CHAPTER 3

Spatial and temporal patterns in the hyporheic zone of the Hunter River

3.1 Introduction

Despite the dominance of the river continuum concept (Vannote *et al.* 1980) in river ecology (Resh and Kobzina 2003), and later the serial discontinuity concept (Ward and Stanford 1983, Stanford and Ward 2001) for epigean ecosystem processes, large-scale studies of longitudinal change in hyporheic physico-chemistry and invertebrate communities have been rare (Boulton *et al.* 1998). However, there are several theories in hyporheic ecology concerning broad-scale faunal and physico-chemical patterns along rivers (Boulton *et al.* 1998, Tabacchi *et al.* 1998, Stanley and Jones 2000). The hyporheic corridor concept considers that hyporheic zones occur along a river continuum like 'beads on a string' (Stanford and Ward 1993). This theory takes into account the often-disjointed occurrences of hyporheic zones along rivers, where areas of upwelling and downwelling are often interspersed with sections of no exchange (e.g., bedrock). Geomorphological processes, such as longitudinal fining of sediments and subsequent loss of stream gradient and interstitial flow velocity, can affect interstitial biological and chemical processes and potentially mean that upland stream hyporheic zones differ markedly from those in lowland rivers (Angradi *et al.* 2001).

Most of our understanding of longitudinal variation in the hyporheic zone comes from studies of reaches less than 20 km in length. To date there have been few studies along stretches of river greater than 100 km. Over a large spatial scale, upwelling regional groundwater can have a dominant influence on hyporheic ecology (Holmes 2000), contributing nutrients, and affecting physico-chemical and biotic properties. However, the cumulative effects of many small-scale site-specific interstitial processes, such as nitrification, may increase the concentration of nutrients in a downstream direction (Fisher *et al.* 1998). Longitudinal changes in temperature, organic matter distribution, and gradients in the influence of groundwater can in turn affect hyporheic invertebrate communities over even a short distance of 11 km (Malard *et al.* 2003). Potentially, over

longer distances the accumulation of taxa from tributaries or regionally upwelling groundwater might further increase the diversity of the hyporheos.

Seasonal fluxes in temperature, groundwater exchange, and stream stage govern some hyporheic ecological processes. Gravel bars are intermittently covered by temporary rises in stream stage dictated by seasonal patterns of rainfall. Seasonal fluctuations can influence the physico-chemical characteristics of the hyporheic zone, but were found not to affect the fauna of the Roseg River (Malard *et al.* 2003), despite lagged seasonal changes in temperature brought about by upwelling deep alluvial and hillslope groundwater (Malard *et al.* 2001). River regulation typically homogenises flow by reducing the frequency and magnitude of spates (Kingsford 2000, Marchant and Hehir 2002).

Given the importance of river stage fluctuations to many aspects of hyporheic ecology (Chapter 1), it may seem surprising that even rivers that are heavily regulated have active hyporheic zones. The Rhône River in France has twenty dams along its reach, yet it harbours some 38 hypogean (groundwater dwelling) taxa (Dole-Olivier *et al.* 1994) and sustains active physico-chemical and microbial processes (Claret and Fontvielle 1997, Claret *et al.* 1999). The hyporheic zone of the regulated South Platte River, Colorado, also actively exchanges water and nutrients with the river and has a diverse invertebrate fauna (Ward and Voelz 1994). A pilot study of the hyporheic zone of the Hunter River found that it too had a surprisingly rich fauna, and interstitial bacteria capable of transforming dissolved nutrients (Boulton 2000a). Perhaps the reason why these rivers retain their active hyporheic zones is because they have maintained their connection to groundwater aquifers. For example, influent groundwater in the Brenno River, Switzerland, mitigated the impacts of regulation on the ecological integrity of the floodplain (Brunke 2002).

3.1.1 Components of an active hyporheic zone

To determine whether the hyporheic zones of the Hunter River are active, it is beneficial to first establish what characterises an 'active' hyporheic zone. Because of the importance of exchange processes from the stream and from groundwater, the hyporheic zone must maintain links to both of these habitats (Chapter 1). Invariant low flow can promote colmation, severing the hyporheic zone from the stream (Brunke 1999), leading to anoxic

conditions in the sediment. Where there is substantial exchange between the stream and hyporheic zone, some physico-chemical variables show predictable trends. For example, the dissolved oxygen concentration of water in the downwelling zone and at the head of gravel bars will be similar to that in the surface water. With depth and distance along interstitial flow-paths, aerobic bacteria and faunal activity consume oxygen, so that upwelling water is usually hypoxic (Figure 3.1). Nutrients also change in concentration with distance from the inwelling zone as they are transformed by microbial activity. Dissolved nitrogen entering an oxygen-rich hyporheic zone can undergo microbially-mediated transformation to nitrate, so that concentrations of nitrate increase with distance from the source of downwelling (Duff and Triska 2000). However, as oxygen declines, denitrification and ammonification take over as the dominant processes and nitrate concentration decreases (Figure 3.1). This can further lead to mineralisation of nitrogen (Webster *et al.* 2003). Interstitial soluble reactive phosphorus (SRP) fluxes are often complex, being determined by interactions among sediment properties, redox conditions, and biota (Hendricks and White 2000). Bacteria are important moderators of phosphorus release and uptake in streams (Dahm *et al.* 1991). In well oxygenated sediments, the SRP concentration can be expected to increase with distance as phosphorus is transformed into its soluble form, but then decrease as microbes adsorb the nutrient (Figure 3.1). The degree to which observed trends resemble expected trends can give an indication of the activity of a hyporheic or parafluvial zone (Findlay 1995, Boulton 2000b).

At this point, it is useful to introduce the concept of 'filtration efficiency', which is a measure of the rate at which dissolved nutrients and physico-chemical variables of a parcel of water are transformed during a period of interstitial flow. To assess filtration efficiency, key indicators, such as DO and NOx concentrations can be measured along subsurface flow-paths. Rapidly declining oxygen concentrations, indicate the presence of interstitial microbial activity, a key component of hyporheic filtration. Similarly, a corresponding increase in nitrogen oxides (NOx) to a point where oxygen becomes limiting, then a subsequent drop in NOx concentration as anaerobic bacteria dominate, can also be indicative of efficient hyporheic filtration.

