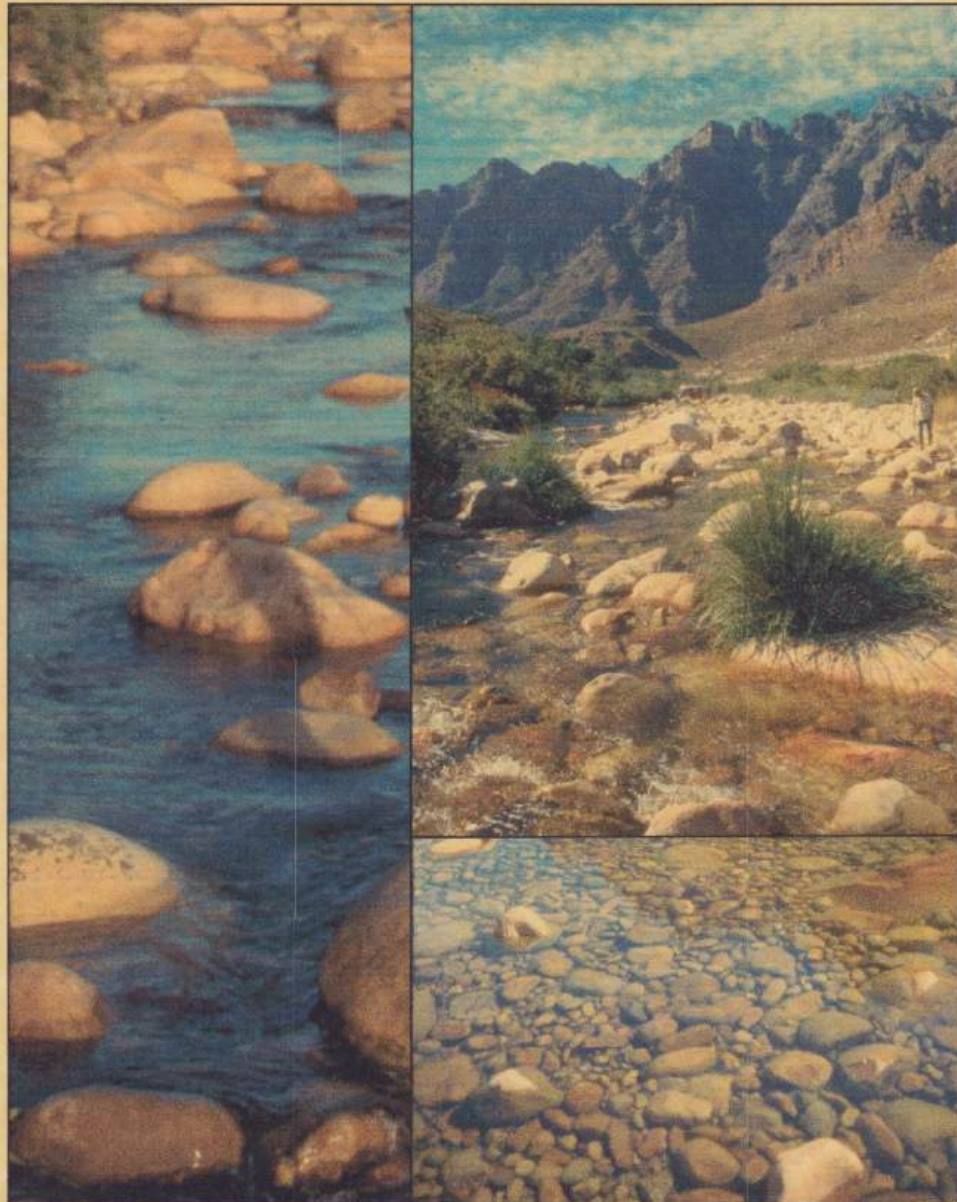


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# Microhabitat Suitability Curves derived for the Mayfly larvae (Ephemeroptera) of a south western Cape foothill river

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# Microhabitat suitability curves derived for the Mayfly larvae (Ephemeroptera) of a south-western Cape foothill river

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**ABSTRACT:** Benthic macroinvertebrate samples were taken from the Molenaars River of the south western Cape (33° 43' 23"; 19° 10' 32"), over three days during April and May 2000. Samples taken at depths ranging from 0.05 to 0.6 m and velocities ranging from 0 to 1.37 m.s<sup>-1</sup> yielded ten species of Ephemeroptera in five families. The abundance data were converted to densities and mean (±SD) density was estimated at 1669±1325 individuals.m<sup>-2</sup>. Microhabitat suitability functions using single-factor and multiple polynomial regression for depth, velocity and Froude number were derived for the eight most common Ephemeropteran species using log-transformed (base 10) density data. Densities for all species exhibited significant correlations (P<0.05) with velocity and Froude numbers where each variable was considered independently. Predicted optimal conditions for macroinvertebrates based on single-factor regression ranged from a velocity of 0.01 m.s<sup>-1</sup> and Froude number 0.01 (*Cloeodes* sp. nov. 1), to 0.99 m.s<sup>-1</sup> and Froude number 1.09 (*Demoreptus capensis*). The distribution by density of only one species (*Lestagella* sp.) was correlated with depth. The interaction terms of the multiple polynomial regressions for velocity and depth (*vd*) were significant (P<0.05) only for *Baetis harrisoni*. Weighted means for velocity and depth weighted by species density were used as additional descriptors of optimal conditions. Comparison of different descriptors of microhabitat suitability revealed that quadratic polynomial regressions fitted the data poorly and tended to over-estimate optimal conditions, while cubic polynomial regressions achieved a better fit and approximated the results obtained using weighted means, but tended to produce mathematical artifacts such as upturning

## Introduction

### *General background*

Changes to the ecological functioning of riverine ecosystems and the decline in biodiversity resulting from human modifications to natural flow regimes have focussed attention on the critical role played by local hydraulics in structuring the distribution, diversity and abundance of the biota. Of primary importance is current velocity, which affects the composition of the substrata, the delivery and cycling of nutrients and gases, the removal of metabolites and the distribution of food resources (Alan 1995; Davis and Barmuta 1989; Newson *et al.* 1998; Statzner *et al.* 1988; Statzner and Higler 1986). As a major physical force acting on the biota, creating conditions of stress and drag, current velocity also plays an important role in shaping the morphological and behavioural adaptations of aquatic organisms (Hynes 1984; Statzner *et*

*al.* 1988; Wiley and Kohler 1984). Alteration the flow regime and thereby local hydraulic conditions can therefore be expected to produce changes in species composition and standing crop of fish and aquatic macroinvertebrates.

A standard analytical technique for recommending environmental flows for rivers impacted by consumptive uses or development was described by Bovee (1986). The distribution of a species across a gradient of any physical habitat variable likely to change given an altered flow regime (i.e. substratum, velocity or depth) is represented on a frequency tally, bar graph or histogram. Based on the assumption that the most 'suitable' or 'optimal' conditions can be identified by the modal range or peak of the distribution, these 'habitat suitability criteria' (Bovee 1986) (in this paper referred to as 'microhabitat suitability curves') can then be used to predict how species composition or standing crop might change in response to an altered flow regime.

Microhabitat suitability curves are derived from a combination of 'utilisation' and 'availability' distributions. Utilisation describes the physical habitat conditions recorded where a particular species was observed or collected. To avoid bias introduced by environmental variability, utilisation is corrected using a distribution describing the availability of the physical habitat variable of interest. Availability is the full range of conditions available to the organism and is derived by randomly sampling the physical habitat conditions in the river at the same time as the biological data are collected (Bovee 1986). 'Suitability' or 'preference' curves for a particular species are then derived from the ratio between the utilisation and availability functions. This ratio is then as a value between 0 (least favourable) and 1 (optimal).

The replicability of the technique and the predictability of its output can be improved by fitting response functions to species distributions. A response function is a way of formally characterising the relationship between a dependent response (in this case the abundance or biomass of a species) and one, or several, explanatory habitat variable/s. The strength and direction of the relationship can thereby be statistically described and tested. Since the data often suggest a curvilinear relationship, polynomial regression (Kleinbaum and Kupper 1978;

Zar 1974) is most often used for this purpose. Using these methods, studies have revealed statistically significant relationships for the distribution by abundance or biomass of species over several physical habitat variables (Gore and Judy 1981; Jowett *et al.* 1991; Jowett and Richardson 1990; Orth and Maughan 1983).

Because microhabitat suitability curves provide a quantitative description of habitat, they are an effective means of translating the microhabitat requirements of species or communities into required flow conditions - and ultimately discharge - by contributing the biological input to hydraulic simulation techniques such as the Physical HABitat SIMulation model (PHABSIM) (Bovee and Milhous 1978). Flow conditions critical to the biota can then be identified, quantified and incorporated into a modified environmental flow regime.

Generally, substratum, depth and velocity have been used as standard explanatory variables. Statzner *et al.* (1988), however, have suggested that predictability and replicability are complicated by the complexity of flow behaviour in a natural river, and propose the use of hydraulic indices such Reynolds and Froude numbers. They suggest that these indices are more appropriate descriptors of flow in ecological studies than mean water column velocity. Furthermore, these indices can be calculated fairly simply from standard measurements. Froude number ( $Fr = v/\sqrt{gd}$ ), the most commonly used index to describe the behaviour of flow, is a dimensionless number which describes the ratio of inertial to gravitational forces and gives an indication of the amount of turbulence (Davis and Barmuta 1989). By integrating the effects of velocity and depth, the Froude number may account for some of the variability evident in biological data which result from the interaction of velocity and depth.

While much of the earlier emphasis in developing microhabitat suitability curves was based on fish (Bovee & Cochnauer 1977; Bovee 1978; ), benthic macroinvertebrates have increasingly become the focus of research (Gore 1978; Gore and Judy 1981; Jowett *et al.* 1991; Jowett and Richardson 1990; Orth and Maughan 1983) because of their widespread occurrence and fundamental importance to the functioning of riverine ecosystems (King and Tharme 1993). Being less mobile than fish, they are less capable of responding to altered flow regimes by avoiding unfavourable conditions and should, therefore, be expected to be more

sensitive than fish to changes in flow (Bovee, cited in King and Tharme 1993).

*Overview of techniques for deriving habitat suitability curves for macroinvertebrates*

A variety of techniques for deriving microhabitat suitability curves for macroinvertebrates has evolved from the basic principles described by Bovee (1986). Orth and Maughan (1983) fitted single factor polynomial regression models to log-transformed macroinvertebrate abundance's, biomass and community diversity indices. The response of ten macroinvertebrate species to depth, velocity, substratum and turbulence (Froude number) was investigated in this manner. A joint preference factor (JPF) derived from the combination of substratum, depth and velocity was found to be significantly correlated with biomass. Orth and Maughan (1983) found that the JPF is a reliable predictor of densities and could be used in place of multivariate preference functions to model the combined effect of the three variables.

In order to provide the input for the PHABSIM model, Gore and Judy (1981) further modified the above technique by relating cumulative mean abundance of the Trichopteran *Nectopsyche lahontonensis* to a predetermined increment of either velocity, depth or substrate. Fourth order polynomials were fitted to the data with the preference defined by the greatest incremental jump in the curve of the polynomial.

A major criticism of single factor habitat suitability functions so far described is that they assume that macroinvertebrates respond independently to velocity and depth (Mathur *et al.* 1985). To overcome this assumption, Gore and Judy (1981) tested the interaction of velocity and depth by adding an interaction term (the product of velocity and depth,  $vd$ ) to an exponential polynomial curve fitted to invertebrate densities. If the correlation coefficient for the interaction term ( $vd$ ) was significantly different from zero, then the interdependence of velocity and depth could be demonstrated. All the tests were statistically significant, suggesting that the interaction term is an important element in the prediction of macroinvertebrate density.

The three approaches described above i.e. the single factor polynomial regression (Orth and Maughan 1983), the incremental approach (Gore and Judy 1981), and the multiple regression (Gore and Judy 1981), were tested by Morin *et al.* (1986), for precision and bias. Bias was

tested by comparing trends in the variability of the residuals. If residual variability differed significantly from zero, then preference curves were considered biased. Precision was tested by comparing the magnitudes of residual variability - high variability suggesting low precision. They found that the least biased and most precise method was the multiple regression approach proposed by Gore and Judy (1981) emphasizing the importance of factoring in the interaction of depth and velocity.

In several studies (Jowett and Richardson; Jowett *et al.* 1991 and Orth and Maughan 1983), weighted means have been used in conjunction with suitability functions to describe optimum physical habitat conditions. Gore (1978) calculated weighted means of velocity and depth weighted by the abundance data of 37 species. The weighted means for velocity and depth were plotted against each other and the optimal conditions for each species defined by a centroid. The optimal conditions for highest community diversity were also calculated and indicator species identified as those species whose centroids were located closest to the centroid for highest diversity. In future samples, the presence of the indicator species would suggest the maintenance of community structure.

Objectives of this study were to derive single factor and multivariate microhabitat suitability curves for the Ephemeroptera of the Molenaars River with respect to the following standard physical habitat variables: velocity, depth and Froude number - with the latter being used as a descriptor of turbulence. Values describing the optimal physical conditions for each species were calculated using weighted means weighted by the density of individual species at each increment of velocity, depth and Froude number in order to compare their performance against the predicted optimum conditions described by the suitability curves.

The Ephemeroptera was chosen as a target group because of their abundance, widespread occurrence, and taxonomic diversity in south western Cape foothill rivers.

