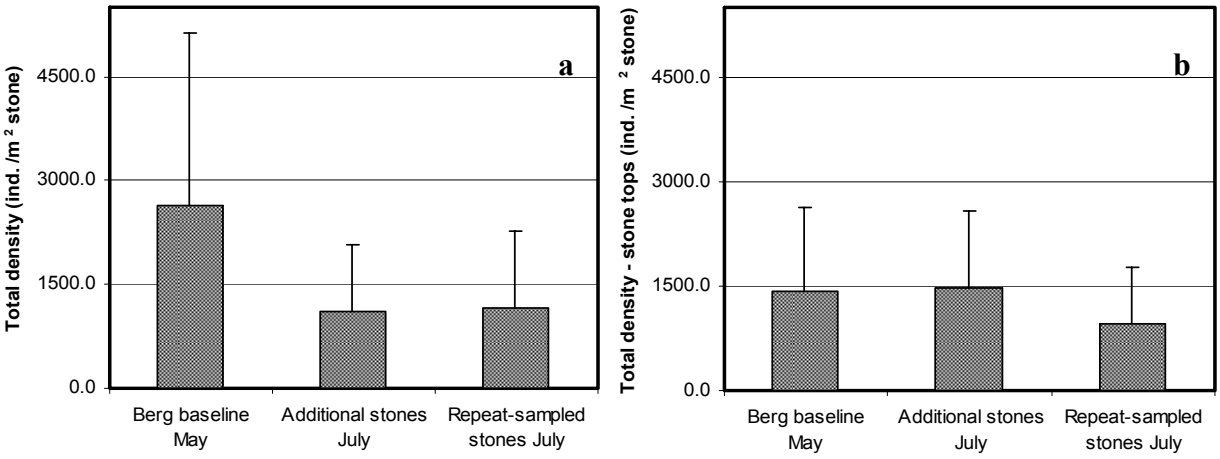


Figure 6.10 Mean total invertebrate densities (standard deviation) in the Berg River in 2004 a) on whole stones and b) on the tops of stones where immovable stones were sampled. Data for the post-flood sampling period are given separately for the Repeat-sampled stones and the Additional (control) stones.

Significant differences (Mann-Whitney U test, adjusted for tied ranks) between Baseline - Additional stones are indicates in bold text. All but four invertebrate taxa declined significantly. Furthermore, for most taxa, the response on Repeat-sampled stones was similar to that on Additional stones, suggesting that the 'sampling effect' on the former was

minor. All but four invertebrate taxa declined significantly. Furthermore, for most taxa, the response on Repeat-sampled stones was similar to that on Additional stones, suggesting that the 'sampling effect' on the former was minor. Large differences in response were particularly noticeable on *Pseudocloeon* spp. *Lithogloea harrisoni* and *Nadinitella crassi*, three taxa that increased in densities over the study period (Table 6.5).

In contrast, densities on the tops of immovable boulders (Figure 6.10b) showed no change in invertebrate densities between the Baseline sampling and post flood Additional stones, but a non-significant 30% decline in the case of Repeat-sampled stones, considerably less than observed in the case of the Molenaars River data, where invertebrate densities on stone tops declined by some 70%.

Although overall invertebrate densities on the top surfaces of immovable boulders were not dramatically altered, actual assemblage changes on stone tops from the Baseline to post-flood periods were more pronounced than those on whole stones (Figure 6.11), with a greater degree of separation of samples according to period of sampling. As with the whole stone PRIMER community analysis, ANOSIM analysis highlighted the differences between Baseline and Post-flood sample sets (Global R = 0.147, p = 0.001, pairwise comparisons indicated in Table 6.6). Repeat-sampled stones were not significantly different from Additional stones (Table 6.6), despite the different mean invertebrate densities on these two groups of post-flood stones indicated in Figure 6.10.

Because of the difference in total invertebrate density between the two groups of stone tops data for the Post-flood survey, SIMPER analysis of the taxa contributing most strongly to the difference between assemblages was conducted separately for the Baseline - Repeat-sampled stones and the Baseline - Additional stones. The results show that, whilst many taxa declined in density over the flood period, as in the case of the whole stone analysis, a greater number of taxa showed an actual increase in density over the study period on this category of stones than on the whole stones analysis (Table 6.7) - over one third of the discriminator taxa in the case of the Repeat-sampled stones, and more than half the taxa on the Additional stones, increased in density. The six most important discriminator taxa were the same in both comparisons (Table 6.7).

Table 6.5 Percentage decrease from the Baseline to the post-flood period, as represented by the Repeat-sampled stones and Additional stones data sets
All taxa are in densities per m^2 stone surface area. Negative values indicate increases in density. Significant differences (Mann-Whitney U test) between Baseline - Additional stones are indicated by p- values in **bold text**.

Taxon / variable	% reduction on repeat sampled stones, relative to baseline	% reduction on additional stones, relative to baseline (Mann-U p value)	
Chlorophyll-*a* (mg/m^2 stone)	64.8	38.7	**(0.002)**
Periphyton AFDW(mg/m^2 stone)	31.5	19.9	(0.746)
Associated organic matter (g/m^2 bed)	70.8	81.4	**(0.000)**
Associated inorganic matter (g/m^2 bed)	82.1	62.5	**(0.001)**
Total invertebrate density	56.3	57.6	**(0.000)**
Species density (# taxa /m^2 stone)	39.8	30.2	**(0.014)**
Demoulinia spp.	93.4	97.8	**(0.000)**
Afroptilum spp.	59.2	75.7	**(0.023)**
Demoreptus capensis	65.9	59.6	(0.232)
Pseudocloeon sp.	-19.0	-437.0	**(0.001)**
Baetis spp.	26.1	26.6	**(0.017)**
Lestagella penicillata	78.3	75.4	**(0.000)**
Lithogloea harrisoni	-49.3	-119.9	**(0.000)**
Nadinitella crassi	-120.7	100.0	**(0.000)**
Aprionyx spp.	88.5	93.6	**(0.000)**
Adenophlebia spp.	87.9	100.0	**(0.000)**
Euthraulus elegans	77.0	90.5	**(0.000)**
Castanophlebia spp.	86.7	75.4	**(0.000)**
Afronurus harrisoni	65.5	81.4	**(0.000)**
Afronurus sp.	92.5	84.9	**(0.000)**
Cheumatopsyche afra	89.6	100.0	**(0.001)**
Cheumatopsyche maculata	77.0	86.3	**(0.002)**
Orthotrichia barnardi	65.4	35.5	(0.399)
Athripsodes bergensis	79.6	88.5	**(0.000)**
Chimarra sp.	95.1	94.0	**(0.000)**
Notonemouridae	4.8	22.4	(0.252)
Simulium spp.	21.5	61.2	(0.157)
Orthocladiinae	53.0	54.9	(0.079)
Tanypodinae	91.4	93.6	**(0.000)**
Chironomini	36.9	58.9	**(0.018)**
Tanytarsini	71.2	77.5	**(0.000)**
Athericidae	92.0	97.6	**(0.000)**
Elmidae larvae	86.8	80.8	**(0.000)**
Elmidae adults	71.4	85.3	**(0.000)**
Helodidae	69.9	67.7	**(0.005)**
Hydraenidae	100.0	100.0	**(0.026)**
Hydraenidae adults	85.7	100.0	**(0.000)**
Hydrachnellae	53.9	60.6	**(0.005)**
Aeshnidae	100	100	**(0.003)**

Table 6.6 ANOSIM Pairwise tests for differences in invertebrate assemblages on the top surfaces of immovable boulders over the pre- to post-flood period. n.s. – not significant

Pairwise comparison	R-statistic	Significance level
Baseline vs. Repeat-sampled stones	0.214	p = 0.001
Baseline vs. Additional stones	0.176	P = 0.001
Additional vs. Repeat-sampled stones	0.033	P = 0.163 (n.s.)

Table 6.7a Discriminator taxa in a SIMPER analysis comparing the dissimilarities between invertebrate assemblages on the tops of immovable boulders, from the Baseline and Post-Flood surveys in the Berg River in 2004: REPEAT SAMPLED STONES. Taxa that cumulatively made up 75% of the dissimilarity between groups are listed, in order of their individual contribution (%) to dissimilarity. Those with the highest Diss / SD ratio were the more consistent discriminator taxa. Results are provided separately for the Baseline - Repeat-sampled stones and the Baseline - Additional stones comparisons. Taxa showing an increase in density over the study period are shaded.

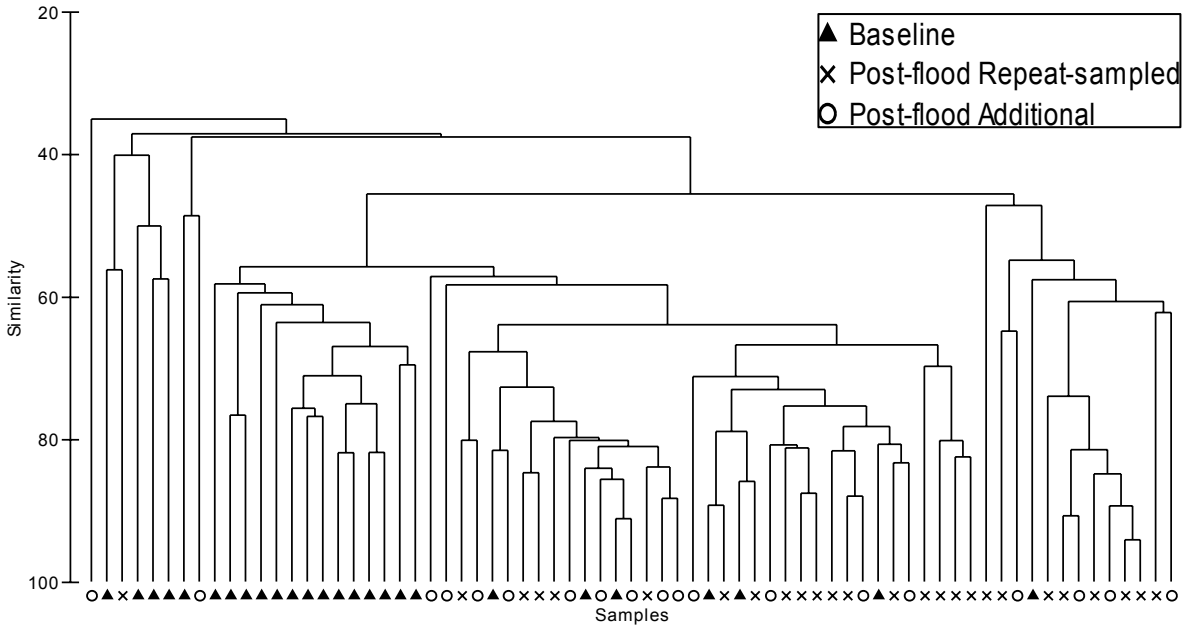
Discriminator taxa	Average abundance (sq. root)		Average dis-similarity	Diss/ SD	Contrib %	Cumul. %
	Baseline survey	Post Flood Repeat-sampled stones				
Baetis spp.	26.47	17.37	11.46	1.24	22.79	22.79
Orthocladiinae	13.77	20.50	11.22	1.44	22.32	45.11
Elmidae larvae	5.56	2.45	4.28	1.06	8.52	53.63
Simulium spp.	1.03	3.59	3.10	0.78	6.17	59.80
Demoulinia spp.	3.84	0.15	3.10	0.73	6.17	65.97
Lestagella penicillata	3.15	1.33	2.49	1.00	4.95	70.91
Tanypodinae	2.19	0.76	2.17	0.53	4.32	75.24
Chironomini	1.62	1.62	2.02	0.80	4.01	79.25
Tanytarsini	0.93	0.99	1.31	0.71	2.60	81.84
Lithogloea harrisoni	0.67	1.10	1.14	0.69	2.28	84.12
Afroptilum spp.	1.43	0.00	1.02	0.47	2.02	86.14
Elmidae adults	1.14	0.13	0.85	0.46	1.70	87.84
Demoreptus capensis	0.54	0.42	0.74	0.47	1.47	89.30
Athripsodes bergensis	0.96	0.13	0.73	0.50	1.45	90.75

Table 6.7b Discriminator taxa in a SIMPER analysis comparing the dissimilarities between invertebrate assemblages on the tops of immovable boulders, from the Baseline and Post-Flood surveys in the Berg River in 2004: ADDITIONAL STONES. Definitions are as per Table 6.7a.

Discriminator taxa	Average abundance (sq. root)		Average dissimilarity	Diss/ SD	Contrib %	Cumul. %
	Baseline survey	Post Flood Additional stones				
Orthocladiinae	13.77	25.34	12.40	1.49	24.34	24.34
Baetis spp.	26.47	19.19	10.66	1.20	20.93	45.27
Elmidae larvae	5.56	5.75	4.18	1.15	8.21	53.48
Lestagella penicillata	3.15	3.65	3.30	0.85	6.48	59.96
Simulium spp.	1.03	3.71	2.84	0.77	5.58	65.54
Demoulinia spp.	3.84	0.00	2.78	0.71	5.45	70.98
Tanypodinae	2.19	0.83	1.74	0.64	3.42	74.40
Chironomini	1.62	1.25	1.67	0.74	3.29	77.69
Lithogloea harrisoni	0.67	1.48	1.44	0.62	2.82	80.51
Demoreptus capensis	0.54	1.36	1.15	0.74	2.25	82.76
Tanytarsini	0.93	1.12	1.09	0.71	2.14	84.90
Afroptilum spp.	1.43	0.25	1.08	0.52	2.11	87.02
Elmidae adults	1.14	0.52	0.92	0.52	1.80	88.82
Hydrachnellae	0.30	0.71	0.69	0.44	1.35	90.17

Table 6.8 A comparison of the degree to which invertebrate assemblages on Repeat-sampled stones were altered from their Baseline condition, according to whether or not stones were moved during floods. The degree of change is represented by the Bray Curtis Similarity coefficient of each repeat-sampled stone, comparing its Baseline to Post-flood assemblage. In post-hoc pairwise comparisons, groups denoted by the same italic letter were not significantly different (Tukey's post-hoc test, p = 0.99)

Stone movement category	Average (median) Bray-Curtis similarity coefficient (%) of repeat-sampled stones, from the Baseline to the post-flood sampling	Significant differences (Tukey's post-hoc test)
1; unmoved in all floods	55.3 (59.2)	*a*
2; moved in Flood 2 but not thereafter	55.6 (58.0)	*a*
3; moved in Flood 2 and Flood 5	43.8 (43.5)	*b*



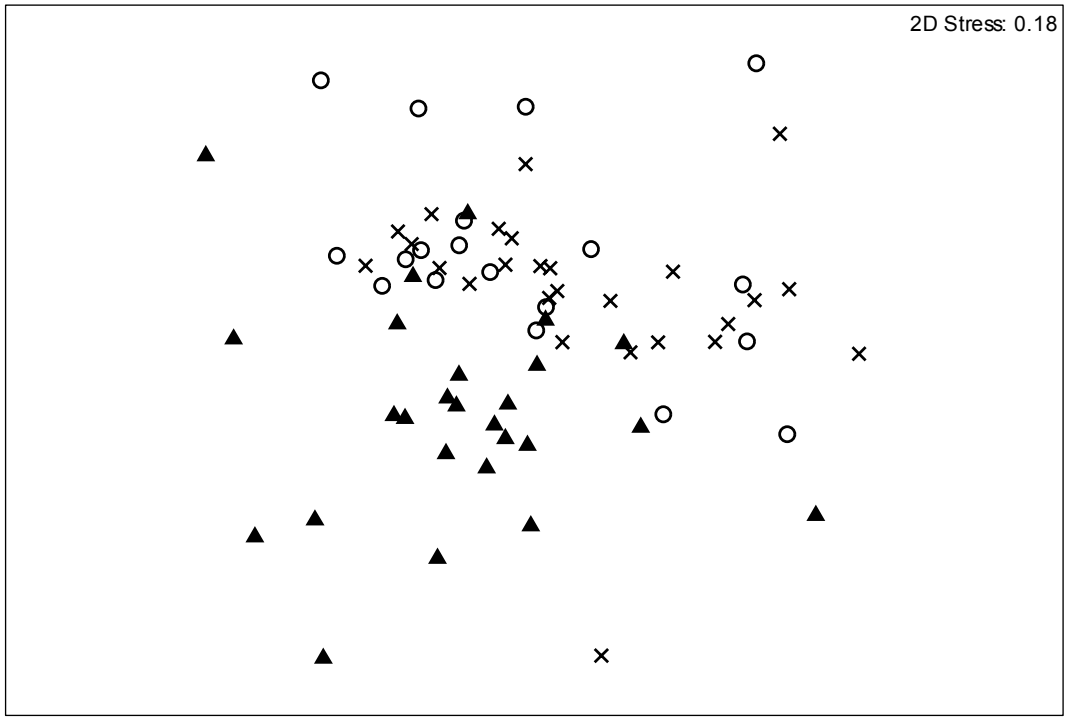


Figure 6.11 Berg River PRIMER results: a) Cluster analysis and b) MDS plots of invertebrate assemblage changes on the top surfaces of immovable boulders over the pre- to post-flood period, based on Bray Curtis similarity coefficients. Both repeat-sampled and additional stones (control) samples for the post-flood period were included in the analysis.

6.3.2.i Effects of stone movement

The results of MDS analysis of the Baseline and Repeat-sampled stones data are presented in Figure 6.12. The individual stone numbers are also indicated, and the distance between the Baseline and the Post-flood position of each stone in Figure 6.12 is representative of how similar it is, or the extent to which it changed, over the study period, in terms of community structure. The results indicate again, the major axis of change being associated with the time period of sampling.

The individual Bray Curtis similarity coefficient for each repeat-sampled stone, from Baseline - Post-flood sampling, was extracted from these multivariate results. Stones were grouped according to their movement characteristics (refer to Table 3.3, section 3.3.1*ii*), and differences in the similarity coefficients across stone movement groupings were examined to test whether stones moved immediately before the post-flood survey were more different from their baseline condition than were those which had not moved over the full study period, or those which moved only once, during the early Class IV flood.

Since the data conformed to the assumptions for parametric testing, an ANOVA was performed on Bray Curtis similarities for the 3 movement groups, indicated in Table 6.8, resulting in a significant difference ($F=5.53$, $p = 0.0065$). A post-hoc Tukey test used to identify significant differences between pairs of samples showed that Movement Group 1 and 2 stones were not significantly different ($p = 0.99$), Movement Group 3 (i.e. moved in flood 5) was significantly different from both Group 1 and 2 stones ($p = 0.009$ and 0.025 for Group 1 vs Group 3 and Group 2 vs Group 3 respectively).

Thus stones which moved immediately before the post-flood sampling were some 10 - 15% more different from their baseline condition than those which did not. An interesting finding was that the Group 2 stones which had moved in Flood 2, but then remained stationery for the month following their movement until the post Flood 5 sampling, were not statistically different from unmoved stones, in terms of their overall assemblage similarities relative to their baseline condition.

Despite the apparent effects of stone movement on the degree of change in assemblage composition, Cluster analysis and MDS of the Post-flood data showed no grouping of samples according to their movement category (Figure 6.13). An ANOSIM on these apriori-determined movement groups (1, 2, 3) revealed only weakly significant differences (Global $R = 0.07$ (significance level $p = 0.04$). Pairwise test results are indicated in Table 6.9 - at the more conservative significance level threshold of $p = 0.01$, suggested for pairwise tests in the ANOSIM procedure, none of the weak differences between movement groups (low R statistic) were significant.

The existence of possible relationships between applied stream power during the peak flood flows of Flood 2 and Flood 5, as well post-flood periphyton, flow and velocity variables and the post-flood invertebrate assemblages was tested by overlaying these variables onto the MDS plot. None of the physical or periphyton measures provided a good match that or suggested any gradients across the data.

Table 6.9 ANOSIM Pairwise tests for differences in invertebrate assemblages across stone movement groups. Group definitions are as per Table 6.8.

Pairwise comparison	R-statistic	Significance level
Group 1 vs Group 2	0.041	p = 0.25
Group 1 vs Group 3	0.088	P = 0.04
Group 2 vs Group 3	0.079	P = 0.05

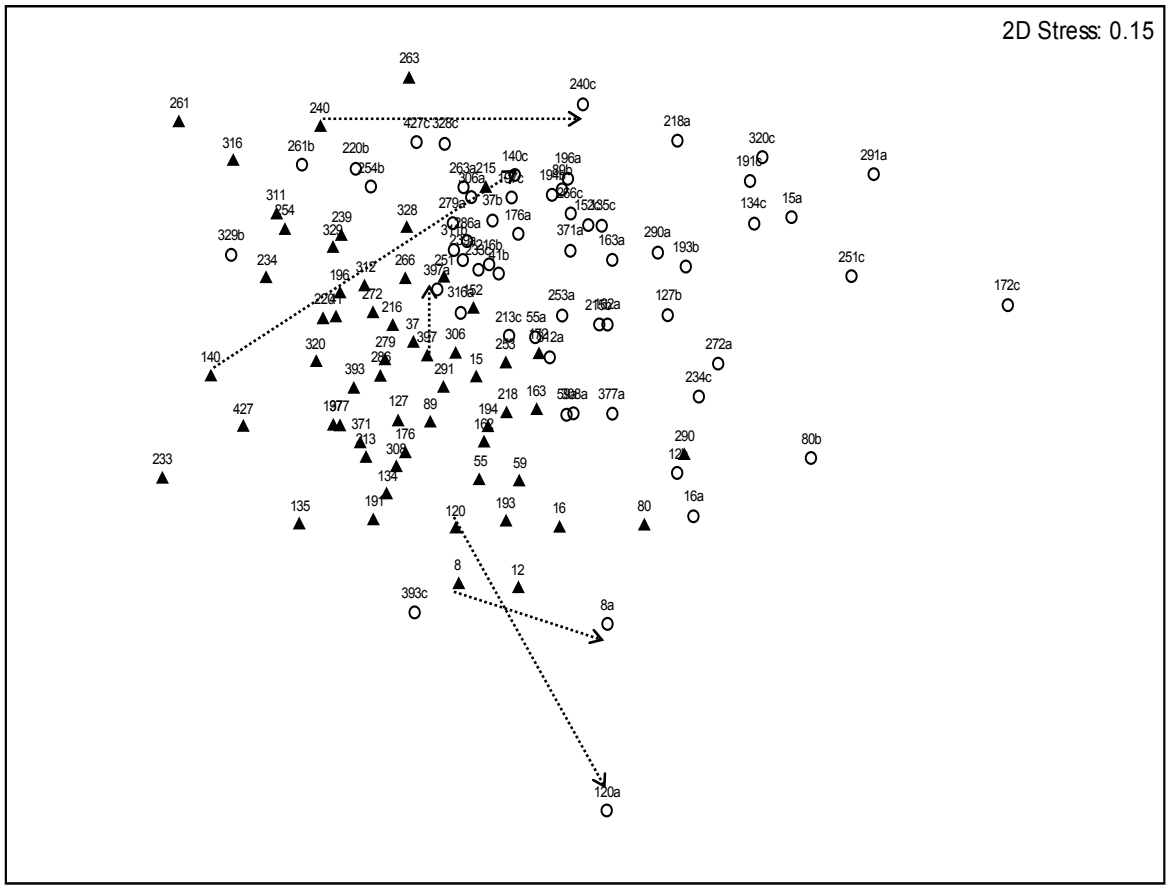


Figure 6.12 Berg River MDS plot of invertebrate assemblage changes over the pre- to post-flood period, based on Bray Curtis similarity coefficients, using Repeat-sampled stone data only.

The distance between the Baseline and the Post-flood position of each stone is representative of how similar it is, or the extent to which it changed, over the study period, in terms of community structure. Examples of this are indicated by arrows from the Baseline to the Post-flood position for a few stones.

Total invertebrate density (inset in Figure 6.13) did show a gradient, but not one that compared well with the movement group of the samples. The BIOENV routine comparing these variables with the invertebrate patterns returned poor correlations.

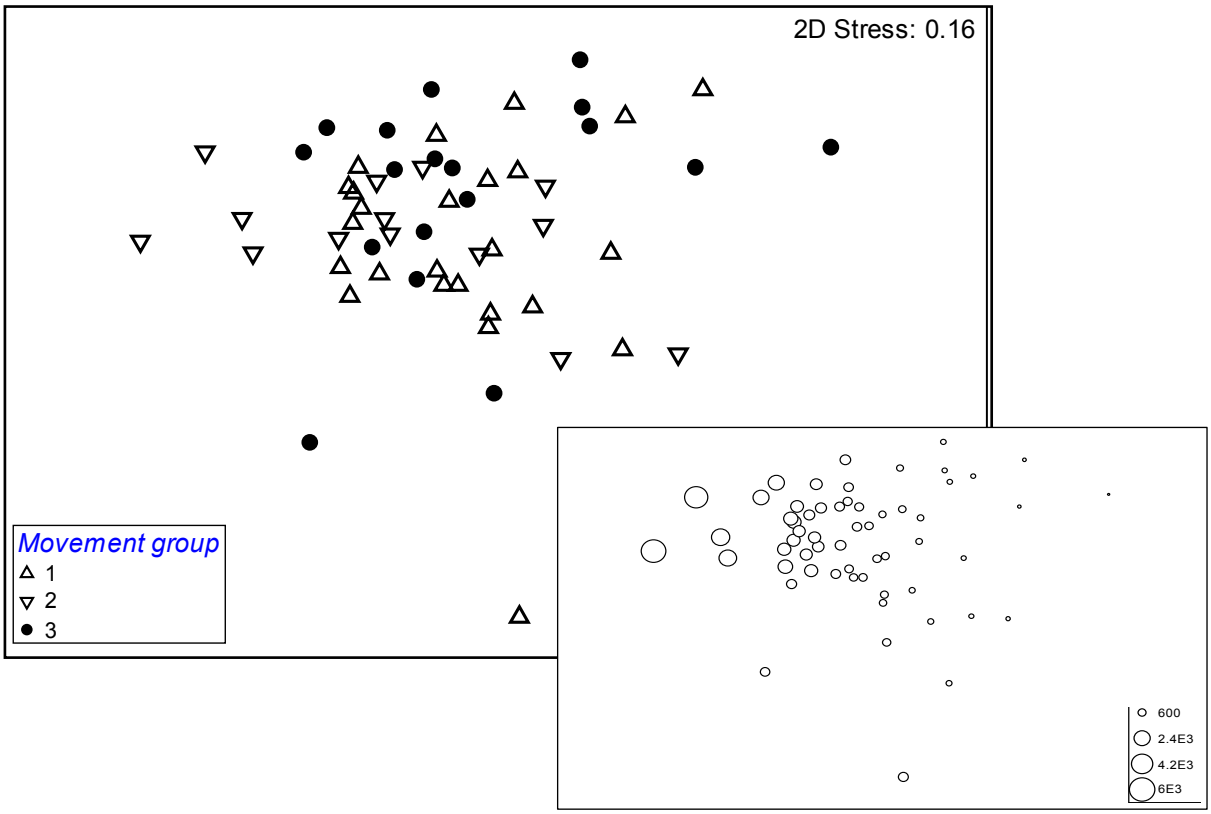


Figure 6.13 Berg River MDS plot of invertebrate assemblages on Repeat-sampled stones in the post-flood period, based on Bray Curtis similarity coefficients, categorised into stone movement groups. Groups 1-3 are defined as per Table 6.5. Inlay: bubble plot of total invertebrate densities superimposed over the MDS plot. The gradient of declining densities does not correspond to differences in stone movement category.

6.4 SPECIES-SPECIFIC RESPONSES TO FLOODS

The exploration of the way in which community structure changed over the study period in the Molenaars and Berg Rivers indicated firstly that community structure was gradually changed over a period characterised by numerous small intra-annual flood events, with significant levels of change only apparent as a cumulative effect of these small shifts (Molenaars River study). Secondly, a period characterised by substantially larger, bed-moving floods was associated with a more obvious alteration of assemblages (Berg River study). In both cases, community change was based largely on different degrees of reduction in the densities of the component species. Some apparently conflicting results were obtained regarding density decreases on top surfaces of large substrata between the two study rivers. Evidence was also provided for community-level differences in the impacts of floods, based on the movement or not of bed substrata, although community-level differences in this regard were not strong. Finally, the evaluation of species-level differences in recovery rates following initial denudation of stones suggested that some taxa recover rapidly, whilst others do not.

This section of the analysis seeks therefore to examine, species by species where sufficient data were available, the changes in densities and in population structure, associated with each sampling occasion in the Molenaars and Berg Rivers, relative to the magnitude of floods and the movement of individual bed particles.

The composite figures that follow (Figure 6.14 a-z) present bar graphs of the mean density (+ standard deviation) in the Molenaars River from each of the five sampling occasions - Baseline, and Pre- and Post- Floods 1 and 4, as well as the frequency distributions describing population size structure at each of the five sampling occasions. For the Molenaars River, only whole stone samples were included in this analysis, since the sample sizes for pre- and post- flood datasets were too small to allow meaningful comparisons to be made. The figures also provide the same density and population structure data for the Berg River, for the two sampling periods (May and July) in that study, but separately for each of the stone movement categories, as outlined in Table 3.3 (section 3.3.1*ii*), and including tops of immovable stones. For ease of reading, these composite figures are presented for the Ephemeroptera (Figure 6.14 a-k) and then for the Trichoptera, Plecoptera, Diptera and Coleoptera (Figure 6.14 l-z).

Significant density changes from Kruskal-Wallis analysis of variance in densities over the five sampling periods on the Molenaars River are presented in Table 6.10. The percentage increase or decrease was calculated for both the Baseline - Post Flood 4 statistic and the Pre-Flood 1 to Post-Flood 4 statistic. Since recovery in many species was only partial, the latter measure is more conservative as it takes into account the potential error associated with initial sampling of stones, referred to as the 'sampling effect'. In Table 6.10, where sample densities at the Pre-Flood 1 survey were lower than the Baseline, the more conservative value for the percentage change has thus been used.

Analysis of variance results for Berg River, comparing Baseline and Post-flood stones, for unmoved stones and those moved in both Flood 2 and Flood 5 are indicated in Table 6.11, for both Repeat-sampled stones and Additional stones. The results of analysis of invertebrate changes on tops of immovable boulders (Category 7 and 8 stones) are also included. The changes in density on stones that moved only once (Category 2 and 5 stones) were not included in the analysis, as separating out impact from possible recovery proved to be too difficult.

Significant differences in population size frequency distributions between the five periods for the Molenaars River and the two periods for the Berg River are presented in Tables 6.12 and 6.13 respectively.

6.4.1 Ephemeroptera:

6.4.1.i Baetidae

Figure 6.14a-e shows the results of this analysis for five Baetidae species or genera. The response of each species, in terms of seasonal changes and flood effects on population density and size structure, is discussed separately in the following passages.

a ***Demoulinia*** spp.

Demoulinia spp. was characterised during the baseline condition by a dominance of relatively small instars (Figure 6.14a), with very few mature nymphs - mature nymphs (black wing buds) were only associated with head width size classes from around 0.8 mm for all the Baetidae. There was a fairly good recovery in densities from the Baseline to the Pre-Flood 1 sampling period (Figure 6.14a), although the recovering population was significantly different with regard to its size distribution, with an increase in mean head width from 0.32 mm to 0.41mm (Table 6.12, frequency distributions for the Baseline and Pre-Flood 1 data shown in Figure 6.14a). This appeared to reflect developmental growth of the population, with the modal head width size class in the Baseline survey of 0.3 mm being replaced by a mode of 0.4 mm head width a month later in the Pre-Flood 1 survey (Figure 6.14a).

Although the differences in density in the Molenaars River were not significantly different over the study period (Kruskal-Wallis, $p > 0.05$, Table 6.10), this (as with many invertebrate data) is at least in part a reflection of the patchiness of distribution even prior to the onset of floods. Overall, there was a decline in density of some 53% (Table 6.10; Figure 6.14a), and the significant frequency distribution changes from the Baseline to subsequent periods suggest that the population that remained was simply maturing, without any new instar recruitment over the study period (Table 6.12).

In the Berg River the population in May 2004 was more mature than that in the Molenaars River in June 2003 (modal head width size class in the Berg River = 0.5 mm vs 0.3 mm in the Molenaars River), but nevertheless still comprised of immature nymphs. Over the flood period, this species was dramatically and significantly reduced in density by between 90 and 100%, as previously indicated in Table 6.5. This reduction was on all categories of stones, irrespective of whether they moved or not (Figure 6.14a, Table 6.11). The remaining population was not significantly different with regard to size distribution (Table 6.13).

b ***Afroptilum*** spp.

In the Molenaars River, the Baseline density of *Afroptilum* spp. was far greater than that of *Demoulinia* spp. (Figure 6.14 a & b), and recovery following initial sampling was characterised by a non-significant increase on stones, although given the high standard deviation of this sample, this apparent increase is considered to have been an artefact of inadequate sampling size. Overall, the population of Afroptilum showed a 58% decrease from the Baseline condition to the end of the study period (Table 6.10). The effect of floods on population structure seemed to emphasis losses of smaller instars: post-flood populations were significantly different from the pre-flood populations in both Flood 1 and Flood 4 (Figure 6.14b; Table 6.12) and were comprised of a greater proportion of older / larger nymphs than the pre-flood populations, with significantly larger individuals

In the Berg River, there was an overall decrease in density of some 60 - 75% (Table 6.5), which was not substantially higher than in the Molenaars River, despite the difference in flood sizes, although in the case of the Berg data this decrease was significant.

Importantly, however, unmoved stones provided a substantial refugium for *Afroptilum* spp. This refugium is demonstrated by the finding that post-flood densities on Category 1 and Category 4 (unmoved) stones were higher but not significantly different from the Baseline condition, whilst those on moved stones (Category 3 and 6) showed a significant decrease by between 97 and 100% (Table 6.11). The species did not remain on the top surfaces of immovable boulders after the Class IV flood (Category 7 and 8 stones). The Post-flood population structure was significantly different from the Baseline situation (Table 6.13), where the frequency-distributional changes suggest both a relative decline in small instars, as a result of flood mortality, and a maturation of the remaining population over the two-month period, with no new recruitment.

c ***Demoreptus capensis***

There was very little change in *D. capensis* densities in the Molenaars River over the study period, with a non-significant increase in population size (Table 6.10, Figure 6.14c). Population structure changed significantly over the study period, reflected in a gradually increasing mean head width, with significant differences in size-frequency distribution between the Baseline and all other surveys (Table 6.12). However, pre-post flood populations for both Flood 1 and Flood 4 were not significantly different (Table 6.12). Despite the increase in mean head width over the study period, the continuous dominance of the smallest size classes suggests an ongoing recruitment of new instars during the season, unlike *Demoulinia* spp. or *Afroptilum* spp.