Declines in oxygen can also change the composition of the interstitial fauna from one dominated by occasional hyporheos (those taxa which may spend part of their life cycle in

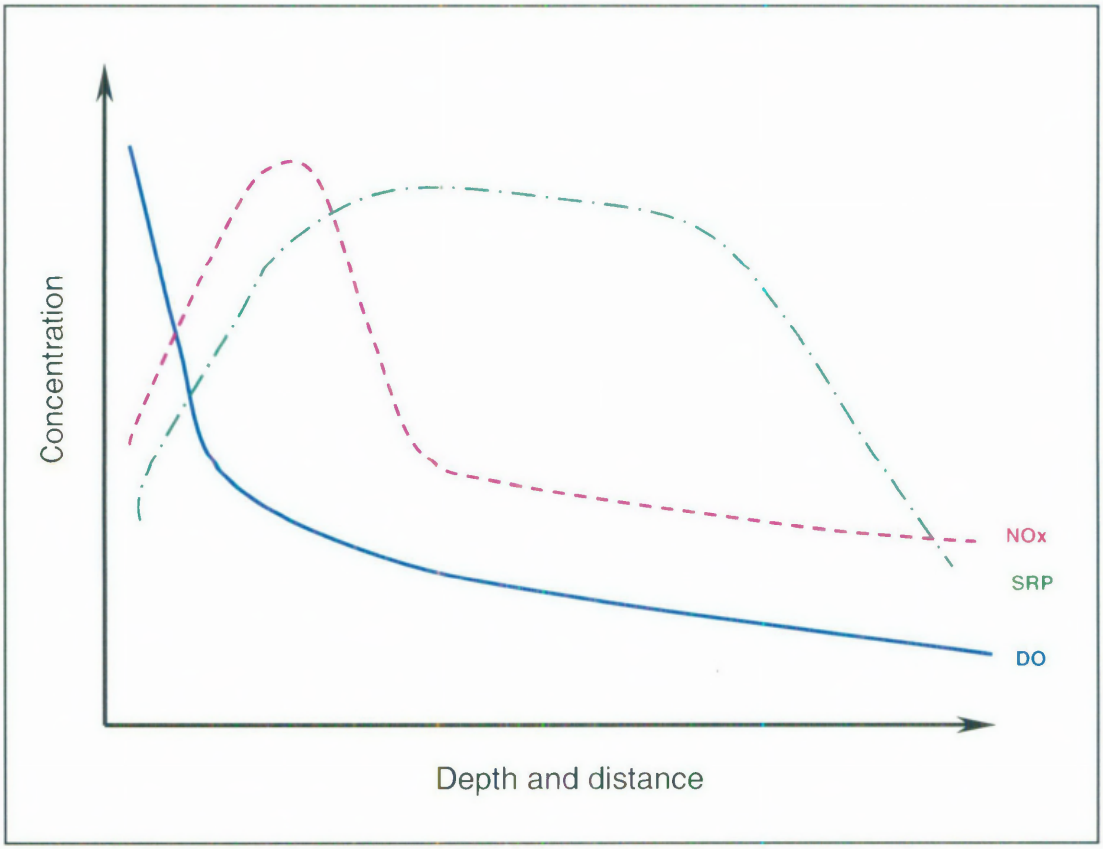


Figure 3.1. Expected trends in the concentrations of soluble reactive phosphorus (SRP), nitrate and nitrite (NOx), and dissolved oxygen (DO) with depth and distance along subsurface flowpaths.

Because hyporheic zones can be patchy, it is important to monitor them at a range of spatial and temporal scales (Boulton *et al.* 1998). This study monitored seven paired hyporheic and parafluvial zones along a 138-km stretch of the Hunter River. Sampling was conducted at the habitat, site, and river scale at 5 times over a year. To determine whether the hyporheic zones of the Hunter River are active, the concentrations of dissolved oxygen, nitrogen oxides (NOx), and soluble reactive phosphorus (SRP) were measured and tested against several hypotheses consistent with the above model (Figure 3.1). Specifically, I tested the model that oxygen declines with depth and distance from the downwelling zone as it is consumed by microbial activity. NOx concentrations will increase with distance along flowpaths to points where oxygen becomes limiting, then the concentration will decline. To test the strength of connections between the surface stream and the hyporheic zone, and to see if there was any longitudinal pattern in faunal distributions, interstitial invertebrate communities were sampled. I predicted that there would be trends of declining epigean taxa with distance along flowpaths, and more groundwater animals at the downstream sites.

3.2 Study sites

Seven sites along the Hunter River were sampled for this study. In a downstream direction, these were Aberdeen (ABER), Denmans (DENM), Bowmans Crossing (BOWM), Downstream of Macquarie Generation (DSMG), Moses Crossing (MOSE), Maison Dieu (MASO), and Dights Crossing (DIGH). Descriptions of these sites can be found in Chapter 2. These sites were selected on the basis of having a riffle and a lateral or central bar. The mean daily flow for the Aberdeen and Jerrys Plain gauging stations is displayed in Figure 3.2 and shows the flow conditions when samples were collected.

3.3 Methods

3.3.1 Field sampling

Seasonal sampling was conducted between May 2000 and May 2001 on the following dates: 17-21 May 2000 (autumn 2000), 14-18 August 2000 (winter), 5-11 November 2000 (spring), 29 January – 3 February 2001 (summer), and 14 – 19 May 2001 (autumn 2001).

Hyporheic sampling of gravel bars (parafluvial) and riffles (hyporheic) was done with a pump sampler (Boulton 1993, Figure 3.3). Six litres of water were extracted, with a hand-operated bilge-pump, via a PVC pipe of 16 mm internal diameter driven into the sediments to the desired depth. Boulton *et al.* (2003a) recommend that at least five samples of 3 – 5 L be collected from a specific area. However, collecting 5 replicates from the two subhabitats (downwelling and upwelling) in the riffle of the Hunter River was not possible due to time limitations, so three 6-L samples were collected from each of the subhabitats. A constant pumping speed was used to minimise variability between sites, times, and habitats (Hunt and Stanley 2000). At downwelling zones, samples were collected from 40 cm and 80 cm. Only 40 cm was sampled in the upwelling zones, as a pilot study revealed little difference in water quality or fauna between 40 cm and 80 cm in this habitat. Sampling locations along a lateral or mid-river gravel bar were –1, 0, 1, 5, 10, and 20+ m from the leading edge of the bar along a predicted flow-path (Figure 3.4). The –1 m samples were taken from 1 m upstream of the upstream edge of the bar, while the 0 m samples were collected from the water-bar margin. The 20+ m location ranged from 20–30 m and was not sampled when bars were less than 20 m long. One 6-L sample was collected 40 and 80 cm below the water table at each of the sampled distances along the bar.