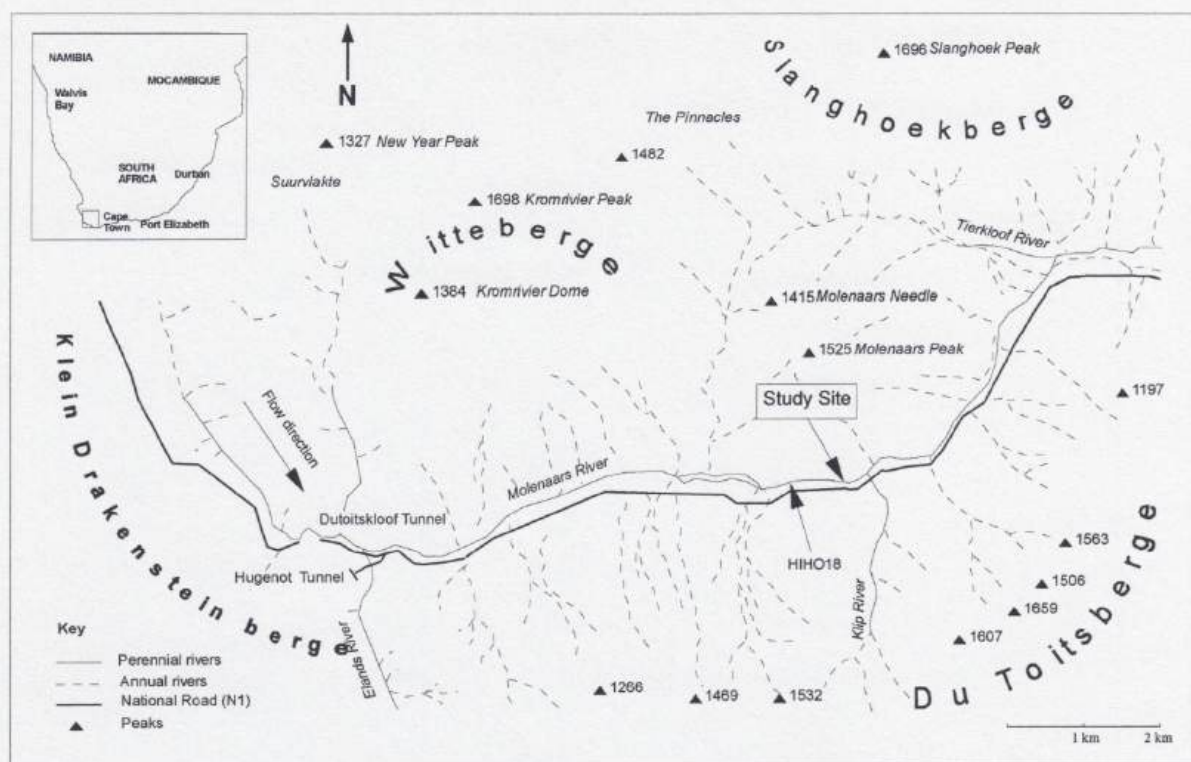
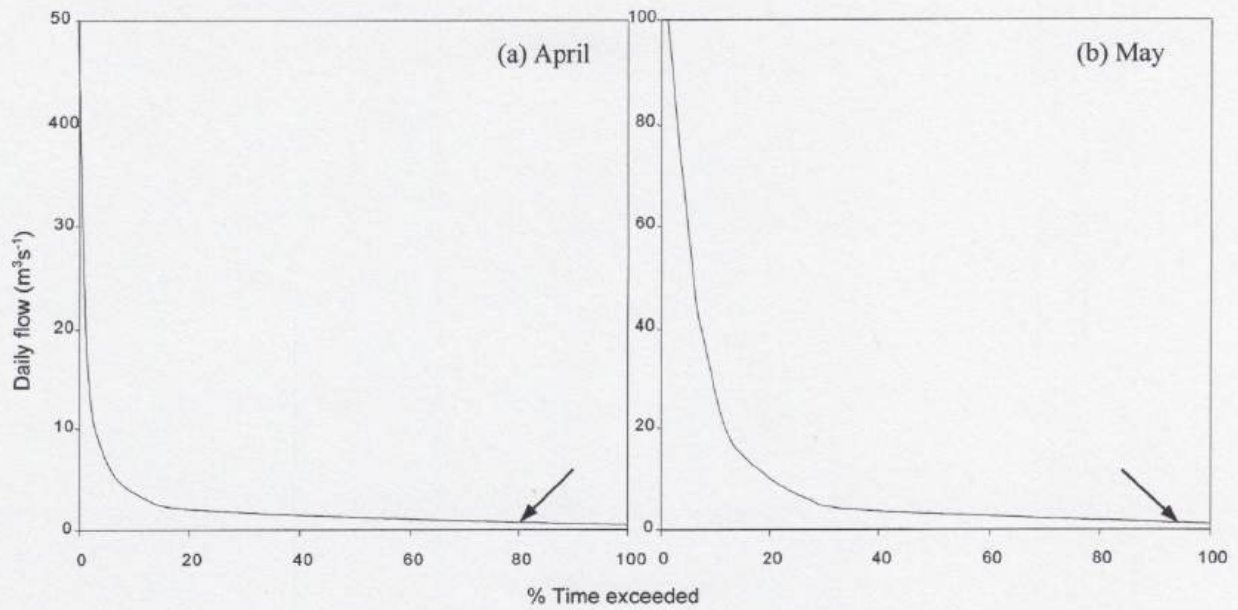


Fig. 1. The Molenaars River, south-western Cape, showing the study site ( $33^{\circ} 43' 23''$ ;  $19^{\circ} 10' 32''$ ) located downstream of the gauging weir HIHO18.

### Study Area

The Molenaars River is a foothill cobble-bed river draining the Du Toits Kloof mountains, situated approximately 60 km east of Cape Town within the south-western Cape winter rainfall region of the fynbos biome. The Molenaars River, draining a catchment area of 113 km<sup>2</sup>, is fairly typical of foothill rivers in the Cape Fold Belt of South Africa (Harrison 1965). The elevation of the catchment is approximately 400 m *amsl* at the study site, with surrounding mountain peaks rising to 1697 m (Slanghoek Peak) and 1838 m (Du Toit's Peak).

The study area ( $33^{\circ} 43' 23''$ ;  $19^{\circ} 10' 32''$ ) indicated in Fig. 1, comprised a 100 m reach of the river, 22 km upstream of its confluence with the Breede River and was found to consist of a sequence of morphological units. Two riffles, upstream and downstream of a pool consisted of a mosaic of emergent boulders and boulder steps among cobbles. Flow types in these areas were predominantly Rippled Surface (RS) and Standing Waves (SW) interspersed by series of Cascades (CAS) over boulder steps and Chutes (CH) between emergent boulders. Flow-



**Fig. 2** Daily flow duration curves for gauging weir H1H018 for (a) April and (b) May calculated from flow data compiled from the years 1969 -2000. Arrows indicate the location on the flow duration curve of the discharge recorded for this study ( $0.6 \text{ m}^3 \text{ s}^{-1}$ ).

types in the pool were predominantly Smooth Boundary Turbulent (SBT) in the centre of the channel with Barely Perceptible Flow (BPF) along the channel margins (see Appendix A for a list of definitions for flowtypes).

Small and large cobble and boulders were the predominant substrata in both the pool and riffle areas. Depositions of sand and particulate organic matter were restricted to the banks and channel margins. The width of the river at the study site ranged from 10 to 20 m with an average gradient of  $0.12 \text{ m.km}^{-1}$ .

A Department of Water Affairs and Forestry gauging station, located approximately 300 m upstream of the study site provided the discharge data for this study. Low-flows occur during late summer - February and March - when monthly flows may vary between  $1.7 - 2.7 \cdot 10^6 \text{ m}^3 \cdot \text{s}^{-1}$ , while high-flows occur during the winter months of June and July when monthly flows vary between  $30 - 35 \cdot 10^6 \text{ m}^3 \cdot \text{s}^{-1}$ . Floods occur during the winter months of June through to September when maximum daily flow rates may exceed  $80 \text{ m}^3 \text{ s}^{-1}$ . The sampling, therefore, took place near the end of the low-flow season and beginning of the high-flow winter months. Discharge during the course of the study remained at  $0.6 \text{ m}^3 \text{ s}^{-1}$  which is exceeded approximately 80% of the time in April and above 90% of the time in May (Fig. 2).



An open canopy of typical riparian species for the fynbos biome lined the left and right banks, which appeared to be fairly stable. Dominant species included: Wild almond (*Brabejum stellatifolium*) and Smalblaar (*Metrosideros angustifolium*). Palmiet (*Prionium serratum*), a rooted emergent reed, occurred along the banks and on channel islands. Black wattle (*Acacia mearnsii*), an exotic invasive that had infested the lower reaches of the river valley, had recently been cleared from this section of the river and was present but not dominant. The main human impacts on the study site were a trout farm and hotel located approximately 1 km upstream of the study site and the National Road (N1), which runs alongside the river approximately 50 m from the wetted area. Deposition of fine particulate organic matter (FPOM) from the outfall of the trout farm may result in the build up of detritus on the stream bed during low flows, although high flows during winter keep the bed well scoured (Simpson 1997).

## Methods

### *Data collection*

Sampling was carried out on three days between 28 April and 04 May 2000. Benthic macroinvertebrate samples were taken from 40 sampling points within the study site using a box sampler with a 0.34 m × 0.34 m (0.1 m<sup>2</sup>) frame size fitted with a collecting bottle of 250 μm mesh diameter. This mesh size allowed the passage of finer organic material, while retaining all but the smallest larval instars of interest to this study. The sampler was positioned on the substratum and the larger particles removed, scrubbed of all fauna and set aside. The remaining particles were disturbed to a depth of 0.1 m. Samples were initially fixed in 4% formalin and taken back to the laboratory where they were transferred to 70% ethanol for preservation. The selected taxa were then separated from the detritus, identified to species level, where possible, and counted under a dissecting microscope.

Since logistical considerations limited the number of samples which could be taken to 40 (compared with 90 – 100 which are generally used to derive suitability curves; Jowett and Richardson 1990; Orth and Maughan 1983), sampling sites were chosen to ensure an even distribution of data points across all velocity and depth ranges. This was difficult in practice

and higher velocity ranges tended to be undersampled due to the higher proportion of slow moving water in the study reach.

Physical habitat variables (velocity and depth) were recorded at each sampling point. A Marsh-McBirney electromagnetic current meter on a metrically calibrated wading rod was used to measure mean current velocity. Since water velocity is assumed to vary logarithmically from zero at the stream bed to a maximum at the water surface, mean current velocity was measured at 0.6 of the water depth from the surface.

#### *Abundance*

The abundance ( $A$ ) of each of the Ephemeropteran species (ten in number) collected at each of the 40 sampling points was determined and converted to densities by multiplication by 10 ( $D=10A$ ) and reported in numbers.m<sup>-2</sup> (Appendix C, Tables 1 a - d and Table 2).

#### *Development of Microhabitat Suitability Curves*

The derivation of microhabitat suitability curves in this study differed in some respects from their original derivation as described by Bovee (1986) and summarized in Fig 3. The original derivation involved the computation of the suitability index or 'preference' as the ratio of utilisation to availability: ( $P_i = U_i/A_i$ ) where,  $P_i$  = an unnormalised index of preference,  $U_i$  the relative frequency of observations;  $A_i$  the relative frequency of  $x_i$  at the time of observation and  $x_i$  the microhabitat variable interval (Bovee 1986). Differences in the availability of habitat between streams can thereby be accounted for, allowing for the comparison of curves for the same species with data compiled from different systems.

Time and manpower constraints in this study did not allow for the collection of availability data. Since sampling sites were systematically chosen to reflect a wide range of environmental conditions in the river and no comparison between study sites was being attempted, it was therefore decided that the physical data from the biological samples would be an adequate reflection of conditions within the 100m reach. Thus the suitability curves in this study are more accurately described as 'utilisation curves'.

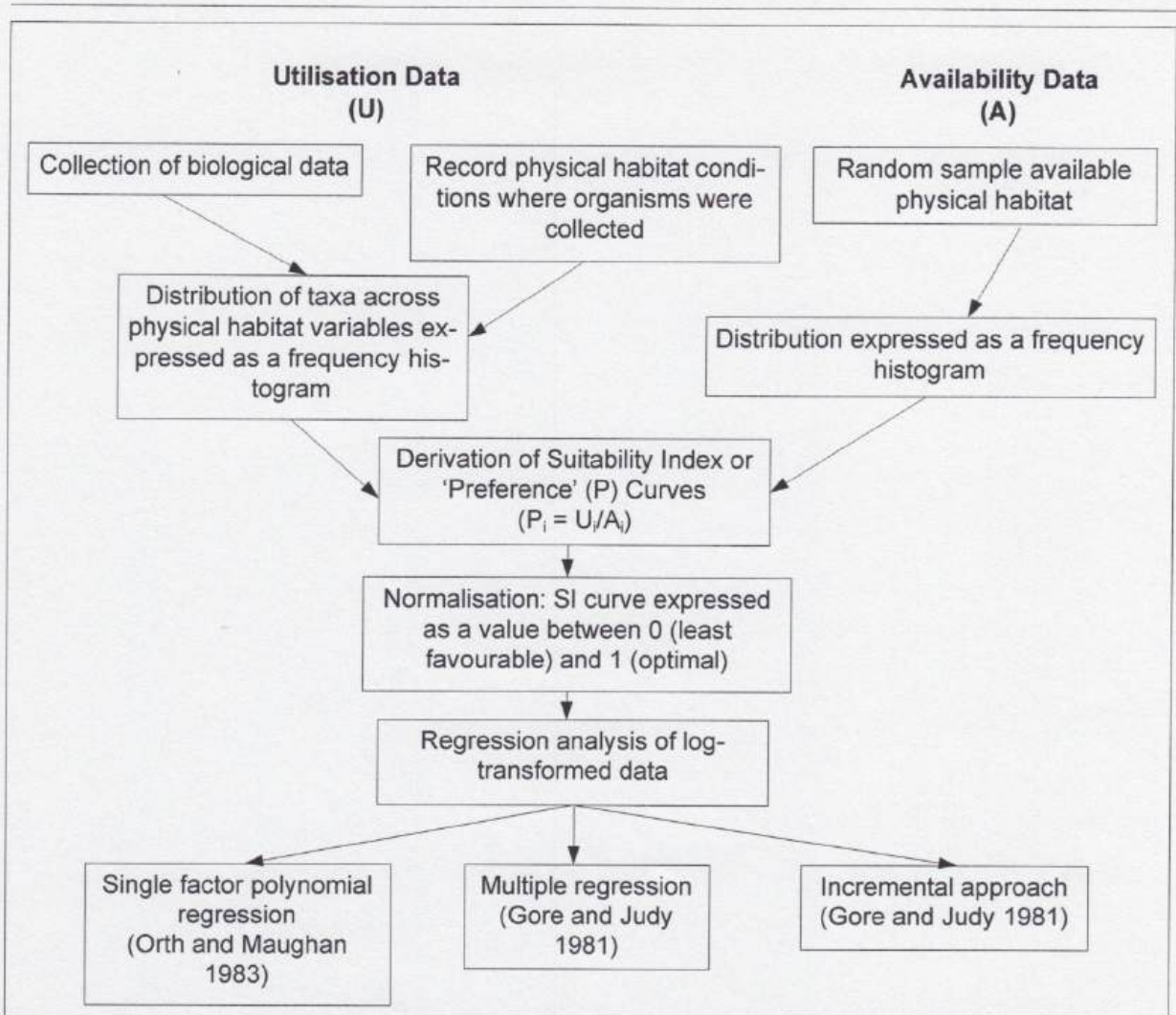


Fig. 3. Summary of the technique for arriving at microhabitat suitability curves as described by Bovee (1986), Gore and Judy (1981), and Orth and Maughan (1983).

A second difference is that the data were not expressed as a true 'index', i.e. they were not normalised. Suitability indices are arrived at by dividing the predicted abundance's by,  $A_{max}$ , the maximum predicted abundance:  $(SI = A/A_{max}$ , Bovee 1986). Thus, the suitability index is expressed as a ratio between 0 and 1. This procedure allows for a more pertinent method of comparing microhabitat suitability between species and sites, but since raw data cannot be displayed, it does not allow for examination of the degree of variability within the data, nor the comparison of relative abundance's between species nor for an evaluation of the goodness of fit.