In the Berg River, the Baseline population of *D. capensis* was comprised of a somewhat more mature cohort than the Molenaars River (0.5 mm modal head width vs 0.3 mm in the Molenaars River; Figure 6.14c). *D. capensis* was one of the four taxa demonstrating a non-significant change in overall density, with a decline of between 60 and 66% (Table 6.5), the former based on comparing Baseline and Additional stones, and the latter comparing Baseline with Repeat-sampled stones. The analysis per stone category, however, showed a somewhat confusing picture - a relative decline on unmoved stones, whilst on the other hand an increase on moved stones and on immovable boulder surfaces - although once again none of these changes were significant (Figure 6.14c, Table 6.11). Analysis of the change in size-frequency distribution from the Baseline to Post-flood periods indicates a strong shift from a normal size distribution dominated by medium sized instars (head width 0.5 mm), to a bimodal distribution with peaks at 0.3 and 0.8 mm, a significant change in frequency distribution (Table 6.13). The results indicate that this species maintained its population density in the face of floods by a combination of continuous recruitment of new instars, as well as through the resistance to floods shown by larger instars, some of which had reached maturity by the end of the study period in July. There was also no indication of a relative refugium provided by unmoved stones in the case of *D. capensis*.

d ***Pseudocloeon* spp.**

Pseudocloeon spp. showed very different responses to the floods in the Molenaars River from its responses in the Berg River, one of the few cases in this study that

demonstrate such a contradiction. In the Molenaars River, the series of small floods had the cumulative effect of reducing population size by some 82% (Table 6.10). Floods appeared to affect larger individuals disproportionally, as demonstrated by changes in frequency distributions and reductions in mean head width pre- and post- floods (Figure 6.14d; Table 6.12). In the Berg River, however, *Pseudocloeon* spp. densities increased significantly from a low base in May (Table 6.5), and was present in higher densities on all categories of stones (Table 6.11; Figure 6.14d), with the exception of top surfaces of immovable boulders. Furthermore, as with *D. capensis* the population size-frequency distribution changed from a normal to a bimodal distribution, indicating both recruitment and survival (resistance) of larger instars (Table 6.13). This result was not statistically significant, although that is probably because of the very low starting densities of this species.

Table 6.10 Percentage decrease (unless increase specified) and results of Kruskal-Wallis analysis of variance between invertebrate density and the five sampling periods in the Molenaars River, for selected taxa.

The % change in density is given as the Baseline - Post Flood 4% change, unless recovery after initial sampling was not adequate, in which case it is given as the Pre-Flood 1 to Post-Flood 4% change. B = Baseline; F1, F4 = Floods 1 and 4, Pre-, Po- = Pre- and Post- Flood sampling periods. H = test statistic. Significant Dunn's post-hoc multiple comparisons are also presented. n.s. = not significant

	% change over study period	H	P value	Dunn's significantly different groups (p-value)
Demoulinia spp.	53%	n.s.		
Afroptilum spp.	58%	13.6	0.009	B - F1Po (0.005)
Demoreptus capensis	10% increase	n.s.		
Pseudocloeon sp.	82%	26.3	0.000	B - F4Pre (0.002) B - F4Po (0.002)
Baetis spp.	16%	16.3	0.003	B - F4Pre (0.034) B - F4Po (0.018)
Lestagella penicillata	No change F1Pre to F4Po	25.3	0.000	B - F1Pre (0.021) B - F1Po (0.006) B - F4Pre (0.004) B - F4Po (0.001)
Lithogloea harrisoni	2500% increase	45.0	0.000	B - F4Pre (0.001) B - F4Po (0.001) F1Pre - F4Pre (0.011) F1Pre - F4Po (0.001)
Aprionyx spp.	99%	9.3	0.054	n.s.
Euthraulus elegans	No change F1Pre to F4Po	17.2	0.002	B - F4Pre (0.000)
Afronurus harrisoni	78%	19.8	0.001	B - F4Po (0.002)

Afronurus sp.	84%	51.6	0.000	B - F1Po (0.014) F1Pre - F1Po (0.014) B - F4Pre (0.000) B - F4Po (0.000) F1Pre - F2Pre (0.001) F1Pre - F2Po (0.000)
Cheumatopsyche afra	Recovery to 66% of Baseline over study period	14.6	0.006	n.s.
Chimarra sp.	Recovery to 64% of Baseline over study period	n.s.		
Athripsodes bergensis	93%	13.6	0.001	B - F4Po (0.043)
Agapetus agilis	47%	13.4	0.010	B - F4Po (0.018)
Notonemouridae	756% increase	n.s.		
Elporia spp.	4%	n.s.		
Simulium spp.	100% increase	11.19	0.025	B - F1Po (0.015)
Orthocladiinae	3%			
Tanypodinae	72%			B - F1Po (0.017) B - F4Pre (0.031) B - F2Po (0.000)
Chironomini	14%	17.0	0.002	B - F1Po (0.049)
Tanytarsini	14%	10.4	0.035	n.s.
Elmidae larvae	Recovery to 83% of Baseline over study period	9.5	0.049	n.s.
Elmidae adults	31%			
Helodidae	10% increase			
Hydrachnellae	51%	n.s.		

Table 6.11 Percentage reduction (+ = increase) and results of Kruskal-Wallis analysis of variance between invertebrate density, from the Baseline condition to the Post-flood sampling on the Berg River, for each stone category, for most taxa. H = Kruskal-Wallis test statistic, p = significance level n.s. = not significant. Dunn's pairwise significant differences are indicated as follows: * p < 0.05; ** p< 0.01; ***p>0.001.

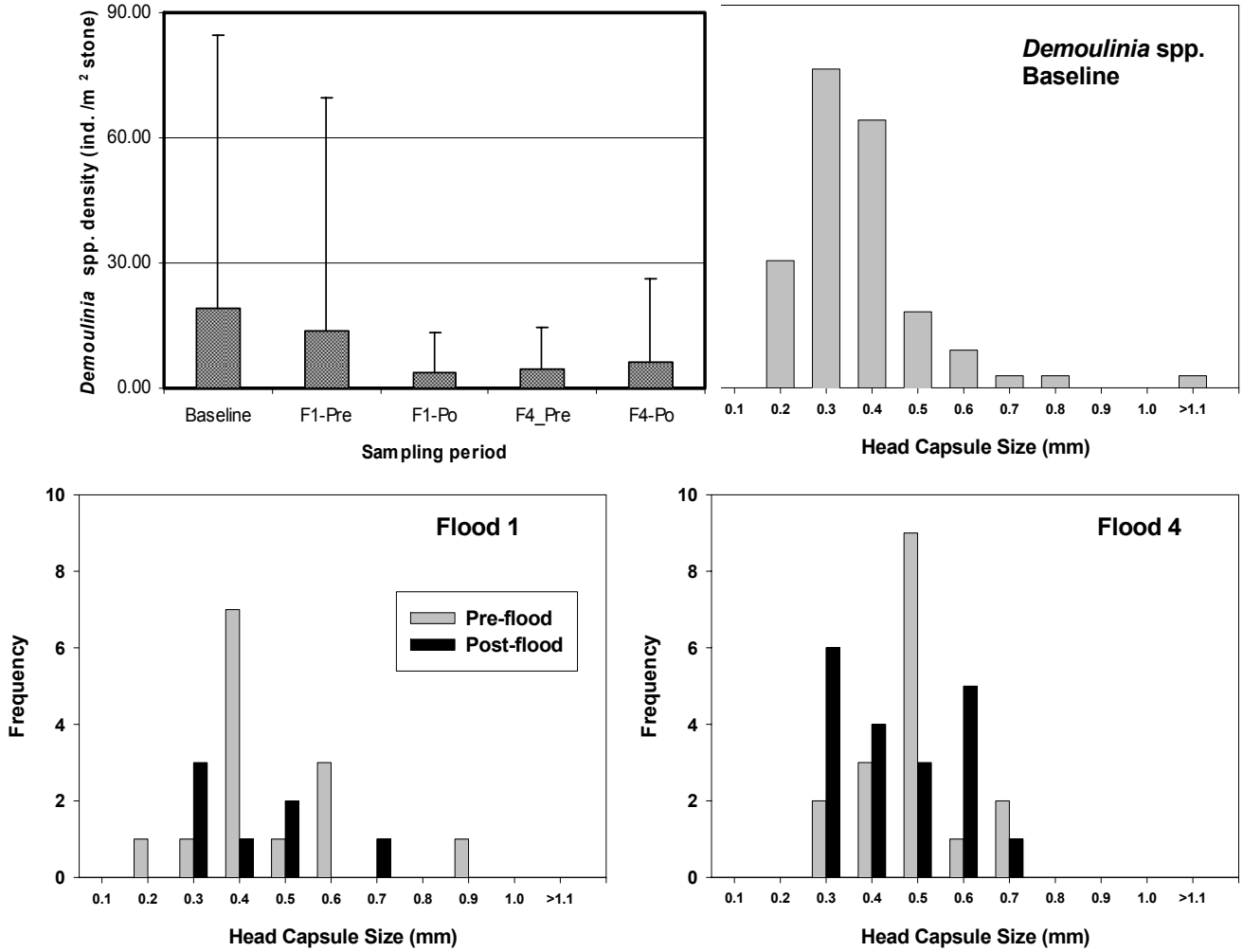
	% decrease on Category 1 / 4 stones (unmoved)				% decrease on Category 3 / 6 stones (moved F2 and F5)				% decrease on Category 7 / 8 stones (immovable boulder tops)			
	Repeat-sampled (Cat1)	Additional (Cat4)	H	P value	Repeat-sampled (Cat3)	Additional (Cat6)	H	P value	Repeat-sampled (Cat7)	Additional (Cat8)	H	P value
Demoulinia spp.	90**	97**	17.6	0.000	95	100**	29.9	0.000	99	100	17.6	0.001
Afroptilum spp.	+43	+25	n.s.		100	97*	16.8	0.000	100	89	n.s.	
Demoreptus capensis	87	80	n.s.		+120	+580	n.s.		+27	+209	n.s.	
Pseudocloeon sp.	1	+367**	16.6	0.003	Not present in Baseline samples				100	+5	n.s.	
Baetis spp.	34	11	n.s.		46*	29	7.0	0.030	57***	41**	15.7	0.000
Lestagella penicillata	67***	64***	21.6	0.000	89***	84***	36.8	0.000	82	+32	n.s.	
Lithogloea harrisoni	+100	+261**	10.7	0.005	22	1	n.s.		+24	+148	n.s.	
Aprionyx spp.	74**	85**	12.9	0.002	100**	98***	25.6	0.000	Not present on top surfaces of boulders			
Euthraulus elegans	71*	77	8.9	0.012	92***	95***	27.3	0.000				
Afronurus harrisoni	54	88**	12.6	0.002	75	89***	20.4	0.000				
Afronurus sp.	89***	79***	23.2	0.000	97***	93***	42.2	0.000				
Cheumatopsyche afra	100	100	n.s.		-	100	n.s.		100	100	n.s.	
Cheumatopsyche maculata	91	75	7.0	0.030	100	89	n.s.		100	n.s.	n.s.	
Orthotrichia barnardi	92	69	n.s.		27	4	n.s.		100	100	n.s.	
Athripsodes bergensis	72*	91**	14.5	0.007	97*	93*	14.7	0.001	n.s.	72	n.s.	
Chimarra sp.	92	51	n.s.		100	99	8.8	0.012	Not present on top surfaces of boulders			
Notonemouridae	28	56	n.s.		16	+57	n.s.					
Simulium spp.	55	73	n.s.		+5	8	n.s.		+635*	+664	8.0	0.018
Orthocladiinae	42	28	n.s.		60	50	n.s.		+40	+124**	9.8	0.008
Tanypodinae	94***	94***	35.8	0.000	90***	94***	29.5	0.000	52	81	n.s.	
Chironomini	17	24	n.s.		14	50			35	41		
Tanytarsini	76**	62	10.4	0.005	85***	84***	21.7	0.000	+5	+28	n.s.	
Elmidae larvae	84***	75**	26.2	0.000	91***	82***	25.0	0.000	75	27	7.3	0.026
Elmidae adults	73*	87*	11.6	0.003	95	79	7.5	0.023	95	70	n.s.	

	% decrease on Category 1 / 4 stones (unmoved)				% decrease on Category 3 / 6 stones (moved F2 and F5)				% decrease on Category 7 / 8 stones (immovable boulder tops)			
	Repeat-sampled (Cat1)	**Additional (Cat4)**	**H**	**P value**	**Repeat-sampled (Cat3)**	**Additional (Cat6)**	**H**	**P value**	**Repeat-sampled (Cat7)**	**Additional (Cat8)**	**H**	**P value**
Helodidae	43	27	n.s.		95	87	n.s.		Not present on top surfaces of boulders			
Hydraenidae	100	100	n.s.		100	100	n.s.					
Hydraenidae adults	100	100	n.s.		100	100	n.s.					
Hydrachnellae	46	43	n.s.		81	25	n.s.		31	+55	n.s.	

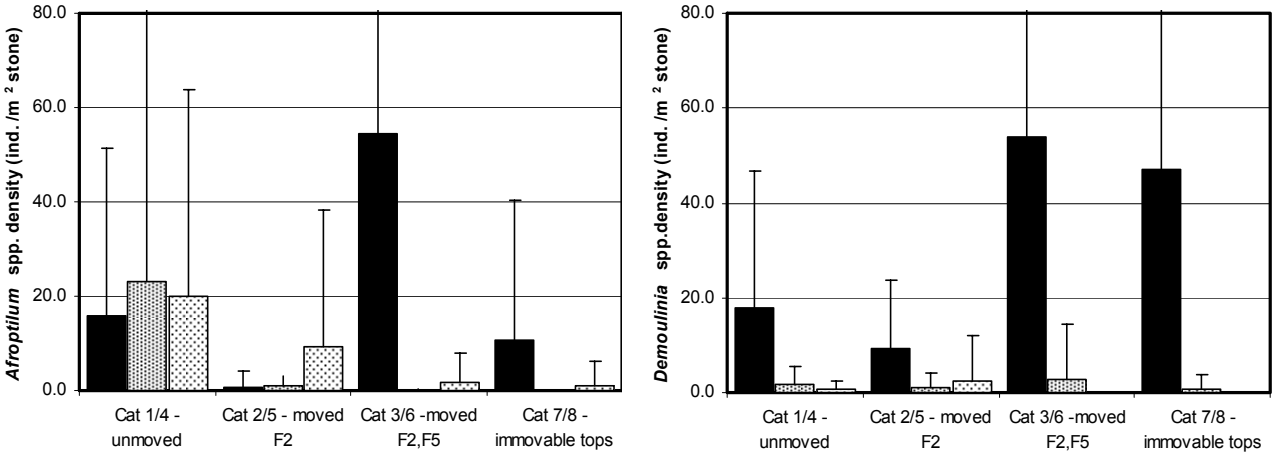
Figure 6.14 a-n Mean species density (+ standard deviation) and population size frequency distributions in the Molenaars River, on each of the five sampling occasions during the 2003 study, followed by mean species density and population size frequency distributions for the two sampling surveys in the Berg River in 2004 analysed separately for each of the stone movement categories.

Data are presented for
a) *Demoulinia* spp., b) *Afroptilum* spp., c) *Demoreptus capensis*; d) *Pseudocloeon* spp.,
e) *Baetis* spp.; f) *Lestagella penicillata*; g) *Lithogloea harrisoni*; h) *Aprionyx* spp.;
i) *Euthraulus elegans*; j) *Afronurus harrisoni*; k) *Afronurus* sp.

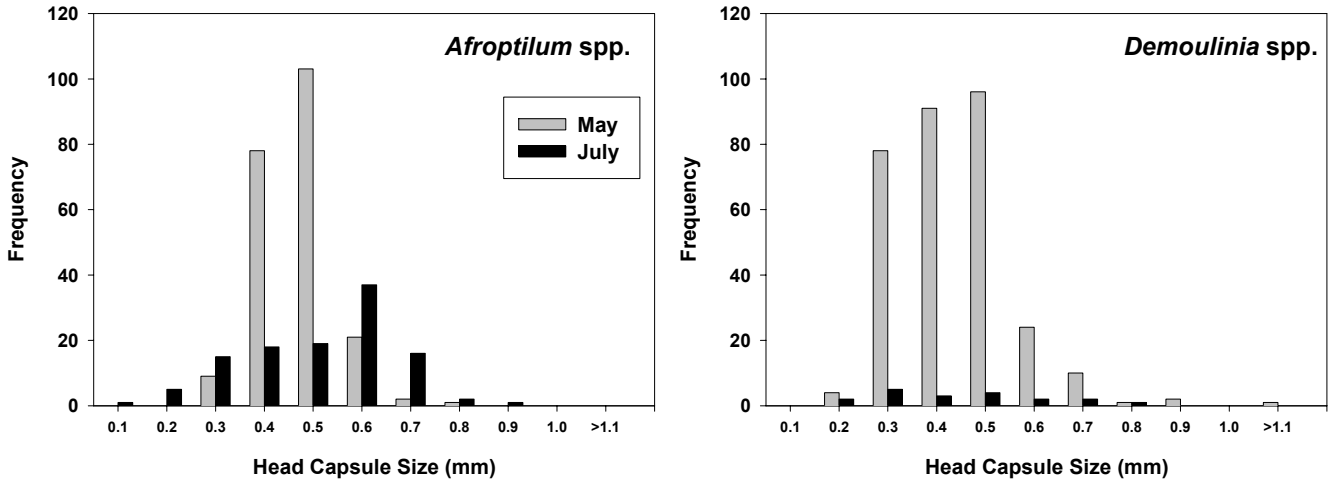
a) *Demoulinia* spp. - Molenaars River



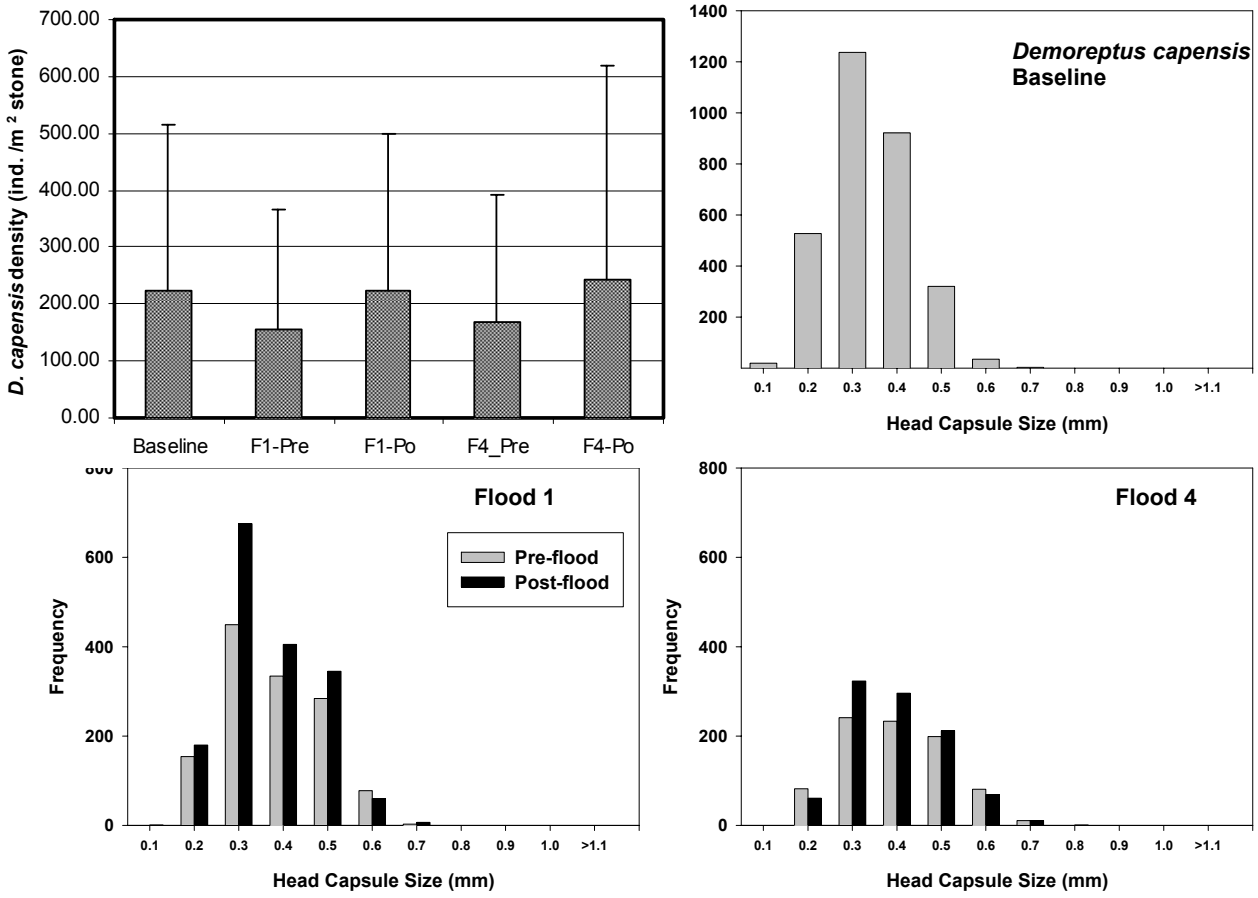
a) *Demoulinia* spp. & b) *Afroptilum spp.* - Berg River



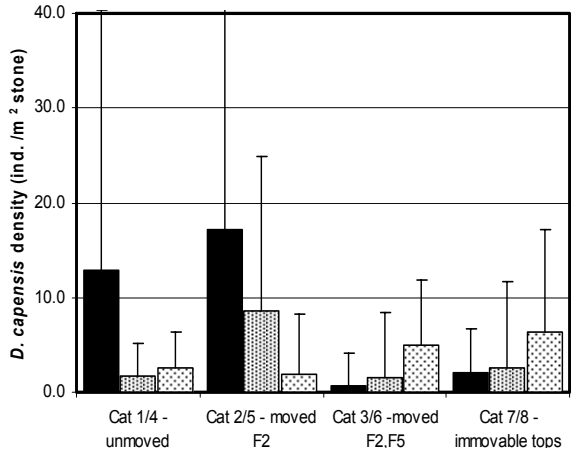
c) *Demoreptus capensis* - Molenaars River

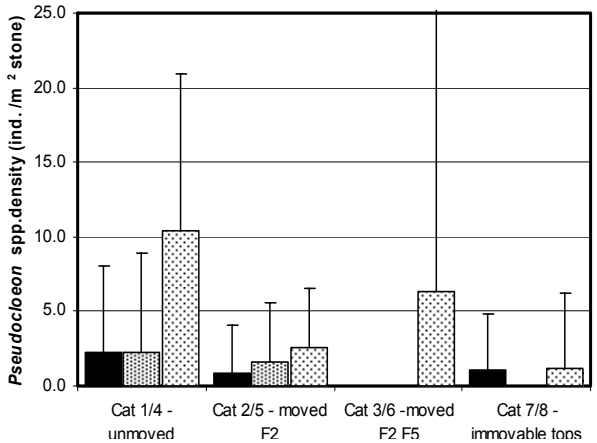


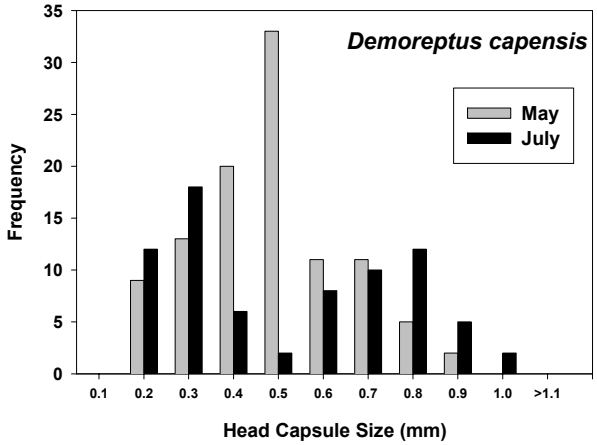
c) *Demoreptus capensis* - Molenaars River