Each sample was collected in three lots of two litres. The initial two litres were elutriated five times through a 125 μm sieve (Figure 3.5). 125mL of this were field filtered through Whatman GF/C filter papers into acid-washed polyethylene bottles and frozen for analysis of nitrate and nitrite nitrogen (NOx), and soluble reactive phosphorus (SRP) in the laboratory. The second two-litre portion was pumped carefully, with little disturbance so that measurements could be taken for dissolved oxygen (DO) and water temperature (using a TPS WP-824 dissolved oxygen meter, TPS, Brisbane, with a YSI5739 probe), and conductivity (EC) and pH (using a TPS MC81 conductivity and pH meter). This sample was subsequently elutriated five times through the sieve along with the third two-litre portion. Material retained by the sieve constituted the faunal sample, which was preserved in 70 % ethanol until processing. Duplicate surface nutrient samples for NOx and SRP were collected in conjunction with DO, pH, EC, and water temperature from the upstream end of the riffle at each site.

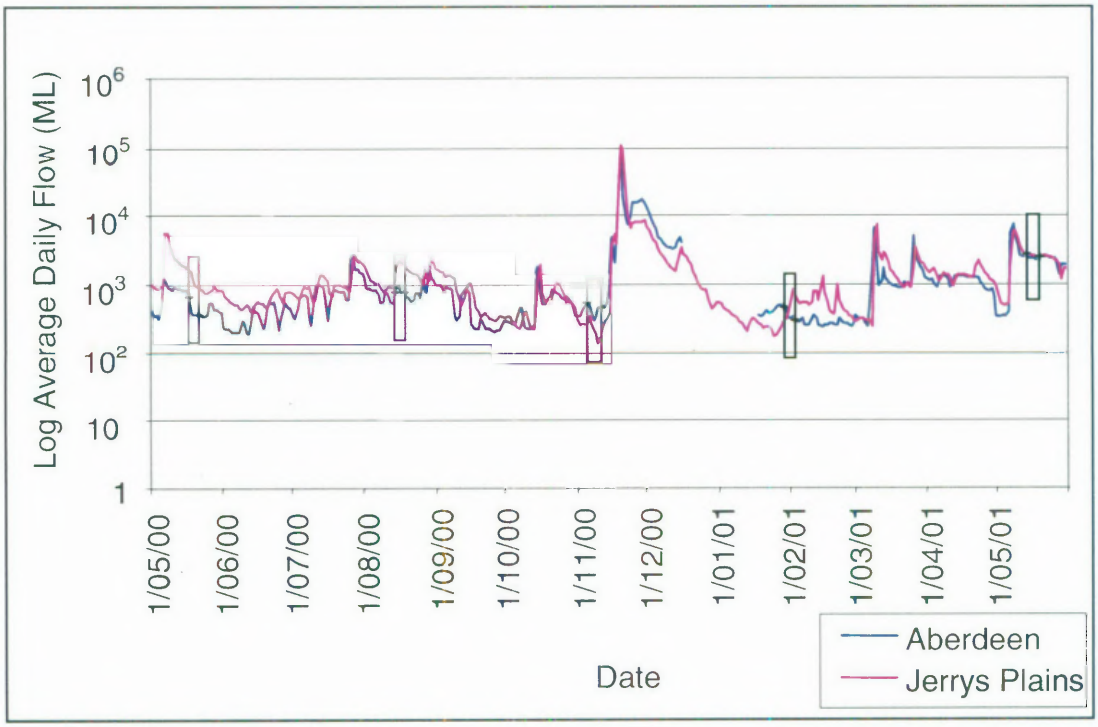


Figure 3.2. Mean daily flow in the Hunter River at Aberdeen and Jerrys Plains (Department of Land and Water Conservation). Boxes indicate sampling occasions.

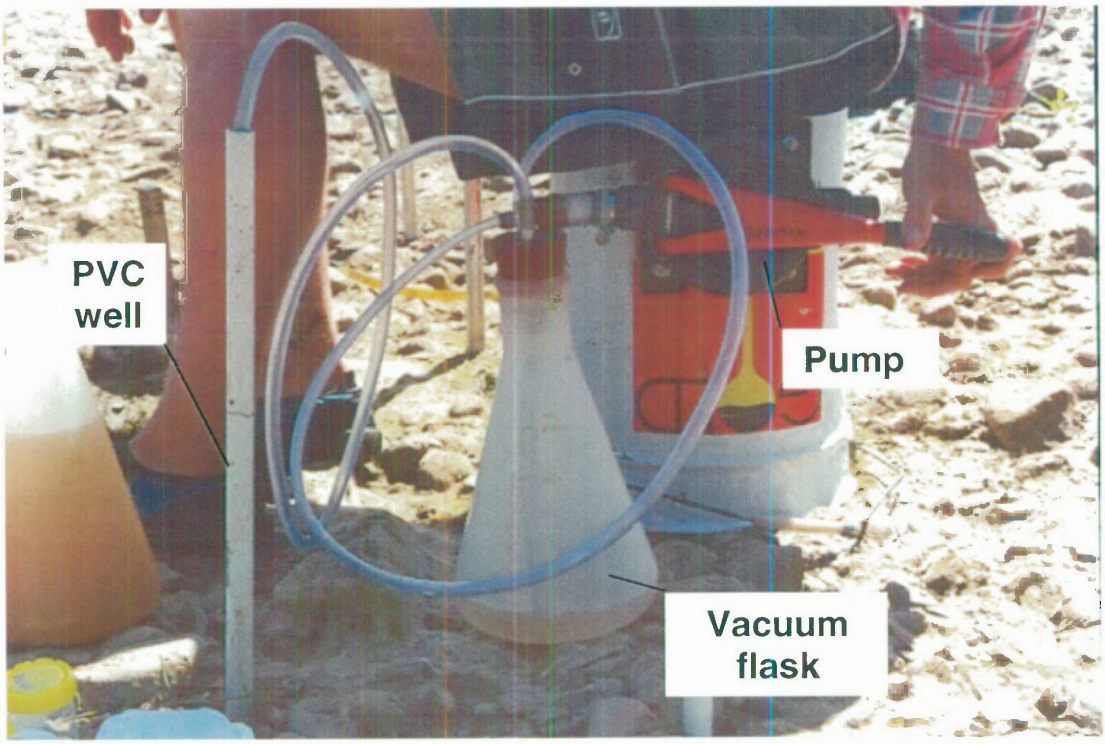


Figure 3.3. The hyporheic pump sampler.