Optimal habitat conditions in this study are therefore defined as those physical habitat conditions associated with the maximum predicted density (the peak of the curve) for each

of the suitability functions, without normalisation.

### *Polynomial regression*

- (a) Polynomial regression (Kleinbaum and Kupper 1978; Zar 1974) was used to perform single factor analysis of the dependence of log-transformed (base 10) macroinvertebrate densities on the physical habitat variables of depth ( $d$ ), velocity ( $v$ ) and Froude number ( $Fr$ ). Regressions were performed on the log-transformed data (Orth and Maughan 1983) to derive quadratic polynomial functions for each of the aforementioned variables using the following function, where  $D$  = density:

$$\log_{10}(D+1) = \alpha + \beta_1 x + \beta_2 x^2 \quad (2)$$

Habitat suitability was derived for those species where the regressions were significant ( $P < 0.05$ ).

- (b) In order to test their performance against quadratic functions, cubic functions were then fitted to the data. Regression was performed on the log-transformed data (Orth and Maughan 1983) to derive cubic polynomial functions for each variable using the expression,

$$\log_{10}(D+1) = \alpha + \beta_1 x + \beta_2 x^2 + \beta_3 x^3 \quad (3)$$

- (c) To account for the interaction of velocity and depth a multiplicative interaction term ( $vd$ ) was added to the quadratic polynomial expression (Gore and Judy 1981) to obtain:

$$\log_{10}(D+1) = \alpha + \beta_1 v + \beta_2 d + \beta_3 v^2 + \beta_4 d^2 + \beta_5 vd \quad (4)$$

If the interaction correlation coefficient  $\beta_5$  was not significantly different from zero ( $H_0: \beta_5 = 0$ ), then the interaction of velocity and depth was assumed to be independent of macroinvertebrate densities.

All analyses were performed using the STATISTICA<sup>®</sup> computer software package.

*Weighted means*

Weighted means were used to describe the typical velocity and depth conditions for each species and a typical value for conditions of highest diversity (Gore 1978; Orth and Maughan 1983). Since the relative importance of each velocity and depth increment measured at each site differed according to the density of animals found there, each increment is assigned a proportionate degree of importance by multiplying it by the density found at that increment. By dividing the weighted physical habitat variables obtained by the sum of the weights, a weighted mean can be obtained. Weighted means for each physical habitat variable and diversity were therefore calculated as follows:

$$x_w = \sum_i w_i x_i / \sum w_i \quad (5)$$

where  $x_w$  = the weighted mean of a habitat variable  $x_i$ , the relative importance of which is determined by  $w_i$ , the weighting variable (i.e. species density or diversity) at site  $i$ .

*Diversity*

For each sample diversity was determined. The Shannon Weaver diversity index ( $H'$ ), the most commonly used index of diversity, was used in this study. It accounts for both species richness and equitability, thus reflecting how evenly individuals are distributed over a range of species (Begon *et al.* 1990) and is calculated using the formula:

$$H' = - \sum_{i=1}^s P_i \log_e P_i \quad (1)$$

where  $P_i$  is the proportion of total individuals in the  $i$ th species and  $s$  is the total number of species at a site.

*Hydraulic index*

Froude number was calculated from:

$$Fr = U / \sqrt{gd} \quad (6)$$

where  $\bar{U}$  is the mean current velocity measured at 0.6 of the depth,  $g$  = acceleration due to gravity, and  $d$  = depth. Where the ratio is small ( $Fr < 1$ ), gravitational forces exceed inertial forces and the flow is described as subcritical or tranquil, where  $Fr = 1$  the flow is critical or transitional and where  $Fr > 1$  inertial forces exceed gravitational forces and the flow becomes turbulent (supercritical) and is characterised by broken white water (Davis and Barmuta 1989).

See Appendix B for a glossary of all statistical and mathematical symbols used here.

## Results

### *Physical habitat variables*

A wide range of microhabitats was available to the benthos in each section of the riffle-pool sequence. Flow in pool areas was slower and deeper with a mean velocity in the pool ( $\pm$  SD) of  $0.08 \pm 0.04$  m.s<sup>-1</sup>. The average depth in the pool was  $0.32 \pm 0.09$  m, although it exceeded 0.6 m in places. As expected, flow in riffles was shallower and faster with a mean velocity of  $0.58 \pm 0.29$  m.s<sup>-1</sup> and depth of  $0.16 \pm 0.17$  m. The maximum velocities recorded in the riffle areas was 1.37 m.s<sup>-1</sup>. Froude numbers were between 0 to 0.05 (mean  $0.03 \pm 0.03$ ) in pools and backwaters and 0.05 to 0.91 (mean  $0.41 \pm 0.25$ ) in riffles. Froude numbers exceeding 1 were only found in shallow turbulent flows over boulder steps (maximum  $Fr$  was 1.71).

### *Invertebrate abundance*

Ten species of Ephemeroptera from five families were found to occur at the study site. Rare

**Table 1** Mean, standard deviation (SD) and coefficient of variation (CV) for counts of Ephemeroptera sampled from 40 points in the Molenaars river during the period 28 April - 04 May 2000.

	Numbers m <sup>-2</sup>	$\pm$ SD	CV
<i>Baetis harrisoni</i>	408	( $\pm$ 387)	1.0
<i>Demoreptus capensis</i>	384	( $\pm$ 441)	1.1
<i>Afromurus sp</i>	104	( $\pm$ 122)	1.1
<i>Lestagella sp</i>	183	( $\pm$ 171)	0.9
<i>Aprionyx peterseni</i>	153	( $\pm$ 241)	1.6
<i>Cheleocloeon excisum</i>	33	( $\pm$ 116)	3.4
<i>Pseudopannota maculosum</i>	10	( $\pm$ 22)	2.1
<i>Castanophlebia sp.</i>	2	( $\pm$ 5)	2.8
<i>Cloeodes sp nov 1</i>	417	( $\pm$ 1152)	2.7
<i>Caenid sp</i>	1	( $\pm$ 7)	6.3
Mean total taxa	1699	( $\pm$ 1325)	0.8

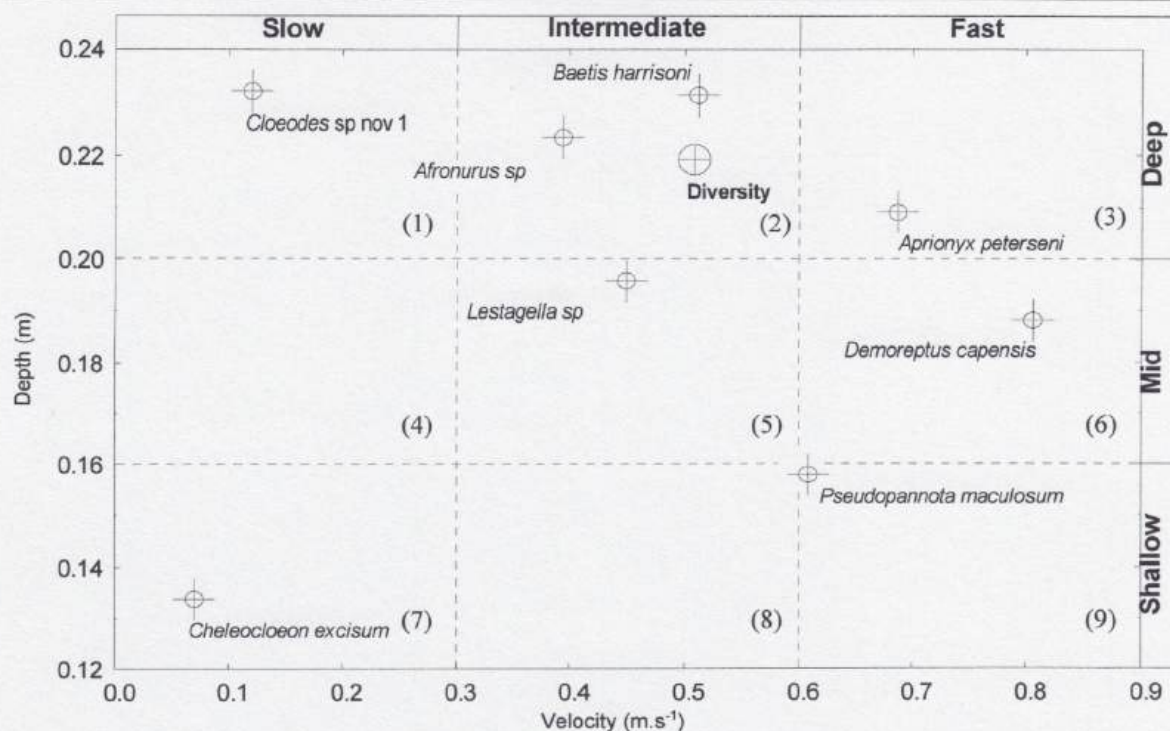
species, including *Castanophlebia* sp. and a species of Caenidae were found in less than five samples and were not included in the analysis. Caenidae were the rarest taxa and were found at only one sampling point. Mean ( $\pm$  SD) invertebrate density from site totals (Table 1) was found to be  $1699 \pm 1325 \text{ m}^{-2}$ . *Cloeodes* sp nov 1 (undescribed) and *Baetis harrisoni* were the most abundant taxa. These accounted for 50 % of all Ephemeroptera, with mean ( $\pm$  SD) abundance's of  $417 \pm 1152$  and  $408 \pm 387$ , respectively. A high coefficient of variation ( $CV$  2.7) for *Cloeodes* sp nov 1 suggested a highly clumped distribution, whereas *B. harrisoni* was more evenly distributed ( $CV$  1.0).

### Weighted means

Table 2 shows the weighted means obtained for depth, velocity and Froude number, weighted by the species density at each sample point. The results are plotted in Fig. 4. Organisms occurred at relatively shallow compared with the available range of depths sampled (0.65 m) and ranged from  $x_d = 0.14 \text{ m}$  for *Caenid* sp. to  $x_d = 0.31 \text{ m}$  for *Castanophlebia* sp. (since both species occurred in fewer than five samples, these estimates may reflect sampling bias and are therefore not included in Fig. 4). Most species had weighted means at depths between  $x_d = 0.13$  and  $x_d = 0.23 \text{ m}$ . Weighted means for velocity ranged from  $x_v = 0.14 \text{ m.s}^{-1}$  (*Cloeodes* sp nov 1) to  $x_v = 0.82 \text{ m.s}^{-1}$  (*Demoreptus capensis* - which had a correspondingly high Froude number:  $x_f = 0.7$ ). The weighted mean for diversity was found at a depth of  $x_d = 0.22 \text{ m}$ , a velocity of  $x_v = 0.51 \text{ m.s}^{-1}$  and Froude number of  $x_f = 0.51$ . The centroids for *B. harrisoni* and *Afromurus* sp. were located closest to the centroid for optimal diversity.

**Table 2** Weighted means for physical habitat variables of depth ( $x_d$ ), velocity ( $x_v$ ) and Froude number ( $x_f$ ) weighted by species density.

	Weighted means ( $x_w$ )		
	Depth $x_d$ (m)	Velocity $x_v$ ( $\text{m.s}^{-1}$ )	Froude $x_f$ Number
<i>Baetis harrisoni</i>	0.23	0.51	0.40
<i>Demoreptus capensis</i>	0.18	0.82	0.70
<i>Afromurus</i> sp.	0.22	0.40	0.31
<i>Lestagella</i> sp.	0.20	0.45	0.36
<i>Aprionyx peterseni</i>	0.21	0.69	0.54
<i>Cheleocloeon excisum</i>	0.13	0.07	0.09
<i>Pseudopannota maculosum</i>	0.16	0.61	0.53
<i>Castanophlebia</i> sp.	0.31	0.47	0.34
<i>Cloeodes</i> sp nov 1	0.23	0.14	0.13
Caenidae sp.	0.14	0.00	0.05



**Fig. 4.** Means of velocity and depth weighted by the density and diversity of each species at 40 sample points. Depth is categorised into 0.04 m increments: shallow 0.12 - 0.16 m; mid 0.16 - 0.20 m; deep 0.20 - 0.24 m. Velocity is categorised into 0.3 m.s<sup>-1</sup> increments: slow 0 - 0.30 m.s<sup>-1</sup>; intermediate 0.3 - 0.6 m.s<sup>-1</sup>; fast 0.6 - 0.9 m.s<sup>-1</sup>. Permutations of depth and velocity categories are numbered (1) - (9).

The velocity and depth ranges for the species sampled were each arbitrarily divided into three categories: shallow-, mid-depth and deep; and slow-, intermediate- and fast-velocities. These categories are based on the minimum and maximum weighted means obtained for the invertebrates and not on the complete range of velocities and depths sampled. The centroids for each species are located in seven of the nine permutations of the velocity and depth categories: (1) slow-velocity, deep species (*Cloeodes* sp nov 1); (2) intermediate-velocity, deep species (*B harrisoni*, *Afronurus* sp. and *Lestagella* sp., including the centroid for diversity), slow-velocity, shallow-depth species (*C. excisum*); (3) fast-velocity, deep species (*Aprionyx peterseni*); (5) intermediate-velocity, mid-depth species (*Lestagella* sp.); (6) fast-velocity, mid-depth species (*Demoreptus capensis*) and (9) shallow-depth fast-velocity species (*P. maculosum*).

#### Microhabitat suitability curves

Microhabitat suitability curves derived for velocity and Froude number are presented in Fig. 5 and 6 (a) - (h) respectively and describe the distribution over these variables for eight of the



ten Ephemeropteran taxa collected. Correlation coefficients and maximum predicted values for each species are reported in tables 3 and 4 respectively.

### Velocity

Polynomial regressions fitted to invertebrate abundances. Use of velocity ( $v$ ) in quadratic and cubic response functions proved significant ( $p < 0.05$ ) for all species except *P. maculosum* (Table 3). The curves suggest that highest invertebrate densities are distributed across a range of velocities, increasing up to a maximum and decreasing thereafter. This range appears to be relatively broad compared with the available range of velocities (*B. harrisoni*, *D. capensis*, *Afronurus* sp and *Lestagella* sp Fig 5 a - d), except for those species occurring in the slower velocity ranges (*C. excisum* and *Cloeodes* sp nov 1, Fig 5 f and h) where most organisms were restricted to velocities less than  $0.4 \text{ m.s}^{-1}$ . *Aprionyx peterseni* (Fig. 1e) appears to be distributed across almost the entire recorded velocity range.

Correlation coefficients ( $R$ ) were highest for *B. harrisoni* (0.63 for the quadratic and 0.71 for the cubic function) and *D. capensis* (0.79 for both the quadratic and cubic functions) and lowest for *P. maculosum* (0.41 and 0.42 for the quadratic and cubic functions respectively).