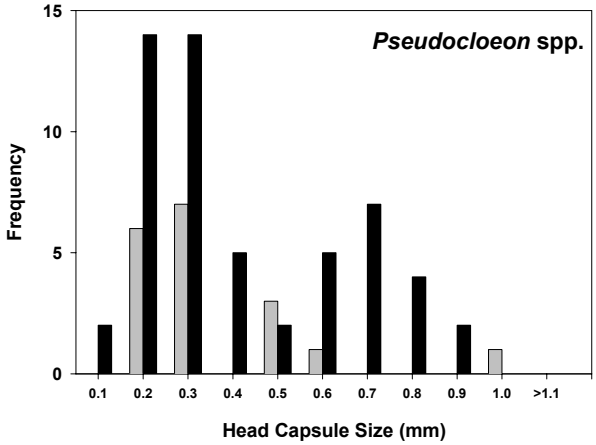


c) *Demoreptus capensis* & d) *Pseudocloeon* spp. - Berg

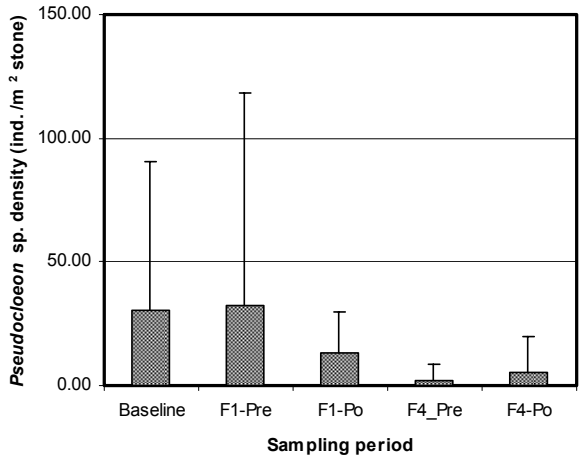


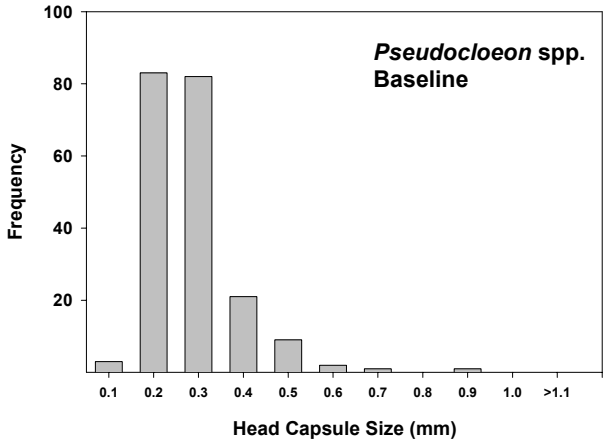


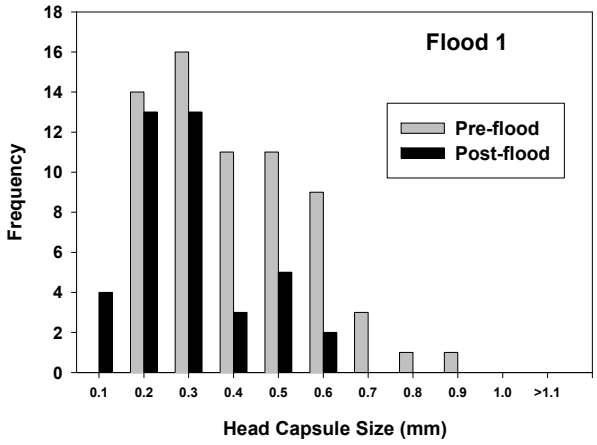


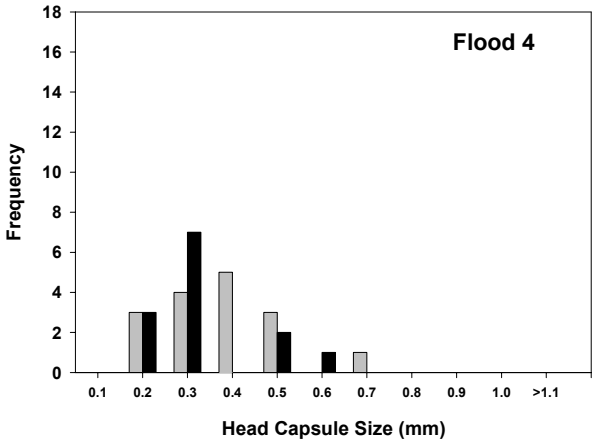


d) *Pseudocloeon* spp. - Molenaars River

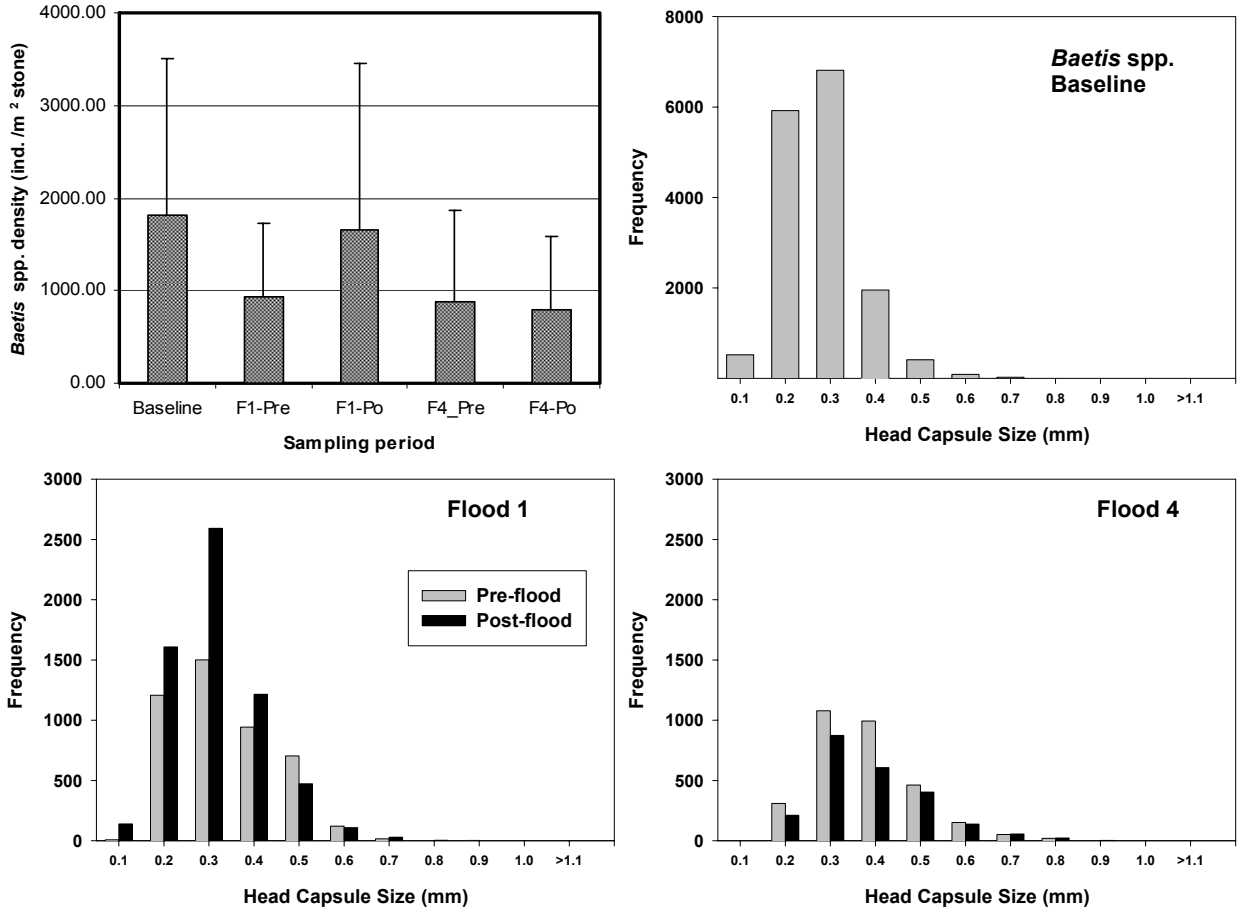




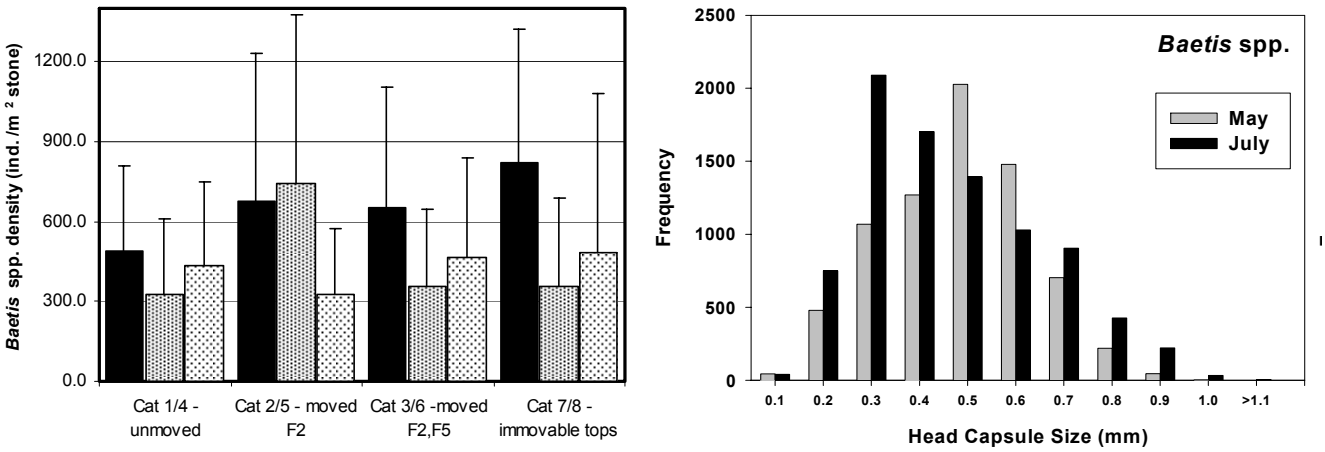




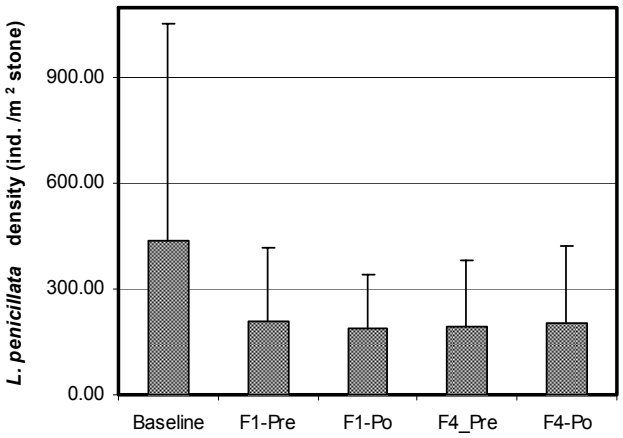
e) *Baetis* spp. - Molenaars River

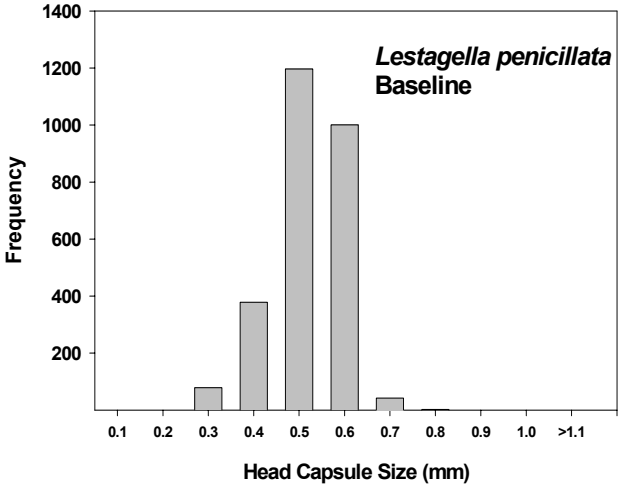


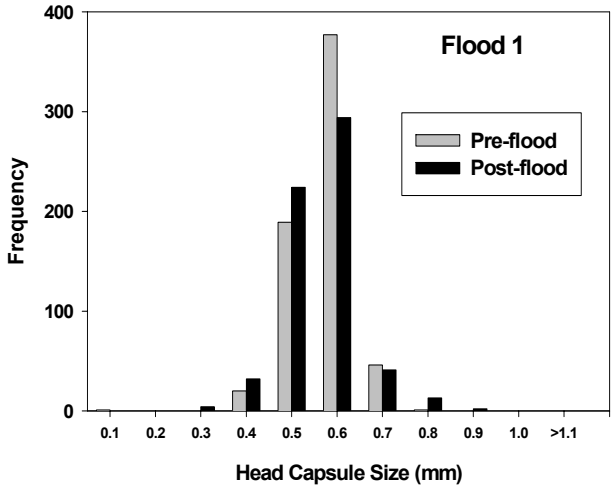
e) *Baetis* spp. - Berg River

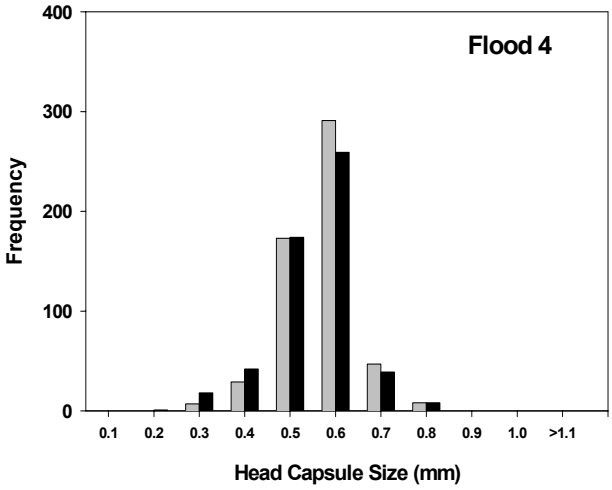


f) *Lestagella penicillata* - Molenaars River

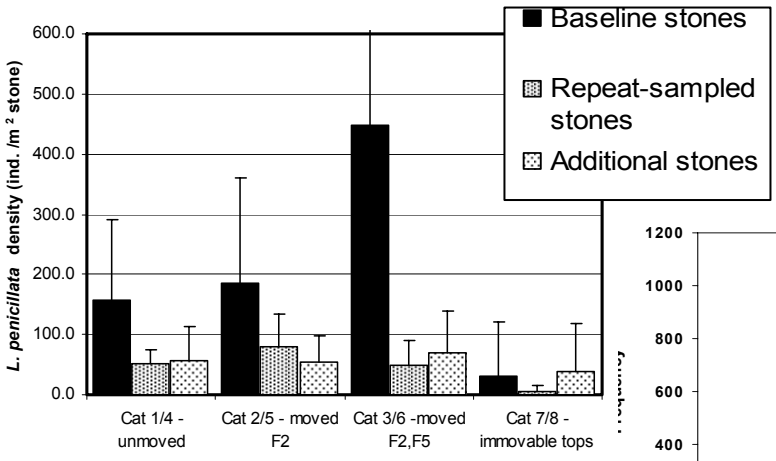


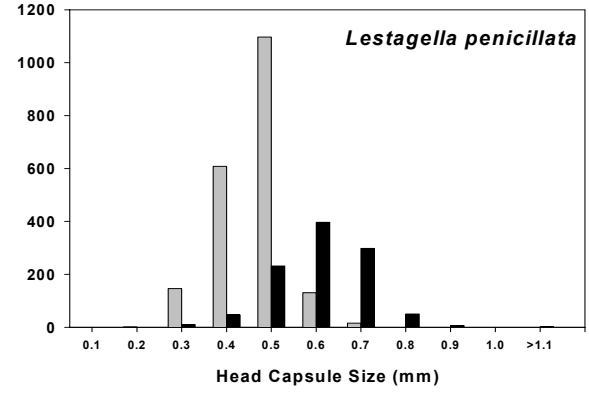




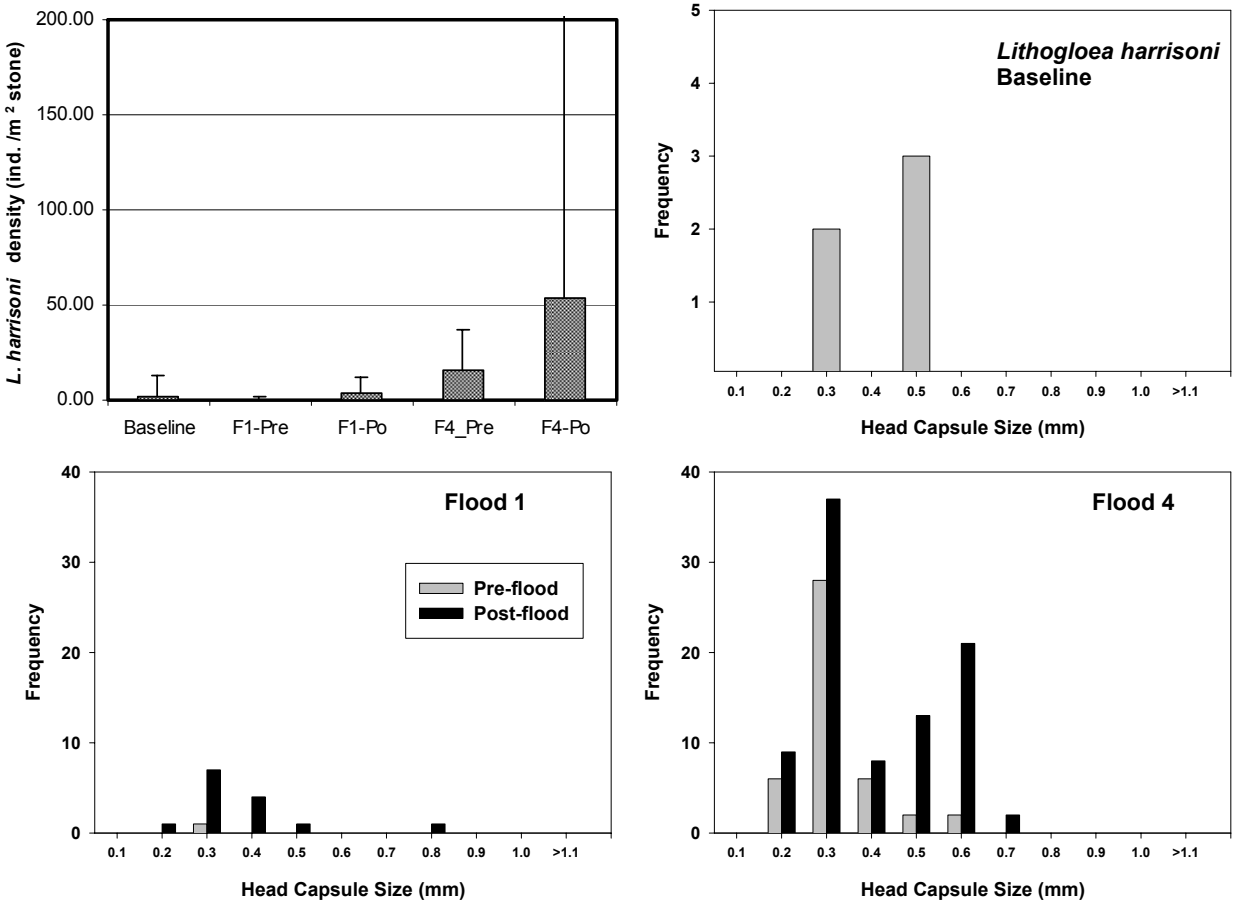


f) *Lestagella penicillata* - Berg River

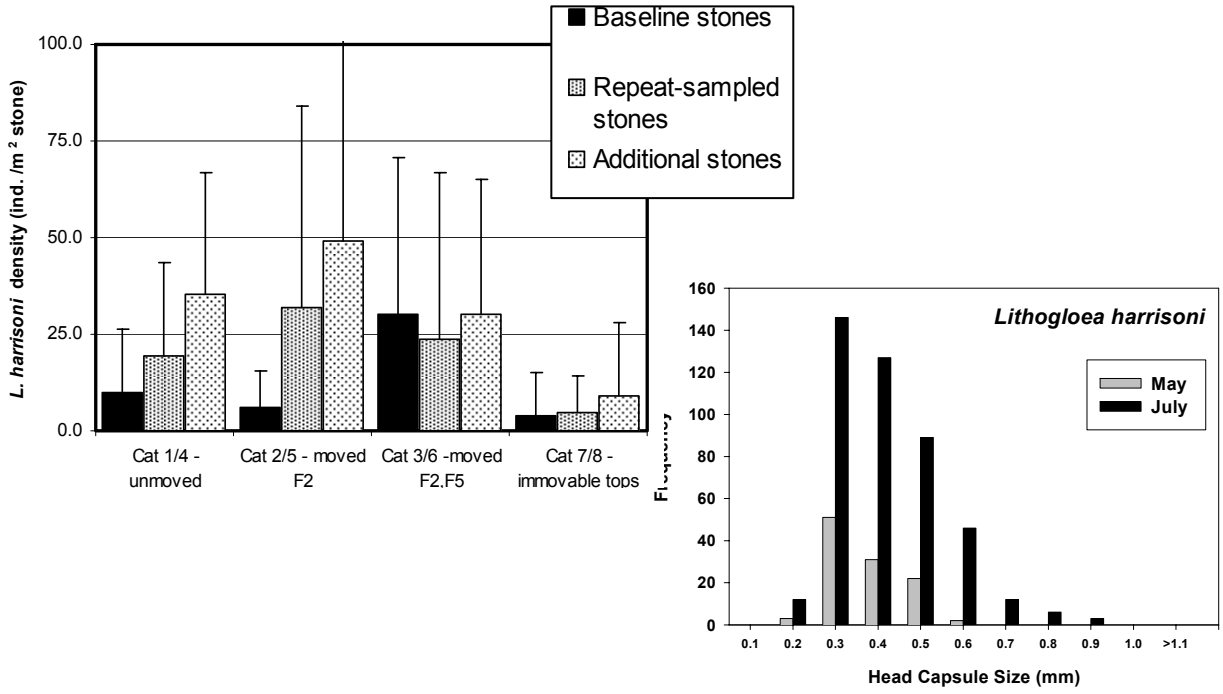




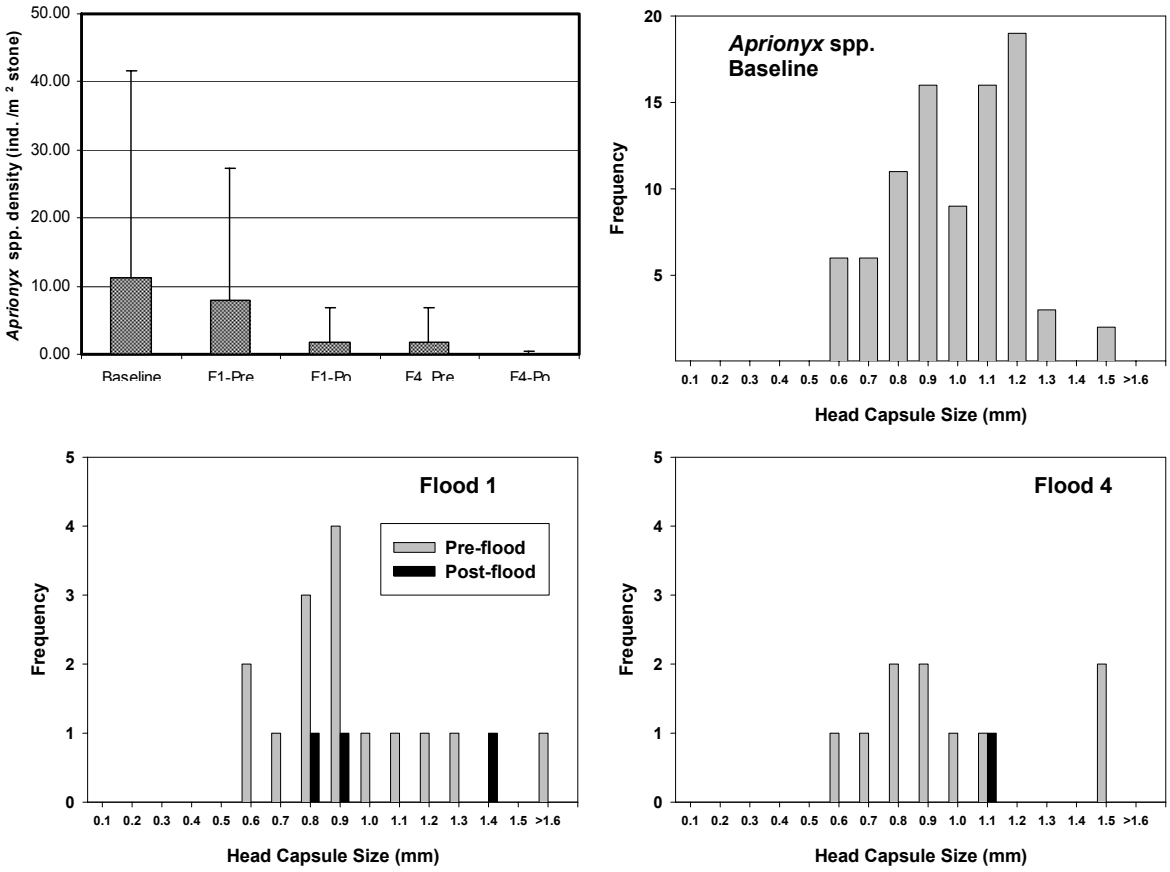
g) *Lithogloea harrisoni* - Molenaars River



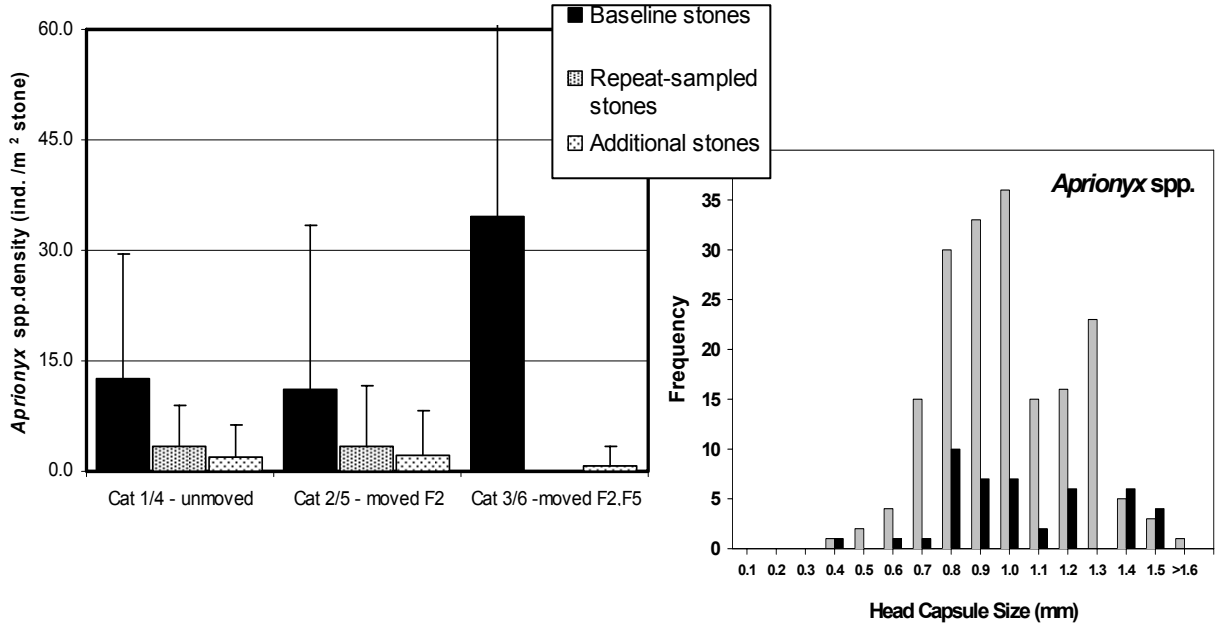
g) *Lithogloea harrisoni* - Berg River



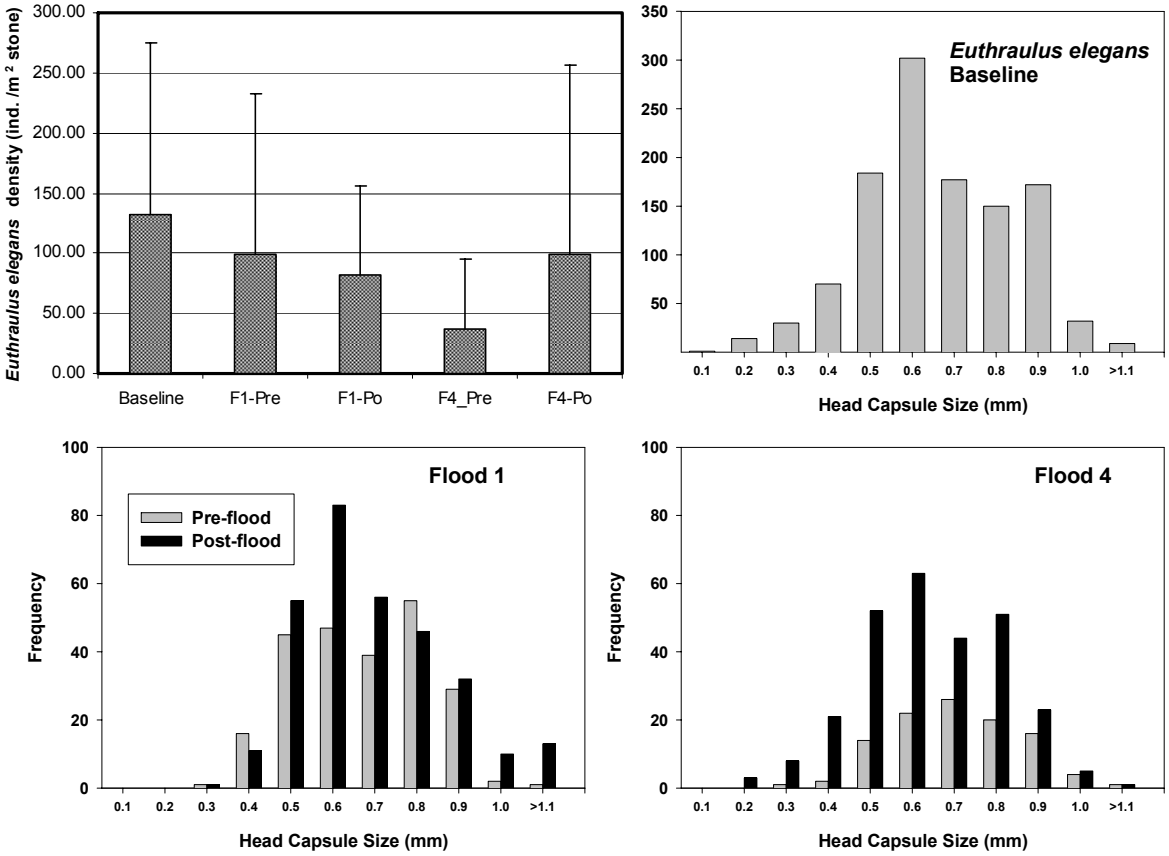
h) *Aprionyx* spp. - Molenaars River



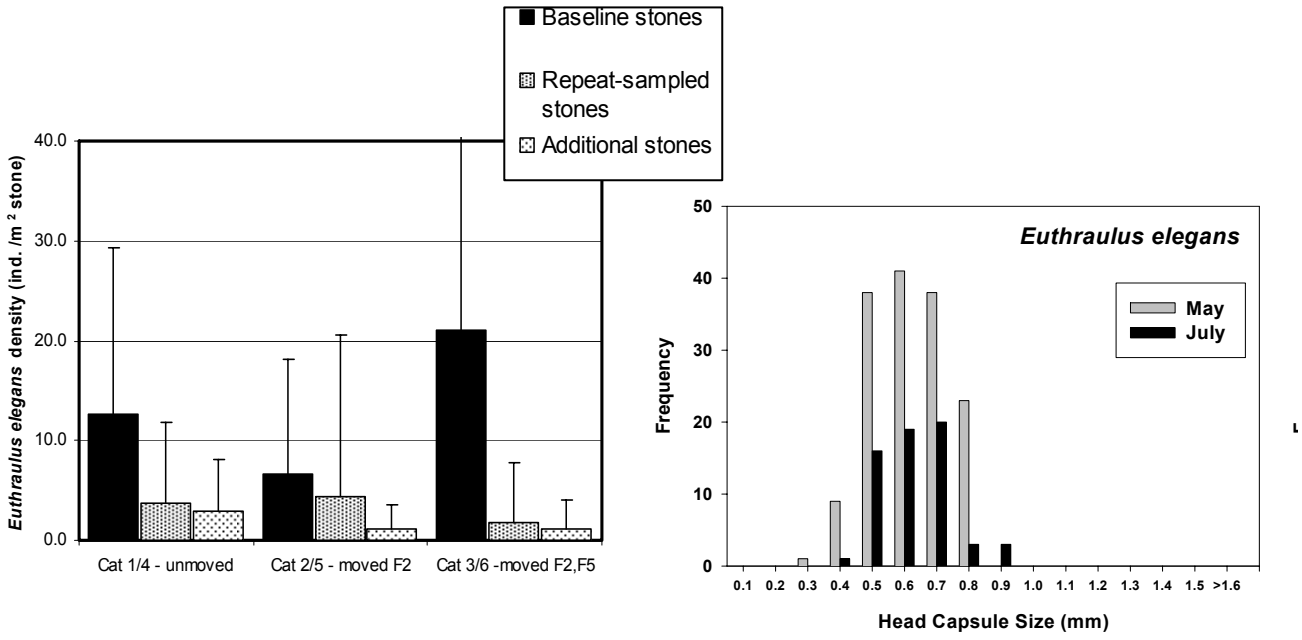
h) *Aprionyx* spp. - Berg River



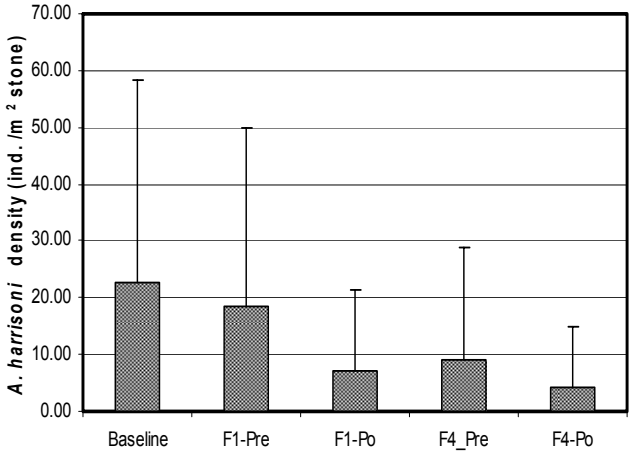
i) *Euthraulus elegans* - Molenaars River

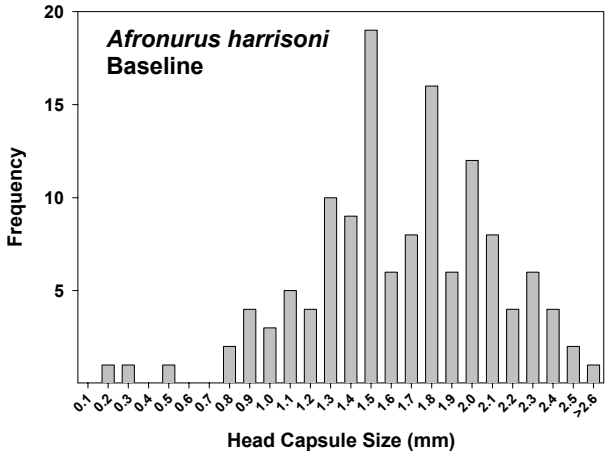


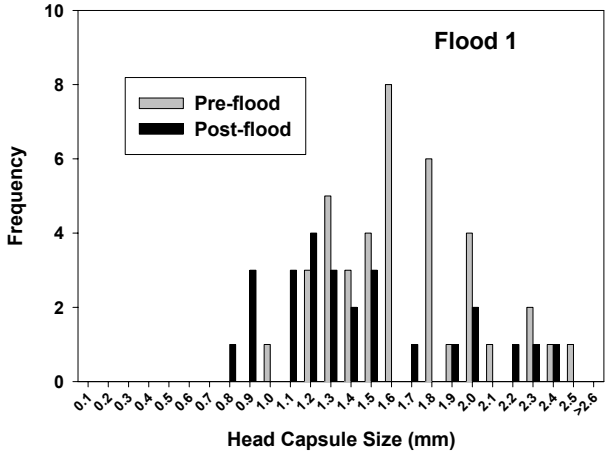
i) *Euthraulus elegans* - Berg River

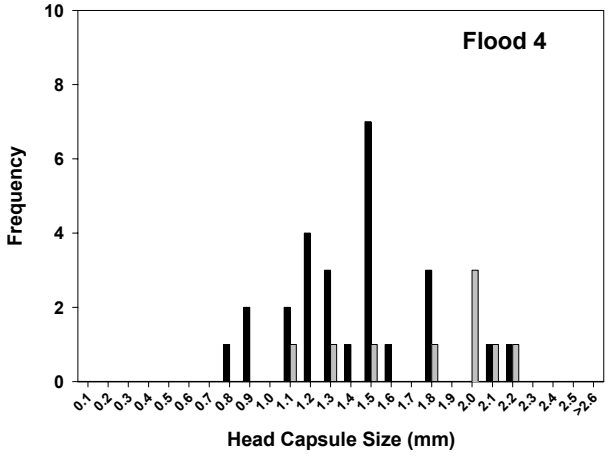


j) *Afronurus harrisoni* - Molenaars River

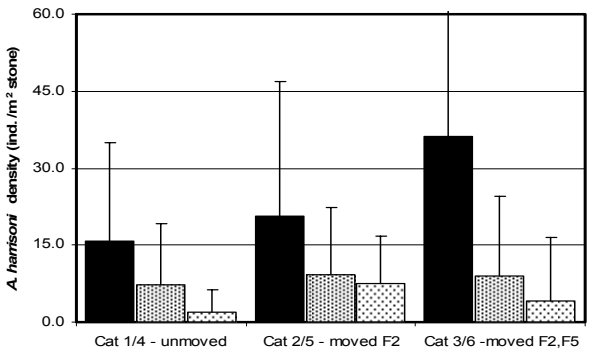


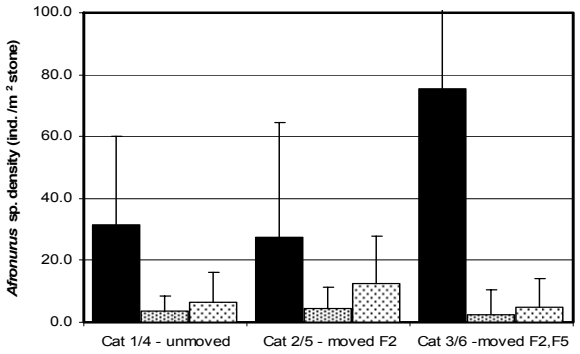


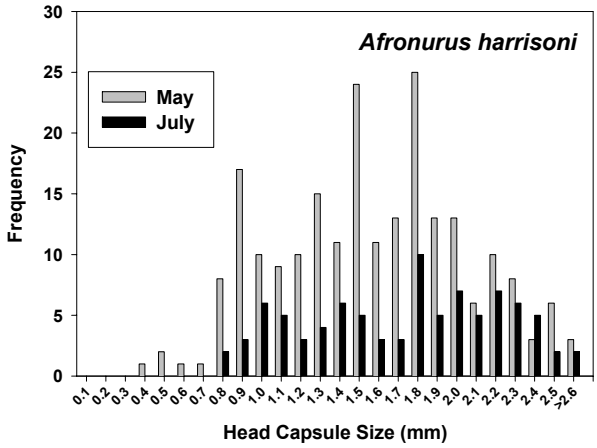


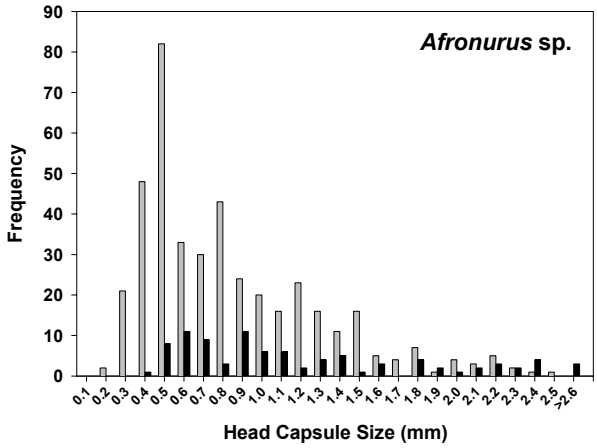


j) *Afronurus harrisoni* & k) *Afronurus* sp.- Berg River

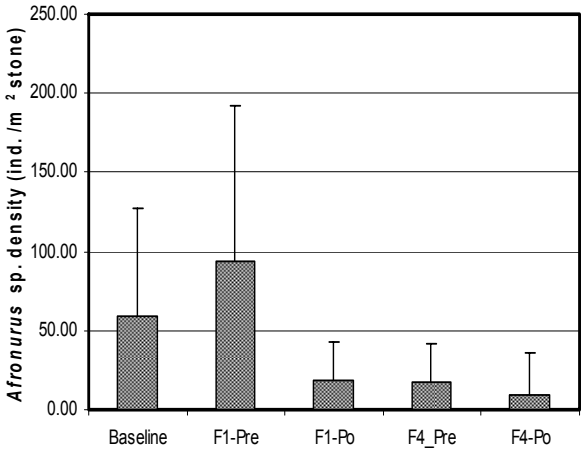


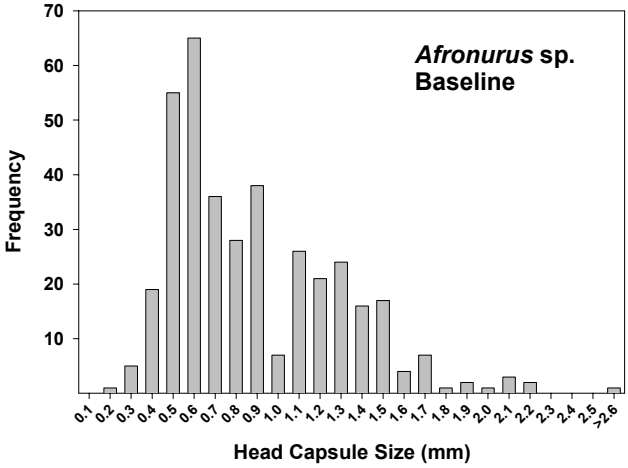


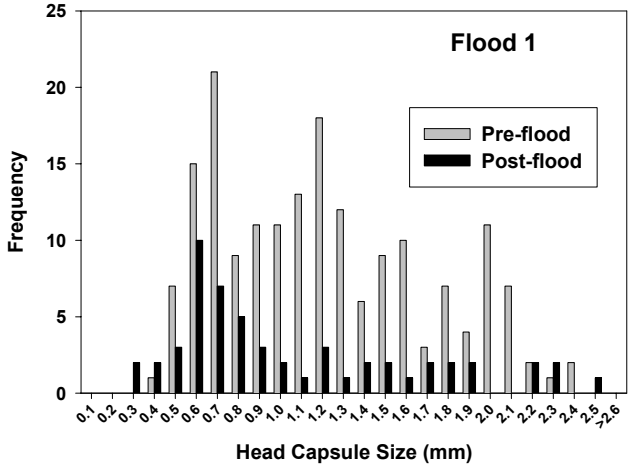


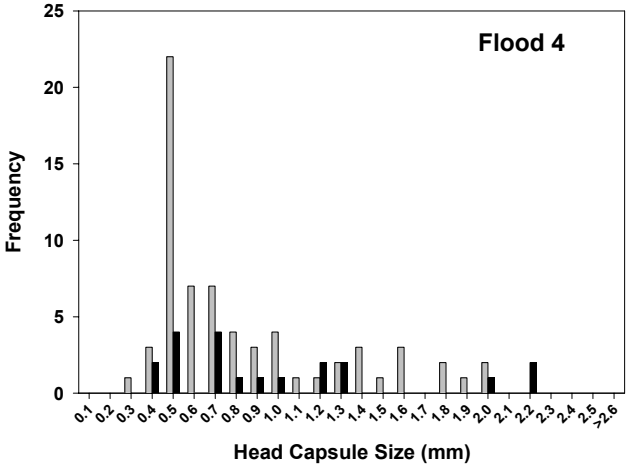


k) *Afronurus* sp. - Molenaars River









e ***Baetis* spp.**

Baetis spp. (largely *B. harrisoni*) was the dominant Baetid mayfly in both the rivers, although in the Molenaars River this taxon occurred at three-times the density of that in the Berg River. In the Molenaars River, *Baetis* spp. did not recover on previously sampled stones after initial sampling (there were significant differences in Baseline - Pre-Flood 1 sampling; Figure 6.2). However, accounting for this by using the Pre-Flood1 to Post-Flood4 data sets, there was a 16% decrease in population size associated with the series of small floods (Table 6.10).

Despite possible flood mortality, small floods in the Molenaars River may also have acted in some way to increase recruitment of young instars: not only were densities of *Baetis* spp. after Flood 1 higher, but Post Flood 1 mean head width was smaller than that prior to the flood, and there was significant difference in the pre-post flood population size-frequency distribution (Table 6.12, Figure 6.14e), with an increase in the dominance of small size classes suggesting recruitment of smaller individuals. The fact that population declined over the study period despite recruitment of new instars, and the fact that the proportion of near-mature instars did not increase suggests that this species is not particularly resistant to floods, unlike *D. capensis* for example, but that continuous recruitment offsets population losses that occur even with small floods.