High flows prevented samples being collected from riffles at MASO in August 2000, and DIGH in August 2000 and February 2001. They also meant that sampling at riffle and bar habitats at DSMG in August 2000 and February 2001 was not possible. In February 2001, meter malfunction prevented the collection of conductivity and pH data from DENM and MASO.

3.3.2 Laboratory processing

Nutrient samples were thawed prior to colorimetric analysis in the laboratory. SRP was analysed using the molybdate blue method (Murphy and Riley 1962), and NOx was analysed using cadmium-copper reduction (Wood *et al.* 1967). Faunal samples were processed under 10 – 400 x magnification and taxa identified as far as possible. Some taxa (e.g. oligochaete worms, microturbellarian flatworms, cyclopoid copepods) were grouped for analysis, as taxonomic studies for these hyporheic groups in Australia are in their infancy.

3.3.3 Hydrological data

The Aberdeen and Jerrys Plains gauging stations were used to obtain flow information for this study. The hydrographs for these two stations were characterised by small fluctuations in discharge. Discharge was highest for the May 2001 sampling occasion (2750 ML), and lowest in November 2000 (180 ML), immediately preceding a large flood (Figure 3.2).

3.3.4 Data analysis

Analysis of variance (ANOVA) was used to compare the means of the dependent variables of temperature, EC, pH, SRP, NOx, DO, invertebrate abundance, and taxonomic diversity among sites, times, and locations. To give a clearer indication of the amount of transformation occurring in the sediments, interstitial SRP, NOx, and DO were analysed as their respective proportions of surface concentrations. If significant transformation occurred, then the difference between the surface water levels of each variable would increase with subsurface residence time. Any seasonal patterns will be indicated by differences among seasonal data. All ANOVAs were computed using SYSTAT for Windows, version 9.01 (SPSS Incorporated).

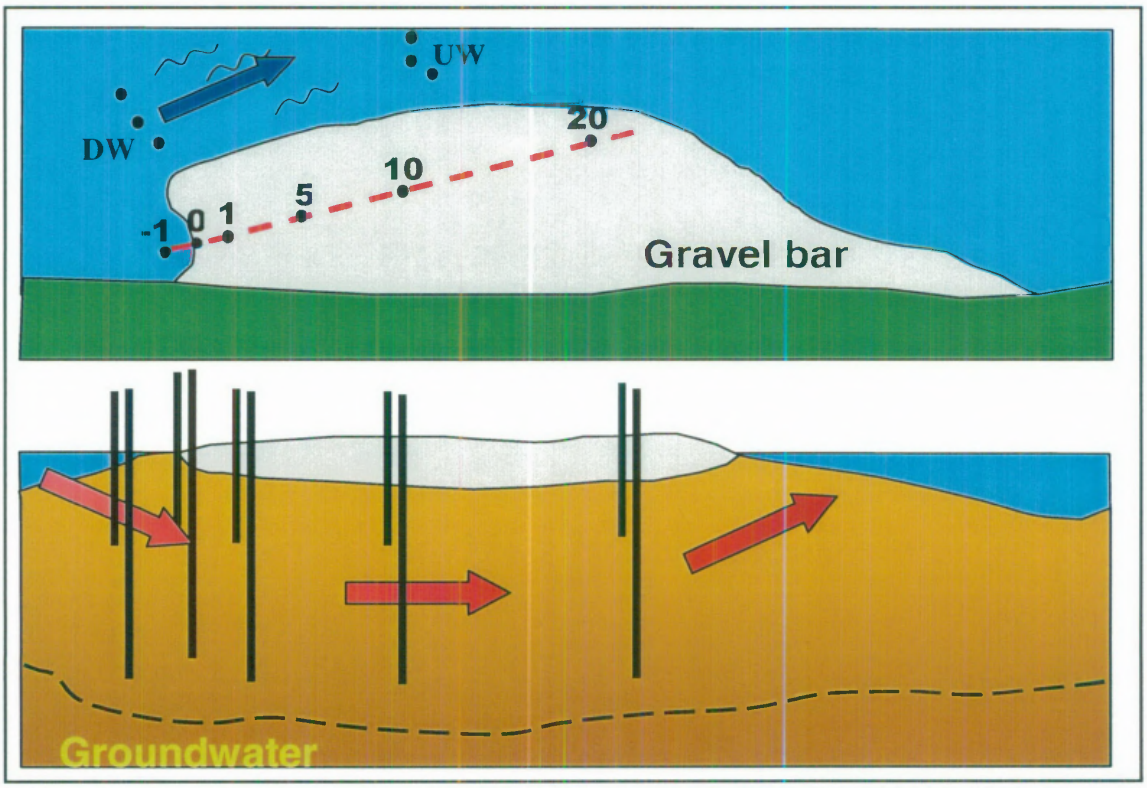


Figure 3.4. Location of sampling points in the riffle and bar within a site. Not to scale.