Suitability functions for most species are convex, either skewed towards the mid to lower velocity ranges ( $0.45 - 0.65 \text{ m.s}^{-1}$ : *B. harrisoni*, *Afronurus* sp., *Lestagella* sp.), or in the single case of *D. capensis*, skewed toward the higher velocities ( $0.97 - 0.99 \text{ m.s}^{-1}$ ). *C. excisum* and *Cloeodes* sp. nov. 1 have curves which are concave, showing highest abundances in the lower velocity ranges ( $< 0.01 \text{ m.s}^{-1}$ ).

**Table 3** Correlation coefficients ( $R$ ) for quadratic and cubic polynomial regression functions (Figs 5 and 6, a - h) derived from Ephemeropteran densities for velocity ( $v$ ), depth ( $d$ ) Froude number ( $Fr$ ) and the interaction term for velocity and depth ( $vd$ ). \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P, 0.001$ .

	Correlation coefficients (R)					
	$v^2$	$v^3$	$d^2$	$Fr^2$	$Fr^3$	$vd$
<i>Baetis harrisoni</i>	0.63***	0.71***	0.28	0.64***	0.68***	0.69***
<i>Demoreptus capensis</i>	0.79***	0.79***	0.36	0.80***	0.82***	0.83***
<i>Afronurus</i> sp.	0.46*	0.61***	0.23	0.19	0.35	0.48
<i>Lestagella</i> sp.	0.49**	0.60***	0.39*	0.30	0.52**	0.60**
<i>Aprionyx peterseni</i>	0.43*	0.51*	0.34	0.47**	0.49*	0.55*
<i>Cheleocloeon exisum</i>	0.44*	0.47*	0.33	0.38	0.44	0.54*
<i>Psuedopannota maculosum</i>	0.41*	0.42	0.26	0.40*	0.40*	0.45
<i>Cloeodes</i> sp. nov. 1	0.45*	0.45*	0.06	0.51**	0.51**	0.54*

### Depth

None of the polynomial regression functions fitted to depth alone proved significant ( $p > 0.05$  in all analyses), suggesting the independence of depth and macroinvertebrate densities (Table 3). These functions were therefore not produced in this study.

### Froude Number

The shape of the curves tended to be similar to the curves for velocity, although tolerance ranges for Froude number appear to be narrower for most species (see Fig 5a *B. harrisoni* and Fig 6c *Afronurus* sp.).

The highest densities of most species are limited to hydraulic conditions where Froude number is  $< 1$  (subcritical conditions). Most species occur within the range of Fr 0.50 - 0.60, with the exception of *D. capensis* which has a maximum predicted Fr of 0.86 - 1.09, suggesting a preference for turbulent conditions in shallow and fast water (supercritical conditions).

### Interaction of Velocity and Depth

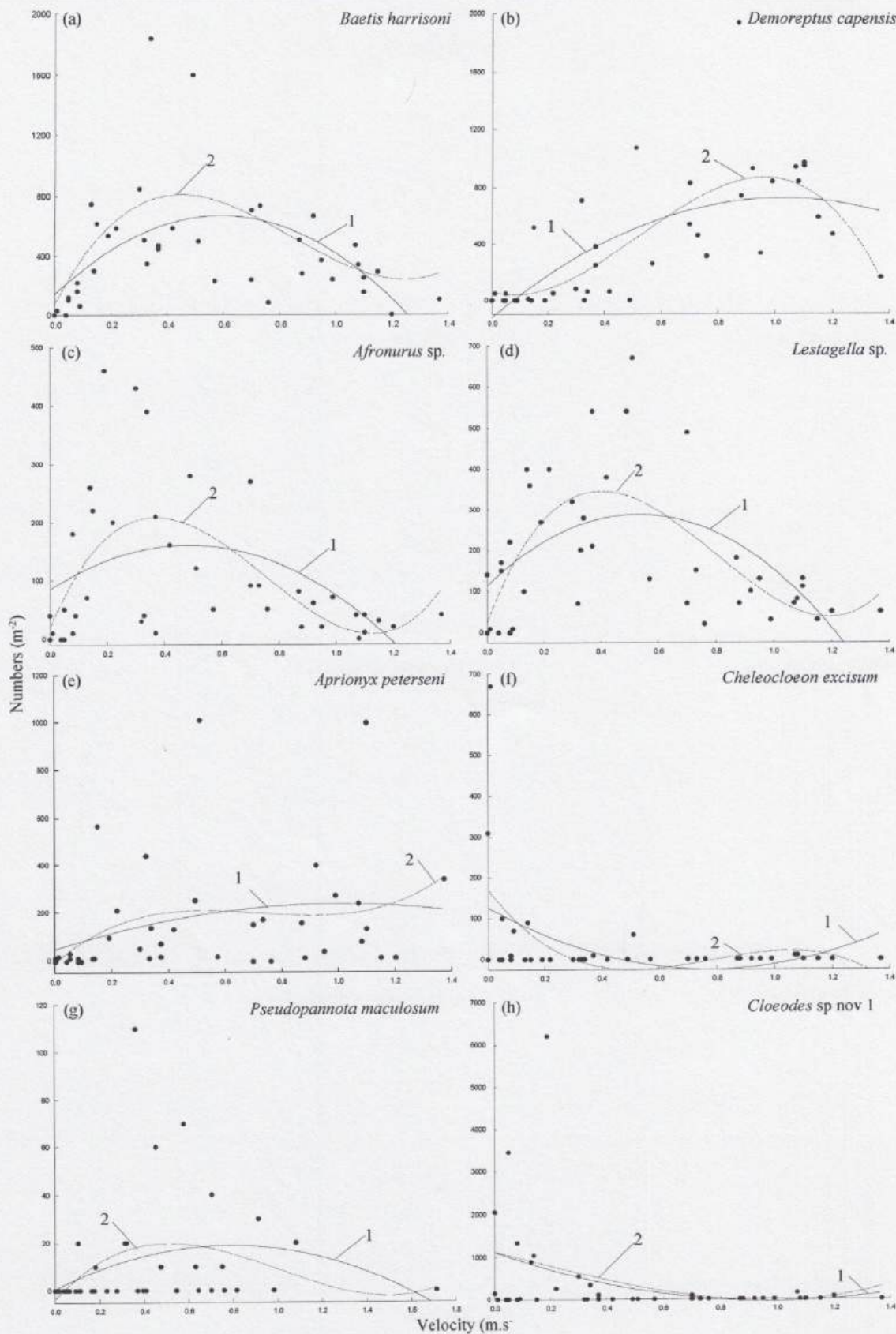
The correlation coefficients for multivariate functions were significant ( $p < 0.05$ ) for all species except *Afronurus* sp. and *P. maculosum*. However, *B. harrisoni* was the only species for which the interaction partial regression coefficient ( $vd$ ) was significant ( $P < 0.05$ ). Response surfaces were derived for *B. harrisoni* and *D. capensis* (Fig. 7) as examples of contrasting microhabitat distributions and not for the remaining species.

**Table 4** Values obtained by inspection for velocity ( $v$ ,  $m.s^{-1}$ ) and Froude number (Fr) at which maxima of Ephemeropteran densities for quadratic and cubic polynomial regressions are predicted.

	Quadratic		Cubic	
	Velocity ( $m.s^{-1}$ )	Froude No.	Velocity ( $m.s^{-1}$ )	Froude No.
<i>Baetis harrisoni</i>	0.64	0.64	0.50	0.49
<i>Demoreptus capensis</i>	0.99	1.09	0.86	0.97
<i>Afronurus</i> sp.	0.59	0	0.31	0.42
<i>Lestagella</i> sp.	0.63	0.44	0.42	0.45
<i>Aprionyx peterseni</i>	0.90	0.86	0.65	0.49
<i>Cheleocloeon exisum</i>	$< 0.01$	$< 0.01$	$< 0.01$	$< 0.01$
<i>Psuedopannota maculosum</i>	0.70	0.64	0.31	0.49
<i>Cloeodes</i> sp nov 1	$< 0.01$	0.01	$< 0.01$	$< 0.01$

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From Fig. 7 it can be seen that highest abundances of *B. harrisoni* occur at velocities between 0.42 and 0.71 m.s<sup>-1</sup> and depths of 0.21 and 0.44 m. Highest densities of this species are predicted to occur at mid-depths and intermediate velocities (in relation to the maximum depth and velocities sampled). Highest densities of *D. capensis* (Fig 7b) were found between velocities of 0.59 and 1.6 m.s<sup>-1</sup> and depths < 0.11 m, suggesting that shallower depths and higher velocities are most suitable for this species



**Fig. 5.** Comparison of microhabitat suitability curves for Ephemeroptera from the Molenaars River fitted for velocity by (1) quadratic and (2) cubic polynomial regressions. Correlation coefficients and significance levels are reported in Table 3

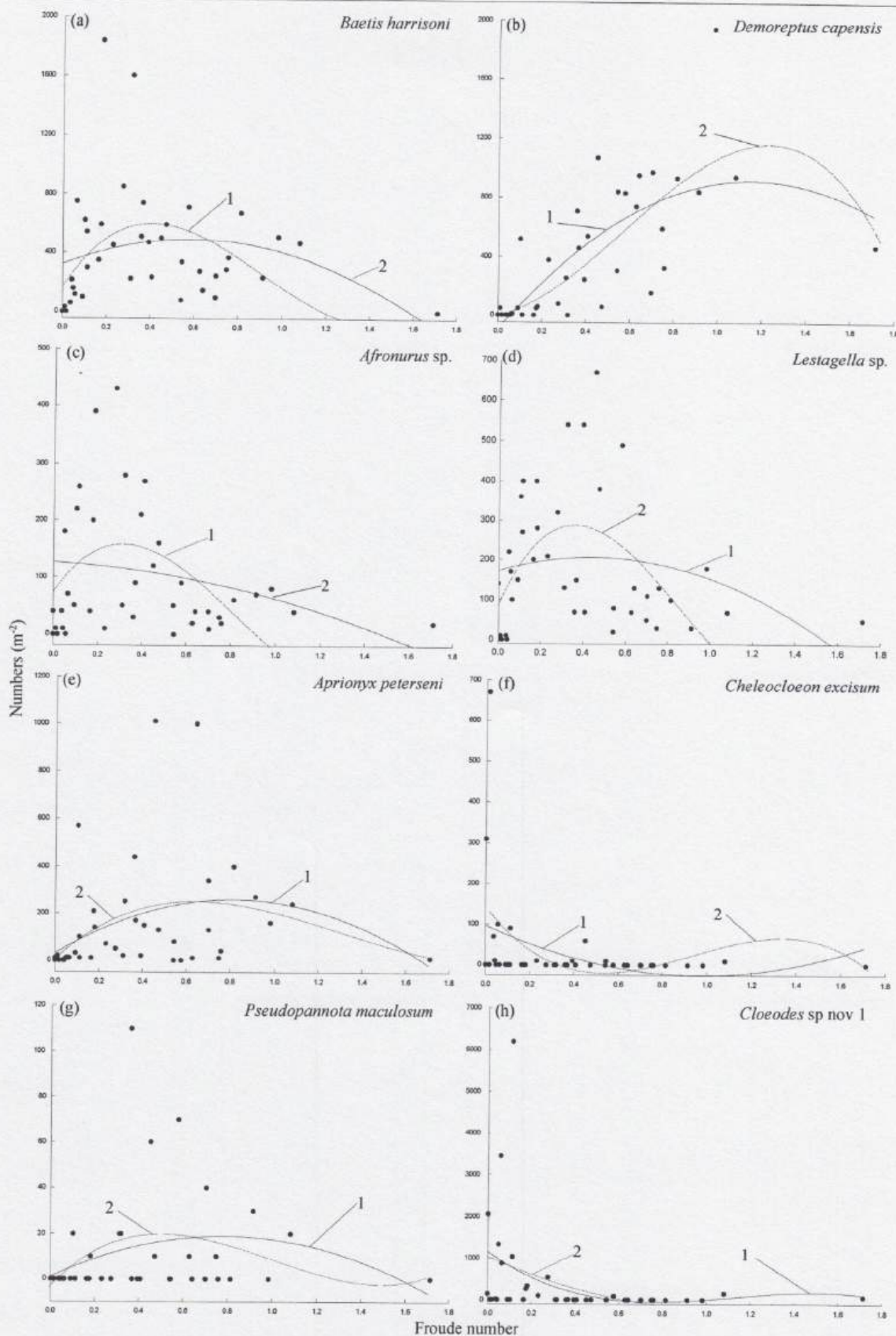
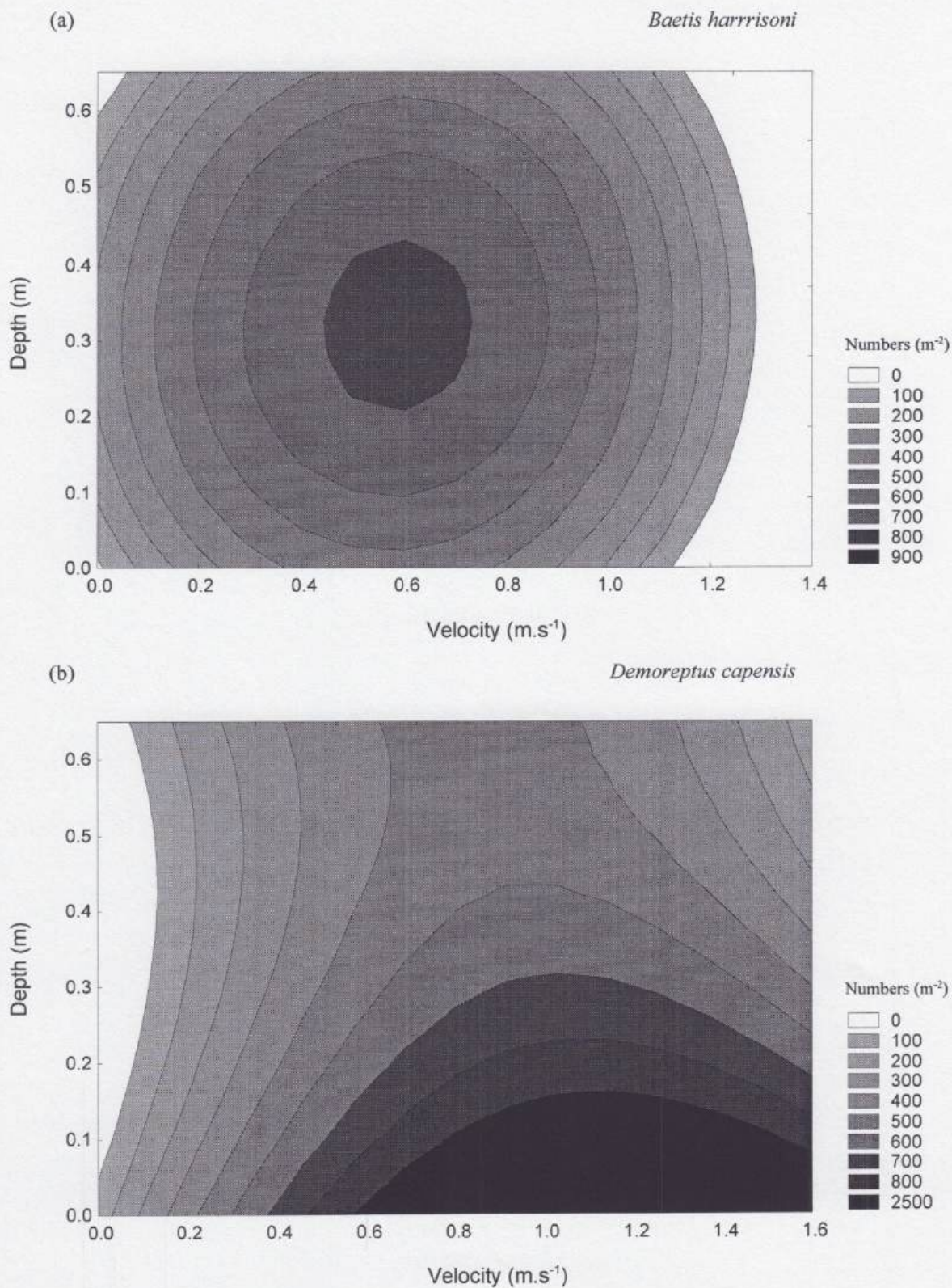