In the Berg River, the population of *Baetis* spp. at the May 2004 Baseline survey was also more mature than its counterpart had been in the Molenaars River in June 2003 (modal head width 0.5 mm in the Berg vs. 0.3 mm in the Molenaars River; Figure 4.16e). Even though the floods were far greater than those on the Molenaars River, the population reduction was only some 26% (Table 6.5). Unmoved stones provided a small refugium - an 11-34% decline on unmoved stones vs. a 29-46% decline on moved stones (Table 6.11; Figure 6.14e). An examination of the change in population structure over the 2-month period indicates a considerable shift towards small instars (Figure 6.14e, Table 6.13), suggesting that massive recruitment was responsible for offsetting population losses during floods. Because of the large population size, a comparison of the size frequency distribution on unmoved (Category 1 and 4) and moved (Category 3 and 6) stones was undertaken (Figure 6.15). This showed a strong tendency for mid-sized to large individuals to be associated with stable stones, whilst new instars recruited readily (and quickly) onto moved stones. Thus not only did unmoved stones represent a relative refugium for *Baetis* spp in terms of population losses, this refugium acts to protect larger individuals from flood-induced mortality. Nevertheless, it is noteworthy that even moved stones were ‘inhabited’ by large, mature nymphs (0.8 mm and larger), as indicated in Figure 6.15.

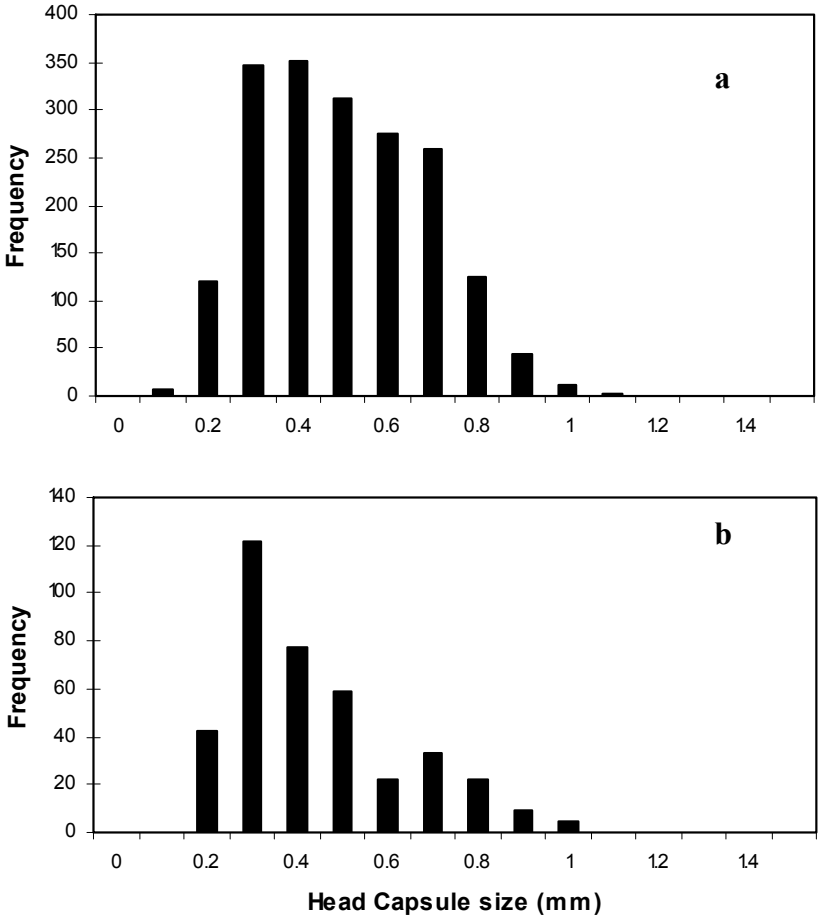


Figure 6.15 Post-flood population size frequency distributions of *Baetis* spp. in the Berg River a) on unmoved stones (Category 1 and 4), and b) on moved stones (Category 3 and 6). Note the scale change on the y-axes of the two graphs.

6.4.1.ii Telagonodidae

Three species of Telagonodidae were present in the Berg and Molenaars Rivers, *Lestagella penicillata* (Figure 6.14f), *Lithogloea harrisoni* (Figure 6.14g) and *Nadinitella crassi*. The latter two species responded to floods in the same manner, but since *N. crassi* was represented in low densities, only data for *L. harrisoni* is presented.

a ***Lestagella penicillata***

In the Pre-Flood 1 survey, *L. penicillata* densities were only 47% of the Baseline density, with a significant difference (see Figure 6.2 and section 6.1.2) indicating a failure of this species to recover. Thereafter, no change in density was observed over the duration of the study in the Molenaars River (Figure 6.14f; Table 6.10). In other words, accounting for the sampling effect of initial Baseline survey sampling can be achieved by comparing the Pre-Flood 1 densities with those of subsequent surveys. The data in Figure 6.1.4f show no change in density from the Pre-Flood 1 to Post-Flood 4 surveys, and this can be considered to the species' response to the series of Class I floods. However, significant

differences in population structure were observed between the Baseline population and all other surveys (Table 6.12), indicating the slow maturation of this species over the season.

In the Berg River, the population of *L. penicillata* was, once again, generally more mature (larger modal head capsule width) than the Molenaars Baseline population. The species was, however, associated with an average 75 - 78% decline in population density over the study period (Table 6.5), the former based on comparing Baseline and Additional stones, and the latter comparing Baseline with Repeat-sampled stones. However, there was a substantially higher loss from stones that moved than from those that did not (Table 6.11). Unmoved stones were associated with a 64 - 67% decline whilst moved stones were associated with an 84 - 89% decline in density, both of which were highly significant (Table 6.11). This difference of some 20% represents a relative refugium afforded by unmoved stones for *L. penicillata*. The significant difference in population structure between the Baseline and the surviving population in the Berg River, post-floods (Figure 6.14f, Table 6.13) indicates maturation of *L. penicillata*, with no recruitment of new instars.

b ***Lithogloea harrisoni***

In contrast to *L. penicillata*, *Lithogloea harrisoni* densities during the Molenaars Baseline survey were very low, but increased exponentially over the study period (Table 6.10). The low numbers precluded adequate testing of changes in population structure, although the pre- to post- Flood 4 period was characterised not only by a large increase in densities, but also by a significant change in population structure (Table 6.12), suggesting that the population at the end of the study period was comprised of more than one cohort (Figure 6.14g).

In the Berg River, the higher densities of *L. harrisoni* provides for a clearer pattern. There was an overall increase in densities over the flood period of between 49 and 120% (Table 6.5), the former based on comparing Baseline and Repeat-sampled stones, and the latter comparing Baseline with Additional stones. Examination of changes associated with different stone movement categories, however, shows that these increases were only on stones that did not move (Category 1 and 4 stones), or which moved once but then had remained stable for a month prior to sampling (Category 2 and 5 stones). Moved stones (Category 3 and 6) were associated with a non-significant decrease in *L. harrisoni* density (Figure 6.14g; Table 6.11). The population size-frequency analysis indicated a significant difference in population structure from the Baseline to post-flood period (Table 6.13). These differences were associated with an increased representation of larger size classes, whilst the modal size class remained 0.3 mm, as with the Baseline condition (Figure 6.14g; Table 6.13). This indicates a substantial and continuous recruitment over the study period, combined with the maturation of the population. These results therefore also suggest that larger individuals were highly resistant to floods.

6.4.1.iii Leptophlebiidae

Five genera of Leptophlebiidae were present in the Molenaars River, of which four were also present in the Berg River. However, two somewhat different responses were identified in relation to changes in density and population structure over the study

period and are presented below. The first of these was best reflected by *Aprionyx* spp. which embodied the more characteristic Leptophlebiid response of the genera including *Choroterpes* spp., *Castanophlebia* spp. and *Adenophlebia* spp. The second was *Euthraulus elegans*, which demonstrated higher resistance to floods.

a ***Aprionyx* spp.**

Aprionyx spp. in the Molenaars Baseline survey (Figure 6.14h) was represented by a range of size classes including nymphs nearing maturity, estimated as head capsule size classes from approximately 1.3 mm and above. Population density at the Pre-Flood 1 survey were close to that of the Baseline condition, but many of the larger individuals were not well represented within the population, probably representing an autumn emergences of mature nymphs during the month between these sampling dates. Notwithstanding this, the number of individuals in the Post- Baseline data sets was very low and this reduces the confidence of these results. Overall, the Pre-Flood 1 population was reduced by 99% over the study period (Table 6.10, Figure 6.14h).

In the Berg River, Baseline samples were again suggestive of two size cohorts within the population (Figure 6.14h), but where most of the population comprised younger instars. Despite an overall 89 - 94% reduction in the population (Table 6.5), based on comparing the Baseline densities with both Repeat-sampled and Additional stones, there were no significant differences in size structure in the Berg River (Table 6.13). However, whilst decreases on moved and unmoved stones were both significant (Table 6.12), *Aprionyx* spp. were reduced to a lesser degree on unmoved stones - a difference of between 13% (using the Baseline vs. Additional stone data set) and 26% (using the Baseline vs. Repeat-sampled stone data set).

b ***Euthraulus elegans***

This species was represented by a comparatively young population during the Baseline sampling in both the Molenaars and Berg Rivers (modal head capsule width 0.6 mm in both cases; Figure 6.14i), although the population in the Molenaars River in June 2003 included pre-emergent nymphs (estimated at head capsule width of 1 mm and above). In the Molenaars River, although there was a dip in the population density in the Pre-Flood 4 survey, there was no change from the Pre-Flood 1 density to the end of the study period (Figure 6.14i; Table 6.10). The population structure varied statistically over the study period (Table 6.12), but the size distribution plots (Figure 6.14i) suggest that this was associated with the maturation of the population, with no new recruitment over the winter period.

Comparing the Baseline densities with both Repeat-sampled and Additional stones, *E. elegans* in the Berg River was reduced by the series of floods by between 77 and 91% (Table 6.5). As with Aprionyx spp., unmoved stones provided a substantial relative refugium, with losses on these stones some 18 - 21% lower than on moved stones (Table 6.11; Figure 6.14i).

6.4.1.iv Heptageniidae

Of the two species of Heptageniidae present in both rivers, *Afronurus* sp. was numerically dominant over *Afronurus harrisoni*, although the latter, both in the Molenaars River in June 2003 and in the Berg River in May 2004, was represented by a more mature population than *Afronurus* sp., as indicated by the greater normality in the frequency distribution as well as the larger modal head width (Figure 6.14j and k).

There was a significant reduction in both *A. harrisoni* in the Molenaars River over the study period, of some 78%, and of *Afronurus* sp. by 84% (Table 6.10), although these were not significant when comparing the Baseline with either Post Flood 1 or Post Flood 4 conditions, again presumably because of high variances associated with small numbers of patchily distributed animals. In the case of the more mature *A. harrisoni*, the decreased density was reflected as a loss of larger individuals (Figure 6.14j). However, with *Afronurus* sp., the post-floods frequency distribution of size data (Figure 6.14k) suggests if anything a loss of small to medium-sized nymphs.

In the Berg River *A. harrisoni* was also associated with a more mature population, and showed a slightly lower population reduction than *Afronurus* sp. (Table 6.5). *A. harrisoni* enjoyed a relative refugium on unmoved stones (Figure 6.14j; Table 6.11), although this was only true comparing Baseline densities against Repeat-sampled stones, and not when the Additional stones data set was compared with the Baseline data.. Nevertheless, on Repeat-sampled stones, there were non-significant population reductions of some 54% on unmoved stones vs. 75% on moved stones (Table 6.11) over the study period, a far smaller reduction than that measured in the small floods of the Molenaars River study. Based on the Additional stones data set, this reduction was much larger - between 88 (unmoved) and 89% (moved stones).

In the case of *Afronurus* sp., there was more agreement between the results based on Baseline vs. Repeat-sampled stones and Baseline vs. Additional stones (Table 6.11). *Afronurus* sp enjoyed an 8 - 14% relative refugium on unmoved stones vs. moved stones.

Size frequency analysis showed very little change in population structure in the case of *A. harrisoni*, suggesting a combination of slow growth over the study period, no new recruitment and a tendency for smaller individuals to succumb to floods. There was a significant difference, however, in the frequency distribution of *Afronurus* sp. before and after the floods, with a substantially increased mean head width (Table 6.13) which combined with visual examination of the plot in Figure 6.14k is strongly suggestive of higher mortality rates for younger instars.

6.4.2 Trichoptera:

Six families of Trichoptera were present in the Berg and Molenaars Rivers at densities that allowed for analysis of changes over the study period. Low genus / species richness within the Families, at least for the autumn / winter assemblages, meant that most of these were represented by only one or two species.

Table 6.12a Results of Kolmogorov Smirnov test for differences in size-frequency distributions over the study period, for taxa on the Molenaars River: sample size, mean head width ± standard deviation (SD) for each of the five sampling periods. Significance levels are provided in Table 6.12b.

	Baseline		Pre-flood 1		Post-flood 1		Pre-flood 4		Post-flood 4	
Taxon	**N**	**Mean ± SD**	**N**	**Mean ± SD**	**N**	**Mean ± SD**	**N**	**Mean ± SD**	**N**	**Mean ± SD**
Demoulinia spp.	68	0.32 ± 0.15	14	0.41 ± 0.17	7	0.38 ± 0.14	17	0.43 ± 0.12	19	0.40 ± 0.13
Afroptilum spp.	4052	0.33 ± 0.09	2359	0.37 ± 0.07	270	0.40 ± 0.10	1165	0.38 ± 0.09	463	0.40 ± 0.10
Demoreptus capensis	3060	0.28 ± 0.09	1302	0.32 ± 0.11	167	0.31 ± 0.10	847	0.34 ± 0.09	97	0.34 ± 0.11
Pseudocloeon spp.	202	0.22 ± 0.11	66	0.34 ± 0.17	40	0.23 ± 0.13	16	0.32 ± 0.13	13	0.27 ± 0.13
Baetis spp.	15726	0.22 ± 0.09	4500	0.28 ± 0.09	6171	0.26 ± 0.10	3072	0.32 ± 0.12	2316	0.33 ± 0.12
Lestagella penicillata	2703	0.47 ± 0.08	634	0.52 ± 0.07	610	0.52 ± 0.09	555	0.52 ± 0.09	541	0.51 ± 0.10
Lithogloea harrisoni	5	0.36 ± 0.11	1	0.27	14	0.33 ± 0.14	44	0.28 ± 0.08	90	0.36 ± 0.15
Aprionyx spp.	88	0.95 ± 0.21	15	0.90 ± 0.30	3	0.98 ± 0.32	10	0.95 ± 0.32	1	1.07
Euthraulus elegans	1141	0.62± 0.18	235	0.62 ± 0.24	307	0.64 ± 0.18	106	0.65 ± 0.16	271	0.58 ± 0.17
Afronurus harrisoni	132	1.62 ± 0.45	40	1.62 ± 0.34	26	1.39 ± 0.44	26	1.38 ± 0.33	9	1.72 ± 0.36
Afronurus spp.	379	0.85 ± 0.41	180	1.17 ± 0.49	55	1.02 ± 0.59	67	0.78 ± 0.46	20	0.93 ± 0.57
Cheumatopsyche afra	45	0.86 ± 0.28	1	1.02	2	0.71 ± 0.28	3	0.90 ± 0.15	8	0.79 ± 0.26
Chimarra spp.	206	1.09 ± 0.57	10	0.81 ± 0.70	11	0.62 ± 0.31	10	0.89 ± 0.57	27	0.92 ± 0.51
Athripsodes bergensis	98	0.48 ± 0.20	14	0.55 ± 0.18	22	0.41 ± 0.18	15	0.33 ± 0.11	2	0.56 ± 0.20
Agapetus agilis	183	0.25 ± 0.10	74	0.26 ± 0.10	43	0.29 ± 0.12	23	0.34 ± 0.14	18	0.25 ± 0.08
Notonemouridae spp.	23	0.58 ± 0.21	3	0.45 ± 0.19	10	0.28 ± 0.18	16	0.41 ± 0.29	48	0.46 ± 0.17
Simulium spp.	1075	0.54 ± 0.21	827	0.44 ± 0.20	522	0.54 ± 0.22	937	0.52 ± 0.24	380	0.50 ± 0.22
Elporia spp.	7716	0.24 ±0.20	1525	0.26 ± 0.12	1272	0.25 ± 0.11	1717	0.28 ± .14	778	0.31 ± 0.15
Tanypodinae spp.	392	0.41 ± 0.18	121	0.49 ± 0.24	53	0.33 ± 0.17	62	0.51 ± 0.23	29	0.33 ± 0.12
Orthocladiinae spp.	3589	0.19 ± 0.05	1697	0.18 ± 0.05	1918	0.17 ± 0.05	1988	0.19 ± 0.07	1544	0.19 ± 0.06

	Baseline		Pre-flood 1		Post-flood 1		Pre-flood 4		Post-flood 4	
Taxon	**N**	**Mean ± SD**	**N**	**Mean ± SD**	**N**	**Mean ± SD**	**N**	**Mean ± SD**	**N**	**Mean ± SD**
Tanytarsini spp.	340	0.21 ± 0.06	74	0.22 ± 0.06	60	0.22 ± 0.06	53	0.22 ± 0.06	72	0.22 ± 0.06
Chironomini spp.	175	0.19 ± 0.09	29	0.25 ± 0.14	12	0.22 ± 0.09	19	0.31 ± 0.09	23	0.19 ± 0.09
Elmidae spp. larvae	894	0.24 ± 0.10	136	0.23 ± 0.10	189	0.21 ± 0.08	238	0.22 ± 0.08	262	0.21 ± 0.06
Elmidae spp. adults	81	0.35 ± 0.08	5	0.23 ± 0.11	18	0.33 ± 0.04	13	0.34 ± 0.05	10	0.37 ± 0.05
Hydrophilidae spp.	17	0.18 ± 0.03	14	0.16 ± 0.02	37	0.16 ± 0.04	18	0.15 ± 0.03	5	0.17 ± 0.025
Hydraenidae spp.	98	0.32 ± 0.04	49	0.33 ± 0.05	2	0.36 ± 0.08	5	0.30 ± 0.01	13	0.33 ± 0.06
Helodidae spp.	71	0.57 ± 0.17	9	0.54 ± 0.14	18	0.49 ± 0.14	13	0.52 ± 0.10	17	0.54 ± 0.10
Hydrachnellae spp.	69	0.20 ± 0.08	39	0.21 ± 0.06	39	0.21 ± 0.04	22	0.17 ± 0.07	16	0.21 ± 0.06

Table 6.12b Results of Kolmogorov Smirnov test for differences in size-frequency distributions over the study period, for taxa on the Molenaars River: significance level for pairwise comparisons between the Baseline and all other periods, and between pre- and post Flood 1 and Flood 2..

Taxon	Baseline v Pre 1	Baseline v Post 1	Baseline v Pre 4	Baseline v Post 4	Pre 1 v Post 1	Pre 4 v Post 4
Demoulinia spp.	p < 0.050	p > 0.100	p < 0.001	p < 0.025	p > 0.100	p > 0.100
Afroptilum spp.	p < 0.001	p < 0.001	p < 0.001	p < 0.001	p < 0.001	p < 0.001
Demoreptus capensis	p < 0.001	p < 0.001	p < 0.001	p < 0.001	0.050 > p < 0.010	P > 0.100
Pseudocloeon spp	p < 0.001	p > 0.100	p < 0.010	p > 0.100	p < 0.005	p > 0.100
Baetis spp	p < 0.001	p < 0.001	p < 0.001	p < 0.001	p < 0.001	p < 0.010
Lestagella penicillata	p < 0.001	p < 0.001	p < 0.001	p < 0.001	p < 0.010	p > 0.100
Lithogloea harrisoni		p > 0.100	p > 0.100	p > 0.100		p < 0.010
Aprionyx spp.	p > 0.100	p > 0.100	p > 0.100		p > 0.100	
Euthraulus elegans	p < 0.050	p > 0.001	p < 0.025	p < 0.001	0.050 > p < 0.010	p < 0.025
Afronurus harrisoni	p > 0.100	p < 0.005	p < 0.005	p > 0.100	p > 0.050	p > 0.100
Afronurus spp.	p < 0.001	p > 0.100	p < 0.001	p > 0.100	p < 0.025	p > 0.100
Cheumatopsyche afra		p > 0.100	p > 0.100	p > 0.100		p > 0.100
Chimarra spp	p < 0.050	p < 0.025	p > 0.100	p > 0.100	p > 0.100	p > 0.100
Athripsodes bergensis	p > 0.100	p > 0.100	p < 0.025	p > 0.100	p > 0.100	p > 0.100
Agapetus agilis	p > 0.100	p > 0.100	p < 0.050	p > 0.100	p > 0.100	p > 0.100
Notonemouridae spp.	p > 0.100	p < 0.005	p > 0.100	p < 0.050	p > 0.100	p < 0.050
Simulium spp	p < 0.001	p < 0.001	p < 0.001	0.050 > p < 0.010	p < 0.025	p > 0.100
Elporia spp	p < 0.001	p < 0.001	p < 0.001	p < 0.001	p < 0.050	p < 0.001
Tanypodinae spp.	p < 0.001	p < 0.001	p < 0.001	p < 0.001	p < 0.025	p < 0.001
Orthocladiinae spp.	p < 0.001	p < 0.001	p < 0.001	p < 0.001	p < 0.001	p < 0.050
Chironomini spp.	p > 0.100	p > 0.100	p < 0.001	p > 0.100	p > 0.100	p < 0.005
Tanytarsini spp.	p > 0.100	0.050 > p < 0.010	p < 0.025	p < 0.050	p > 0.100	p > 0.100
Elmidae spp. Larvae	p > 0.100	p < 0.001	p < 0.001	p < 0.001	p < 0.025	p > 0.100
Elmidae spp. Adults	0.050 > p < 0.010	p > 0.100	p > 0.100	p > 0.100	p > 0.100	p > 0.100
Hydrophilidae spp	p > 0.100	p > 0.100	p > 0.100	p > 0.100	p > 0.100	p > 0.100
Hydraenidae spp.	p > 0.100	p > 0.100	0.050 > p < 0.010	p > 0.100	p > 0.100	p > 0.100
Helodidae spp.	p > 0.100	p > 0.100	p > 0.100	p > 0.100	p > 0.100	p > 0.100
Hydrachnellae spp.	p > 0.100	p > 0.100	p > 0.100	p > 0.100	p > 0.100	p > 0.100

Table 6.13 Results of Kolmogorov Smirnov test for differences in size-frequency distributions for taxa on the Berg River: sample size (N), mean head width ± standard deviation (SD) and significance level for comparison between the Baseline and Post-flood periods.

	May (Baseline)		July (Post-floods)		
Taxon	**N**	**Mean ± SD**	**N**	**Mean ± SD**	**P-value**
Demoulinia spp.	307	0.40 ± 0.12	19	0.40 ± 0.17	>0.100
Afroptilum spp.	214	0.43 ± 0.46	114	0.46 ± 0.15	<0.001
Demoreptus capensis	104	0.44 ± 0.17	75	0.47 ± 0.26	<0.025
Pseudocloeon spp.	18	0.31 ± 0.23	55	0.36 ± 0.24	>0.100
Baetis spp.	7333	0.44 ± 0.15	8594	0.41 ± 0.19	<0.001
Lestagella penicillata	1997	0.42 ± 0.07	1038	0.56 ± 0.10	<0.001
Lithogloea harrisoni	109	0.33 ± 0.09	441	0.38 ± 0.12	<0.001
Aprionyx spp.	184	0.95 ± 0.22	45	0.99 ± 0.28	>0.100
Euthraulus elegans	150	0.57 ± 0.12	62	0.57 ± 0.11	>0.100
Afronurus harrisoni	220	1.54 ± 0.49	89	1.68 ± 0.49	<0.100
Afronurus sp.	418	0.80 ± 0.46	91	1.15 ± 0.64	<0.001
Cheumatopsyche afra	36	0.75 ± 0.35	1	0.75 ± 0.00	
Cheumatopsyche	84	0.61 ± 0.33	22	0.83 ± 0.30	<0.001
Chimarra spp.	140	0.78 ± 0.49	18	0.98 ± 0.36	<0.005
Athripsodes bergensis	237	0.26 ± 0.04	102	0.16 ± 0.05	<0.001
Notonemouridae	80	0.58 ± 0.18	67	0.56 ± 0.29	<0.025
Simulium spp.	496	0.54 ± 0.19	568	0.55 ± 0.22	<0.010
Orthocladiinae	6986	0.19 ± 0.07	9180	0.22 ± 0.07	<0.001
Tanypodinae	816	0.34 ± 0.14	105	0.31 ± 0.16	<0.010
Chironomini	251	0.23 ± 0.08	136	0.20 ± 0.07	<0.010
Tanytarsini	433	0.25 ± 0.09	106	0.24 ± 0.09	>0.100
Elmidae (larvae)	2046	0.23 ± 0.07	281	0.25 ± 0.06	<0.001
Elmidae (adults)	330	0.32 ± 0.08	88	0.34 ± 0.06	<0.100
Helodidae	232	0.37 ± 0.11	106	0.50 ± 0.10	<0.001
Hydrachnellae	91	0.25 ± 0.09	35	0.31 ± 0.11	<0.100

6.4.2.i Hydropsychidae - Cheumatopsyche afra and *C. maculata*

Cheumatopsyche afra occurs at the study site in both the Berg and Molenaars Rivers, although in the Berg River it co-occurs with *C. maculata*. In the Molenaars River, *C. afra* was very patchily distributed, as indicated by the high standard deviation in the Baseline density in Figure 6.14*l*. The size-frequency distribution indicates that there was a range in the maturity level at this time.

The Post-Flood 1 densities of *C. afra* were indicative of a complete failure of this species to recover on previously denuded stones within a month of initial sampling, although the patchy distribution of the Baseline data precluded statistically significant results. By the Post Flood 4 survey, i.e. notwithstanding the four small floods, densities had gradually recovered to 34% of the Baseline condition. This recovery was as a result of the colonisation on river substrata by mature individuals, not from new recruitment, as evident

from the size frequency data in Figure 6.14*l*. Excluding the initial sampling effect, therefore, it can be considered that Class I floods did not cause a change in *C. afra* densities in the Molenaars River.

In the Berg River, the size frequency data for *C. afra*, although different from that in the Molenaars River in 2003, had the a similar modal size class - 0.8 mm - which is assumed to correspond to mid- late instars, given the broader spread of size classes within the population. However, in nearly 200 Post-flood samples, only one individual was collected, illustrating a different fate of this species in the face of larger floods than those which occurred in the Molenaars River in 2003.

In the Berg River *C. maculata*, on the other hand, was characterised by a population dominated by early instars (Figure 6.14m). A reduction in density over the study period in the order of 86% was observed when comparing Baseline with Additional stones. Repeat-sampled stones were not used for comparison, given the strong sampling effect evident in the Molenaars study. The difference in density decreases on moved and unmoved stones (Table 6.11, using Baseline - Additional stones only) was 14%, which represents the relative refugium offered to this species on unmoved stones. Finally, population losses appeared to affect small instars disproportionally, with a significant decline over the study period in mean head capsule width, accompanied by a shift in the modal size class from 0.3 mm to 0.8 mm, a change that is unlikely to represent mere developmental growth.

6.4.2.ii Philopotamidae - Chimarra spp.

Chimarra spp. displayed a similar response to initial sampling as *C. afra*, with a slow recovery over the sampling period. Interestingly, densities after Flood 1 and Flood 4 were marginally higher then the pre-flood densities, suggesting that small floods might have aided, rather than inhibited, recolonisation (Figure 6.14 n).

In the Berg River study, once again only Additional stones were used in the analysis because of the sampling effect demonstrated in the Molenaars River study. Table 6.11 indicates a large difference in density decreases on unmoved (51%) vs. moved (99%) stones, thus indicating the relative refugium potential of unmoved stones for this species (Figure 6.14 n). Although the sample size in the post-flood survey was very small, comparison of the head capsule size-frequency distribution for the two periods indicates the larger effect of the floods on small instars, with a significant change in distribution (Table 6.13) and larger mean head width in the later survey.

6.4.2.iii Glossossomatidae - Agapetus agilis

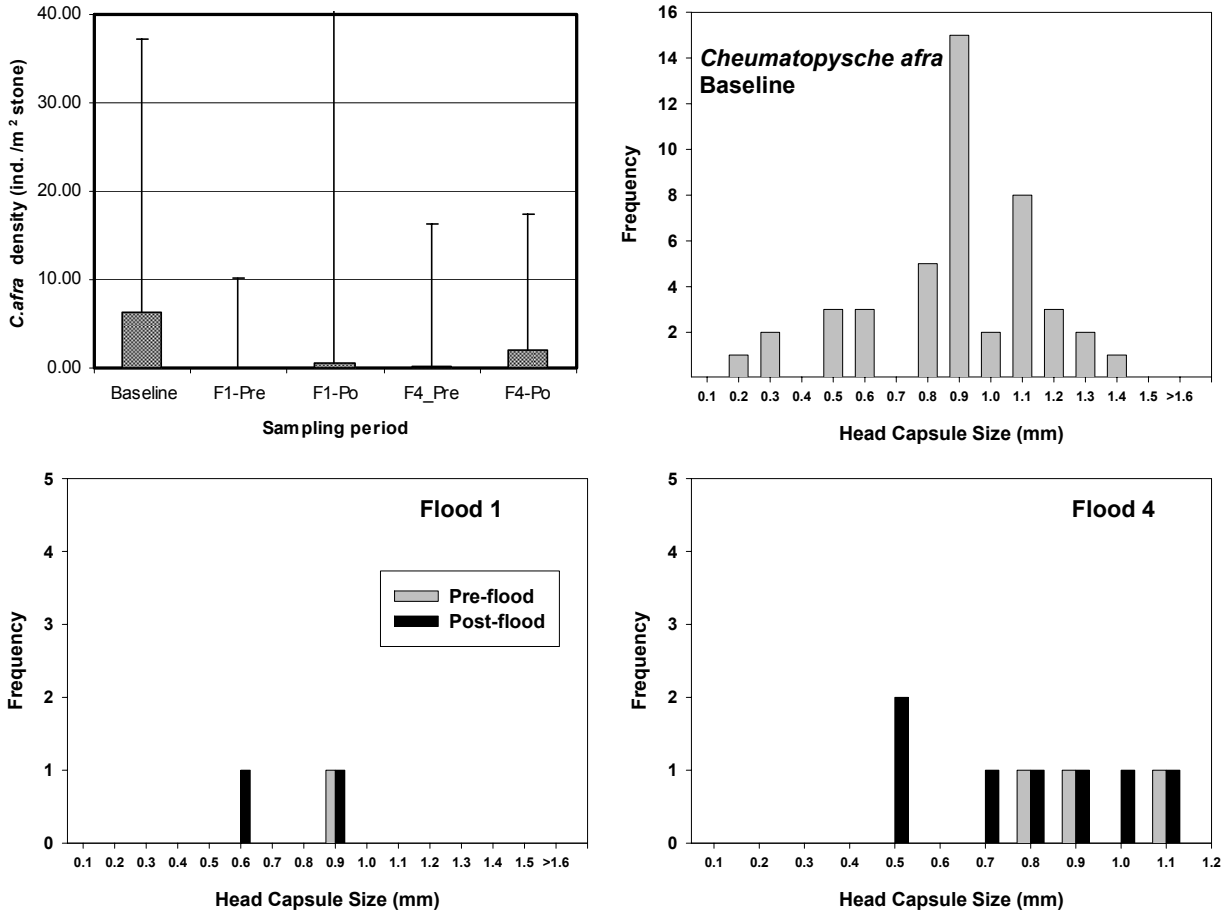
The *Agapetus agilis* population in the Molenaars River during the Baseline survey was dominated by young instars (Figure 6.14o). Recovery on denuded stones was slow following initial sampling, but increased after the first flood. However, the population on the resampled stones thereafter declined over the study period. The shifts in head capsule size frequency distribution from unimodal to bimodal over the study period suggests that recruitment of new instars and developmental growth was taking place, despite which the

data suggest an overall decrease in population from Pre-Flood 1 to Post-Flood 4 of some 47%.

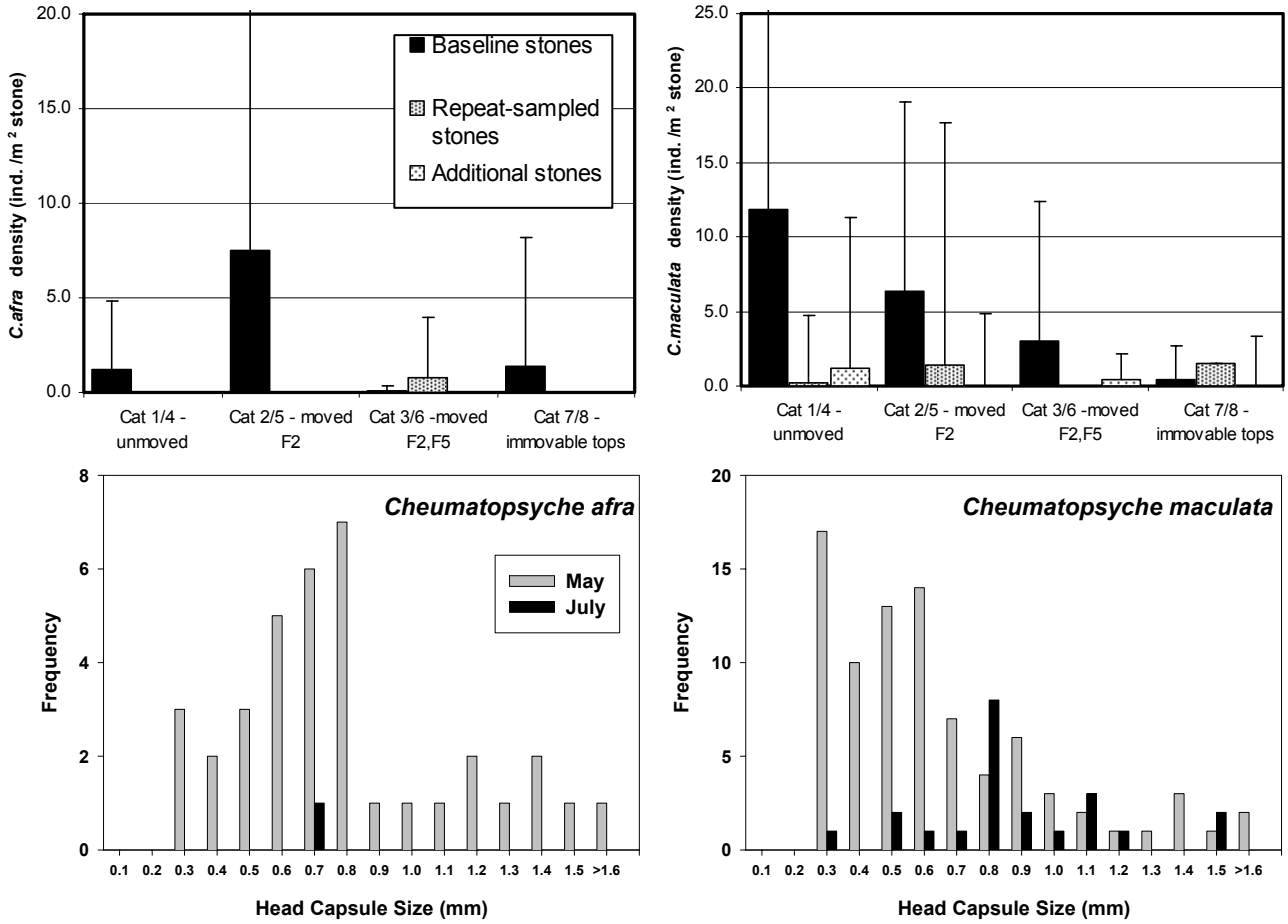
The density data for the Berg River were too low to allow for size-frequency analysis or statistical analysis of difference. The bar graphs are included, however, simply to indicate that in this river, *A. agilis* increased over the study period, especially on unmoved stones (Figure 6.14o).