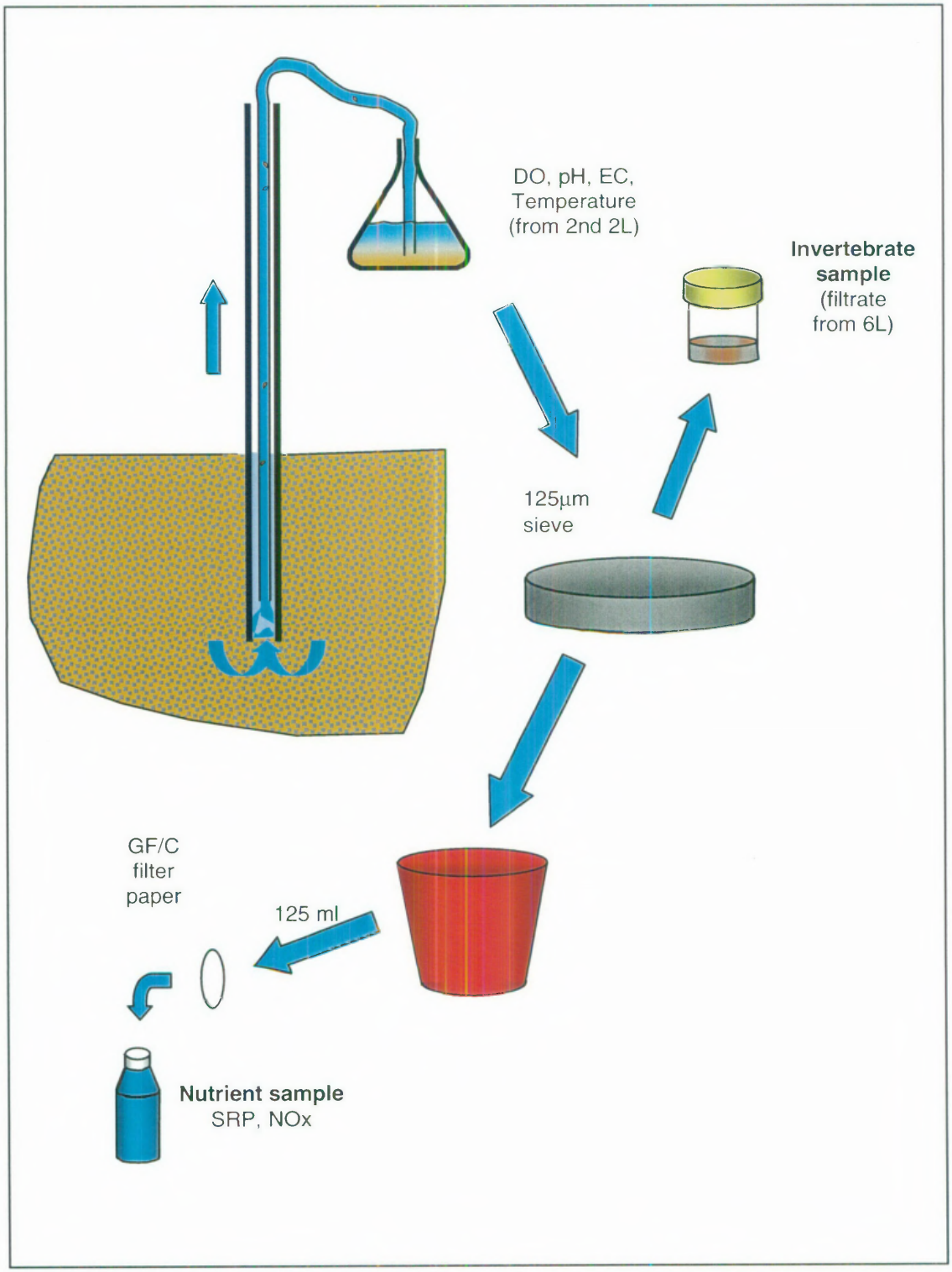


Figure 3.5. Pictorial representation of sample collection using the pump sampler. Refer to section 3.3.1 for more detail.

To test for differences among sites and times at bar and riffle habitats, a two-factor restricted mixed ANOVA (Quinn and Keough 2002) was used. For these analyses, time was a random factor with 5 levels (May 2000, August 2000, November 2000, February 2001, and May 2001). Its estimated mean square (EMS) was tested over EMS of the error term. The EMS of Site (Site was fixed with 7 levels numbered in a downstream direction) was tested over the EMS of the Time-Site interaction to determine its F ratio. All habitats and depths were pooled for the analyses of bar samples to test for longitudinal variation among sites, and temporal variation among seasons. If there is a significant amount of transformation occurring in a bar or riffle, then an observable change in water chemistry can be expected. For analyses of riffle physico-chemical data, the three habitats were also pooled within site. Surface SRP, NOx, DO, temperature, conductivity, and pH were analysed with two-factor (Site, Time) ANOVAs. However, there was a large amount of data missing for interstitial pH, temperature, and EC, mostly due to meter malfunction, but also from inaccessibility to some sites during high flows. For these variables, two separate one-way ANOVAs were conducted to assess large-scale spatial and temporal patterns for each habitat, using first Site, then Time as the factors. Prior to analysis, all physico-chemical data were tested for normality using Wilk-Shapiro tests using Statistix for Windows version 7 (Analytical Software). Box-plots and residual plots were examined to identify heteroscedasticity. Where necessary, data were transformed to comply with the assumptions of ANOVA (Underwood 1997).

To test for differences among riffle habitats within sites, and among seasons, two-factor mixed ANOVAs were used. Time, a random factor, was crossed with Habitat, which was fixed. Habitat had three levels; downwelling at 40 cm depth, downwelling at 80 cm depth, and upwelling at 40 cm depth.

Trends along bars were analysed using analysis of covariance (ANCOVA) with Statistix for Windows version 7 (Analytical Software 2000). Separate analyses were done for each site and depth. The model was specified as Time, with distance along the bar being the covariate.

Powerful multivariate analysis methods such as MANOVA, the multivariate equivalent of ANOVA, have existed since the 1930s (Anderson 2001). However, many of the

assumptions required for MANOVA are not met by multi-species abundance data (Clarke and Warwick 2001, Baldwin *et al.*1998). MANOVA's assumption of normality precluded it from being used in the current study because most samples had low numbers of only a few taxa, and zeros dominated the data matrix. To overcome this, I used three non-parametric multivariate analytical techniques, computed using PRIMER version 5.2.9 (Plymouth Marine Laboratories, Plymouth, UK). Non-metric multidimensional scaling (nMDS) was used to display similarity data among samples of invertebrates represented in two dimensions (Clarke and Warwick 2001). Where invertebrate communities in each sample share taxa with similar abundances, they will appear near each other on an nMDS plot. To test the significance of differences among groups of samples, an analysis of similarities (ANOSIM) was performed using the Bray-Curtis similarity matrices from which the nMDS plots were obtained.