Fig. 6. Comparison of microhabitat suitability curves for Ephemeroptera from the Molenaars River fitted for Froude number by (1) quadratic and (2) cubic polynomial regressions. Correlation coefficients and significance levels are reported in Table 3



**Fig. 7.** Comparison of response surfaces derived from multivariate polynomial regressions including the interactive term ( $vd$ ) for (a) *B. harrisoni* ( $1.633+4.244v-0.884d-4.091v^2-0.812d^2+4.163vd$ ) and (b) *D. capensis* ( $1.379+4.896v-7.492d-2.920v^2+7.330d^2+3.189vd$ )

## Discussion

The relationship between mean water column velocity and the microdistribution of aquatic invertebrates has been questioned by some authors (Statzner 1981; Macan 1974), primarily because stream organisms (with the exception of Simuliidae and Blephariceridae) are believed to occupy the viscous sublayer on the lower surface of stones (Statzner 1981). This suggests that the organisms are able to find sheltered refuges from the current, taking advantage of small-scale flows created by the substratum irrespective of mean water column velocity. Nowell and Jumars (cited in Allan 1995), however, have proposed that the viscous sublayer is an artifact of experimental conditions where flow is laminar. Under conditions of increasing turbulence (the predominating condition in natural streams), this viscous sublayer becomes thinned to the point where it may be of no consequence to the invertebrates at all, particularly when flows exceed  $0.2 \text{ m}\cdot\text{s}^{-1}$  (Allan 1995). However, while the flow microenvironment within the hyporheos does afford some refuge from the prevailing flow conditions, direct exposure of benthic invertebrates to mean current velocities can be assumed to take place for at least part of the time: Glozier and Culp (1989), for example, demonstrated significant diel movement by two mayfly species from the lower surfaces of the substratum during the day to the upper surfaces at night, and large numbers of at least one species of Ephemeroptera were observed grazing the periphyton on upper surfaces of rocks in the pool areas during the course of this study (pers.obs.).

One of the assumptions of the present study is, therefore, that while the measurement of mean water column velocity may not give a true reflection of the flow conditions experienced by the organism, it is in at least a limited sense, representative of these conditions. The statistically significant relationships between mean water column velocity and the distribution of the benthos obtained in this study appear to support this assumption. However, the discrepancies between measured water column velocity and flow near the bed may explain the relatively broad distributions (Fig., 5, a-h and 6, a-h) observed for invertebrate densities across physical habitat variables and the relatively low correlation coefficients in some cases. Actual tolerance ranges for individual species may therefore be far narrower and well below the velocities reported here, especially for samples taken from deeper water where mean

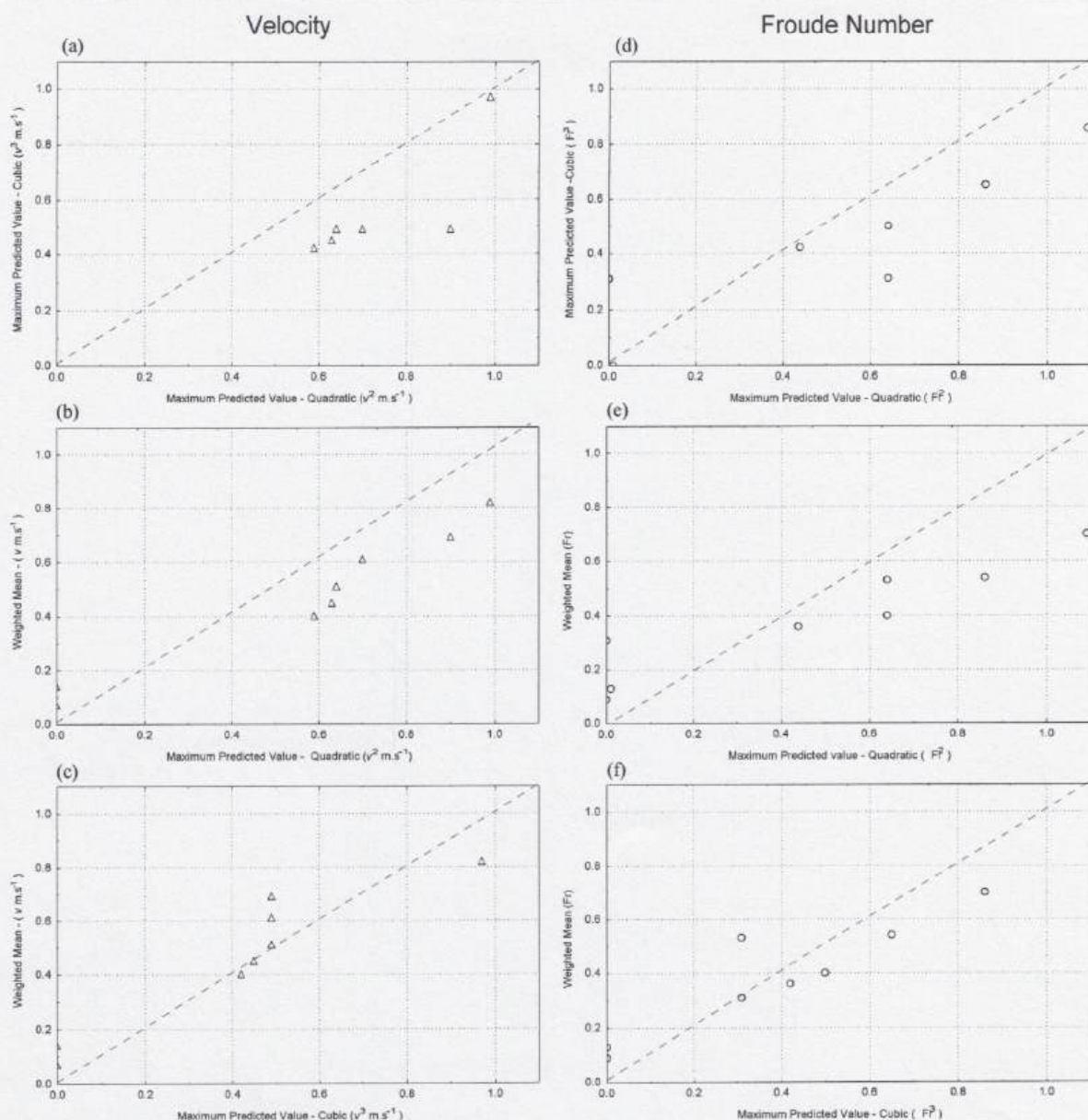
water column velocity is less representative of conditions near the bottom.

The weighted means for velocity and depth reported here for highest diversity are slightly lower than (0.51 m.s<sup>-1</sup> and 0.22 m respectively, Table 4), but compare favourably with, the findings of Gore (1978; 0.76 m.s<sup>-1</sup> velocity 0.28 m) and Orth and Maughan (1983; 0.6 m.s<sup>-1</sup> and 0.34 m). The discrepancies in these findings are probably due to the comparison of different species, but confirm the critical importance of the shallower depths (< 0.3 m) and mid-velocity ranges (0.5 - 0.7 m.s<sup>-1</sup>) to most stream invertebrate species.

The performance of different descriptors of microhabitat suitability as reflected in maximum predicted density for a specific physical habitat variable are summarized in Fig. 8 a - f. Quadratic polynomial regressions tend to overestimate velocity and Froude number optima in relation to cubic polynomial regressions (Fig. 8 a and d) and weighted means (Fig. 8 b and e) and appear to fit the data poorly (Fig.s. 5 and 6 a - h). They also display very high y-intercepts for certain species predicting higher than expected densities for these species in the lower velocity ranges. This is particularly evident for the quadratic functions fitted to the distributions for Froude number of *B. harrisoni* (Fig. 6a), *Afronurus* sp. (Fig. 6c) and *Lestagella* sp. (Fig 6d) where the tolerance ranges are narrower. Slauson (1988), suggests correcting this by forcing the regression through the origin which can be achieved by omitting the intercept term ( $\alpha$ ). However, Slauson (1988) points out that this tends to give an inflated r-squared since the intercept was not estimated. Also, omission of the intercept term also does not represent skewed data effectively.

The optima for cubic polynomial regressions approximate those values obtained from the weighted means of velocity and Froude number (Fig. 8 c and f), but are in some instances slightly higher. While achieving a better fit, cubic polynomials tend to display mathematical artifacts such as upturning. However, unless there is reason to suspect a bimodal distribution of the species such as a differential distribution of size class, upturning (or 'curve tails') can be safely ignored. Decisions to omit curve tails should be based on a biological understanding of the species and an examination of the raw data (King and Tharme 1993).





**Fig. 8.** Comparison of values for velocity (a - c) and Froude number (d - f) at which expected values of habitat suitability appear to be maximum for: weighted means, quadratic polynomial regression and cubic polynomial regression. The physical habitat value (velocity or Froude number) for which a particular model predicts maximum is plotted on the x-axis with the corresponding value for the model being compared on the y-axis. Where both predictions agree, the point falls on the broken line.

The disadvantages of using a single-figure descriptors (i.e. weighted means) of microhabitat suitability are clear if the weighted means of velocity for *A. peterseni* (Fig. 4) are compared with the suitability curve for this species (Fig 5e). Examination of optimal velocity conditions for *A. peterseni* described by the weighted mean (Fig. 4) can be found at 0.69  $\text{m.s}^{-1}$ , whereas the suitability curve for this species (Fig. 5e) and correlation coefficient, as well as the distribution of the raw data, suggests that the relationship between velocity and the density of

*A. peterseni* while being significant ( $P < 0.05$ ) is relatively weak ( $R$  0.51, Table 3), showing little or no trend toward any particular velocity value. Because they do not reflect the distribution of the species over the whole range of a particular variable, weighted means give no indication of strength of the relationship.

#### *Interaction of velocity and depth*

Microhabitat suitability curves have been criticised (Mathur *et al.* 1985) for not factoring in the interaction of depth and velocity. Single factor polynomial regressions were favoured above multivariate techniques because of early limitations in computer hardware and software (Hanson 1988). However, readily available software packages for analysing and visualising two dimensional data have simplified matters considerably.

The suitability of a certain depth for a particular species may depend on the velocity at that depth. This is due to the reduced thickness of the viscous sublayer with increasing turbulence (Allan 1995) and the subsequent exposure of organisms to higher velocities under conditions of higher turbulence. Since turbulence increases with increasing height of the roughness elements in relation to the speed and depth of the water (Davis and Barmuta 1989), the interaction of depth and velocity is an important factor in determining invertebrate distributions.

Bovee (1986) recommended restricting bivariate analyses to quadratic polynomial regressions since cubic polynomial regressions and higher produced bimodal response surfaces. However, in this study, the bivariate quadratic functions tended to demonstrate similar weaknesses to single factor quadratic functions, i.e., suggesting high densities at low physical habitat values (in this case depth, see *D. capensis* Fig. 7 b).

The only significant interaction term ( $vd$ ) for multivariate quadratic polynomial regressions was obtained for *B. harrisoni* ( $P < 0.05$ ). An examination of Fig. 7 (a) reveals that the optimum velocity range described by single factor polynomial regression and weighted means (0.64 and 0.51  $m.s^{-1}$  respectively) are only valid for depths between 0.25 and 0.45 m. Although the interaction term for *D. capensis* was not statistically significant ( $P > 0.05$ ), it

<sup>1</sup> Since the dataset was small in this particular study an overreliance on statistical significance was avoided (Day and Quinn 1989).

was decided to include the results of the multiple regression analysis (Fig. 7 b and Appendix B) for reasons of biological significance<sup>1</sup>. Fig 7 (b) suggests that highest abundances of *D. capensis* can be found between 0.6 and >1.6 m.s<sup>-1</sup> only where depths are < 0.15 m. This is confirmed by the location of highest abundances of *D. capensis* in the higher Froude number ranges (>1 Table 4). The usefulness of including the interaction term in regressions and the danger in interpreting microhabitat suitability on the basis single-factor regression is therefore evident. However, the absence of significance for most interactive terms suggest that the interaction of velocity and depth and its effect on invertebrate distributions may be better integrated by hydraulic indices such as Froude number for which all correlation's were significant (Table 3).

#### *Limitations and recommendations*

Although weighted means supported the results obtained using cubic polynomial regression, the use of weighted means to describe habitat suitability is not recommended since they merely describe 'average' conditions and give no reflection of the variability within the data or the strength and trend of the relationship. Similarly, the use of an indicator species is questionable since an indicator species merely represents 'average' or 'typical' conditions for diversity. The results from this study suggest that there is high variability in the selection of microhabitat conditions even within families and the presence of a single 'indicator' species may not adequately reflect the conditions required for the maintenance of community structure. Furthermore, the effect of losing species from a community cannot be predicted unless the species which is lost and its function within that community is understood (Harris 1999). The analysis of a representative group of species whose microhabitat requirements are known may be more effective than the use of a single indicator species.

A major criticism of microhabitat suitability curves (Mathur *et al.* 1985) are the weak correlation's between observed and predicted abundances. These weak correlation's may be partly related to the inherent imprecision and bias of the models themselves (Morin *et al.* 1986), but may also be related to the patchiness of lotic communities, a feature evident from the high coefficients of variation for density of several species in this study (Table 1). Patchy distributions are a common feature of freshwater communities (Hildrew and Giller 1994) due

to variability in a multitude of environmental factors. It is therefore difficult to investigate any single factor in isolation. The influence of other factors not considered here such as food preference (Macan 1974), competition (McAuliffe 1984; Hemphill 1988), predation (Peckarsky, Horn and Statzner 1990), recent disturbance events and colonisation rates, should therefore not be ruled out when considering invertebrate distributions.

A further complication in the development of habitat suitability curves and one which may lead to a lack of significance and low correlation's is the coarseness of standard sampling procedures for benthic macroinvertebrates (Davis and Barmuta 1989). The use of a box sampler mixes spatial scales and makes the characterisation of substratum difficult. Individual rocks may be more appropriate than box samplers as sampling units for the derivation of microhabitat suitability curves.