Figure 6.14l-z Mean species density (+ standard deviation) and population size frequency distributions in the Molenaars River, on each of the five sampling occasions during the 2003 study, followed by mean species density and population size frequency distributions for the two sampling surveys in the Berg River in 2004 analysed separately for each of the stone movement categories.
Data are presented for
l) Cheumatopsyche afra; m) Cheumatopsyche maculata; n) Chimarra sp.;
o) Agapetus agilis; p) Notonemouridae; q) *Simulium* spp.; r) Tanypodinae;
s) Orthocladiinae; t) Tanytarsini; u) Chironomini; v) *Elporia* spp.; w) Elmidae larvae;
x) Elmidae adults; y) Helodidae z) Hydrachnellae

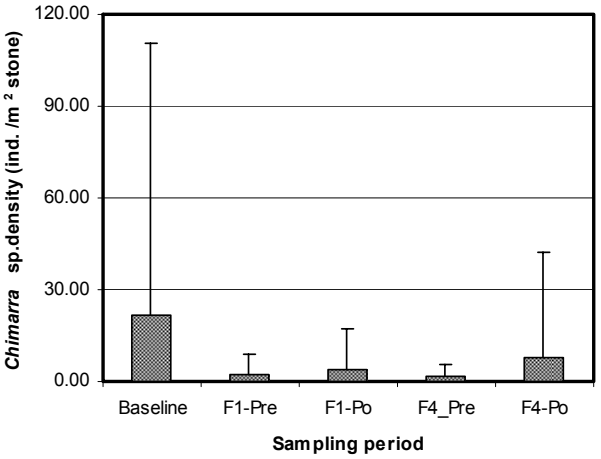
l) *Cheumatopsyche afra* - Molenaars River

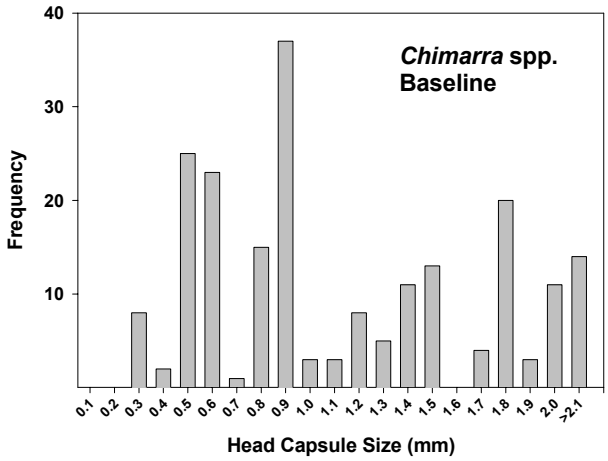


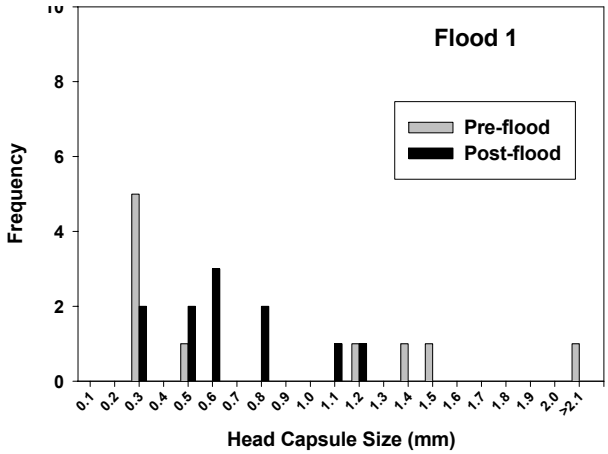
l) *Cheumatopsyche afra* & m) *Cheumatopsyche maculata* - Berg River