ANOSIM is a multivariate test that does not have the same strict assumptions as MANOVA (Clarke and Warwick 2001) and uses ranked similarities to compare within- and between-group variation (Clarke 1993). 'Global R' tests for overall differences between groups, and its significance is determined by comparing it with values calculated for randomly chosen permutations of the data amongst the groups (Hillman and Quinn 2002). Performing a high number of permutations can increase confidence in the probability of R's significance. For all of the ANOSIMs performed, the maximum number of permutations was set to 10 000.

The ANOSIM function allows a maximum of two factors for either crossed or nested designs. For this reason I have computed several separate ANOSIMs for each analysis (Dahl and Dahl 2002). This necessitated the groupings of lower factors within higher factors of the model. Sites were analysed separately from each other, and both bar and riffle were analysed separately within each Site. For riffle fauna, two-way crossed ANOSIMs of *a priori* selected Time and Habitat groups were calculated from Bray-Curtis similarity matrices of log (x+1) transformed data. The number of permutations was set to 10 000. Because bar fauna had more than two factors of interest (Time, Distance, and Depth), two separate crossed ANOSIM analyses were done for each site: Time x Distance, and Time x Depth. Distance x Depth was not analysed because this interaction was not of primary interest to this study.

Once the significance of each grouping is established, it is often useful to determine which species, or set of species, contributed to the grouping. SIMPER (SIMilarity PERcentages) is a technique that allows determination of the species responsible for groupings (Clarke and Warwick 2001) and was used for the Hunter River samples.

3.4 Results

3.4.1 Trends among sites and times

This section compares river-scale patterns among sites and times in the physico-chemical variables in surface water, parafluvial (bar) zones, and riffle hyporheic zones. Average values for each variable measured from the surface water can be found in the table accompanying the graph for each of the sites.

Temperature in the riffle and bar displayed seasonal trends, peaking in February 2001 at 26 °C, and having a low of 14 °C in August 2000 ($F_{4,258} = 433.545$, $P < 0.001$ for riffle, $F_{4,375} = 624.55$, $P < 0.001$ for bar). There were also strong longitudinal trends in interstitial temperature in the hyporheic zone, with temperatures increasing with distance downstream from an average of 17 °C at ABER to 20 °C at MASO ($F_{6,251} = 2.801$, $P = 0.012$). However, mean hyporheic temperature at DIGH was 4 °C lower than that at MASO. Parafluvial water temperatures on the other hand, increased to a peak of 22 °C at DSMG, then fall to 18 °C at DIGH ($F_{6,373} = 5.44$, $P < 0.001$).

Mean interstitial pH in the riffle and bar varied over time with pH in both habitats peaking at 8.0 in November 2000 ($F_{4,241} = 10.08$, $P < 0.001$ for riffle, and $F_{4,339} = 10.94$, $P < 0.001$ for bar). Mean pH differed along the river in bar and riffle habitats, though not in any discernable downstream trend ($F_{6,239} = 2.955$, $P = 0.008$ for riffle, and $F_{6,337} = 7.033$, $P < 0.001$ for bar). Both habitats displayed a bimodal pH, peaking at 8.0 at DENM and MOSE.

Mean EC below the riffle differed with time and distance downstream but displayed no seasonal or longitudinal trends ($F_{6,337} = 7.512$, $P < 0.001$ among Sites, and $F_{4,339} = 19.83$, $P < 0.001$ among Times). Similar patterns occurred in the bars ($F_{6,239} = 7.29$, $P < 0.001$ among Sites, and $F_{6,239} = 7.29$, $P < 0.001$ among Times)

Surface DO was relatively high at all sites, being between 80 and 110 % saturation. Exceptions to this occurred in May at DENM when surface water was supersaturated, probably by algal photosynthesis, to 159 %. High oxygen concentrations were also recorded at DSMG in November 2000 (126 %), and at BOWM in February (121 %). DO in the surface water was consistently lower from autumn to summer 2000 across all sites ($F_{4,33} = 6.717$, $P < 0.001$). DO increased again in autumn 2001. There were no differences among sites with surface DO concentrations. Interstitial DO in bars at May 2001 differed to those in May, August, and November 2000 ($P < 0.001$, Table 3.1). Bar DO also differed among sites ($P < 0.001$, Table 3.1) but displayed no clear downstream trend. Generally, DO in bars at BOWM and DSMG were similar to all sites downstream. Bar DO concentration decreased with Site in the following order: DENM, MASO, MOSE, BOWM, DSMG, ABER, and DIGH. In contrast to this, DO in riffle habitats did not differ among sites (P=0.075, Table 3.1).

Surface water concentrations of SRP did not differ down the length of the river ($F_{5,23} = 0.124$, $P = 0.985$) and ranged from 0.008 mg/L to 0.076 mg/L. Concentrations were higher in autumn 2000 than the other four times ($F_{4,33} = 2.839$, $P = 0.040$). Neither interstitial riffle nor bar SRP concentrations differed among sites, but did differ with Time ($P < 0.001$, Table 3.1). Bar SRP in May and November 2000 did not differ to each other ($P = 0.437$) and were higher than all other times (both > 150 % of surface). SRP in the bar was lowest (less than 65 % of surface water concentration) in autumn 2001, which differed to SRP in winter ($P < 0.001$).

In the surface water, NOx concentrations ranged from 0.0003 mg/L (DIGH, spring) to 0.348 mg/L (DSMG, summer). NOx concentrations in surface water did not differ among sites ($F_{6,22} = 1.043$, $P = 0.425$), but displayed strong temporal variation ($F_{4,33} = 25.924$, $P < 0.001$). February and May 2001 concentrations were highest, followed by August and May 2000. November 2000 was much lower than at other times. NOx concentrations were relatively homogenous among sites in both of the hyporheic habitats (both $P > 0.05$, Table 3.1). Strong temporal variations characterised NOx concentrations in the bar ($P < 0.001$, Table 3.1), with NOx concentrations being higher in spring, then autumn 2000, winter, summer, and autumn 2001.