Ideally availability data should be determined independently of use data using the random sampling techniques described by Bovee (1986). Microhabitat suitability curves need to be developed for each river and site to account for differences in species composition, temperature and water quality regimes. The development of microhabitat suitability curves should be done in conjunction with habitat mapping (Gore and Judy 1981), or comparison with availability data, to be most effective in determining environmental flows. However, more studies need to be directed at investigating the relationship between 'use' and 'availability'. This relationship remains unclear (Mathur *et al.* 1985) and may be critical to the prediction of the effects of altered flow regimes on aquatic communities.

Patterns of microhabitat use and relative abundance of macroinvertebrates can also be expected to vary from year to year and between seasons as well as rivers (Orth 1987). While it is impossible to control for all variables, suitability curves should be compiled from data which are accumulated over several seasons in order to take this into account. Orth (1987) has also suggested that critical flows, (i.e. flows when microhabitat is most limited) need to be identified to avoid underestimating the amount of habitat available during such times.

Suitability curves should not be relied upon to account for all aspects of instream environ-

mental flows. For example, suitability curves do not account for flows which may be sufficient to maintain high levels of diversity, but may not be sufficient to provide flushing flows to clear accumulated sediment from the hyporheos, thereby maintaining important sites for colonisation and refugia during spates (Simpson 1997).

### *Conclusions*

The results presented in this study, indicate that there may be a set of flow conditions which are most likely to maintain the present composition of the Ephemeropteran community in the river during the months in which the river was sampled i.e. the maintenance of relatively shallow riffle areas (<0.3 m) with velocities exceeding  $0.3 \text{ m.s}^{-1}$ . Should flow conditions become reduced below these values it is likely that species such as *D. capensis* with higher velocity tolerances will become reduced in numbers and community composition will shift in favour of the slow water – shallow species such as *C. excisum* and *Cloeodes* sp. nov. 1. However, microhabitat suitability curves for the same species need to be derived for other rivers in the south- western Cape before the validity of the present functions can be confirmed.

Despite the assumed sensitivity of the curves to the site and time of sampling, as well as to the type of model or descriptor used, they represent a useful way of providing biologically meaningful data for environmental flow assessments. In order to confirm their usefulness, studies will need to be conducted which investigate the response of the biota after the implementation of specified flow regimes. Also, microhabitat suitability curves need to be linked to models which predict how available habitat varies with discharge. Current methodologies which are able to do this, such as the Instream Flow Incremental Methodology (IFIM, Bovee 1986), link microhabitat suitability curves to simulated changes in the availability of physical habitat in cells in a cross-sectional profile of the channel at incremental changes in flow. However, these models were developed in the United States and are inappropriate for developing countries where time and manpower constraints are limiting. Until new, more appropriate models have been developed and tested, a conservative estimation of habitat requirements using the techniques prescribed here will need to suffice for informing management decisions and conserving species diversity in local rivers.

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**APPENDIX B**  
**GLOSSARY OF SYMBOLS**

**Table 1** Glossary of mathematical and statistical symbols. Each of the symbols used in this study are defined here.

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$A_{\max}$	maximum predicted abundance/ density	
$A_i$	the relative frequency of sites with the value $x_i$	
$\alpha$	y intercept in regression equation	
$\beta$	partial regression coefficient of re- gression equation	
$d$	depth	
Fr	Froude number	Fr < 1 subcritical flow Fr = 1 critical flow Fr > 1 supercritical flow
$g$	acceleration due to gravity ( $9.8 \text{ m s}^{-2}$ )	
$P_i$	unnormalised index of preference	
$U_i$	relative frequency of $x_i$	
$v$	velocity	
$\bar{U}$	mean water column velocity at 0.6 depth from the surface	
$w_i$	weighting variable at site $i$	
$x_d$	weighted mean depth	
$x_f$	weighted mean Froude number	
$x_v$	weighted mean velocity	
$x_w$	weighted mean of a habitat vari- able ( $x$ )	

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**APPENDIX A**  
**DESCRIPTIONS OF FLOWTYPES**

**Table 1** Categories of flow types identified in the reach (Rowntree 1996)

<b>Flow Type</b>	<b>Definition</b>
Rippled Surface (RS)	The water surface has regular smooth disturbances which form low transverse ripples across the direction of flow
Standing Waves (SW)	Standing waves which may or may not be broken at the crest
Cascades (CAS)	Water tumbling down a stepped series of boulders, large cobble or bedrock
Chutes (CH)	Water forced between two rocks, usually large cobble or boulders; flowing fast with the fall too low to be considered free falling.
Smooth Boundary Turbulent (SBT)	The water surface remains smooth, medium to slow streaming flow takes place throughout the water profile, turbulence can be seen as the upward movement of fine suspended particles.
Barely Perceptible Flow (BPF)	Smooth surface flow, only perceptible through the movement of floating objects

**APPENDIX C**  
**Ephemeropteran taxa densities and physical  
habitat variables**

**Table 1 (a)** Ephemeropteran taxa densities (numbers.m<sup>-2</sup>), velocity (m.s<sup>-1</sup>), depth (m) and Froude number for sample points 1 - 10.

Family	Sample No.	BRBSMo1	BRBSMo2	BRBSMo3	BRBSMo4	BRBSMo5	BRBSMo6	BRBSMo7	BRBSMo8	BRBSMo9	BRBSMo10
	Velocity (v)	1.08	0.32	0.99	0.19	0.04	0.13	0	1.07	1.37	0.37
	Depth (d)	0.4	0.08	0.12	0.3	0.5	0.41	0.14	0.1	0.39	0.09
	Fr (v <sup>1/2</sup> /gd)	0.55	0.36	0.91	0.11	0.02	0.06	0.00	1.08	0.70	0.39
Baetidae	<i>Baetis harrisoni</i>	340	510	240	540	0	750	0	470	100	470
	<i>Cloeodes sp nov 1</i>	0	0	0	6200	0	880	140	150	0	0
	<i>Pseudopannota maculosum</i>	0	110	30	0	0	0	0	20	0	0
	<i>Demoreptus capensis</i>	840	710	840	0	0	10	0	940	160	250
	<i>Cheleocloeon exisum</i>	10	0	0	0	0	0	310	10	0	10
Heptageniidae	<i>Afronurus sp.</i>	0	30	70	460	0	70	0	40	40	210
Ephemerellidae	<i>Lestagella sp.</i>	80	70	30	270	0	100	0	70	50	540
Leptophlebiidae	<i>Aprionyx peterseni</i>	80	440	270	100	0	10	0	240	340	20
	<i>Castanophlebia sp.</i>	0	0	0	30	0	0	0	0	10	0
Caenidae	Caenidae sp	0	0	0	0	0	0	50	0	0	0
	<b>Total</b>	1350	1870	1480	7600	0	1820	500	1940	700	1500
	<b>Diversity</b>	1.01	1.42	1.23	0.721	0	1.06	0.62	1.43	1.38	1.4

**Table 1 (b)** Ephemeropteran taxa densities (numbers.m<sup>-2</sup>), velocity (m.s<sup>-1</sup>), depth (m) and Froude number for sample points 11 - 20.

Family	Sample No.	BRBSMo11	BRBSMo12	BRBSMo13	BRBSMo14	BRBSMo15	BRBSMo16	BRBSMo17	BRBSMo18	BRBSMo19	BRBSMo20
	Velocity (v)	0.33	0.34	0.08	0.42	0.3	1.15	0	0.05	0.14	0.09
	Depth (d)	0.41	0.36	0.28	0.08	0.12	0.24	0.24	0.03	0.16	0.6
	Fr (v <sup>1/2</sup> /gd)	0.16	0.18	0.05	0.47	0.28	0.75	0.00	0.09	0.11	0.04
Baetidae	<i>Baetis harrisoni</i>	350	1840	160	590	850	290	0	100	300	60
	<i>Cloeodes sp nov 1</i>	0	340	1340	0	540	0	2060	0	1040	20
	<i>Pseudopannota maculosum</i>	0	10	0	10	0	10	0	0	0	0
	<i>Demoreptus capensis</i>	0	60	0	60	80	590	0	50	0	0
	<i>Cheleocloeon exisum</i>	0	0	0	0	0	0	0	0	90	70
Heptageniidae	<i>Afronurus sp.</i>	40	390	180	160	430	30	40	50	260	40
Ephemerellidae	<i>Lestagella sp.</i>	200	280	220	380	320	30	140	150	400	10
Leptophlebiidae	<i>Aprionyx peterseni</i>	10	140	10	130	50	10	10	30	10	0
	<i>Castanophlebia sp</i>	0	0	10	0	0	0	0	0	0	10
Caenidae	Caenidae sp	0	0	0	0	0	0	0	0	0	0
	<b>Total</b>	600	3060	1920	1330	2270	960	2250	380	2100	210
	<b>Diversity</b>	0.929	1.27	0.983	1.38	1.5	0.972	0.349	1.45	1.36	1.55



**Table 1 (c)** Ephemeropteran taxa densities (numbers.m<sup>-2</sup>), velocity (m.s<sup>-1</sup>), depth (m) and Froude number for sample points 21 - 30.

Family	Sample No.	BRBSMo21	BRBSMo22	BRBSMo23	BRBSMo24	BRBSMo25	BRBSMo26	BRBSMo27	BRBSMo28	BRBSMo29	BRBSMo30
	Velocity (v)	0.37	0.08	0.49	0.76	0.95	0.57	0.7	0.22	1.2	0.87
	Depth (d)	0.26	0.36	0.24	0.2	0.16	0.34	0.3	0.16	0.05	0.08
	Fr (v <sup>1/3</sup> /gd)	0.23	0.04	0.32	0.54	0.76	0.31	0.41	0.18	1.71	0.98
Baetidae	<i>Baetis harrisoni</i>	450	220	1600	80	370	230	240	590	0	510
	<i>Cloeodes sp nov 1</i>	100	0	0	0	0	0	0	260	70	0
	<i>Pseudopannota maculosum</i>	0	0	20	0	0	20	0	0	0	0
	<i>Demoreptus capensis</i>	380	0	0	310	330	260	540	50	470	1940
	<i>Cheleocloeon exisum</i>	10	10	0	0	0	0	0	0	0	0
Heptageniidae	<i>Afronurus sp.</i>	10	10	280	50	20	50	270	200	20	80
Ephemerellidae	<i>Lestagella sp.</i>	210	0	540	20	130	130	70	400	50	180
Leptophlebiidae	<i>Aprionyx peterseni</i>	70	0	250	0	40	20	150	210	10	160
	<i>Castanophlebia sp</i>	0	0	0	0	0	0	0	0	0	0
Caenidae	<i>Caenidae sp</i>	0	0	0	0	0	0	0	0	0	0
	<b>Total</b>	1230	240	2690	460	890	710	1270	1710	620	2870
	<b>Diversity</b>	1.48	0.345	1.12	0.948	1.24	1.43	1.42	1.61	0.837	1.01

**Table 1 (d)** Ephemeropteran taxa densities (numbers.m<sup>-2</sup>), velocity (m.s<sup>-1</sup>), depth (m) and Froude number for sample points 31 - 40.

Family	Sample No.	BRBSMo31	BRBSMo32	BRBSMo33	BRBSMo34	BRBSMo35	BRBSMo36	BRBSMo37	BRBSMo38	BRBSMo39	BRBSMo40
	Velocity (v)	0.92	0.7	1.1	1.1	0.88	0.73	0.51	0.01	0.05	0.15
	Depth (d)	0.13	0.15	0.3	0.25	0.2	0.4	0.13	0.08	0.08	0.22
	Fr (v <sup>1/3</sup> /gd)	0.82	0.58	0.64	0.70	0.63	0.37	0.45	0.01	0.06	0.10
Baetidae	<i>Baetis harrisoni</i>	670	710	150	250	280	740	500	30	120	620
	<i>Cloeodes sp nov 1</i>	0	90	0	0	0	10	0	0	3450	0
	<i>Pseudopannota maculosum</i>	0	70	0	40	10	0	60	0	0	20
	<i>Demoreptus capensis</i>	930	830	950	970	740	460	1070	50	0	520
	<i>Cheleocloeon exisum</i>	0	0	0	0	0	0	60	670	100	0
Heptageniidae	<i>Afronurus sp.</i>	60	90	40	10	20	90	120	10	0	220
Ephemerellidae	<i>Lestagella sp.</i>	100	490	130	110	70	150	670	10	170	360
Leptophlebiidae	<i>Aprionyx peterseni</i>	400	0	1000	130	10	170	1010	20	10	570
	<i>Castanophlebia sp</i>	10	10	0	0	0	0	0	0	0	0
Caenidae	<i>Caenidae sp</i>	0	0	0	0	0	0	0	0	0	0
	<b>Total</b>	2170	2290	2270	1510	1130	1620	3490	790	3850	2310
	<b>Diversity</b>	1.3	1.45	1.14	1.11	0.95	1.36	1.57	0.642	0.454	1.59

**Table 2** Total, mean and standard deviation (SD) of Ephemeropteran densities (numbers.m<sup>-2</sup>)

Family	Species	Total	Mean	(±SD)
Baetidae	<i>Baetis harrisoni</i>	16320	408	(±387)
	<i>Cloeodes</i> sp nov 1.	16690	417	(±1152)
	<i>Pseudopannota maculosum</i>	430	10	(±22)
	<i>Demoreptus capensis</i>	15390	384	(±441)
	<i>Chelecloleon exisum</i>	1350	33	(±116)
Heptageniidae	<i>Afronurus</i> sp.	4190	104	(±122)
Ephemerellidae	<i>Lestagella</i> sp.	7330	183	(±171)
Leptophlebiidae	<i>Aprionyx peterseni</i>	6130	153	(±241)
Caenidae	<i>Castanophlebia</i> sp.	80	2	(±5)
	<i>Caenidae</i> sp.	50	1	(±7)

**APPENDIX D**  
**Regression summaries of Microhabitat Suitability**  
**Functions**

**Table 1** Regression summary for *Beatis harrisoni* densities by velocity, depth and Froude number for quadratic and cubic functions as well as interaction terms. Significance level (P) and Standard Error (St.Err.) for the individual regression coefficients (B) are

R= .62946620 R <sup>2</sup> = .39622770 Adjusted R <sup>2</sup> = .36359136 F(2,37)=12.141 p<.00009 Std.Error of estimate: .67452						
	BETA	St. Err.	B	St. Err.	t(37)	p-level
a			1.40452	0.22411	6.26698	2.73E-07 *
v	2.37472	0.48193	4.82705	0.9796	4.92758	1.76E-05 *
v <sup>2</sup>	-2.2873	0.48193	-3.7588	0.79196	-4.7462	3.08E-05 *