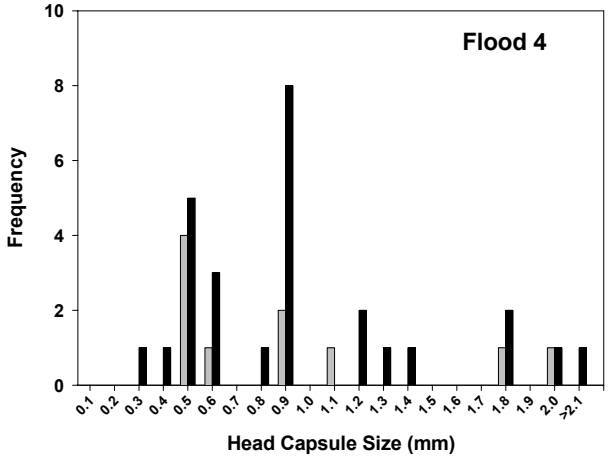


n) *Chimarra sp.* - Molenaars River

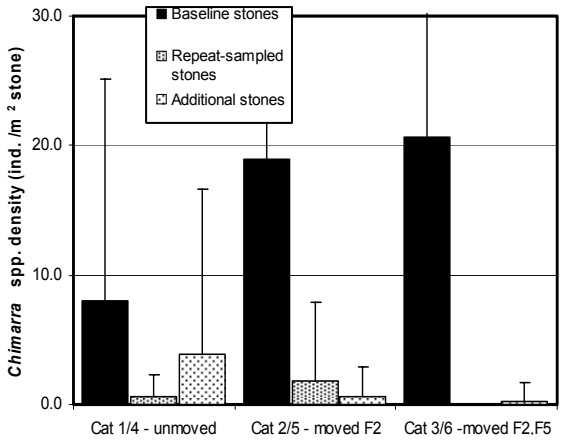


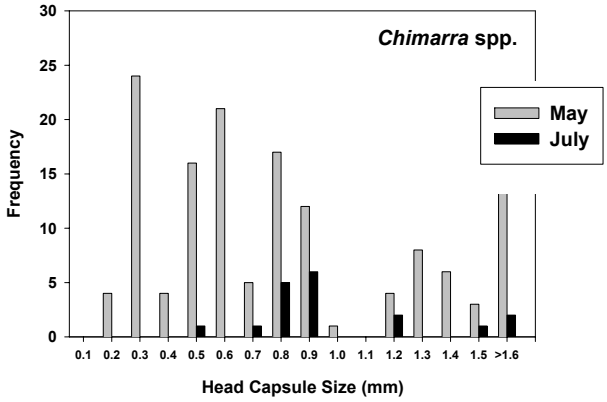




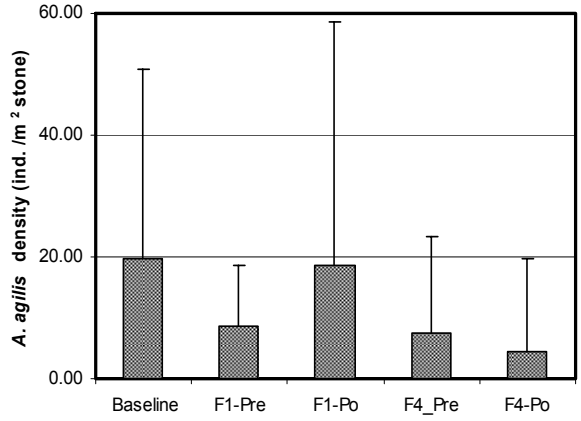


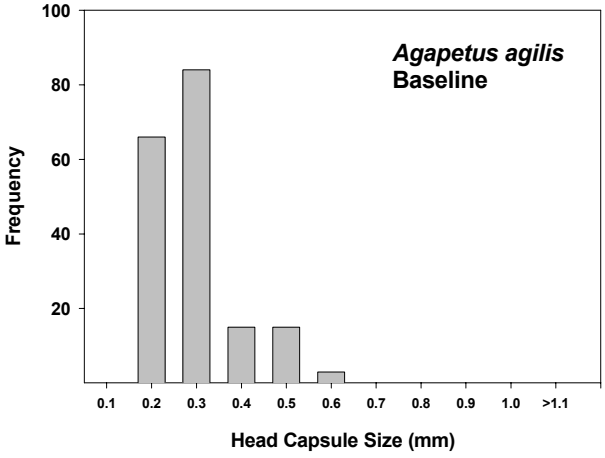
n) *Chimarra sp* - Berg River

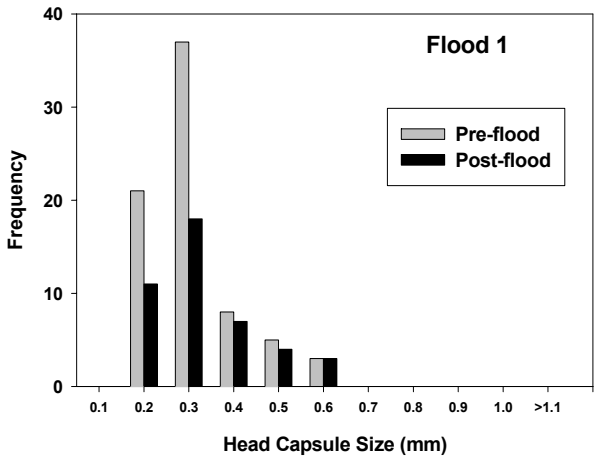


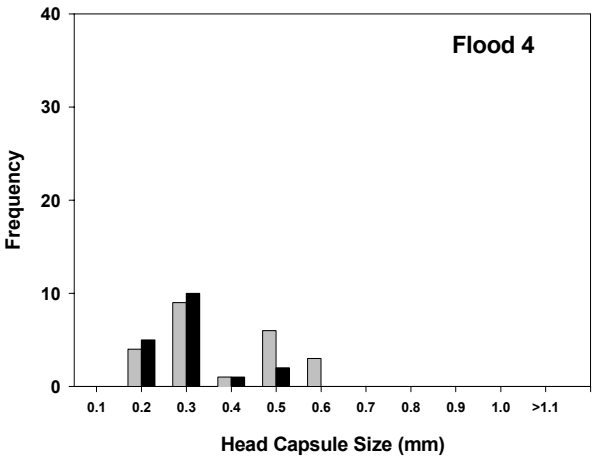


o) *Agapetus agilis* - Molenaars River

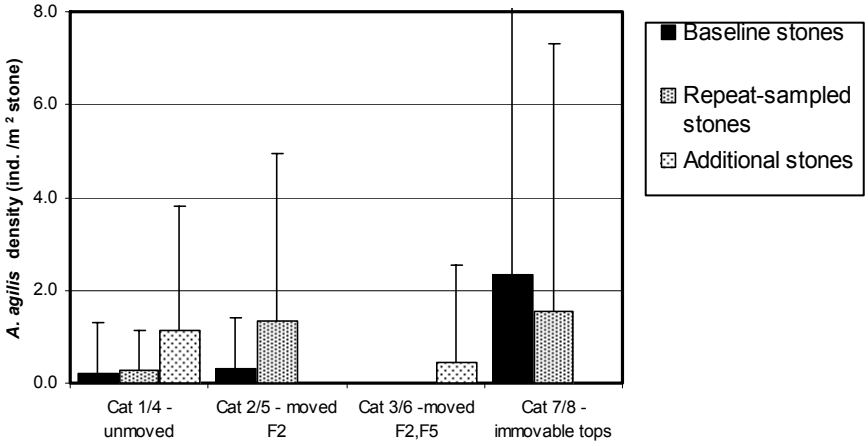




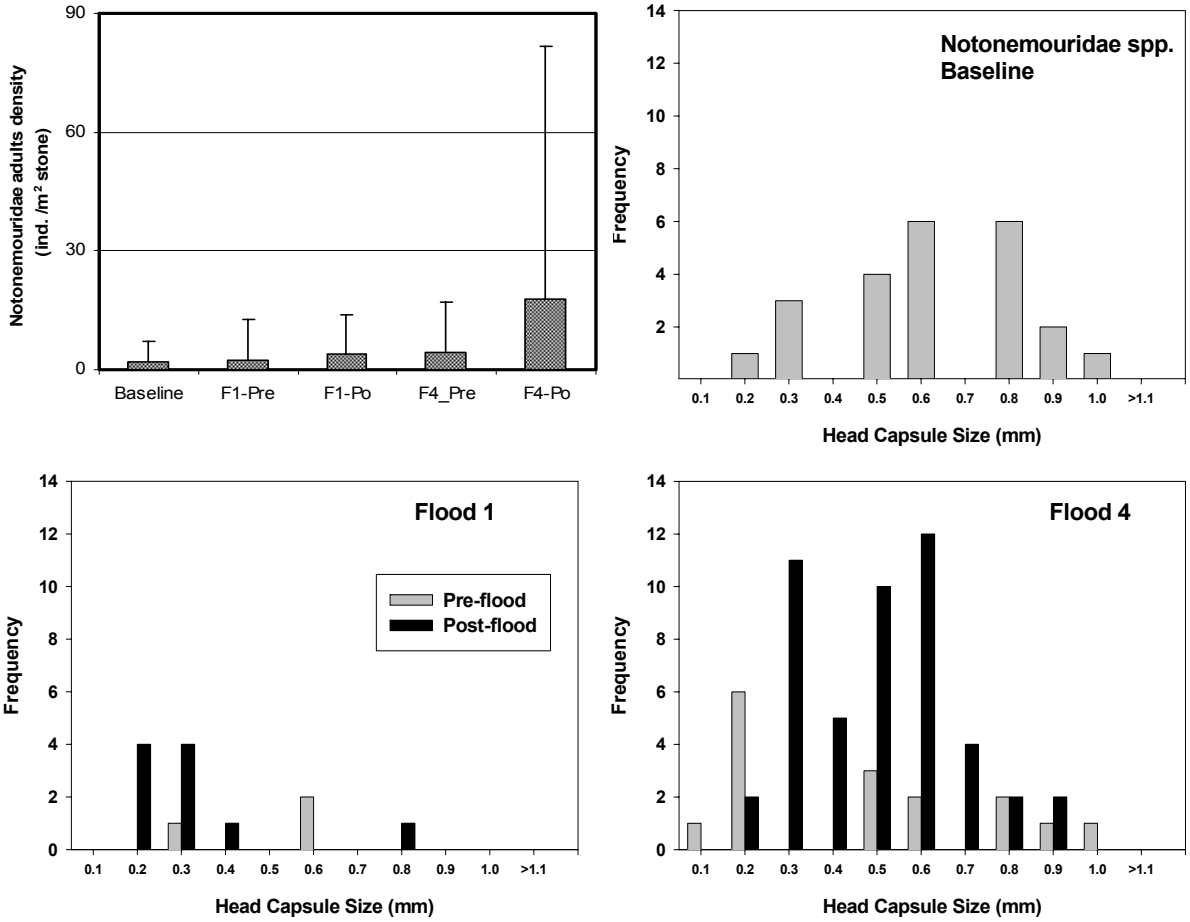




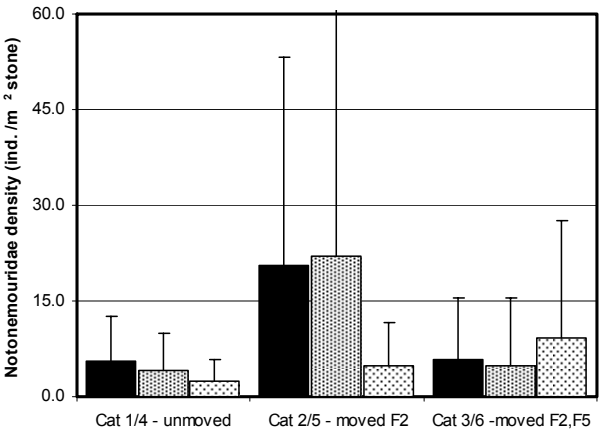
o) *Agapetus agilis* - Berg River

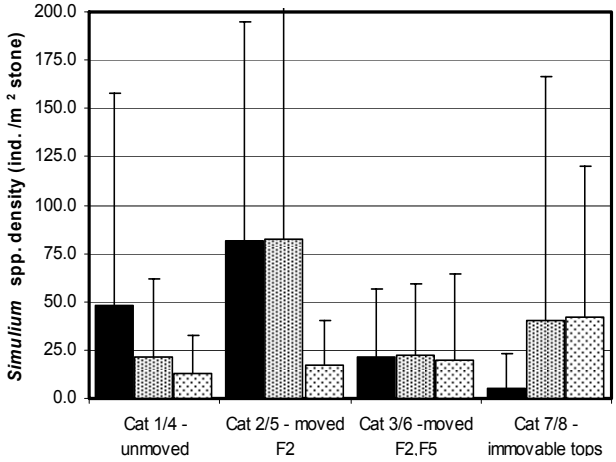


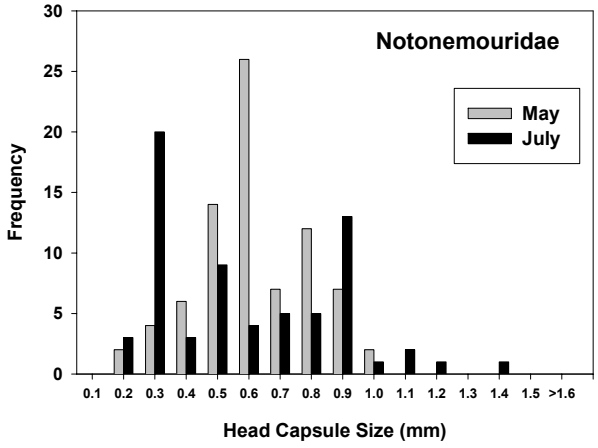
p) Notonemouridae - Molenaars River

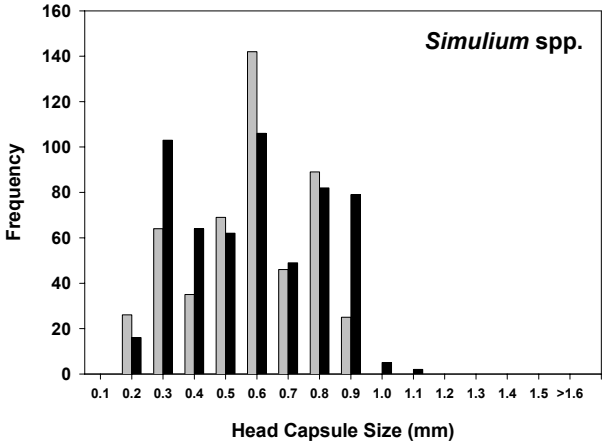


p) Notonemouridae & q) *Simulium* spp. - Berg River

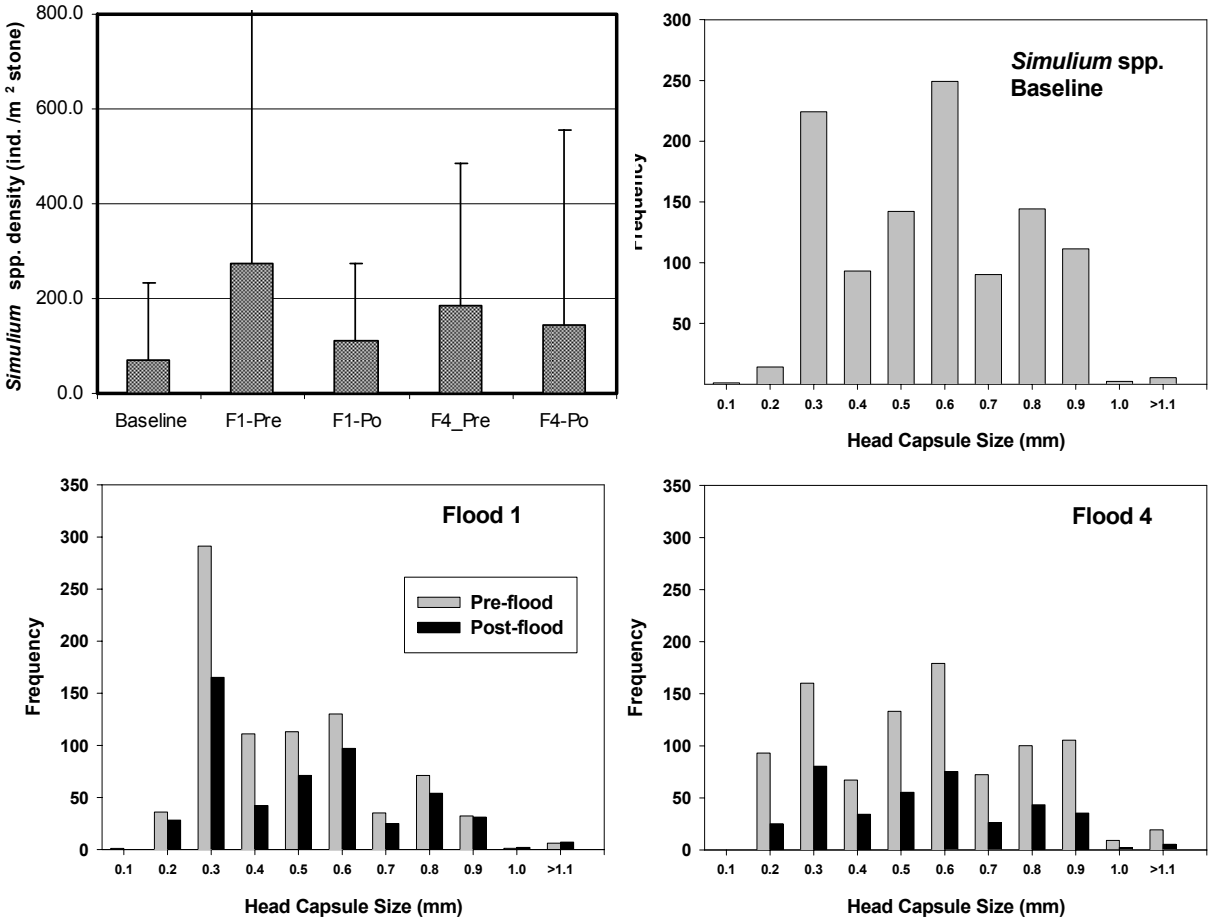




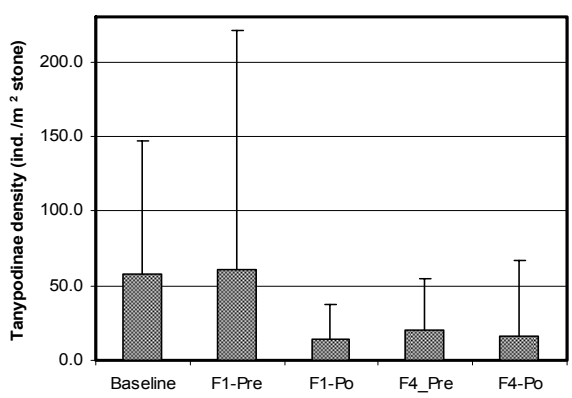


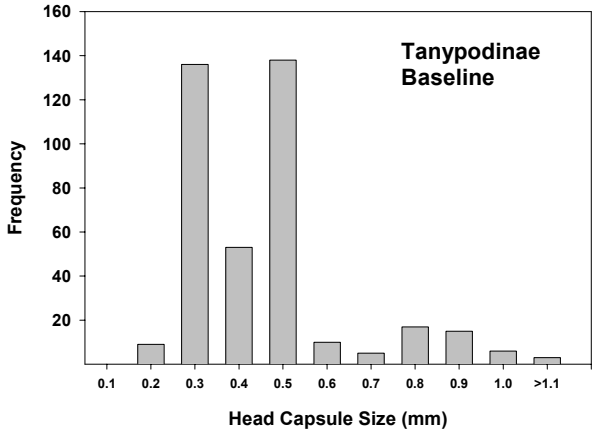


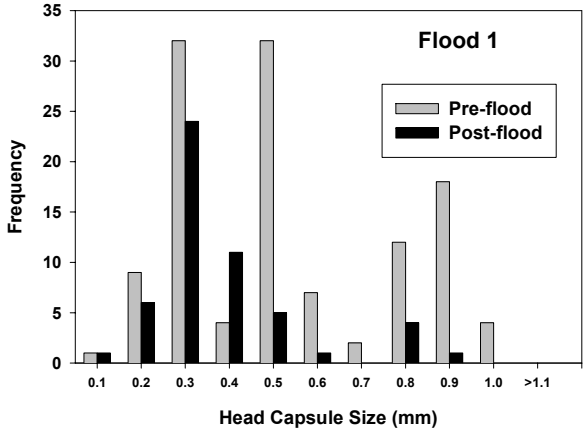
q) *Simulium* spp. - Molenaars River

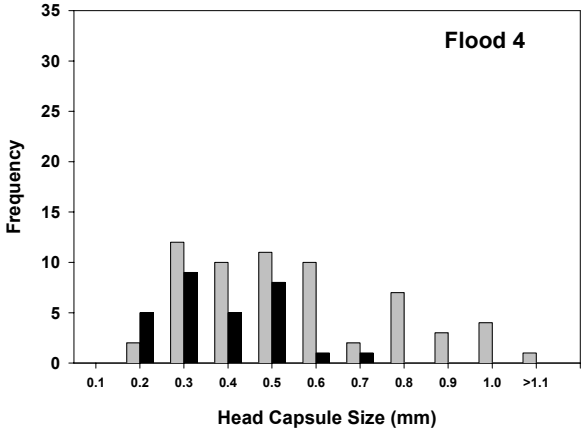


r) Tanypodinae - Molenaars River

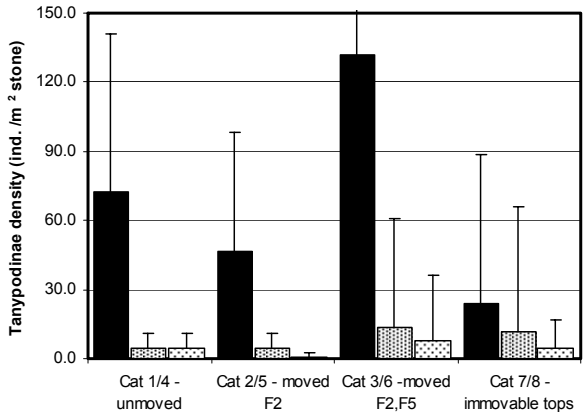


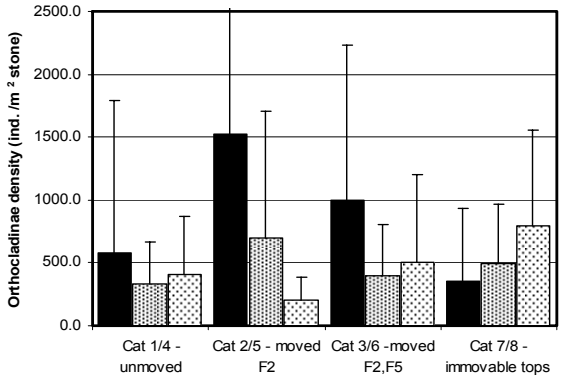


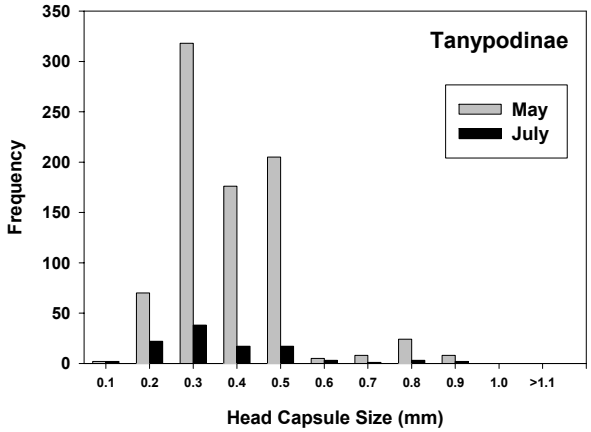


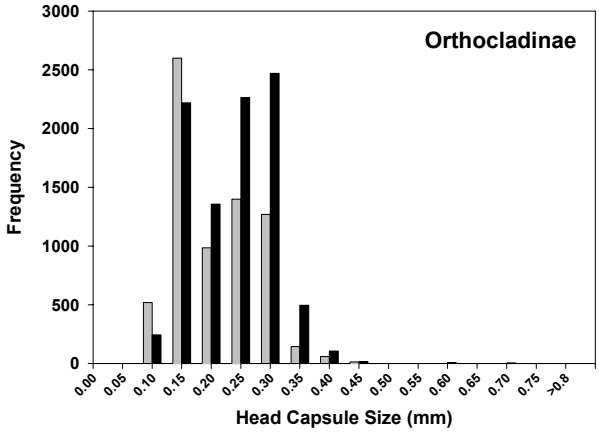


r) Tanypodinae & s) Orthocladiinae - Berg River

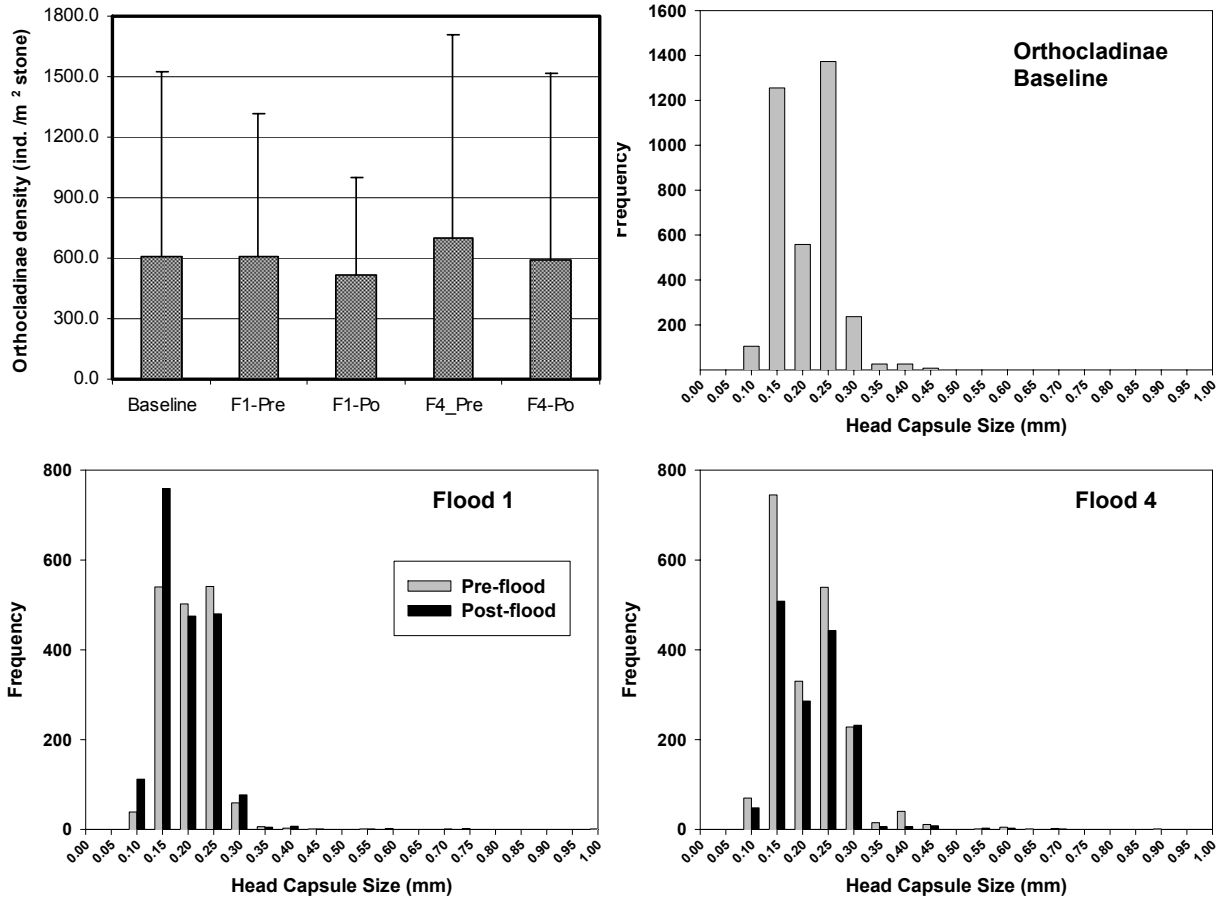




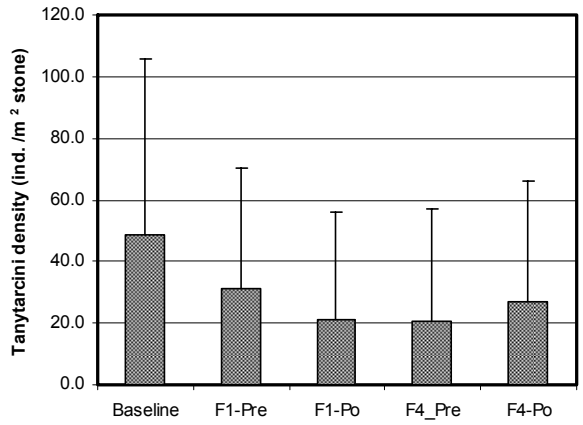


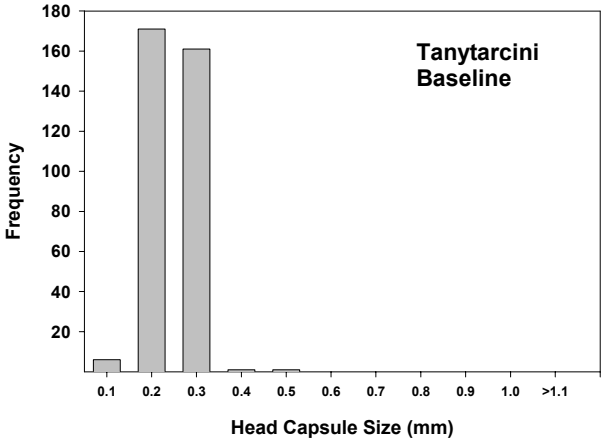


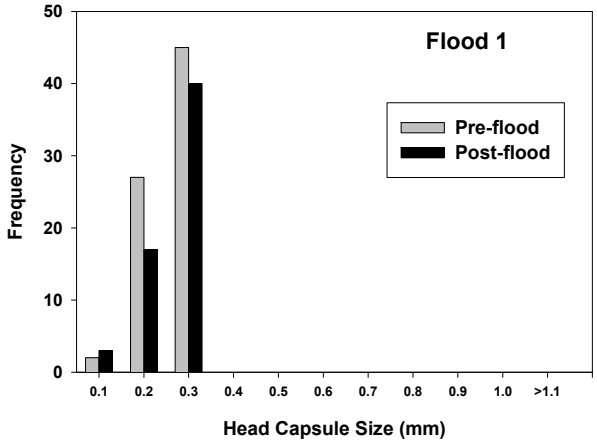
s) Orthocladiinae - Molenaars River

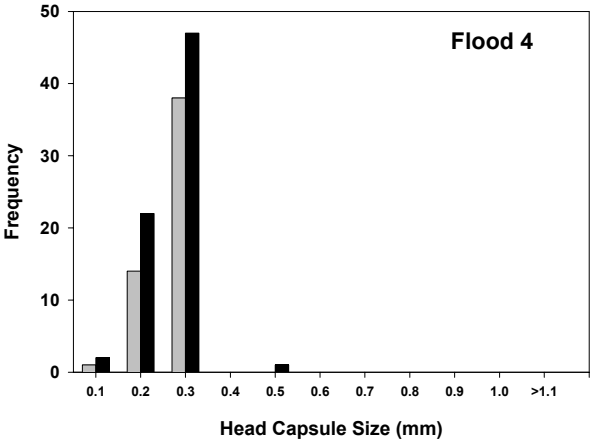


t) Tanytarsini - Molenaars River

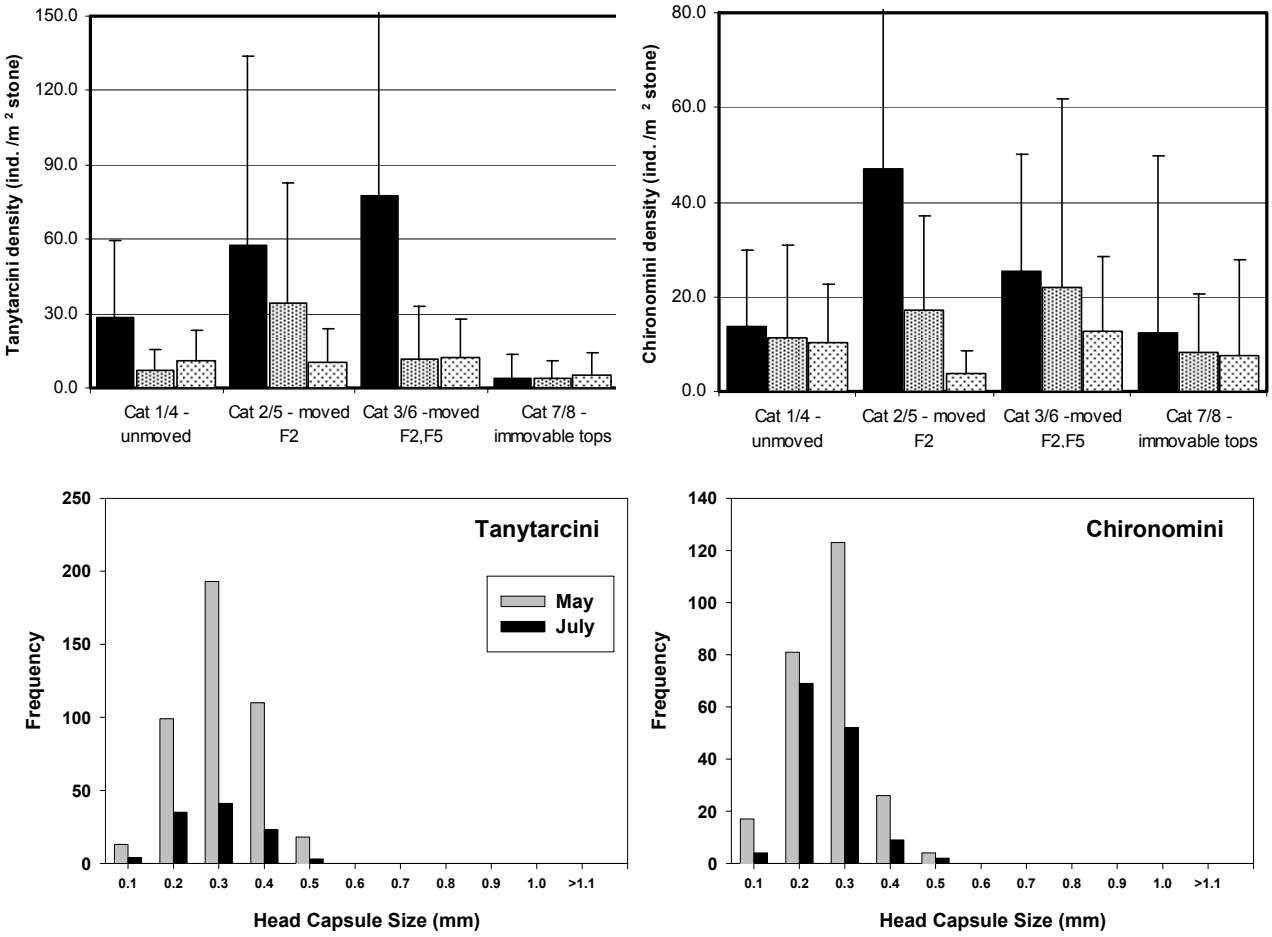




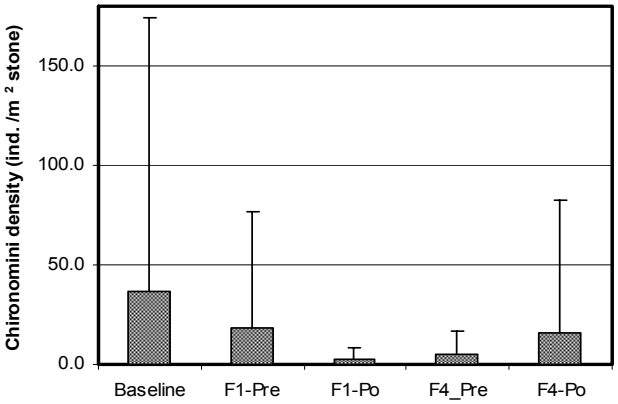


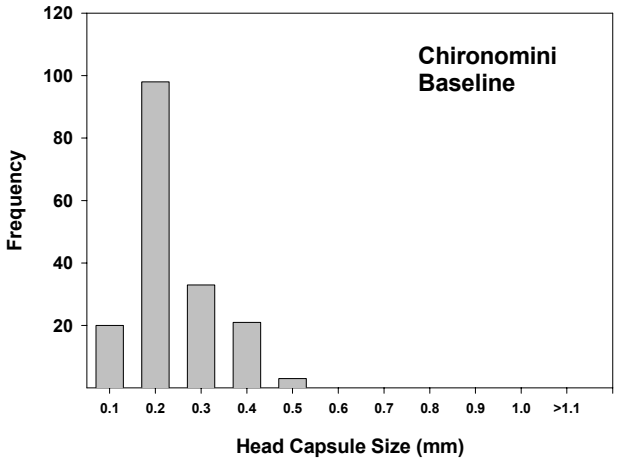


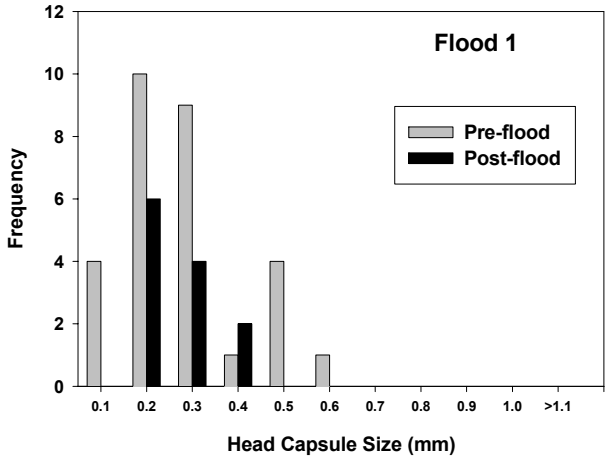
t) Tanytarsini & u) Chironomini - Berg River

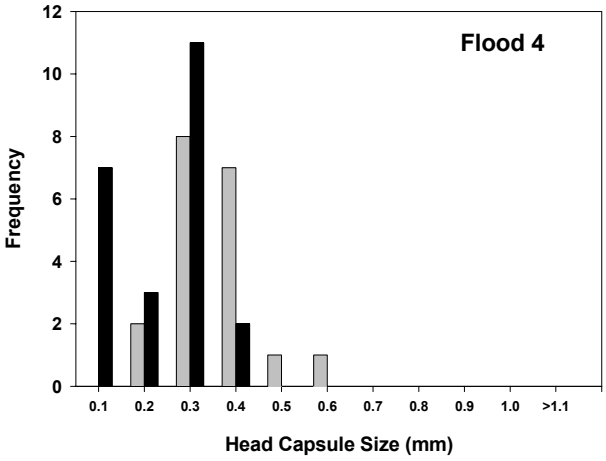


u) Chironomini - Molenaars River

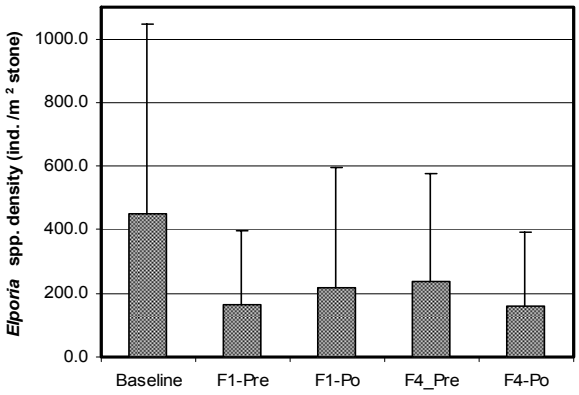


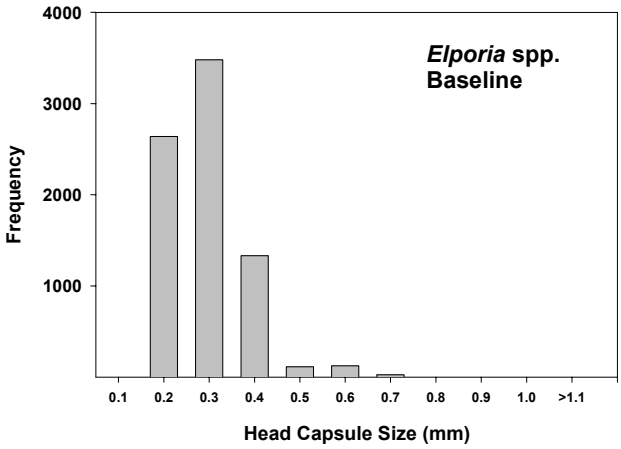


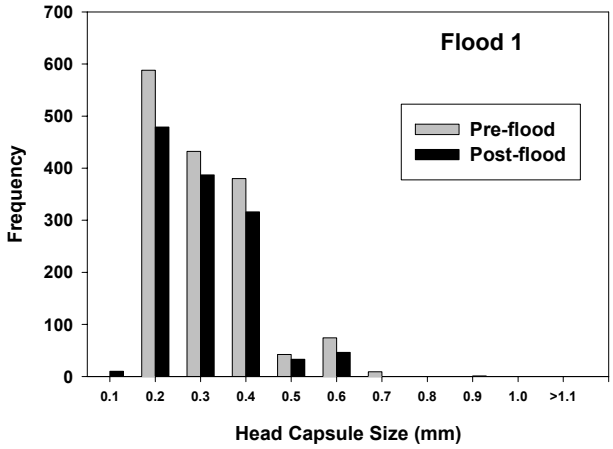


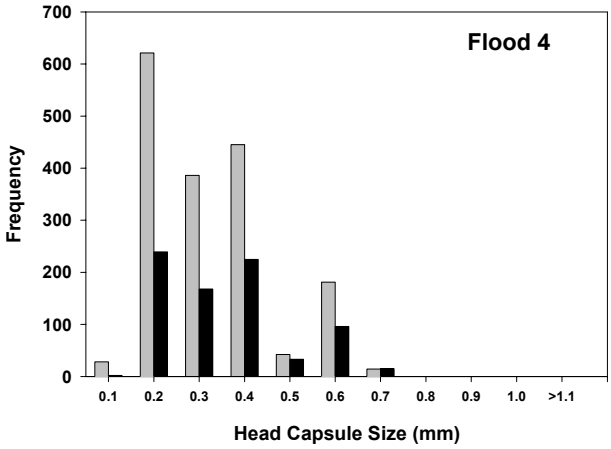


v) *Elporia* spp. - Molenaars River

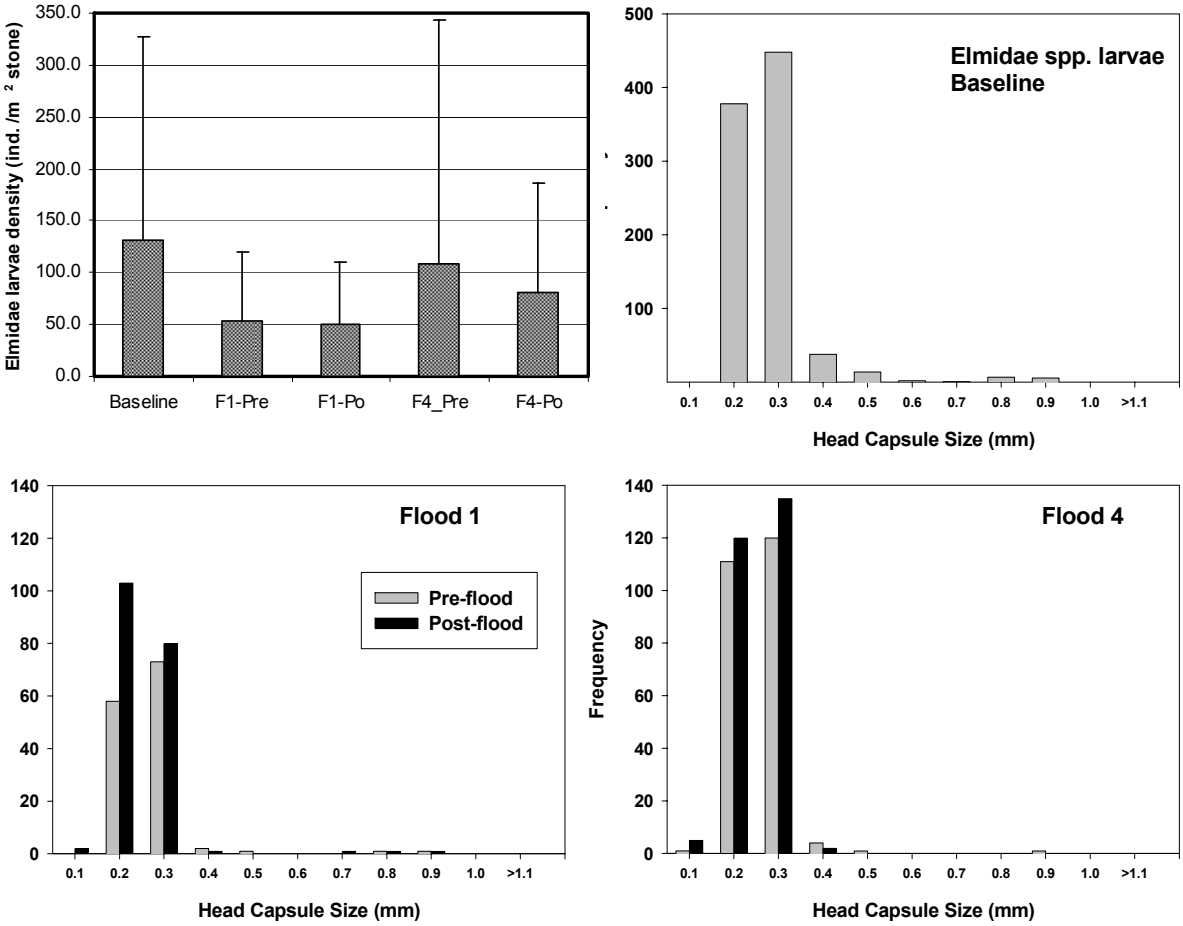




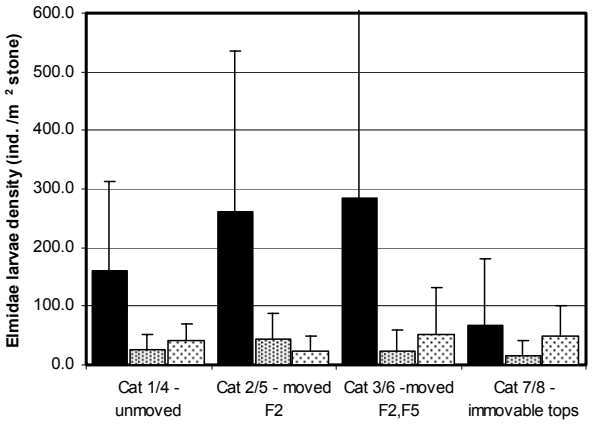


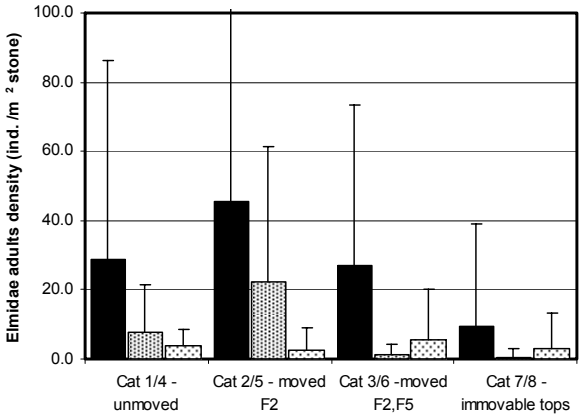


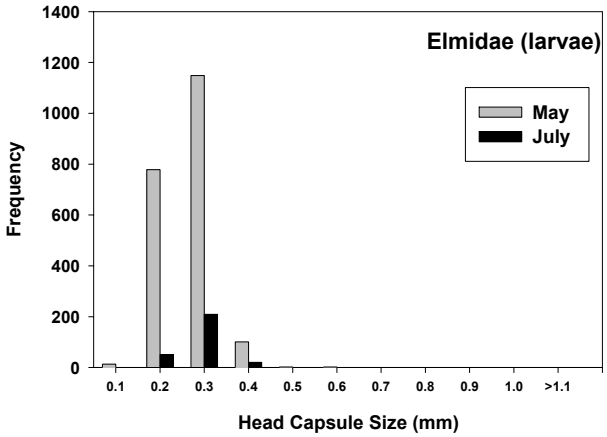
w) Elmidae larvae - Molenaars River

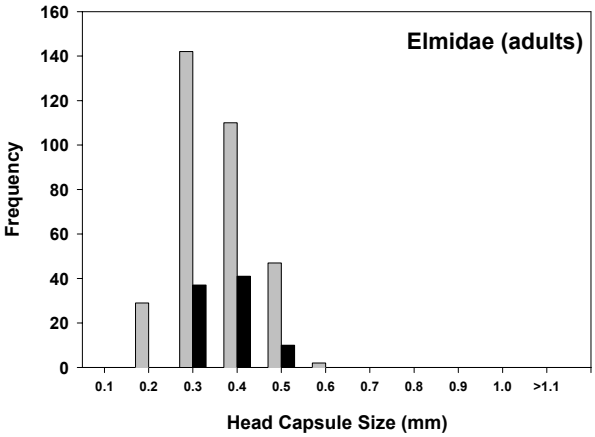


w) Elmidae larvae & x) Elmidae adults- Berg River

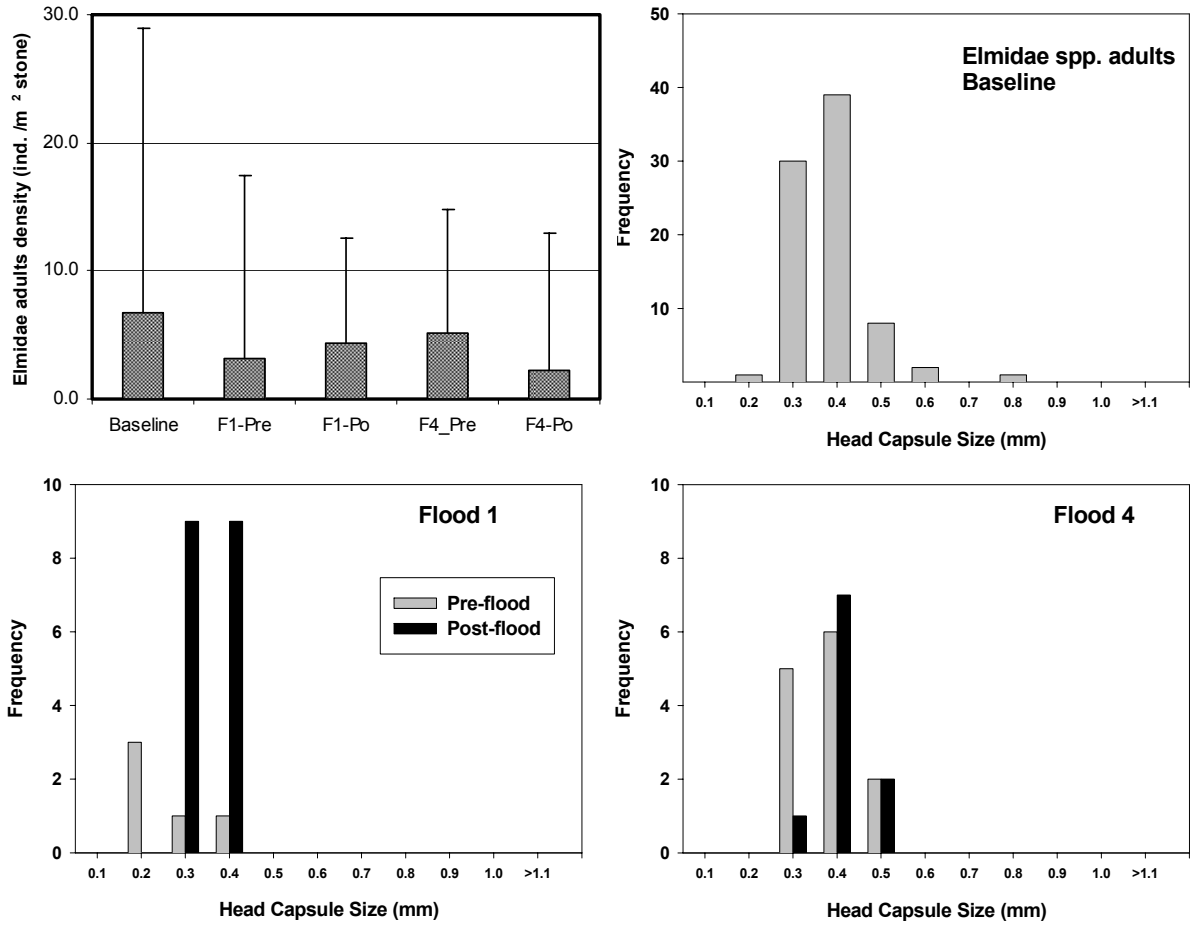




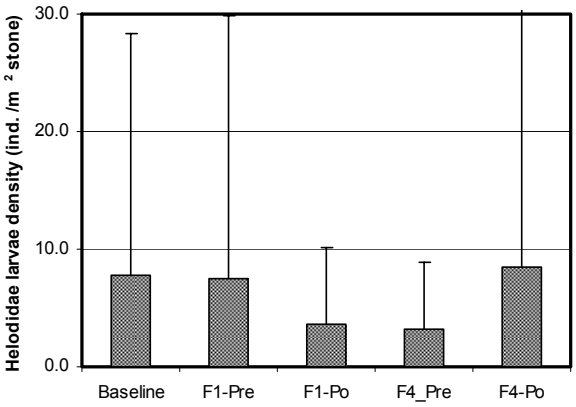


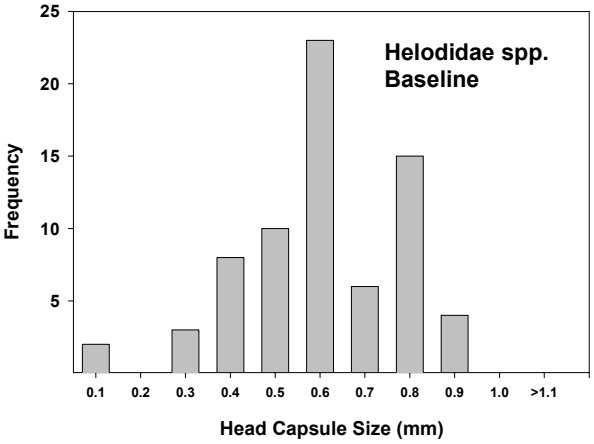


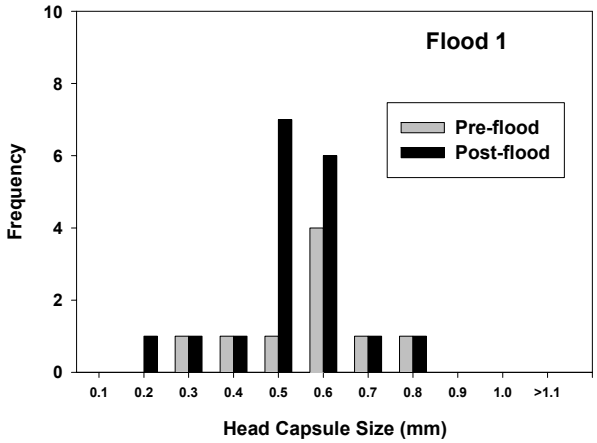
x) Elmidae adults - Molenaars River

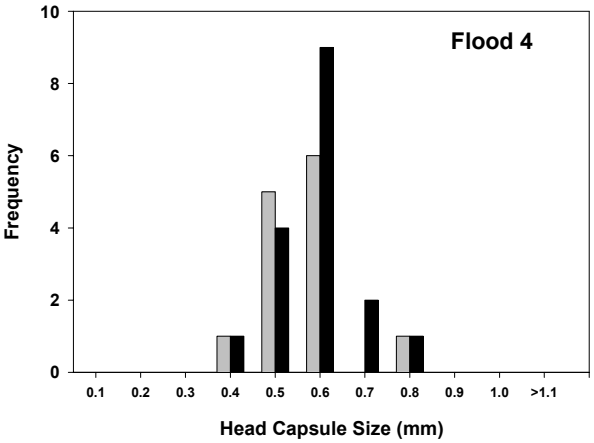


y) Helodidae - Molenaars River

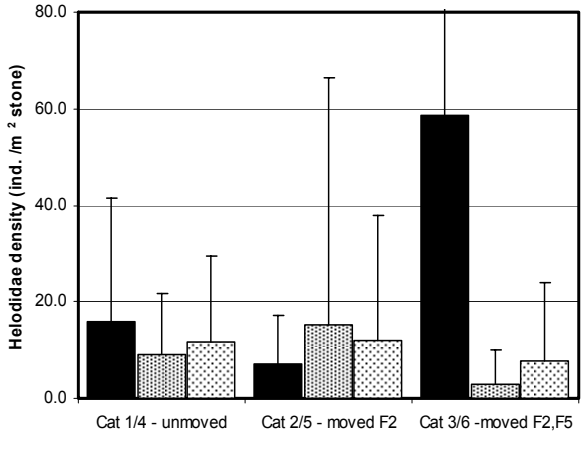


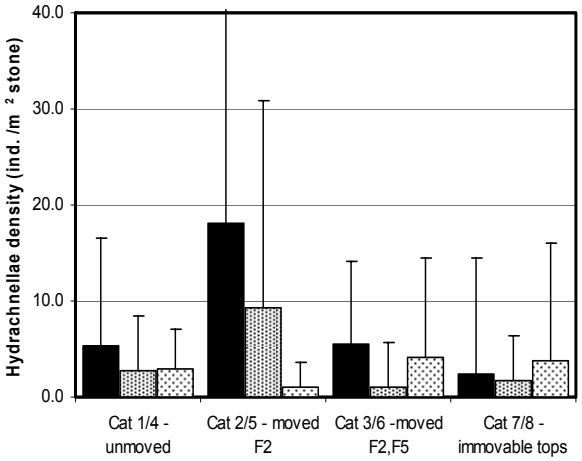


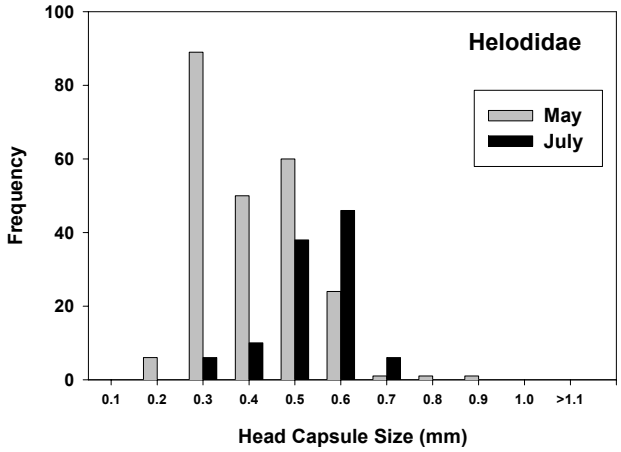


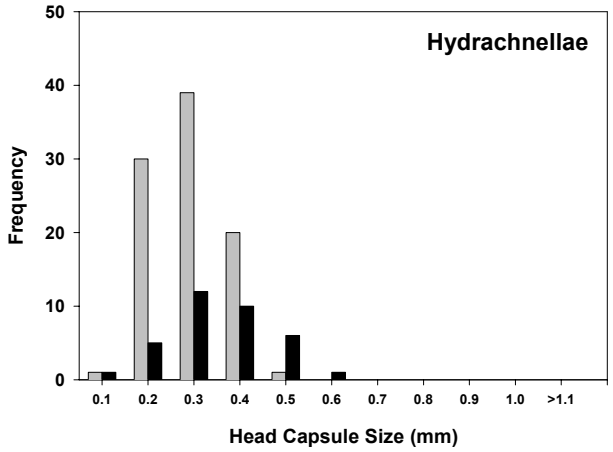


y) Helodidae & z) Hydrachnellae- Berg River

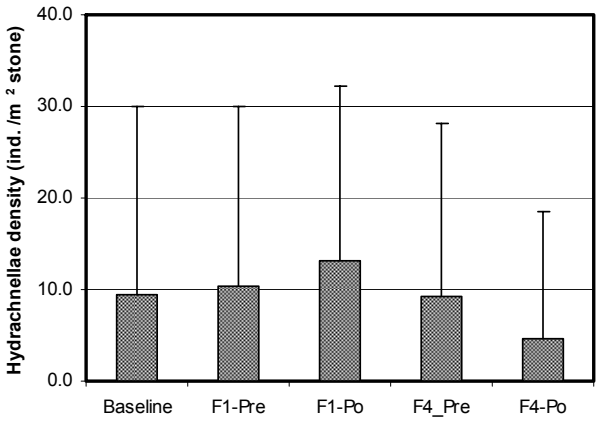


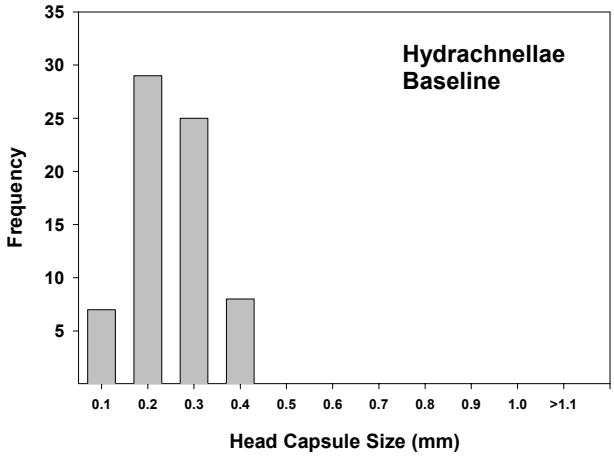


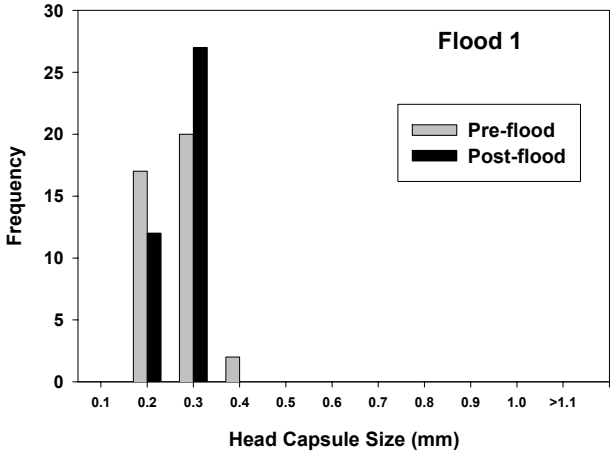


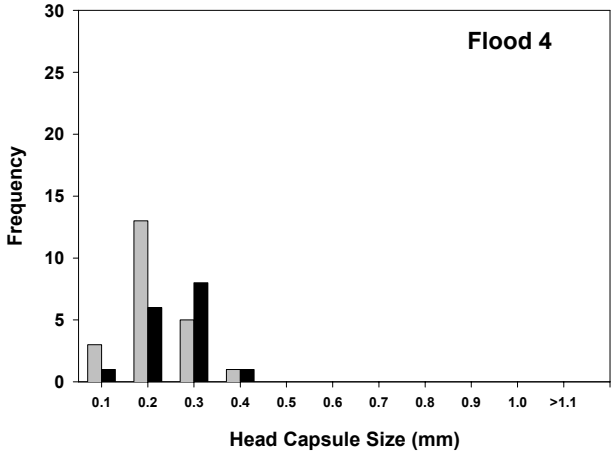


z) Hydrachnellae- Molenaars River









6.4.3 Notonemouridae:

This Plecopteran Family was in all likelihood represented by more than one species. Figure 6.14p indicates a large increase over the study period in the Molenaars River - an impressive 750%, albeit off a very low standing crop. However the large standard deviation in the Post-Flood 4 data set, and the fact that this increase was not significant (Table 6.10) suggests that the sample size may not be sufficiently large to accurately reflect actual increases in the notonemourid population, and the results should be thus treated with caution.

In the Berg River, Notonemouridae was one of the four taxa demonstrating a non-significant change in overall density, with a decline of between 5 and 22% (Table 6.5), the former based on comparing Baseline and Repeat-sampled stones, and the latter comparing Baseline with Additional stones. Although mean Post-flood densities on Repeat-sampled stones were nearly identical for all stones categories (Figure 6.14p), unmoved stones were associated with a larger percentage decline in Notonemouridae density than those which moved during floods (Figure 6.14p), although none of the changes were significant. There was a significant difference in head width frequency distributions between the pre- and post-flood population (Table 6.13), and the shift again from a single peak at 0.6 mm to a bimodal distribution, with peaks of 0.3 and 0.9 mm suggests a combination of resistance to floods and ongoing recruitment of new instars over the winter season. Of course, the resistance by the existing population and recruitment of new instars may reflect not only one species, but a staggering of the appearance on the stream bed of co-existing species.