A total of 71 invertebrate taxa was found in the hyporheic and parafluvial habitats during this study (Figure 3.6). Only taxonomic richness in parafluvial zones differed among sites ($P = 0.040$, Table 3.1), with the 2 upstream sites being richest (more than 6 taxa per sample). DSMG had the lowest diversity, averaging 2 taxa. The richness in the bars was least in winter and summer. Except for summer, taxonomic diversity in riffles increased temporally ($P < 0.001$, Table 3.1), rising from 4 taxa in May 2000, to over 6 in May 2001.

Invertebrate abundance displayed no longitudinal trends among sites for bar or riffle samples (Table 3.1). Abundance increased with Time in bars ($P < 0.001$, Table 3.1) and riffles ($P < 0.001$, Table 3.1), except for during summer.

3.4.2 Aberdeen (ABER)

The DO of ABER surface water ranged between 83.2 and 97.9 % saturation (Figure 3.7). In riffle habitats, DO was more similar to surface concentrations in the 40 cm downwelling habitat (65.5 ± 9 % surface, mean ± SE) than the 80 cm downwelling (45.8 ± 6.5 %) and 40 cm upwelling zones (10.8 ± 3.8 %, Table 3.4, $P < 0.001$, Figure 3.7). DO decreased along the bar at both 40 cm (ANCOVA $F_{1,24} = 106.85$, $P < 0.001$) and 80 cm (ANCOVA $F_{1,24} = 36.93$, $P < 0.001$) depths (Figure 3.7). DO along the bar at 40 cm fell from 74.8 ± 18.7 % of surface to 8.5 ± 3.5 % surface when averaged over the five times. At 80 cm DO was lower, with an average range of 44.1 ± 11.4 % to 7.1 ± 4.0 %. Strong temporal variation was apparent in the bar habitat at 40 cm (ANCOVA $F_{4,24} = 24.9$, $P < 0.001$) , with higher concentrations in August 2000 and both dates in 2001. There were differences with Time at 80 cm too (ANCOVA $F_{4,24} = 5.51$, $P = 0.003$), when DO was higher in February and May 2001. In the riffle, DO increased between autumn 2000 and winter, and between summer and autumn 2001 for all habitats except for upwelling in autumn 2001 ($P < 0.001$, Table 3.2).

Interstitial pH in the bar at ABER did not differ with distance at either 40 cm (ANCOVA $F_{1,24} = 0.07$, $P = 0.800$) or 80 cm (ANCOVA $F_{1,24} = 0.42$, $P = 0.525$, Figure 3.7). Bar pH was lowest during May and increased through the year (ANCOVA $F_{4,24} = 9.72$, $P < 0.001$ for 40 cm, $F_{4,24} = 5.58$, $P = 0.003$ for 80 cm). Riffle pH was highest at the downwelling zone at 40 cm ($P = 0.002$, Table 3.2) and in May 2001 ($P < 0.001$, Table 3.2).

Table 3.1. ANOVA results for Time x Site interactions for riffle and bar habitats. Bold numbers are significant at P = 0.05.

Variable	Source	SS	df	MS	F-Ratio	P
Bar						
DO - Log (x+1)						
	T	39.741	4	9.935	53.029	**0.000**
	S	20.542	6	3.424	18.273	**0.000**
	T*S	81.288	22	3.695	19.722	**0.000**
	Error	65.012	347	0.187		
SRP						
	T	182806.115	3	60935.372	33.135	**0.000**
	S	340657.261	6	56776.210	1.186	0.348
	T*S	1100784.803	23	47860.209	26.025	**0.000**
	Error	638137.343	347	1839.013		
NOx - Log (x+1)						
	T	13.977	4	3.494	26.119	**0.000**
	S	24.865	6	4.144	2.266	0.075
	T*S	40.235	22	1.829	13.670	**0.000**
	Error	46.422	347	0.134		
Invertebrate abundance - Log(x+1)						
	T	19.597	4	7.899	18.787	**0.000**
	S	12.727	6	2.121	2.374	0.064
	T*S	19.656	22	0.893	3.426	**0.000**
	Error	90.489	347	0.261		
Taxonomic richness						
	T	168.334	4	42.084	8.867	**0.000**
	S	479.505	6	79.918	4.464	**0.004**
	T*S	393.871	22	17.903	3.772	**0.000**
	Error	1646.858	347	4.746		
Riffle						
DO - Log (x+1)						
	T	1.565	4	0.391	2.510	**0.043**
	S	3.225	6	0.537	0.603	0.725
	T*S	16.944	19	0.862	5.722	**0.000**
	Error	36.938	237	0.156		
SRP - Log (x+1)						
	T	1.091	3	0.364	16.687	**0.000**
	S	2.027	5	0.405	0.726	0.612
	T*S	11.724	21	0.558	25.621	**0.000**
	Error	5.237	237	0.022		
NOx - Log (x+1)						
	T	4.124	3	1.375	15.166	**0.000**
	S	3.827	5	0.765	0.848	0.531
	T*S	18.957	21	0.903	9.960	**0.000**
	Error	21.480	237	0.091		
Invertebrate abundance - Log(x+1)						
	T	4.771	2	2.386	8.760	**0.000**
	S	10.300	6	1.717	1.354	0.278
	T*S	26.619	21	1.268	4.654	**0.000**
	Error	64.546	237	0.272		
Taxonomic richness						
	T	209.191	4	52.298	7.557	**0.000**
	S	261.221	6	43.537	2.024	0.112
	T*S	408.769	19	21.514	3.109	**0.000**
	Error	1640.167	237	6.921		