R= .70775199 R <sup>2</sup> = .50091288 Adjusted R <sup>2</sup> = .45932229 F(3,36)=12.044 p<.00001 Std.Error of estimate: .62172						
	BETA	St. Err.	B	St. Err.	t(36)	p-level
a			1.03852	0.24579	4.22524	0.000155 *
v	4.6819	0.94987	9.51682	1.93079	4.92899	1.87E-05 *
v <sup>2</sup>	-8.23027	2.20785	-13.525	3.62823	-3.7277	0.000662 *
v <sup>3</sup>	3.78214	1.37636	5.1588	1.87734	2.74793	0.009312 *

R= .28347195 R <sup>2</sup> = .08035635 Adjusted R <sup>2</sup> = .03064588 F(2,37)=1.6165 p<.21231 Std.Error of estimate: .83246						
	BETA	St. Err.	B	St. Err.	t(37)	p-level
a			1.70453	0.42871	3.97591	0.000313 *
d	0.94569	0.57103	5.88775	3.55513	1.65613	0.106154 *
d <sup>2</sup>	-1.01932	0.57103	-11.188	6.26737	-1.7851	0.082452

R= .69242608 R <sup>2</sup> = .47945387 Adjusted R <sup>2</sup> = .40290297 F(5,34)=6.2632 p<.00032 Std.Error of estimate: .65335						
	BETA	St. Err.	B	St. Err.	t(34)	p-level
a			1.63385	0.45205	3.61432	0.000963 *
v	2.08826	0.4945	4.24476	1.00515	4.22299	0.00017 *
d	-0.14209	0.56587	-0.8847	3.523	-0.2511	0.803242
vd	0.60328	0.29622	4.16351	2.04436	2.03658	0.04954 *
v <sup>2</sup>	-2.48947	0.49975	-4.091	0.82126	-4.9814	1.82E-05 *
d <sup>2</sup>	-0.07403	0.51224	-0.8125	5.62218	-0.1445	0.885947

R= .63861861 R <sup>2</sup> = .40783373 Adjusted R <sup>2</sup> = .37582475 F(2,37)=12.741 p<.00006 Std.Error of estimate: .66800						
	BETA	St. Err.	B	St. Err.	t(37)	p-level
a			1.69618	0.19141	8.86172	1.11E-10 *
Fr	1.44312	0.30937	3.28388	0.70399	4.66465	3.96E-05 *
Fr <sup>2</sup>	-1.56106	0.30937	-2.5471	0.50478	-5.0459	1.22E-05 *

R= .67556072 R <sup>2</sup> = .45638229 Adjusted R <sup>2</sup> = .41108081 F(3,36)=10.074 p<.00006 Std.Error of estimate: .64886						
	BETA	St. Err.	B	St. Err.	t(36)	p-level
a			1.46995	0.22469	6.5422	1.32E-07 *
Fr	2.6528	0.73855	6.03657	1.68061	3.59189	0.000973 *
Fr <sup>2</sup>	-4.66932	1.75936	-7.6186	2.87063	-2.654	0.011767 *
Fr <sup>3</sup>	2.07621	1.15792	2.1416	1.19439	1.79305	0.08137

**Table 2** Regression summary for *Demoreptus capensis* densities by velocity, depth and Froude number for quadratic and cubic functions as well as interaction terms. Significance level (P) and Standard Error (St.Err.) for the individual regression coefficients (B) are shown.

R= .78701205 R<sup>2</sup>= .61938797 Adjusted R<sup>2</sup>= .59881435  
 F(2,37)=30.106 p<.00000 Std.Error of estimate: .77392

	BETA	St. Err.	B	St. Err.	t(37)	p-level
a			0.21103	0.25714	0.82067	0.41708931
v	1.82851	0.38263	5.37116	1.12397	4.77874	2.78873E-05 *
v <sup>2</sup>	-1.14305	0.38263	-2.7145	0.90868	-2.9873	0.00497299 *

R= .78865866 R<sup>2</sup>= .62198249 Adjusted R<sup>2</sup>= .59048103  
 F(3,36)=19.745 p<.00000 Std.Error of estimate: .78192

	BETA	St. Err.	B	St. Err.	t(36)	p-level
a			0.2943	0.30912	0.95204	0.34742525
v	1.46529	0.82667	4.30423	2.4283	1.77252	0.08477047
v <sup>2</sup>	-0.20745	1.92149	-0.4926	4.56314	-0.108	0.91462499
v <sup>3</sup>	-0.59542	1.19784	-1.1736	2.36109	-0.4971	0.6221571

R= .36526848 R<sup>2</sup>= .13342106 Adjusted R<sup>2</sup>= .08657896  
 F(2,37)=2.8483 p<.07071 Std.Error of estimate: 1.1678

	BETA	St. Err.	B	St. Err.	t(37)	p-level
a			2.06045	0.6014	3.42609	0.00151404 *
d	0.15892	0.55431	1.42978	4.98714	0.28669	0.7759468
d <sup>2</sup>	-0.51536	0.55431	-8.1741	8.79186	-0.9297	0.35853186

R= .83943233 R<sup>2</sup>= .70464663 Adjusted R<sup>2</sup>= .66121232  
 F(5,34)=16.223 p<.00000 Std.Error of estimate: .71120

	BETA	St. Err.	B	St. Err.	t(34)	p-level
a			1.37957	0.49207	2.80361	0.00828991 *
v	1.66678	0.37248	4.89607	1.09415	4.47479	8.1498E-05 *
d	-0.83281	0.42624	-7.4928	3.83491	-1.9538	0.05898641
vd	0.31978	0.22313	3.18926	2.22536	1.43314	0.16094862
v <sup>2</sup>	-1.22988	0.37644	-2.9207	0.89397	-3.2671	0.00248626 *
d <sup>2</sup>	0.4622	0.38585	7.33092	6.11994	1.19787	0.23925044

R= .80662377 R<sup>2</sup>= .65064190 Adjusted R<sup>2</sup>= .63175768  
 F(2,37)=34.454 p<.00000 Std.Error of estimate: .74147

	BETA	St. Err.	B	St. Err.	t(37)	p-level
a			0.36998	0.21246	1.74143	0.08991732
Fr	1.64024	0.23763	5.39379	0.78142	6.90257	3.8237E-08 *
Fr <sup>2</sup>	-1.04876	0.23763	-2.4729	0.5603	-4.4135	8.4878E-05 *

R= .81930016 R<sup>2</sup>= .67125276 Adjusted R<sup>2</sup>= .64385715  
 F(3,36)=24.502 p<.00000 Std.Error of estimate: .72918

	BETA	St. Err.	B	St. Err.	t(36)	p-level
a			0.15697	0.2525	0.62165	0.53808933
Fr	2.42843	0.57433	7.98568	1.88865	4.22825	0.00015406 *
Fr <sup>2</sup>	-3.07401	1.36817	-7.2482	3.22598	-2.2468	0.03087821 *
Fr <sup>3</sup>	1.35279	0.90046	2.0165	1.34224	1.50234	0.14173126

**Table 3** Regression summary for *Afronurus* sp. densities by velocity, depth and Froude number for quadratic and cubic functions as well as interaction terms. Significance level (P) and Standard Error (St.Err.) for the individual regression coefficients (B) are shown.

R= .46131941 R <sup>2</sup> = .21281560 Adjusted R <sup>2</sup> = .17026509 F(2,37)=5.0015 p<.01195 Std.Error of estimate: .65350						
	BETA	St. Err.	B	St. Err.	t(37)	p-level
a			1.23006	0.21713	5.66506	1.7848E-06 *
v	1.65292	0.55028	2.85082	0.94907	3.0038	0.00476186 *
v <sup>2</sup>	-1.7382	0.55028	-2.4237	0.76728	-3.1588	0.00315103 *

R= .61343148 R <sup>2</sup> = .37629818 Adjusted R <sup>2</sup> = .32432303 F(3,36)=7.2400 p<.00064 Std.Error of estimate: .58972						
	BETA	St. Err.	B	St. Err.	t(36)	p-level
a			0.84197	0.23314	3.61148	0.00092063 *
v	4.53612	1.06186	7.82353	1.8314	4.27188	0.00013535 *
v <sup>2</sup>	-9.16491	2.46815	-12.779	3.44147	-3.7133	0.00068967 *
v <sup>3</sup>	4.7264	1.53862	5.47004	1.7807	3.07184	0.00403694 *

R= .23742976 R <sup>2</sup> = .05637289 Adjusted R <sup>2</sup> = .00536602 F(2,37)=1.1052 p<.34183 Std.Error of estimate: .71549						
	BETA	St. Err.	B	St. Err.	t(37)	p-level
a			1.3995	0.36847	3.7981	0.00052574 *
d	0.61691	0.57843	3.25886	3.05559	1.06653	0.29309627
d <sup>2</sup>	-0.75835	0.57843	-7.0623	5.38672	-1.3111	0.1979191

R= .48879315 R <sup>2</sup> = .23891874 Adjusted R <sup>2</sup> = .12699503 F(5,34)=2.1347 p<.08495 Std.Error of estimate: .67032						
	BETA	St. Err.	B	St. Err.	t(34)	p-level
a			0.99165	0.46379	2.13815	0.03977613 *
v	1.54388	0.59793	2.66276	1.03126	2.58205	0.01430283 *
d	0.60144	0.68423	3.17714	3.61449	0.879	0.38557151
vd	-0.16853	0.35818	-0.9869	2.09746	-0.4705	0.64100105
v <sup>2</sup>	-1.52818	0.60429	-2.1308	0.84259	-2.5289	0.01624919 *
d <sup>2</sup>	-0.61938	0.61939	-5.7681	5.76819	-1	0.32438496

R= .19307922 R <sup>2</sup> = .03727958 Adjusted R <sup>2</sup> = ---- F(2,37)=.71638 p<.49517 Std.Error of estimate: .72269						
	BETA	St. Err.	B	St. Err.	t(37)	p-level
a			1.49435	0.20708	7.21644	1.462E-08 *
Fr	0.44604	0.39447	0.86121	0.76163	1.13075	0.26543701
Fr <sup>2</sup>	-0.47038	0.39447	-0.6512	0.54611	-1.1924	0.24067844

R= .35366672 R <sup>2</sup> = .12508015 Adjusted R <sup>2</sup> = .05217016 F(3,36)=1.7155 p<.18113 Std.Error of estimate: .69845						
	BETA	St. Err.	B	St. Err.	t(36)	p-level
a			1.23622	0.24186	5.11128	1.0689E-05 *
Fr	2.07283	0.93695	4.0022	1.80906	2.21231	0.03337584 *
Fr <sup>2</sup>	-4.6504	2.23199	-6.4381	3.09003	-2.0835	0.04436403 *
Fr <sup>3</sup>	2.7921	1.46898	2.4437	1.28568	1.90071	0.06537019

**Table 4** Regression summary for *Lestagella* sp. densities by velocity, depth and Froude number for quadratic and cubic functions as well as interaction terms. Significance level (P) and Standard Error (St.Err.) for the individual regression coefficients (B) are shown.

R= .48748902 R <sup>2</sup> = .23764555 Adjusted R <sup>2</sup> = .19643720						
F(2,37)=5.7669 p<.00661 Std.Error of estimate: .63914						
	BETA	St. Err.	B	St. Err.	t(37)	p-level
a			1.41434	0.21236	6.6601	8.0758E-08 *
v	1.83554	0.54153	3.14624	0.92822	3.38955	0.00167605 *
v <sup>2</sup>	-1.80027	0.54153	-2.4947	0.75042	-3.3244	0.00200666 *
R= .60528827 R <sup>2</sup> = .36637389 Adjusted R <sup>2</sup> = .31357171						
F(3,36)=6.9386 p<.00084 Std.Error of estimate: .59072						
	BETA	St. Err.	B	St. Err.	t(36)	p-level
a			1.07209	0.23353	4.59071	5.2095E-05 *
v	4.39398	1.07027	7.5316	1.83452	4.10549	0.00022133 *
v <sup>2</sup>	-8.39046	2.4877	-11.627	3.44733	-3.3728	0.00179129 *
v <sup>3</sup>	4.19403	1.55081	4.82395	1.78374	2.70441	0.01038349 *
R= .39331631 R <sup>2</sup> = .15469772 Adjusted R <sup>2</sup> = .10900571						
F(2,37)=3.3857 p<.04464 Std.Error of estimate: .67301						
	BETA	St. Err.	B	St. Err.	t(37)	p-level
a			1.8192	0.3466	5.24876	6.5255E-06 *
d	0.63426	0.54746	3.32987	2.87416	1.15855	0.25406247
d <sup>2</sup>	-0.96179	0.54746	-8.9016	5.06688	-1.7568	0.08722186
R= .60407424 R <sup>2</sup> = .36490569 Adjusted R <sup>2</sup> = .27150947						
F(5,34)=3.9071 p<.00662 Std.Error of estimate: .60855						
	BETA	St. Err.	B	St. Err.	t(34)	p-level
a			1.8769	0.42105	4.45767	8.5702E-05 *
v	1.39961	0.5462	2.39903	0.93623	2.56244	0.01499427 *
d	-0.19882	0.62503	-1.0438	3.28142	-0.3181	0.75235271
vd	0.51713	0.3272	3.00955	1.90418	1.5805	0.12325235
v <sup>2</sup>	-1.80892	0.55201	-2.5067	0.76495	-3.277	0.00242139 *
d <sup>2</sup>	-0.27106	0.5658	-2.5087	5.23666	-0.4791	0.63496172
R= .30762530 R <sup>2</sup> = .09463332 Adjusted R <sup>2</sup> = .04569458						
F(2,37)=1.9337 p<.15895 Std.Error of estimate: .69651						
	BETA	St. Err.	B	St. Err.	t(37)	p-level
a			1.66668	0.19957	8.35119	4.8875E-10 *
Fr	0.74882	0.38254	1.43689	0.73404	1.95751	0.0578622
Fr <sup>2</sup>	-0.71285	0.38254	-0.9808	0.52633	-1.8635	0.07034629
R= .52041479 R <sup>2</sup> = .27083156 Adjusted R <sup>2</sup> = .21006752						
F(3,36)=4.4571 p<.00921 Std.Error of estimate: .63369						
	BETA	St. Err.	B	St. Err.	t(36)	p-level
a			1.30326	0.21944	5.93915	8.3802E-07 *
Fr	3.05336	0.85536	5.85899	1.64132	3.56968	0.00103569 *
Fr <sup>2</sup>	-6.63433	2.03761	-9.1281	2.80352	-3.2559	0.00246497 *
Fr <sup>3</sup>	3.95534	1.34105	3.44041	1.16647	2.94943	0.00556458 *

**Table 5** Regression summary for *Aprionyx peterseni* densities by velocity, depth and Froude number for quadratic and cubic functions as well as interaction terms. Significance level (P) and Standard Error (St.Err.) for the individual regression coefficients (B) are shown.