6.4.4 Diptera:

6.4.4.i Simuliidae - *Simulium* spp.

Even with the effect of initial sampling of stones in the Molenaars River, *Simulium* spp. increased by 100% over the study period (Figure 6.14q). This genus was extremely quick to recover after initial denudation of stones, and also demonstrated remarkable microhabitat specificity: a Wilcoxon's Test for dependent samples was conducted on the data collected from Repeat-sampled stones from the Pre-Flood 1 survey and their original assemblages collected during the Baseline survey - a set of 24 whole stones. There was no significant difference in *Simulium* spp. densities (Wilcoxon's $Z = 1.53$, $p = 0.125$), indicating complete recovery. More than this, *Simulium* spp. densities actually increased, but the recolonising animals were largely restricted to almost exactly those stones which were colonised in the initial Baseline survey (Figure 6.16). In addition, the densities of recolonising *Simulium* spp. followed the initial Baseline survey densities very closely. In the Baseline survey 11 of 24 stones were bare of *Simulium* spp.. Of these 11, only two stones (numbers 183 and 235 in Figure 6.16) were colonised by *Simulium* spp. during the month interval until the second sampling date, and then only at very low densities. Both these results indicate the enormous resilience and strong micro-habitat specificity in this group. Size-frequency analysis suggests ongoing recruitment throughout the study period

in the Molenaars River.

In the Berg River, *Simulium* spp., as with the Notonemouridae and *D. capensis* already mentioned, exhibited a non-significant overall decrease in density over the flood period of between 22 and 61% (Table 6.5), the former based on comparing Baseline and Repeat-sampled stones, and the latter comparing Baseline with Additional stones. Examination of the changes in relation to stone movement categories (Table 6.11) indicated that *Simulium* spp. fared better on moved stones, where negligible decreases and even increases in density were observed in the Post-flood survey (Figure 6.14q). In this regard, Category 2 stones - repeat-sampled stones which moved in Flood 2, but remained stable thereafter, supported substantially greater densities of *Simulium* spp. than any other stone category. Of equal importance was the significant, large percentage increase in *Simulium* spp. densities on the tops of immovable boulders (Figure 6.14 q, Table 6.11). There were no obvious differences in the size-frequency distribution of *Simulium* spp. on these different stone categories after the floods, unlike the case for *Baetis* spp. Size-frequency analysis comparing the pre- and post-flood periods indicated a very slight increase in mean head capsule width (Table 6.13) but the distribution in Figure 6.14q suggests both developmental growth and recruitment over the study period.

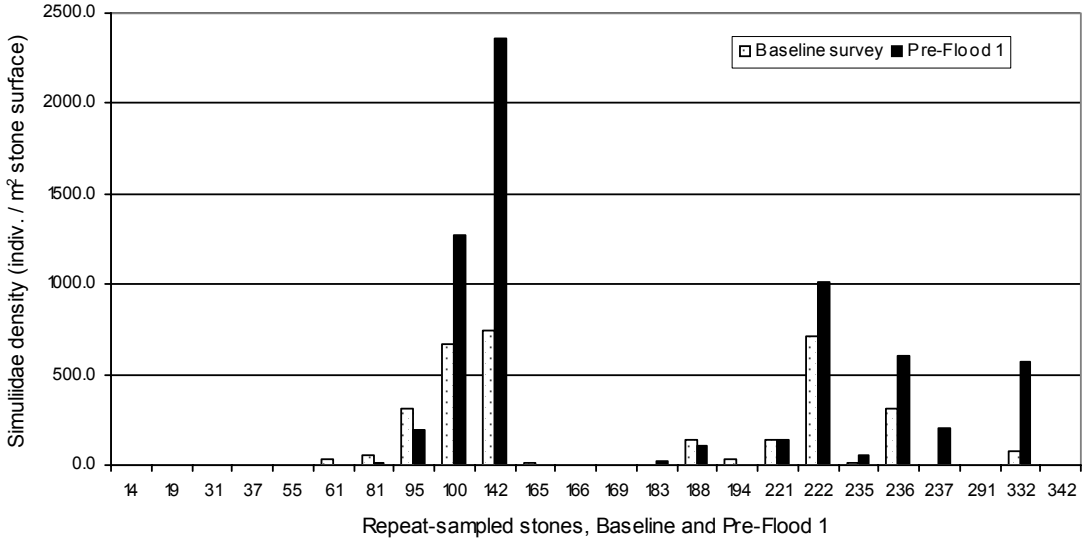


Figure 6.16 Molenaars River Baseline and pre-Flood 1 *Simulium* spp. densities on individual repeat-sampled stones, demonstrating the recovery after initial denudation of stones during the Baseline survey, and illustrating the strong microhabitat specificity of this taxon. Individual stone numbers are listed along the z-axis.

6.4.4.ii Chironomidae

The major sub-Families of Chironomidae in the Berg and Molenaars Rivers are the Orthocladiinae, the predatory Tanypodinae and the Chironominae, which are easily differentiated into two Tribes: the tube-dwelling Tanytarsini and Chironomini. Responses to floods were separately examined for each of these four groups.

a ***Tanypodinae***

Tanypodinae in the Molenaars River recovery fairly well after the Baseline survey, but were significantly reduced by some 70% of their starting density (Table 6.10), with the major losses occurring on smaller instars (Figure 6.14r). A similar pattern was evident in the Berg River, although in this case density reductions by the larger floods amounted to between 90 and 94% of the Baseline condition, with no refugium offered by unmoved stones (Table 6.11).

b ***Orthocladiinae***

Densities of Orthocladiinae in the Molenaars River remained remarkably constant over the full study period (Figure 6.14s, Table 6.10), and although there were statistically significant differences in size-frequency distributions (Table 6.11), there were no more than five pupae collected in all 10 000 animals examined over the Molenaars River study, indicating that the population either remained static in terms of developmental growth, or that any losses were matched by new recruitment.

The Orthocladiinae were the last of the four taxa already mentioned that exhibited a non-significant overall decrease in density over the flood period, of between 53 and 55% (Table 6.5), the former based on comparing Baseline and Repeat-sampled stones, and the latter comparing Baseline with Additional stones. Examination of the changes in relation to stone movement categories (Table 6.11; Figure 6.14s) indicated that Orthocladiinae enjoyed an approximate 20% relative refugium from flood-induced density reductions on unmoved stones, with immovable boulder tops representing a haven from the effects of floods - on these stones Orthoclad densities increased by between 40% (Repeat-sampled stones) and 124% (Additional stones, this increase being significant). In the Berg study, the significant difference in size-frequency distributions can be visually interpreted as reflecting both recruitment of young instars and developmental growth over the flood period.

c ***Tanytarsini***

Tanytarsini did not recover completely on sampled stones between the Baseline and Pre-Flood 1 sampling periods, although the differences in density between these periods was not significant (Figure 6.14t; Table 6.10). Over the remaining study period however, there was only a small decrease in density of 14%. An interesting feature was the size-frequency distribution of this group, since very few large animals (0.4 - 0.5 mm) were present throughout the study period, even by the time of the fourth flood, where stones were dominated by animals of 0.3 mm.

In the Berg River, Tanytarsini were substantially reduced by floods, of between 71 and 77% (Table 6.5), the former based on comparing Baseline and Additional stones, and the latter comparing Baseline with Repeat-sampled stones. Examination of the changes in relation to stone movement categories (Table 6.11; Figure 6.14t) indicated that Tanytarsini enjoyed 10 - 20% relative refugium from flood-induced density reductions on unmoved stones, with immovable boulder tops representing a haven from the effects of floods, as

was the case with orthoclads, although the Tanytarsini were represented in very low densities on boulders. The population structure showed a more even spread of size classes than in the case of the Molenaars River (Figure 6/14t), but was unchanged over the sampling period (Table 6.13).

d ***Chironomini***

This group of chironomids did also not recover well on previously denuded stones, and was represented unevenly over the study period, although seemingly not in response to flood events (Figure 6.14u). Population size frequency distribution analysis indicated significant changes between the Baseline and Pre-flood 4 surveys that were suggestive of new recruitment as well as developmental growth.

The picture in the Berg River study was somewhat confusing. Comparing Category 1 / 4 stones (unmoved) with Category 3 / 6 stone s (moved in Floods 2 and 5) showed that there was very little difference in the degree of reduction in densities between these groups - no relative refugium. Only the category 2 and 5 stones were associated with significant and substantial decreases in density. These stones represent a mixture of having been moved in Flood 2 and having remained stationary over the Flood 5 immediately preceding the post-flood data collection. Differentiating between movement vs non-movement flood effects is thus not possible for this category of stones. Overall, the reduction in densities over the flood period (Table 6.5) was between 37% (comparing Baseline and Repeat-sampled stones) and 59% (comparing Baseline and Additional stones).

6.4.4.iii Elporia spp.

Elporia spp. were inadequately represented in the Berg River at any time over the study period to allow for flood effects to be examined. In the Molenaars River, as with the mayfly *Lestagella penicillata*, *Elporia* spp. recovered in the month following after initial sampling to only 34% of the Baseline density, where after no change in the population as a result of floods was observed (Figure 6.14v). There were significant changes in size-frequency distribution over the full study period, which suggested continuous strong recruitment of young instars as well as developmental growth.

6.4.5 Coleoptera:

6.4.5.i Elmidae

As reported in section 6.1.2, Elmidae larvae were one of the few groups that were significantly lower on re-sampled stones at the Pre-Flood 1 sampling (Figure 6.2). Thereafter, no effects of floods were apparent, and in fact this group increased to 63% of the initial Baseline density, despite the floods over the study period (Figure 6.14w). Elmidae adults followed a similar pattern of inadequate recovery following the Baseline sampling, but their densities declined slightly from the Pre-Flood 1 sampling, with an overall recovery of only 31% of the Baseline density (Figure 6.14x).

In the Berg River both larvae and adults decreased on all categories of stones, with unmoved stones providing a small (7%) relative refugium for larvae, but no consistent refugium was apparent in the case of adults.

6.4.5.ii Helodidae

Whilst Helodidae densities were variable over the study period, the Baseline and Pre-Flood 1 densities were similar, and there were no significant changes over the flood events (Figure 6.14y). Size-frequency distributions also did not change significantly (Table 6.12).

In the Berg River Helodidae decreased by between 68 and 70% overall, but were substantially more affected by floods on stones that moved (Figure 6.14y; Table 6.11), with more than 50% difference in density reductions between these two categories of stones. The change in size-frequency distribution was significant, and represented developmental growth, with an increase in average head capsule width from 0.37 mm in May to 0.50 in July (Table 6.13).

6.4.6 Acarina: Hydrachnellae (Order: Acariformes)

Hydrachnellae (water mites) was the only non-insect group included in the study of invertebrate responses to floods. In the Molenaars River there was little change in density for much of the study period, although densities were non-significantly reduced immediately after Flood 4 (Figure 6.14z; Table 6.10). No significant differences in population structure were found over the study period in either river. In the Berg River there was a significant decrease of between 54 and 61%. However, with regard to differences in responses on moved vs. unmoved stones, the results were somewhat contradictory (Table 6.11), with higher densities being found on Additional stones that had moved (Category 6 stones) than any other.

6.5 INFLUENCE OF APPLIED STREAM POWER ON INVERTEBRATE DENSITIES

The relationship between applied power and post-flood density of invertebrates was examined only on unmoved stones, since the analysis was aimed at testing whether, outside of disturbance associated with particle movement, there was a relationship between the magnitude of forces acting on a particle and the 'erosion' of animals from that particle.

The range of applied stream power values calculated for unmoved stones, at the peak of each of the monitored floods, were as follows: 2000 10 000 Watts m^{-3} on those stones sampled immediately after Flood 1 on the Molenaars River; a range of 4000 - 20 000 Watts m^{-3} on Flood 4 sampled stones. In Flood 5 on Berg River the range of values was some 12 000 - 31 000 Watts m^{-3} on unmoved, Repeat-sampled stones, but the range was lower, between 14 000 - 24 000 Watts m^{-3} on unmoved, Additional stones. As the applied power at the bed is discharge dependent, this increase in applied stream power ranges with increasing flood size is unsurprising.

In the case of the Berg River, all stream power values were high. Even though the range

reported here was for the stones from which biological samples were taken, which were all situated within the main channel, there were only nine stones out of the 433 stones monitored over the flood where the applied power during Flood 5 was under 10 000 Watts m^{-3}. This suggests that, in terms of applied power, there were no patches within the stream bed that were associated with low flow forces, which may have sheltered animals - applied stream power values during winter baseflow conditions averaged around 100 Watts m^{-3}.

Relationships between post-flood invertebrate densities and stream power were hard to decipher for three reasons. In some instances inadequate recovery on repeat-sampled stones led to very low densities, for example, *Cheumatopsyche afra*. In the case of the Berg River samples, however, the control offered by the Additional stones data set did not include these problems. Secondly, patchiness in the distribution of most of the taxa resulted in zero-densities on some stones that may or may not have been related to the magnitude of forces acting on the stones, thus obscuring possible relationships with applied stream power. Finally, the analysis could only test the relationship between actual post-flood invertebrate density and applied stream power, not the change in density of the different invertebrate taxa, since it is obviously impossible to measure both pre- and post-flood densities on individual stones. Given the probably very wide differences in starting densities, immediately before the flood, the analysis was limited therefore to examining whether the post flood distribution of invertebrates matched the distribution of forces on the stream bed, rather than the effect of different magnitudes of force on the degree of reduction in invertebrate density from a bed particle.

Whilst there were few significant relationships between the density of any taxon and the maximum applied stream power at that stone during the immediately preceding flood, most taxa demonstrated either non-significant negative relationships between density and applied power, or no relationship at all. Examples are provided in Figures 6.17 to 6.19. Note that correlation coefficients and regression equations are indicated on these figures only where these were found to be statistically significant.

Figure 6.17 shows the relationship between applied stream power and immediately-post flood densities for *Afroptilum* spp. and *Demoulinia* spp., on unmoved stones, after each of the three floods monitored for this study - Floods 1 and 4 on the Molenaars River and Flood 5 on the Berg River. Both species were reduced by some 50% in density over the four small floods of the Molenaars River. In the Berg River, both species were scoured from stones that moved, whilst on unmoved stones *Afroptilum,* enjoyed complete refugium and its densities remained unchanged on these stones. *Demoulinia* was virtually absent from all stones in the Berg River after the floods (Figure 6.14 a and b). There is a suggestion in Figure 6.17 that *Afroptilum* spp. densities respond weakly to the magnitude of applied stream power on a river stone, if one examines all three floods together (note different values for stream power along the x-axis), although none of these relationships were significant. On the other hand, *Demoulinia* spp. density showed no relationship to applied stream power.

For the Leptophlebiidae (Figure 6.18), different species were present at different densities in the two rivers. However, *Euthraulus elegans* was the only one which remained present in high densities in the Molenaars River, over the study period, whilst *Adenophlebia* spp. and *Aprionyx* spp. declined progressively over time, perhaps in relation to a late autumn emergence. *Adenophlebia* spp. was one of the few species that showed a significant negative correlation with applied stream power during Flood 1 in the Molenaars River (Figure 6.18 ii), whilst *E. elegans* showed no such relationship. In the Berg River, both species enjoyed a relative refugium on unmoved stones. The same trend as in the Molenaars was present - *E. elegans* showing no relationship to applied power; *Adenophlebia* spp. responding negatively, although this relationship was not significant in the Berg River.

Finally, two taxa that are frequently associated with the upper surfaces of river substrata, Simulium spp. and Elmidae larvae, are presented in Figure 6.19, in relation to changing applied power values. No correlation between densities and stream power were suggested.

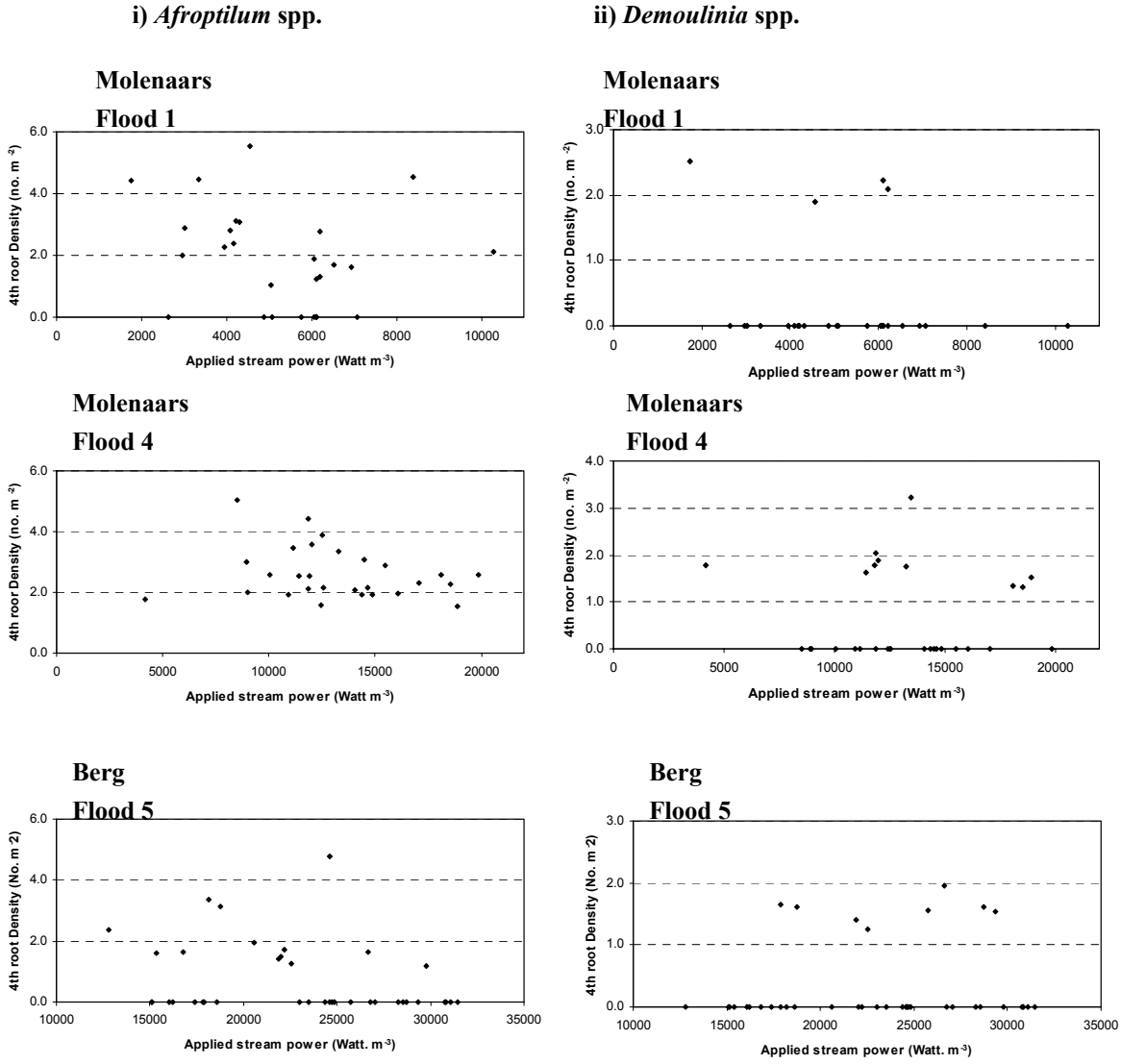


Figure 6.17 Relationship between the applied power at the bed, calculated for each stone sampled immediately after Flood 1, Flood 4 in the Molenaars River, and Flood 5 in the Berg River, against the post-flood density of invertebrates on the sampled stones, for i) *Afroptilum* spp. and ii) *Demoulinia* spp.

i) *Euthraulus elegans* **ii) *Adenophlebia* spp.**

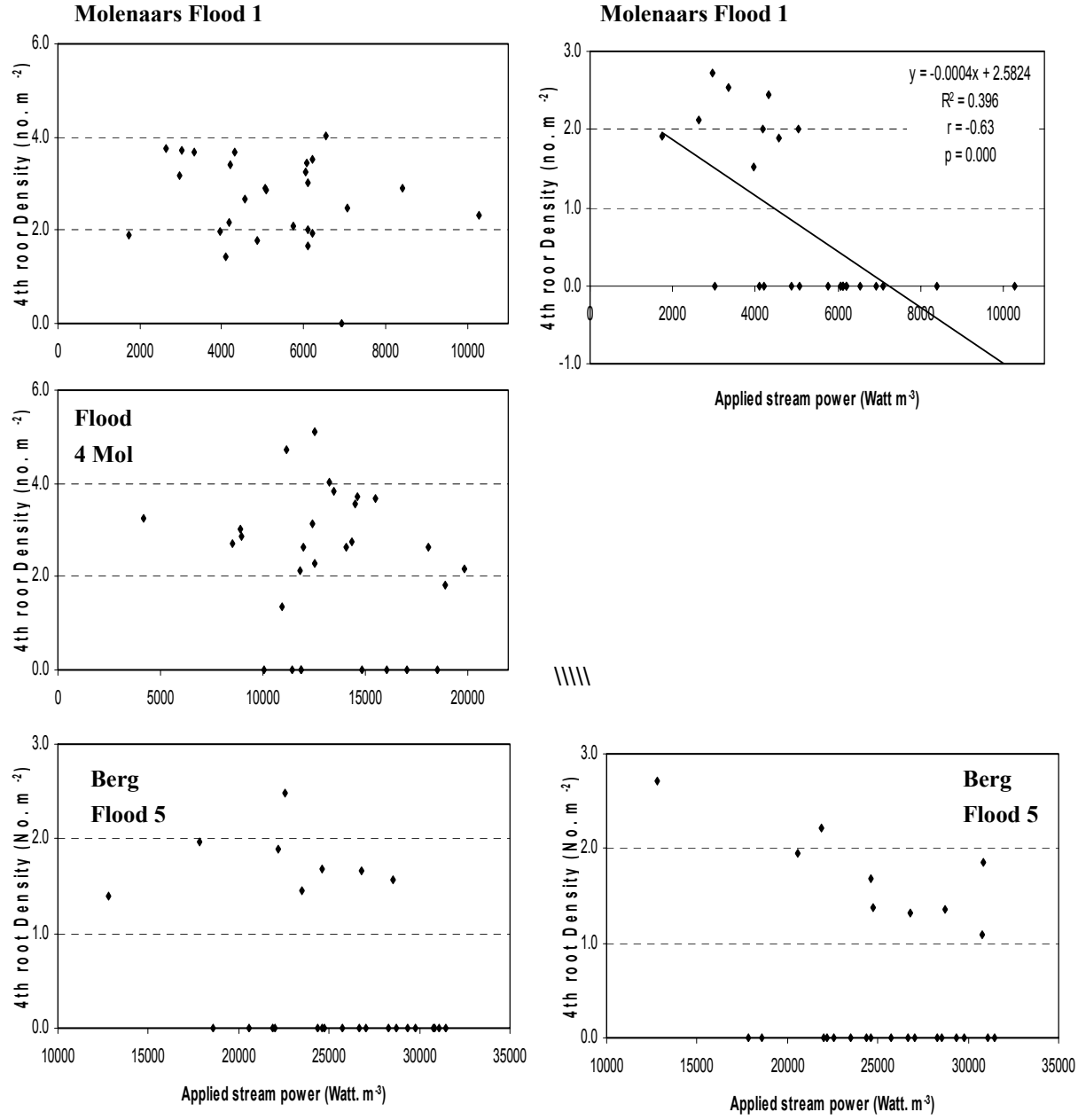


Figure 6.18 Relationship between the applied power at the bed, calculated for each stone sampled immediately after Flood 1, Flood 4 in the Molenaars River, and Flood 5 in the Berg River, against the post-flood density of invertebrates on the sampled stones, for i) *Euthraulus elegans* and ii) *Adenophlebia* spp.

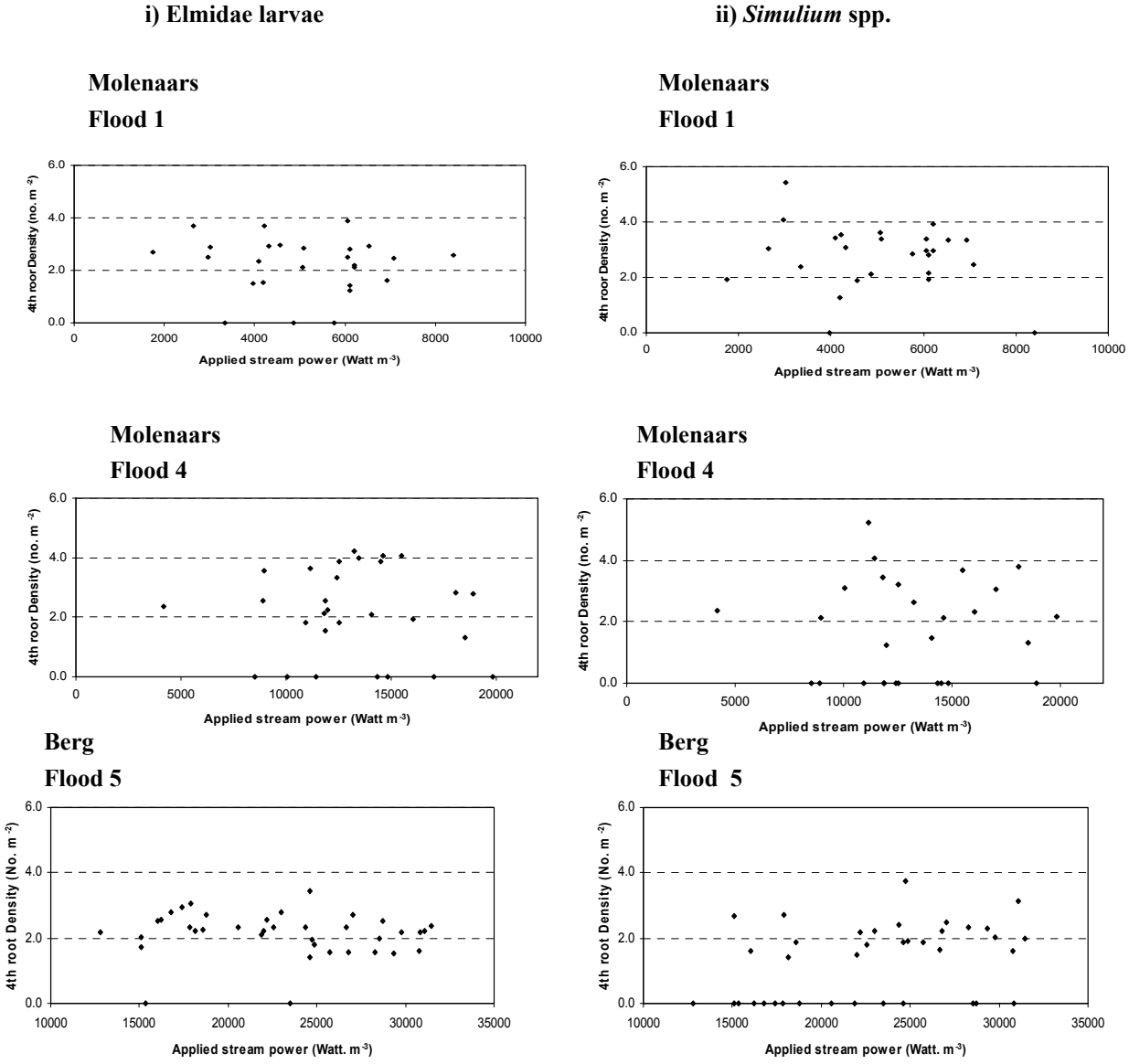


Figure 6.19 Relationship between the applied power at the bed, calculated for each stone sampled immediately after Flood 1, Flood 4 in the Molenaars River, and Flood 5 in the Berg River, against the post-flood density of invertebrates on the sampled stones, for i) Elmidae larvae and ii) *Simulium* sp.

6.6 DISCUSSION

Sampling design and confidence in the results

In the Molenaars River, 50 samples were taken at each of four pre- or post-flood sampling surveys, and 200 samples were collected at the initial Baseline survey, in order to assess flood-related impacts on invertebrate fauna. Due to the constraints of time and resources, however, only 30 stones, including samples from whole stones and tops of immovable boulders, were processed for each survey, with 70 stones being processed of the 200 Baseline samples collected. In this study, therefore, two of the randomly selected subsets of approximately 23 whole-stone samples from the Baseline data set were compared, to check that each subset produced the same representation of invertebrate community structure, and hence that this sample size was adequate for subsequent analysis of flood effects. The non-significant difference between the subsets of Baseline data samples (with the exception of two taxa) lends itself to the conclusion that this sample size was sufficient to use for further comparisons between pre- or post-flood assemblages or between these and the baseline data.

Comparison of the data sets from all time periods for the Molenaars River study shows a gradually declining population over the four sampling periods following the Baseline survey (Figure 6.7). Despite this, there were no significant differences in density between Pre-Flood 1 densities and Post Flood 4 densities in the majority of invertebrate taxa of the Molenaars River, taken individually, with a few exceptions (Figure 6.2). Indeed, multivariate analysis only discerned significant change in invertebrate community structure as a cumulative effect of four floods in the Molenaars River, suggesting that these small floods had little effect on invertebrate assemblages. An alternative, and quite probable, reason for the failure to discern statistically significant change could be the large variance associated with estimates of population density at each time interval over the study (even after data transformation), which may have overshadowed changes resulting from small floods. To dismiss the non-significant declines in density, therefore, and conclude that the series of Class I floods had no effect on invertebrate taxa would thus not be correct.

An important feature of the Molenaars River study was the sampling design - that of repeat-sampling marked stones. At the level of community structure, the biotope signature observed in the distribution of species assemblages on the repeat-sampled stones of the Pre-Flood 1 survey was very similar to that of the Baseline survey, as shown by the results of multi-variate analysis (Figure 6.1). This robust analysis indicates that the relationships between species and their hydraulic environment became re-established very rapidly on repeat-sampled stones after initial sampling. In relation to univariate measures such as invertebrate density data, there were no significant differences between Baseline and Pre-Flood 1 densities of total invertebrate density and that of individual species for all but five taxa, also suggesting that recovery on repeat-sampled stones within the month-long period after initial sampling was adequate. These results suggest that such an approach to flood studies may have merit.

However, despite the similarity in the spread of samples from the Baseline and Pre-Flood 1 sampling, the actual pairs of invertebrate samples, i.e. taken from each individual stone sampled at Baseline and again at Pre-Flood 1, were only on average 67% similar, based on multivariate analysis, after root-root transformation. This could be seen as evidence for the absence of a full recovery, and thus the conclusion that the study approach was flawed, in terms of quantifying flood effects. Also, even the non-significant decreases in densities of individual taxa between the Baseline and Pre-Flood 1 surveys may, again, simply be the result of large variances in density estimates, especially in patchily distributed taxa. Closer examination of the species data showed a combination of complete recovery by some species, as well as a failure by others to recover on sampled stones. Examples of the failure for species to recover on repeat-sampled stones were *Lestagella penicillata* and *Elporia* spp. Neither reached more than 46% of the Baseline condition at any subsequent point after the Baseline survey. This was despite the fact that these taxa were associated with immature populations, which implies that there were unlikely to be losses to pupal or adult stages and despite evidence of recruitment of new instars over the winter period, at least in the latter species. Niemi *et al.* (1990) concluded that a complicating feature of pre-post disturbance studies is the fact that pre-disturbance densities are almost never re-attained because of natural temporal fluctuations and new gradients in resources. In the Molenaars River, exponential increases in *Lithogloea harrisoni* over the whole study period are a case in point (see also Johnson & Vaughn, 1995).

These considerations throw some doubt over the results from the Molenaars River, suggesting on the one hand that the failure to find statistically significant changes in density should not be disregarded as evidence for flood effects, because of variability in density distribution, but on the other hand that the effects of floods might well be over-estimated on repeat-sampled stones, because of a failure of many taxa to recover after the initial sampling. This 'sampling effect' can be considerably reduced by using the Pre-Flood 1 data as an alternative baseline condition against which to compare subsequent changes, and this indeed became the approach of this study.

Some concerns remain even after that, however. For example, the lack of change in *Elporia* spp. from Pre-Flood 1 (the alternative baseline condition) to Post-Flood 4 (Figure 6.14v) suggests a stable population throughout the winter. However, the size-frequency distribution for this species shows that it was recruiting new instars continuously, but no portion of the population developed to pupal stage over the study period. An alternative explanation for the stability in the *Elporia* spp. population density on the repeat-sampled stones, therefore, could be that larger individuals were relocating to non-sampled stones on the river bed more generally, because of possibly poorer stone conditioning and food resource availability on previously sampled stones. This topic is discussed further with reference to invertebrate resilience. A control sample of previously unsampled stones at each sampling occasion would have provided important comparative information in this regard, but was not collected.

With regard to the Berg River study, a control sample collected simultaneously

with the repeat-sampled stones revealed that any 'sampling effect' was not significant compared with the effects of the preceding floods on invertebrate assemblages (Figures 6.8 and 6.11) or on the densities of individual taxa. There were some small exceptions to this: Chlorophyll a was lower on Repeat-sampled stones than on Additional stones, suggesting that the initial effects of stone scrubbing and marking may have been carried through to the Post-flood period. Also, densities of some taxa that increased in densities over the study period, viz. *Pseudocloeon* spp. *Lithogloea harrisoni* and *Nadinitella crassi*, were also higher on Additional stones than on Repeat-sampled stones, although both data sets showed the same trend. Overall, therefore, the Repeat-sampled stones can be considered to provide a reliable measure of the magnitude of invertebrate response to flood disturbance, in the case where larger within-year floods occur, as the magnitude of the disturbance effect reduces the 'sampling effect' to a relatively small error.

The Additional Stones data set allowed for testing of the accuracy in predictive power of the hydraulic model, since the movement status of each of these stones was determined theoretically using the model, and the invertebrate responses, grouped into 'moved' and 'unmoved' categories were compared with those of the Repeat-sampled stones, whose movement status was obviously known through the actual recording of stone dislocation during floods. In all respects the two post-flood datasets showed the same pattern of change when compared with the Baseline condition, in each movement category. The similarity in flood responses of the invertebrates on Repeat-sampled and on Additional stones, in both movement categories, indicates that the hydraulic model has considerable potential for application in future disturbance studies, thus avoiding the error associated with the sampling effect of a repeat-sampled study design.

The Molenaars River study as a field experiment in post disturbance recovery

In many respects, the Molenaars River study emulates the sorts of artificial disturbance experiments of researchers over the past two decades (e.g. Robinson & Minshall, 1986; Boulton *et al.,* 1988; Lake *et al.,* 1989; Lake & Schreiber, 1991; Gawne & Lake, 1996; Matthaei *et al.,* 1996; Mathooko, 1998) which have examined invertebrate assemblages on artificially disturbed substrata at increasing time since disturbance, by manually disturbing individual particles or patches of river bed. In this regard, the data collected in this study may provide useful information, specifically on the differences in recovery rates on previously denuded stones, which are relevant in flood studies. Such small-scale experimental disturbance studies are considered to simulate the effects of disturbance fairly adequately, especially since the dominant effect of floods is the overturning of individual stones (Downes *et al.,* 1998a; Matthaei *et al.,* 1999a). In this study then, the artificial disturbance of stones was effected during the Baseline sampling through the removal of all invertebrates from stones. The intensity of this artificial disturbance in the Molenaars River would be more akin to the acid-washing treatment of Boulton *et al.* (1988), than to the simple overturning of stream particles of other studies, or possibly might emulate an extreme scouring event in streams that carry high concentrations of suspensoids, because the sampling process included removal of animals, then cleaning

and drying the stones sufficiently to mark them permanently.

Whilst Lake *et al.* (1989) found that 30 days was sufficient for full recovery of trapped organic material, invertebrate density and species density, Boulton *et al.* (1988) found that invertebrate species density but not total invertebrate density, had returned to pre-disturbance levels in 32 days, on his acid-scoured stones. Similarly periphyton was also reduced after 32 days than prior to the disturbance treatment. Robinson & Minshall (1986) concluded that a time period of over 27 days between disturbances may be adequate for equilibrium conditions to be established in invertebrate assemblages, but not periphyton. In this Molenaars River study, periphyton was not sampled, but organic matter did return to pre-disturbance levels within 30 days, whilst invertebrate taxa were variously more or less abundant after 30 days, with most taxa present in lower densities than at the pre-disturbance time. Community composition was on average 67% similar to the pre-disturbance condition (Bray Curtis Similarity on root-root transformed data). The recovery rates of the invertebrate taxa following initial disturbance were also variable. In this study therefore, recovery was slower than that measured in other studies, and affected by a range of factors, discussed below.

Factors affecting recovery rates are well described in the literature (e.g. Niemi *et al.,* 1990), and include the presence of refugia, scale of disturbance and life-history traits of the recolonising population. In addition, the extent to which food resources are rapidly re-established may influence the effect of disturbance on invertebrates (Robinson & Minshall, 1986; Death, 2003). The scale of disturbance and the presence of refugia may in many ways be considered corollaries, since refugia are defined as habitats or factors that reduce the effects of disturbance (Sedell *et al.,* 1990). In this artificial disturbance study, although the magnitude of disturbance of both invertebrates and their potential food resources on each stone was severe (total denudation), the scale of disturbance was small and its corollary, the availability of refugia was high - refugia were widely available in the form of all river-bed stones that were not sampled. Thus the key factor influencing recovery in this study would be the life history traits of the invertebrate taxa.

Mobility, or the propensity for dispersal, is logically one of the most important resilience attributes affecting the time to recovery after a disturbance (e.g. Lancaster & Hildrew, 1993b; Townsend & Hildrew, 1994; Winterbottom *et al.,* 1997a). The Simuliidae and Chironomidae are well recorded early colonisers of disturbed substrata because of their mobility (Fisher *et al.,* 1982; Biggs & Stokseth, 1996), and these groups recovered well in the Molenaars River study after initial denudation of stones. On the other hand, the poor recovery by Elmidae larvae (Coleoptera), *Elporia* spp. (Diptera: Blephariceridae), *Lestagella penicillata* (Ephemeroptera: Telagonodidae) and both *Cheumatopsyche afra* and *Chimarra* spp., two net-spinning caddisflies, probably reflects the much poorer mobility of these animals than for example the Baetid mayflies, chironomids and simuliids. Neither *Elporia* spp. nor Elmidae swims, but both groups move rather by crawling across the stream bed, and hence would take far longer to redistribute across the stream bed than more mobile, swimming and / or actively drifting taxa like the Baetidae and Simuliidae. *Lestagella penicillata* is a poor swimmer and tends to have a very clumped

distribution over the stream bed (pers. obs.). Similarly, since *C. afra and Chimarra* spp. utilise built structures for capture of prey, they are less likely to range across the river than groups which browse or graze. The series of small floods during the Molenaars River study period may have served effectively to increase the mobility of these taxa, allowing some redistribution of these groups onto denuded stones, for example *C. afra and Chimarra* spp., whose densities on previously sampled stones increased with each time interval after the initial denudation and were greatest two months and four floods after the Baseline sampling survey. Winterbottom *et al.* (1997a) demonstrated that in some species mobility was increased as a function of discharge. In this light, a re-examination of the artificial disturbance study of Lake *et al.* (1989), where 'total recovery' of invertebrate fauna occurred within 33 days of disturbance, might find that the small spates that occurred during the recovery period may have been a substantial contributing factor to the rapid recovery found in this study.

Townsend's (1989) definition of disturbance as being the 'opening up of space' for recolonisation, which may take place at a range of scales, is particularly applicable in these sorts of studies. Unoccupied space may be associated with the supply of resources, or critical to the capture of resources, and thus desirable for either competing species or for new recruits from within the stream bed. This is likely to be especially important where invertebrate densities are high, at which times recolonisation of substrata may take place in mere hours (Robinson & Minshall, 1986).

In this regard, both the initial density of an organism, but also life history characteristics that determine the availability of new recruits at the time of the disturbance, would be expected to influence recovery rates. The recolonising populations of a number of taxa, *inter alia Agapetus agilis*, *Simulium* spp., *Chimarra* spp. and *Lithogloea harrisoni* had a smaller mean or modal head size in the Pre-Flood 1 samples than in the Baseline survey, suggesting that the previously denuded stones may have been recolonised predominantly by young instars. For example, Simuliidae are year-round breeders in Southern African rivers (De Moor, 1994) and drift, particularly of younger instars, is substantial and constitutes an important mechanism for the dispersion and spatial differentiation of different developmental stages (De Moor *et al.,* 1986). Similarly, the moderate and massive increases in Notonemouridae and *L. harrisoni* densities respectively, over the study period in the Molenaars River, and the frequency distribution of larval sizes, indicate the sequential hatching off eggs or migration of new instars from the hyporheos, which would provide a ready supply of individuals to colonise opened up space. On the other hand, new instars of *Cheumatopsyche* spp. tend to appear on the stream bed only later in the winter months (pers. obs.), and thus would not contribute to resilience of this group during early winter floods. Further, whilst the baetid mayflies *Demoulinia* spp. and *Afroptilum* spp. recovered rapidly on previously sampled stones prior to the onset of floods (Figure 6.14 a,b), they were susceptible to even the small floods during this study, and having no new recruitment, suffered large population losses over the season.

An additional factor in determining invertebrate resilience in this study was potentially the post-disturbance conditioning - in terms of algae and detritus, as well as the peri-

phyton composition - of previously denuded stones. Recovery pathways of algal communities following disturbance by floods or drought include recolonisation by immigrant propagules, as well as *in-situ* recovery and growth of remnant residues of the algal mat (Biggs & Stokseth, 1996; Peterson, 1996; Stanley *et al.,* 2004). In relation to floods, adnate forms of algae, mostly diatoms, are usually more resistant to scour and often provide a remnant layer for early (Grimm & Fisher, 1989; Peterson, 1996), except in the case of very large scouring floods. Non-attached, motile and loose flocculent assemblages have low resistance to floods, but under non-flood conditions drifting unattached diatoms resettle rapidly (Peterson, 1996). Propagule attachment has been shown to be a function of velocity and is highest in slow-flowing (>0.3 m s^{-1}) habitats (Biggs & Stokseth, 1996; Opsahl *et al.,* 2003). An idealized sequence of recovery of algal assemblages post disturbance is suggested by Stevenson (1996) to be re-growth of adnate forms, mostly diatoms and basal cells of filamentous green algae that persist through the disturbance event, to fast-growing apically-attached forms that stand erect on substrata, and finally to stalked, filamentous or motile forms (Stevenson, 1996).

Although algae are tolerant of desiccation (Peterson, 1996; Stanley *et al.,* 2004), mortality after sudden drying can occur within 0.5 to 4 hours (Stanley *et al.,* 2004), depending on the degree of heat exposure. All 'movable' stones in this study were removed from the stream for marking, and remained in the sun for at least two hours. In addition, all organic material was burnt off the area of each stone that was to be marked with paint, by means of a gas torch, to ensure that the paint marker remained on the stone. Thus there were in all probability very few remnant algal cells on denuded stones during the Baseline survey, and recovery during the period that followed must have been largely a result of immigration from drifting propagules (Robson, 2000). This feature, together with the prevailing autumn low-flow conditions, would have influenced the composition of algal assemblages on repeat-sampled stones. Thus the recovery process of stream periphyton during the Molenaars River study would probably have excluded in-situ recovery of adnate algal forms, but rather have given rise to a loose flocculent assemblage (Peterson, 1996), with low representation of adnate and mucilaginous forms, which are slower to recover from drifting propagules. Because different grazers are associated with exploitation of different algal life forms (Steinman, 1996), this feature may well have influenced the resilience or recovery recorded for different grazer taxa, as is hypothesised in the case of scraper-grazer taxa, *Elporia* spp., Elmidae and *Agapetus agilis*.

Mention has already been made of the slow recovery of *Elporia* spp. and Elmidae. Similarly, the cased-caddis *Agapetus agilis* would also fit this pattern of slow recovery, since despite signs of strong recruitment of new instars over the study period (Figure 6.14o), this species also ended up with low densities on Repeat-sampled stones, relative to the Baseline condition. This may have been in part a reflection of low mobility. However, as algal scraper-grazers (Schael, 2005), these groups are thought to favour the utilisation of adnate or prostrate algal growth forms (Steinman, 1996). For example, species within the genus *Agapetus* have been found to show a preference for, or significantly affect accrual rates of adnate diatoms, which were not affected or ingested by

grazing mayflies (Poff & Ward, 1992; Peterson *et al.,* 2001). In this study, therefore, the failure of these groups to recover on Repeat-sampled stones may thus also reflect the fact that the species composition algal assemblages, or the dominant life forms, that were re-established on denuded stones did not correspond to the preferred food source of these particular grazer groups. Resource quality has been shown to influence invertebrate colonisation of substrata in other studies (e.g. Negishi & Richardson, 2005).

In a slightly different vein, *Baetis* spp., by far the dominant taxon in the Molenaars River and present on almost every stone sampled, at all survey times, was the only species of Baetidae that had lower densities on repeat-sampled stones in the Pre-Flood 1 sampling than during the Baseline survey, and these were significantly so. In contrast, rapid recovery of numerically subordinate taxa, *Demoulinia* spp., *Afroptilum* spp., *Pseudocloeon* spp. and *Demoreptus capensis* occurred from the Baseline to Pre-Flood 1 sampling times. The extent to which baetid species compete for resources in Western Cape rivers is a subject for mere speculation, but these taxa are all fairly similar with regard to mouthpart morphology. If *Baetis* spp. were a dominant competitor among the Baetidae mayflies, as suggested by its numerical dominance within the invertebrate assemblages, then its apparent failure to recover might simply reflect its selection against possibly poorer resources associated with denuded stones - these stones in fact becoming space available for the lesser competitor species of Baetidae. In this instance, recovering periphyton assemblages may have been too sparse to support high densities of grazers, as was found in the study of Robinson & Minshall (1986). In the Molenaars River, periphyton biomass was not sampled, but in the Berg River study, one of the few differences between the post-flood repeat-sampled stones and the control set (Additional stones) was in the significantly lower periphyton biomass on the former, suggesting slow post-sampling recovery.

Competition between hydropsychid caddisflies and Simuliidae is better documented. Hydropsychids have been shown to be superior competitors, either through aggression or because their collecting nets interfere with simuliid feeding (Hemphill & Cooper, 1986; Hemphill, 1988; Zhang *et al.,* 1998) and mature hydropsychids are reported to constitute a significant predator regulating simuliid population size (De Moor, 1992). Simuliidae also exhibit intraspecific competition (Wiley & Kohler, 1981), although this more often leads to redistribution of individuals on a bed particle rather than displacement. In this study, both groups share the fast run / riffle biotopes, and there was a significant positive correlation between *Simulium* spp. density and that of *Cheumatopsyche afra* in the Molenaars River during the Baseline survey, a finding similar to that of De Moor (1992) who showed substantial overlap in habitat utilisation between these groups. The rapid recovery by *Simulium* spp. on repeat-sampled stones one month after initial sampling is consistent with the other research findings indicating the high resilience and high mobility of this taxon (Hemphill & Cooper, 1986; Hemphill, 1988), and the increase in population density of this group is explained by the continuous recruitment of new instars over the study period. The pattern of recolonisation of stones by *Simulium* spp., with almost exactly the same distribution of densities over the stream bed (Figure 6.16) is a marvellous demonstration of

the strong microhabitat preference. A second aspect of this pattern of recovery on denuded stones is also noteworthy: recolonisation of stones was more substantial on those stones that had previously supported *C. afra*, which species did not recover on denuded stones at all within the first month post Baseline sampling. The largest increases in *Simulium* spp. density were on those stones which had the greatest Baseline densities of *C. afra*. This suggests that in the absence of *C. afra, Simulium* spp. was able to expand its population size on stones that provided the optimal hydraulic conditions for resource utilisation. Other studies (e.g. Johnson & Vaughn, 1995) have also found a shift in relative densities of Hydropsychidae and Simuliidae after substratum disturbance in favour of the latter. These results are additional evidence for the idea that competitive displacement of Simuliidae by hydropsychid caddisflies in stream ecosystems is mediated by the effects of disturbance and the greater resilience of Simuliidae, thus allowing for long-term co-existence of these groups within the same microhabitat (Wiley & Kohler, 1981; Hemphill & Cooper, 1986; Hemphill, 1988; Zhang *et al.,* 1998; Robinson *et al.,* 2004).

Invertebrate responses to floods

In the Molenaars River study, the series floods that occurred over the invertebrate study period (Floods 1-4: Table 3.4, Figure 3.9) were very small, with less than 3% bed movement. The maximum average daily discharge for these floods was between 3 and 8 $m^3 s^{-1}$. To put this into perspective, baseflow during this dry winter ranged between 1 and 4 $m^3 s^{-1}$, although this higher value was only measured at the end of winter. However, the fourth flood had an instantaneous peak discharge of some 29 $m^3 s^{-1}$, more than an order of magnitude higher than the winter baseflows during July.

These minor floods affected the recovery of invertebrates on denuded substrata to different degrees. In some of the taxa which had shown little recovery in the month after the initial Baseline sampling, the increased velocities associated with the floods may have increased effective mobility and facilitated recolonisation (*sensu* Winterbottom *et al.,* 1997a), as discussed previously. In other groups, a poor or only moderate level of recovery after initial Baseline sampling may have been associated with the life-history stages present in the river (e.g. absence of new recruits or sub-adult stages) and / or the poorer conditioning of the repeat-sampled stones, which may have been avoided by mobile taxa that are able to track resources efficiently (e.g. *Baetis* spp.).

Where recovery after initial sampling was rapid, the taxa exhibited various responses from apparent flood-induced emergence, or susceptibility of only large instars to floods, through various levels of susceptibility of the population to increased flows, including no measurable response to increased flows.

These species-specific responses to small flood flows are summarised in Table 6.14. Here the extent of recovery after initial sampling, i.e. in the absence of floods, is provided as an indicator of the resilience of a species, whilst, in the case of resilient species, the susceptibility to flow is a measure of the extent to which the series of floods subsequently reduced population densities. This is based on the percentage reductions

provided in Table 6.10, but is provided here as categories of percentages, because of the low level of significance in the results. Where post Baseline sampling recovery was poor, floods either facilitated recovery or appeared to have no effect on recovery, and this is also indicated in Table 6.14.

It should be noted that these data must be considered preliminary, since the patchiness of invertebrate distributions, especially when abundances were low, as well as the wide variance associated with estimates of population density precluded statistically significant results in most instances. Nevertheless, they do represent the first specie-level data for flood-related responses on invertebrates in Western Cape rivers.

In the Berg River in 2004 there were two large intra-annual floods during the study period that moved between 25 and 43% of the river bed (Tables 3.5 and 6.2), and three minor spates (DRIFT Class I and II) that moved less than 3% of bed sediments. The larger floods represented a low and a high DRIFT Class IV flood, and moved all size categories of river bed materials, but to different degrees (Table 6.2).

Many studies have used a level of 40 or 50% of bed movement as a *threshold* for defining disturbance (e.g. Townsend *et al.,* 1997b; Gjerløv *et al.,* 2003). In comparison, therefore, the Class IV floods on the Berg River could be viewed as reasonably small disturbance events. On the other hand, the Berg River has much larger substratum particle sizes than most of the comparative studies on disturbance (see the literature review) and thus greater bed stability. As a result, whilst the magnitude of forces acting on the bed, and potentially affecting invertebrates through increased shear stresses, might be similar to, or indeed considerably greater than, other studies, this might not result in equivalent bed movement. For example, in a New Zealand study of similar design to this present one (Matthaei *et al.,* 1999a), a flood with return period of six months was associated with some 68 - 72% bed movement.

The floods in the Berg River were associated with some 58% decrease in total invertebrate density, cumulative for the two-month period. Nearly all individual invertebrate taxa declined significantly, whilst three mayfly taxa increased in densities on stones over the study period - *Lithogloea harrisoni* and *Nadinitella crassi* (Telagonodidae) and *Pseudocloeon* spp. (Baetidae).

Table 6.14 Summarised species-specific responses to small early winter floods in the Molenaars River, 2003.

The resilience of different taxa is indicated categorically as 'high', 'medium' or 'low', based on the extent of recovery observed in the month after initial Baseline sampling, but prior to floods. Susceptibility to flow is also provided within categories of percentages, because of the low level of significance in the results, based on values in Table 6.10. These categories are as follows: ≈- no change (± 24% increase or decrease), ↓ (25 - 69% decrease); ↓↓ (70 - 84% decrease); ↓↓↓ (85 - 100+% decrease). Arrows facing upwards indicate increases in density.

Species / taxon	Susceptibility to floods	
	Description	**Change in density over flood period**
Species showing high resilience (good / full recovery after initial sampling, before floods)		
Afroptilum spp.	differential loss small instars	↓
Demoreptus capensis	recruitment of new instars	≈
Pseudocloeon sp.		↓↓
Euthraulus elegans		≈
Lithogloea harrisoni	recruitment of new instars	↑↑↑
Afronurus harrisoni	differential loss large instars or flood-mediated emergence	↓↓
Afronurus sp.		↓↓
Notonemouridae	recruitment of new instars	↑↑↑
Simulium spp.	recruitment of new instars	↑↑↑
Orthocladiinae		≈
Tanypodinae		↓↓
Helodidae		≈
Hydrachnellae		↓
Species showing medium resilience (moderate recovery after initial sampling, before floods)		
Baetis spp.	may be associated with food quality	↓
Demoulinia spp.		↓
Lestagella penicillata		≈
Aprionyx spp.	Autumn emergence - small numbers depleted by floods	↓↓↓
Tanytarsini		≈
Chironomini		≈
Species showing low resilience (poor or no recovery after initial sampling, before floods)		
Cheumatopsyche afra		food-facilitated partial recovery
Chimarra sp.		flood-facilitated partial recovery
Agapetus agilis	recruitment of new instars	pattern not clear
Elporia spp.	recruitment of new instars	≈
Elmidae larvae		flood-facilitated partial recovery
Elmidae adults		↓

Interestingly, the large floods on the Berg River appeared to exceed a disturbance threshold for other taxa that were not affected by the smaller floods on the Molenaars River, viz. *Simulium* spp., Notonemouridae and *Demoreptus capensis*. These taxa increased in densities over the two month study on the Molenaars River, but declined in the Berg River. In addition the Orthocladiinae and Helodidae, whose densities remained stable in the Molenaars River study, were reduced by the larger floods in the Berg River study.

The Berg River study allowed for the effects of stone movement or non-movement during floods to be described, in relation to the magnitude of the disturbance-response by invertebrates. The percentage decrease in total invertebrate density on stones that were unmoved over the whole study period, relative to those that moved in both large floods was 40% and 62% respectively, a difference of some 20%. This is an interesting result for two reasons.

Firstly, the difference in densities on moved vs. unmoved stones is much less than anticipated, or put differently, the fact that moved stones, sampled immediately after a flood, retained nearly 40% of their Baseline densities is an unexpected result. It indicates that, despite obvious flood-induced mortality, many taxa were still present in reasonable densities on moved stones, presumably either because they never left that stone or because they colonised the stone in its new location during or at the end of the flood. This leads to the question of how local persistence over the course of a flood is possible in the case of moved stones in the Berg River, since these stones could hardly be considered to constitute instream refugia.

Most studies of instream refugia, that is, excluding the hyporheic zone and floodplain areas, identify as most important either stable particles (which moved stones were not) or hydraulic refugia such as patches of stream where shear stress remains low over the course of a flood (Lancaster, 1990; Lancaster & Hildrew, 1993a, b; Rempel *et al.,* 1999; Lancaster, 2000). Almost all studies that have demonstrated hydraulic refugium use during high flows have done so by means of artificially created refugia (Robertson *et al.,* 1995; Winterbottom *et al.,* 1997a; Winterbottom *et al.,* 1997b; Lancaster, 2000; Negishi & Richardson, 2005), although Matthaei *et al.* (2003) were able to identify stable patches of stream bed that acted as refugia for periphyton and invertebrate grazers (see also Palmer *et al.,* 1995). Nonetheless, these indicate that invertebrate densities in refugia were higher after floods than in non-refugium patches.

In relation to Lancaster & Hildrew's (1993b) refugium-based description of different stream types (see section 2.5.3, Figure 2.4), the Berg River may have fitted the Type III stream - that is, having a range of low and high shear stress points at low flows, but with all portions of the bed reflecting high shear stress (albeit measured as applied stream power) at high discharges and hence exhibiting a low refugium potential. Indeed, none of the more than 400 points in the Berg River were characterised by low or unchanging applied stream power during flood flows, relative to the baseflow condition. Even small stones that were located within the hydraulic shelter of large bed particles were nevertheless associated

with elevated applied stream power. In addition, the moved stones were often simply overturned or moved less than 0.5 m from their original locations, thus remaining in unsheltered positions within the main channel.

The fact that invertebrate densities on moved, unsheltered stones were greater than expected indicates that, even in bed-moving spates, invertebrates that are eroded from the bed are not necessarily lost from the stream reach, even in the absence of obvious hydraulic shelter. Rather, displacement may result in come sort of 'scramble for cover', which may be more or less successful depending on the particular attributes of different species, for example, mobility. In addition, some taxa may simply remain on a moving stone, awaiting the return of low flow conditions to redistribute over the stream to preferred micro-habitats. An additional explanation, at least in the case of some taxa, could be that moved stones represent a less densely inhabited environment preferable for colonisation by young instars moving into the surface layers of the bed from the hyporheos, immediately after a flood. These species-specific responses are discussed below.

These results thus differ markedly from the small, experimentally-based, refugium studies that indicate higher densities in instream refugia during floods (e.g. Palmer *et al.,* 1996; Winterbottom *et al.,* 1997b; Negishi & Richardson, 2005), since they provide no evidence of higher densities in some parts of the stream than in others. The current understanding of how invertebrates are affected by flood flows once they are dislodged from the substratum and entrained into the water column is poor, and difficult to research (Lancaster *et al.,* 1996; Bond *et al.,* 2000), although some behavioural studies indicate active responses to entrainment (Lancaster, 1999). Speculatively, the high turbulence associated with the large roughness elements in the Berg River may create hydraulic dead zones (*sensu* Lancaster *et al.,* 1996) that influence both invertebrate drifting distances as well as their re-entry into the bed. These are also considered to be instream refugia, but their transient nature makes them impossible to sample in empirical studies. Additional investigation of flood-related drift behaviour in these study rivers may help to explain reach-level resistance of invertebrates.

Secondly these results indicate a relative refugium afforded by stable stones. Whilst this was only some 20% for total invertebrates, it was shown to be more or less important for different taxa. The responses to floods on both unmoved stones vs. those moved in both large floods are summarised in Table 6.15, for invertebrate taxa which were represented in sufficient densities in order to show patterns. The susceptibility to flow is a measure of the extent to which the series of floods reduced population densities, and is based on the percentage reductions provided in Table 6.11, but is provided as categories of percentages, because of the preliminary nature of the results. The summary is provided separately for Repeat-sampled stones (potentially overestimating the effect of floods because of the error associated with repeat sampling the same stone) and Additional (independent) stones, although the responses were highly similar in both cases.

For many taxa there was little difference in the level of reduction on the two categories of (moved and unmoved) stones, but possibly for different reasons. Species like *Demoulinia*

spp., *Cheumatopsyche afra*, and Tanypodinae were mostly reduced to near-zero densities by the floods - apparently as a result of erosion of individuals by flood forces, rather than through pupation or emergence of subimagos, as indicated by the population size frequency data. Others like the Chironomidae and Elmidae that may be more resistant to shear forces because of their size, may have simply held onto moving stones. Indeed, these taxa are well known to be difficult to dislodge from stones when sampling even by light brushing and often have to be removed by forceps.

In the case of taxa whose populations were augmented by new instars (e.g. *Baetis* spp., *Demoreptus capensis*, Notonemouridae and *Simulium* spp.) moved stones may have represented open space for young recruits, thus reducing the numerical differences in density between moved and unmoved stones. In this instance, colonisation of 'open space' presupposed that the substrata (moved stones) were initially denuded and then colonised by young instars from the hyporheos. The only data with large enough sample sizes to test this was that for *Baetis* spp., where moved stones were found to support substantially smaller individuals than unmoved stones (Figure 6.15). This still does not indicate when such stones were colonised. Samples were taken as soon after a flood as was practically possible, often in still considerably elevated flows, but it is possible that animals had already begun to redistribute themselves over the stream bed. A final explanation for the higher than expected densities on moved stones could be that more mobile taxa may have been able to counteract the effects of initial removal from the riverbed by flood waters, by rapidly returning to the substratum (e.g. *Simulium* spp., *D. capensis*).

Invertebrate densities on the top surfaces of large immovable boulders did not decrease over the flood period, but changed in composition quite substantially, with *Baetis* spp. declining and being replaced in dominance by orthoclad chironomids. Other groups that increased in density on these surfaces were *Simulium* spp., *Lithogloea harrisoni, Lestagella penicillata*, *D. capensis* and other chironomids.

In relation to the type of refugium offered by unmoved stones - whether this was the top surface or the whole stones - the stones were generally subject to similar forces as those stones that moved during the floods, measured as applied stream power. This type of refugium - that of large stable particles (*sensu* Townsend *et al.,* 1997b; Francoeur *et al.,* 1998) - does not therefore constitute an hydraulic refuge, but rather one that may be associated either with more resistant taxa (e.g. *Lestagella penicillata*, *Lithogloea harrisoni*), with retreat- or case-building taxa (e.g. Tanytarsini, *Cheumatopsyche maculata*, *Chimarra* spp.), or with taxa that escape hydraulic forces by hiding within the sediments underneath these stones, and which would be exposed to the force of the flood if a particle were to move (e.g. Helodidae, *Euthraulus elegans*).

Table 6.15 Summarised species-specific responses to winter floods in the Berg River, 2004, showing the relative refugium from flood mortality afforded by unmoved stones. Susceptibility to flow is based on percentage reduction in population density, and provided within categories of percentages. These categories are as follows: ≈- no change (± 24% increase or decrease), ↓ (25 - 69% decrease); ↓↓ (70 - 84% decrease); ↓↓↓ (85 - 100+% decrease). Arrows facing upwards indicate increases in density.

	UNMOVED STONES		STONES MOVED IN BOTH LARGE FLOODS	
	Repeat-sampled	**Additional**	**Repeat-sampled**	**Additional**
No relative refugium offered on unmoved stones				
Demoreptus capensis	↓↓↓	↓↓	↑↑↑	↑↑↑
Notonemouridae	↓	↓	≈	↑
Simulium spp.	↓	↓↓	≈	≈
Demoulinia spp.	↓↓↓	↓↓↓	↓↓↓	↓↓↓
Cheumatopsyche afra	↓↓↓	↓↓↓	Not present in Baseline	
Tanypodinae	↓↓↓	↓↓↓	↓↓↓	↓↓↓
Orthocladiinae	↓	↓	↓	↓
Elmidae adults	↓↓	↓↓↓	↓↓↓	↓↓
Elmidae larvae	↓↓	↓↓	↓↓↓	↓↓
Low relative refugium offered on unmoved stones				
Cheumatopsyche maculata	↓↓↓	↓↓	↓↓↓	↓↓↓
Athripsodes bergensis	↓↓	↓↓↓	↓↓↓	↓↓↓
Afronurus sp.	↓↓↓	↓↓	↓↓↓	↓↓↓
Aprionyx spp.	↓↓	↓↓↓	↓↓↓	↓↓↓
Chironomini	≈	≈	≈	↓
Baetis spp.	↓	≈	↓	↓
Hydrachnellae	↓	↓	↓↓	↓
Euthraulus elegans	↓↓	↓↓	↓↓↓	↓↓↓
Chimarra sp.	↓↓↓	↓	↓↓↓	↓↓↓
Afronurus harrisoni	↓	↓↓↓	↓↓	↓↓↓
Tanytarsini	↓↓	↓	↓↓↓	↓↓
Moderate to high relative refugium offered on unmoved stones				
Lestagella penicillata	↓	↓	↓↓↓	↓↓↓
Helodidae	↓	↓	↓↓↓	↓↓↓
Afroptilum spp.	↑	↑	↓↓↓	↓↓↓
Lithogloea harrisoni	↑↑↑	↑↑↑	↓	≈

These results contrast with those of Bond & Downes (2000) who found that a caddisfly that preferentially colonised large rocks was disproportionately dislodged from these substrata compared to smaller rocks. In the present study *Cheumatopsyche maculata* also preferred larger rocks, but they afforded this species a small relative refugium during floods - notwithstanding which the population declined by 77% over the flood season.

At a community level, stones that moved or remained unmoved appeared to differ very little, and were not distinguishable using multivariate analysis. This result needs to be interpreted in the light of the different starting conditions on moved and unmoved stones: from the Baseline survey, it became clear that stones that were destined to move were generally smaller, but, more importantly, had higher invertebrate densities than those that were destined to remain stationary over the flood period. The relatively greater reduction of densities on moved stones thus had the effect of 'cancelling out' this initial starting difference, thus ensuring that the distribution of taxa after floods was generally more homogenous across different stone size classes. The failure to discriminate between assemblages on moved and non-moved stones after the floods is probably due to this effect. It is noteworthy, however, that a number of taxa virtually only survived floods because of the relative refugium of unmoved stones - viz. Leptophlebiidae, most Trichoptera, and the mayfly *Afroptilum* spp. Similarly, *Lithogloea harrisoni*, which appears on the river bed at the start of winter, only increased in population density on unmoved stones.

Relationship between invertebrate density on unmoved stones and the distribution of forces over the stream bed

Bond & Downes (2000) provided evidence that hydraulic forces acting on even fixed substrata may play as great a role in disturbance as rock tumbling, since densities of the species they examined were not different on fixed or movable substrata. The results of this study agree, since bed particle movement was not necessary in the series of small non-bed moving spates in the Molenaars River to cause a reduction in invertebrate populations, and in the Berg River there was not a great deal of difference in densities of many taxa on moved and unmoved stones. This contrasts with Cobb *et al.* (1992) who found that insect densities started to decline with a substratum displacement of about 10%.

Laboratory methods have been used to examine the responses of invertebrates to increasing flow forces (Lancaster, 1999), but no field experiments have attempted to quantify this relationship. In this study, the attempt to find a relationship between invertebrate density and the distribution of applied stream power on unmoved river stones during a flood was not easy, and marred by a number of limitations. The chief one of these was that it is not possible to measure invertebrate density on a single stone both before and after a flood, as the measurement of the first will denude the stone of invertebrates, precluding further data collection. Thus the study could only examine the relationship between applied power and post-flood densities, not the change in density over the flood.

Even so, the results provide no substantial evidence that invertebrates change their

distribution over the stream bed as a result of increasing flow forces. This may be in part explained by the following:

Behavioural changes in distribution along a hydraulic gradient undertaken by individuals in response to increases in flow have been shown, for example, by Lancaster (1999) in her laboratory study.

Also, underwater observations of *Elporia* spp (Blephariceridae) movement in the Molenaars River during the ascending limb of one of the floods showed individuals on the uppermost surfaces to be progressively relocating downwards towards the bed, which might have been in response to the increased flows (pers. obs.).

Redistribution of animals immediately after a flood may have confounded the effects of applied power on density distributions.

7 CONCLUSIONS AND RECOMMENDATIONS

In what can only be regarded as a very preliminary investigation of invertebrate responses to floods, field observations of invertebrate responses to three floods indicate:

- Increased forces associated with even small spates effect a degree of reduction in invertebrate populations, which cumulatively alter population dynamics over the winter season, although there are large differences in the extent to which species perceive small floods as disturbance.
- Large floods are associated with greater population reductions and affect all stream invertebrates.
- Movement of substratum particles is not a threshold for disturbance-responses, since almost all taxa were reduced on unmoved as well as moved substrata
- However, there is a wide difference in the relative refugium afforded to different taxa, as a result of some substrata remaining stable over a flood.
- Resistance to floods at a reach level is considerable, indicated by a 58% overall reduction in invertebrate density (or 42% survival) as a result of two floods that moved between 25 and 43% of the river bed particles, in all size classes.
- Resistance to floods may be exaggerated by the immigration of new individuals of some species, in the form of new recruits of small instars from the hyporheos or upstream reaches, which would constitute a resilience response to floods in these taxa.
- No direct relationship was found between invertebrate densities after a flood and the distribution of maximum forces acting on bed particles during the flood, measured as unit applied stream power, possibly as a result of micro-scale movements of invertebrate within / on the same substratum particle.

These results add to the current understanding of how floods may affect ecological processes regarding species interactions, since they clearly demonstrate substantial differences in the disturbance-response between different and potentially competing species. The preliminary species-specific results may aid in setting flow requirements in rivers, during Environmental Water Requirements studies, particularly where there is evidence of species interactions, or where pest species (Chironomidae, Simuliidae) may proliferate under regimes of little disturbance.

However, the observational data effectively represent only three replicates in what might be a very variable set of responses to floods, dependent on not only the specifics of the flood hydrograph (peak and duration), but the timing with the season, initial population densities, etc. Seasonal and interannual differences in these aspects of the hydrological regime and biotic responses are likely to be considerable, and these need to be investigated to substantiate these results.

The successful outcome of the hydraulic model developed to describe incipient motion, in terms of its ability to indicate the movement status of previously unmarked river stones,

raises the potential for simpler studies on flood responses to be undertaken in the future, free from the complicating error effects of repeat-sampled stones. This will enable large sample sizes to be processed, with more robust results.

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