R= .42746635 R <sup>2</sup> = .18272748 Adjusted R <sup>2</sup> = .13855059 F(2,37)=4.1363 p<.02392 Std.Error of estimate: .83241						
	BETA	St. Err.	B	St. Err.	t(37)	p-level
a			0.91005	0.27658	3.2904	0.00220332 *
v	1.11931	0.56069	2.41334	1.20892	1.99628	0.05330151
v <sup>2</sup>	-0.77153	0.56069	-1.3449	0.97735	-1.376	0.17708513

R= .51130335 R <sup>2</sup> = .26143112 Adjusted R <sup>2</sup> = .19988371 F(3,36)=4.2476 p<.01143 Std.Error of estimate: .80223						
	BETA	St. Err.	B	St. Err.	t(36)	p-level
a			0.57343	0.31715	1.80805	0.07895968
v	3.1198	1.15551	6.72661	2.49139	2.69994	0.01049965 *
v <sup>2</sup>	-5.92451	2.68582	-10.327	4.6817	-2.2058	0.03386382 *
v <sup>3</sup>	3.27938	1.67432	4.74465	2.42243	1.95863	0.05793791

R= .34778497 R <sup>2</sup> = .12095438 Adjusted R <sup>2</sup> = .07343840 F(2,37)=2.5456 p<.09209 Std.Error of estimate: .86330						
	BETA	St. Err.	B	St. Err.	t(37)	p-level
a			1.33138	0.44459	2.99459	0.00487867 *
d	0.66941	0.55828	4.42073	3.68683	1.19906	0.23812744
d <sup>2</sup>	-0.93801	0.55828	-10.92	6.49953	-1.6802	0.10135012

R= .55436868 R <sup>2</sup> = .30732463 Adjusted R <sup>2</sup> = .20546060 F(5,34)=3.0170 p<.02329 Std.Error of estimate: .79943						
	BETA	St. Err.	B	St. Err.	t(34)	p-level
a			1.53612	0.55312	2.77718	0.00885707 *
v	0.68848	0.57043	1.48443	1.2299	1.20696	0.23577958
d	-0.31739	0.65275	-2.096	4.31071	-0.4862	0.62992316
vd	0.62147	0.34171	4.54945	2.50146	1.81871	0.0777731
v <sup>2</sup>	-0.86059	0.57649	-1.5001	1.00489	-1.4928	0.14470975
d <sup>2</sup>	-0.14535	0.5909	-1.6921	6.87925	-0.246	0.80717808

R= .47412170 R <sup>2</sup> = .22479138 Adjusted R <sup>2</sup> = .18288821 F(2,37)=5.3645 p<.00900 Std.Error of estimate: .81071						
	BETA	St. Err.	B	St. Err.	t(37)	p-level
a			0.94692	0.2323	4.07633	0.00023275 *
Fr	1.12275	0.35397	2.71001	0.85439	3.17187	0.00304174 *
Fr <sup>2</sup>	-0.90626	0.35397	-1.5685	0.61262	-2.5602	0.01467598 *

R= .49055477 R <sup>2</sup> = .24064398 Adjusted R <sup>2</sup> = .17736431 F(3,36)=3.8029 p<.01820 Std.Error of estimate: .81345						
	BETA	St. Err.	B	St. Err.	t(36)	p-level
a			0.8098	0.28168	2.87488	0.00674589 *
Fr	1.814	0.87288	4.37849	2.1069	2.07817	0.04488285 *
Fr <sup>2</sup>	-2.68241	2.07937	-4.6425	3.59877	-1.29	0.20527123 *
Fr <sup>3</sup>	1.18641	1.36853	1.29808	1.49735	0.86692	0.39172783



**Table 6** Regression summary for *Cheleocloeon excisum* densities by velocity, depth and Froude number for quadratic and cubic functions as well as interaction terms. Significance level (P) and Standard Error (St.Err.) for the individual regression coefficients (B) are shown.

R= .44077190 R <sup>2</sup> = .19427987 Adjusted R <sup>2</sup> = .15072743 F(2,37)=4.4608 p<.01838 Std.Error of estimate: .75074						
	BETA	St. Err.	B	St. Err.	t(37)	p-level
a			1.0909	0.24944	4.37334	9.5807E-05 *
v	-1.25098	0.55672	-2.45	1.09031	-2.2471	0.03068706 *
v <sup>2</sup>	0.91585	0.55672	1.45008	0.88146	1.64508	0.10842338

R= .47336889 R <sup>2</sup> = .22407811 Adjusted R <sup>2</sup> = .15941795 F(3,36)=3.4655 p<.02607 Std.Error of estimate: .74689						
	BETA	St. Err.	B	St. Err.	t(36)	p-level
a			1.27904	0.29528	4.33167	0.0001133 *
v	-2.48192	1.18437	-4.8607	2.31953	-2.0956	0.04321608 *
v <sup>2</sup>	4.08655	2.7529	6.47033	4.35874	1.48445	0.14639319
v <sup>3</sup>	-2.01785	1.71614	-2.6518	2.25532	-1.1758	0.24738792

R= .33388871 R <sup>2</sup> = .11148167 Adjusted R <sup>2</sup> = .06345366 F(2,37)=2.3212 p<.11229 Std.Error of estimate: .78838						
	BETA	St. Err.	B	St. Err.	t(37)	p-level
a			1.26283	0.40601	3.11036	0.00358852 *
d	-1.2066	0.56128	-7.2378	3.36685	-2.1497	0.03818309 *
d <sup>2</sup>	1.13724	0.56128	12.026	5.93544	2.02614	0.05000556 *

R= .54243834 R <sup>2</sup> = .29423936 Adjusted R <sup>2</sup> = .19045103 F(5,34)=2.8350 p<.03033 Std.Error of estimate: .73298						
	BETA	St. Err.	B	St. Err.	t(34)	p-level
a			2.06193	0.50714	4.06578	0.00026806 *
v	-1.28413	0.57579	-2.5149	1.12766	-2.2302	0.03244061 *
d	-1.3495	0.65889	-8.095	3.95236	-2.0481	0.04833128 *
vd	0.44622	0.34492	2.96712	2.29352	1.2937	0.20448989
v <sup>2</sup>	0.6323	0.58191	1.00113	0.92135	1.08659	0.28486344
d <sup>2</sup>	1.03527	0.59645	10.9478	6.30738	1.73572	0.09166975

R= .38005944 R <sup>2</sup> = .14444518 Adjusted R <sup>2</sup> = .09819897 F(2,37)=3.1234 p<.05579 Std.Error of estimate: .77361						
	BETA	St. Err.	B	St. Err.	t(37)	p-level
a			0.90987	0.22167	4.10469	0.000214 *
Fr	-0.79353	0.37186	-1.7398	0.81529	-2.1339	0.03954278 *
Fr <sup>2</sup>	0.52628	0.37186	0.82734	0.58459	1.41526	0.16535509

R= .43753772 R <sup>2</sup> = .19143926 Adjusted R <sup>2</sup> = .12405920 F(3,36)=2.8412 p<.05140 Std.Error of estimate: .76244						
	BETA	St. Err.	B	St. Err.	t(36)	p-level
a			1.12432	0.26402	4.25848	0.00014085 *
Fr	-1.98369	0.90072	-4.3491	1.97479	-2.2023	0.03413131 *
Fr <sup>2</sup>	3.58438	2.14568	5.63483	3.37311	1.67051	0.10349108
Fr <sup>3</sup>	-2.0427	1.41217	-2.0301	1.40346	-1.4465	0.15669017

**Table 7** Regression summary for *Pseudopannota maculosum* densities by velocity, depth and Froude number for quadratic and cubic functions as well as interaction terms. Significance level (P) and Standard Error (St.Err.) for the individual regression coefficients (B) are

R= .41353786 R <sup>2</sup> = .17101356 Adjusted R <sup>2</sup> = .12620348 F(2,37)=3.8164 p<.03113 Std.Error of estimate: .64618						
	BETA	St. Err.	B	St. Err.	t(37)	p-level
a			-0.0576	0.2147	-0.2681	0.79007947
v	1.48544	0.5647	2.46858	0.93845	2.63049	0.01235368 *
v <sup>2</sup>	-1.30588	0.5647	-1.7545	0.75869	-2.3125	0.02641471 *

R= .42086420 R <sup>2</sup> = .17712667 Adjusted R <sup>2</sup> = .10855389 F(3,36)=2.5830 p<.06838 Std.Error of estimate: .65267						
	BETA	St. Err.	B	St. Err.	t(36)	p-level
a			-0.1299	0.25803	-0.5034	0.61777836
v	2.04297	1.21967	3.39511	2.02692	1.67501	0.1025981
v <sup>2</sup>	-2.74201	2.83497	-3.684	3.80888	-0.9672	0.33989331
v <sup>3</sup>	0.91396	1.7673	1.0192	1.97081	0.51715	0.60821497

R= .26470639 R <sup>2</sup> = .07006947 Adjusted R <sup>2</sup> = .01980296 F(2,37)=1.3940 p<.26082 Std.Error of estimate: .68439						
	BETA	St. Err.	B	St. Err.	t(37)	p-level
a			0.4522	0.35246	1.28299	0.2074758
d	0.29165	0.57421	1.48451	2.92277	0.50791	0.61453003
d <sup>2</sup>	-0.53248	0.57421	-4.7781	5.15257	-0.9273	0.3597734

R= .45156186 R <sup>2</sup> = .20390811 Adjusted R <sup>2</sup> = .08683577 F(5,34)=1.7417 p<.15170 Std.Error of estimate: .66057						
	BETA	St. Err.	B	St. Err.	t(34)	p-level
a			-0.0034	0.45705	-0.0074	0.99412549
v	1.40951	0.61153	2.3424	1.01627	2.3049	0.02740546 *
d	0.14493	0.69979	0.73772	3.56195	0.20711	0.8371582
vd	-0.1525	0.36633	-0.8605	2.06697	-0.4163	0.67981166
v <sup>2</sup>	-1.12912	0.61803	-1.517	0.83034	-1.827	0.07649498
d <sup>2</sup>	-0.25797	0.63347	-2.3148	5.68434	-0.4072	0.68639648

R= .40563582 R <sup>2</sup> = .16454042 Adjusted R <sup>2</sup> = .11938044 F(2,37)=3.6435 p<.03594 Std.Error of estimate: .64870						
	BETA	St. Err.	B	St. Err.	t(37)	p-level
a			0.04848	0.18587	0.26085	0.79565692
Fr	0.97822	0.36747	1.8199	0.68365	2.66204	0.01142519 *
Fr <sup>2</sup>	-0.82541	0.36747	-1.1011	0.49019	-2.2462	0.03074885 *

R= .41728323 R <sup>2</sup> = .17412529 Adjusted R <sup>2</sup> = .10530240 F(3,36)=2.5300 p<.07253 Std.Error of estimate: .65386						
	BETA	of BETA	B	of B	t(36)	p-level
a			-0.0337	0.226419	-0.14882	0.882527
Fr	1.51572	0.910313	2.819864	1.693558	1.665054	0.104583
Fr <sup>2</sup>	-2.2065	2.168528	-2.9434	2.892747	-1.01751	0.315701
Fr <sup>3</sup>	0.922521	1.427213	0.777976	1.203591	0.646379	0.522134

**Table 8** Regression summary for *Cloeodes* sp. nov. 1. densities by velocity, depth and Froude number for quadratic and cubic functions as well as interaction terms. Significance level (P) and Standard Error (St.Err.) for the individual regression coefficients (B) are shown.

R= .45162034 R <sup>2</sup> = .20396094 Adjusted R <sup>2</sup> = .16093180 F(2,37)=4.7401 p<.01470 Std.Error of estimate: 1.2167						
	BETA	St. Err.	B	St. Err.	t(37)	p-level
a			1.98649	0.40425	4.91405	1.8392E-05 *
v	-1.01643	0.55336	-3.2456	1.76695	-1.8368	0.07427905
v <sup>2</sup>	0.61762	0.55336	1.59438	1.4285	1.11612	0.27156678

R= .45559131 R <sup>2</sup> = .20756345 Adjusted R <sup>2</sup> = .14152707 F(3,36)=3.1432 p<.03693 Std.Error of estimate: 1.2306						
	BETA	St. Err.	B	St. Err.	t(36)	p-level
a			1.87983	0.48652	3.86382	0.00044772 *
v	-0.58843	1.1969	-1.8789	3.82185	-0.4916	0.62596577
v <sup>2</sup>	-0.48484	2.78205	-1.2516	7.18182	-0.1743	0.86262554
v <sup>3</sup>	0.70161	1.73431	1.50333	3.71605	0.40455	0.68820238

R= .06223417 R <sup>2</sup> = .00387309 Adjusted R <sup>2</sup> = ----- F(2,37)=.07193 p<.93073 Std.Error of estimate: 1.3610						
	BETA	St. Err.	B	St. Err.	t(37)	p-level
a			0.81479	0.70091	1.16249	0.25248134
d	0.20215	0.5943	1.97706	5.8123	0.34015	0.73566622
d <sup>2</sup>	-0.22183	0.5943	-3.8246	10.2466	-0.3733	0.71108526

R= .54605964 R <sup>2</sup> = .29818113 Adjusted R <sup>2</sup> = .19497247 F(5,34)=2.8891 p<.02803 Std.Error of estimate: 1.1917						
	BETA	St. Err.	B	St. Err.	t(34)	p-level
a			0.84301	0.82454	1.0224	0.31381249
v	-1.06783	0.57418	-3.4097	1.83341	-1.8598	0.07158981
d	1.24117	0.65705	12.1388	6.42599	1.88901	0.06744468
vd	-0.55398	0.34395	-6.0059	3.72895	-1.6106	0.11651009
v <sup>2</sup>	1.0559	0.58028	2.72579	1.49799	1.81963	0.07763037
d <sup>2</sup>	-1.11649	0.59479	-19.25	10.2549	-1.8771	0.06910235

R= .51556452 R <sup>2</sup> = .26580677 Adjusted R <sup>2</sup> = .22612065 F(2,37)=6.6977 p<.00329 Std.Error of estimate: 1.1684						
	BETA	St. Err.	B	St. Err.	t(37)	p-level
a			1.99709	0.3348	5.96507	7.0012E-07 *
Fr	-1.23962	0.34448	-4.4312	1.23139	-3.5985	0.00093195 *
Fr <sup>2</sup>	1.03715	0.34448	2.65834	0.88294	3.01077	0.00467514 *

R= .51959888 R <sup>2</sup> = .26998299 Adjusted R <sup>2</sup> = .20914824 F(3,36)=4.4380 p<.00939 Std.Error of estimate: 1.1812						
	BETA	St. Err.	B	St. Err.	t(36)	p-level
a			2.10132	0.40902	5.13744	9.8652E-06 *
Fr	-1.59441	0.85585	-5.6994	3.05936	-1.8629	0.07064468
Fr <sup>2</sup>	1.94879	2.0388	4.99496	5.22567	0.95585	0.34552205
Fr <sup>3</sup>	-0.60894	1.34183	-0.9867	2.17425	-0.4538	0.65268785