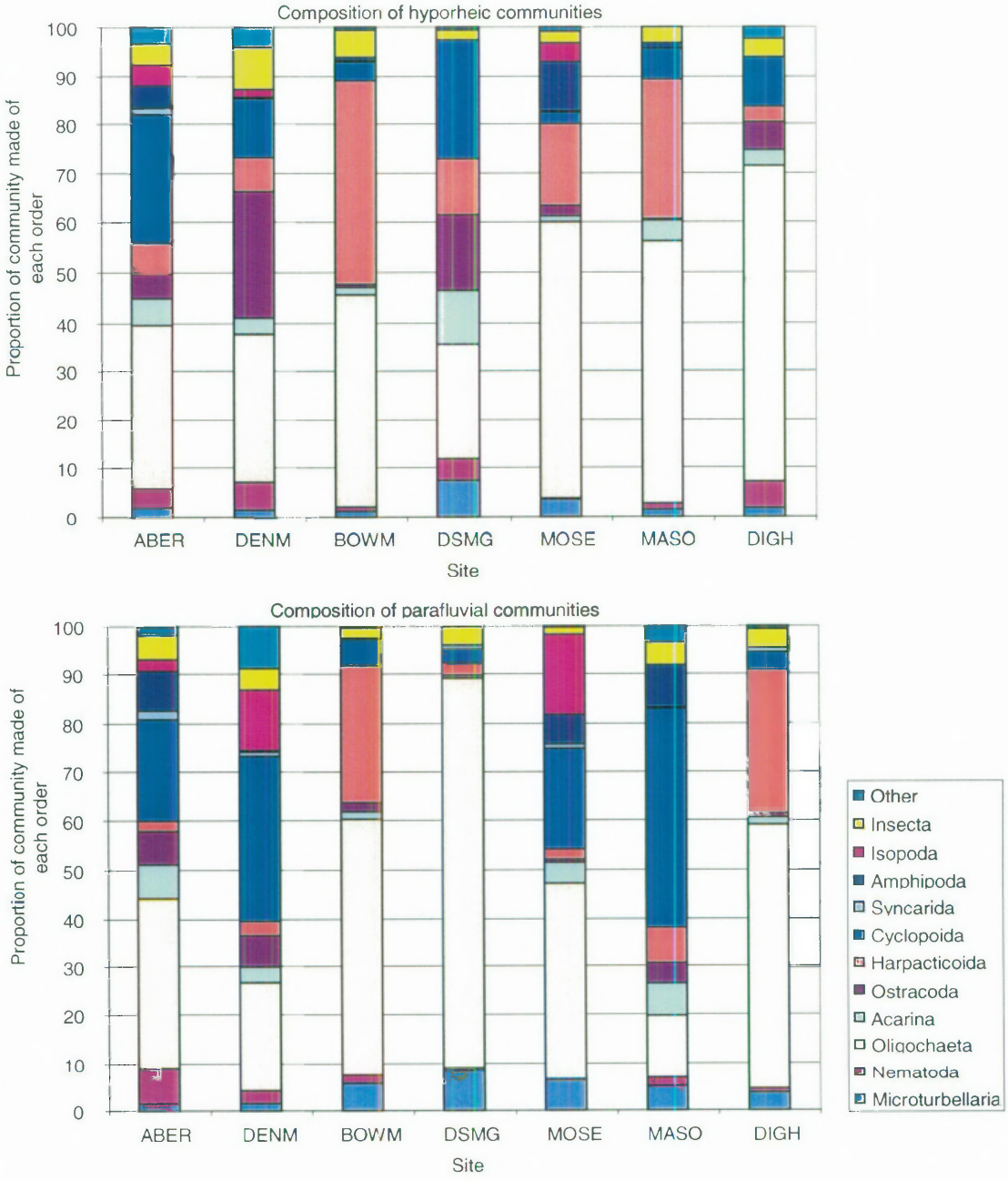


Figure 3.6. Composition of invertebrate communities in hyporheic and parafluvial habitats at seven Hunter River sites.

Temperature in the hyporheic zone and parafluvial zone fluctuated as expected with the seasons, ranging from 11 °C in May 2000 to a maximum of 23 °C in February 2001 (Table 3.2, Figure 3.7). Interstitial temperature also displayed spatial patterns, being higher in the upwelling zone ($P < 0.001$, Table 3.2) than in the downwelling zone. Temperature in the bar increased with parafluvial distance along the flowpath at 80 cm (ANCOVA $F_{1,24} = 11.68$) but not at 40 cm (ANCOVA $F_{1,24} = 0.21$, $P = 0.651$, Figure 3.7).

Hyporheic EC was highest during May and August 2000 ($P < 0.001$, Table 3.2, Figure 3.7) and did not differ among zones ($P = 0.058$, Table 3.2, Figure 3.7). Parafluvial EC did not differ significantly with distance along the bar (ANCOVA $F_{1,24} = 0.11$, $P = 0.739$; ANCOVA $F_{1,24} = 0.57$, $P = 0.460$). However, at 80 cm depth, the EC during May 2000 was significantly lower than at any other time.

Surface NOx concentrations at ABER ranged from 0.028 ± 0.006 mg/L in spring 2000 to 0.316 ± 0.204 mg/L in autumn 2001 (Figure 3.7). In the riffle, interstitial concentrations were generally highest in the 40-cm DW, then the 80-cm DW, and 40-cm UW ($P = 0.012$, Table 3.2, Figure 3.7). A strong Time x Site interaction indicates temporal variation in NOx at each habitat ($P = 0.009$, Table 3.2). NOx concentrations were not significantly different along the bar at 40 cm depth (ANCOVA $F_{1,24} = 0.74$, $P = 0.398$, Figure 3.7). At 80 cm, NOx was higher nearer the upstream end of the bar (ANCOVA $F_{1,24} = 7.61$, $P = 0.011$, Figure 3.7). NOx concentrations in November 2000 were higher than those of other times for bar (ANCOVA $F_{4,24} = 19.54$, $P < 0.001$) and riffles ($P < 0.001$, Table 3.2). In the bar, there was a weak negative correlation between NOx and DO ($r_{59} = -0.418$, $P = 0.022$).

SRP concentrations in the surface water ranged between 0.016 ± 0.001 mg/L in May 2000 and 0.118 ± 0.094 mg/L in May 2001 (Figure 3.7). Concentrations in the three riffle habitats decreased with Time ($P < 0.001$, Table 3.2, Figure 3.7), but there was no difference between Habitat ($P = 0.544$, Table 3.2, Figure 3.7). SRP did not differ with distance along the bar but showed significant variation with Time for both the 40 (ANCOVA $F_{4,24} = 38.50$, $P < 0.001$) and 80 cm depths (ANCOVA $F_{4,24} = 27.54$, $P < 0.001$). Here, autumn 2000 consistently had the highest SRP concentrations (Figure 3.7). Parafluvial concentrations of SRP correlated negatively with DO ($r_{59} = -0.394$, $P = 0.031$).

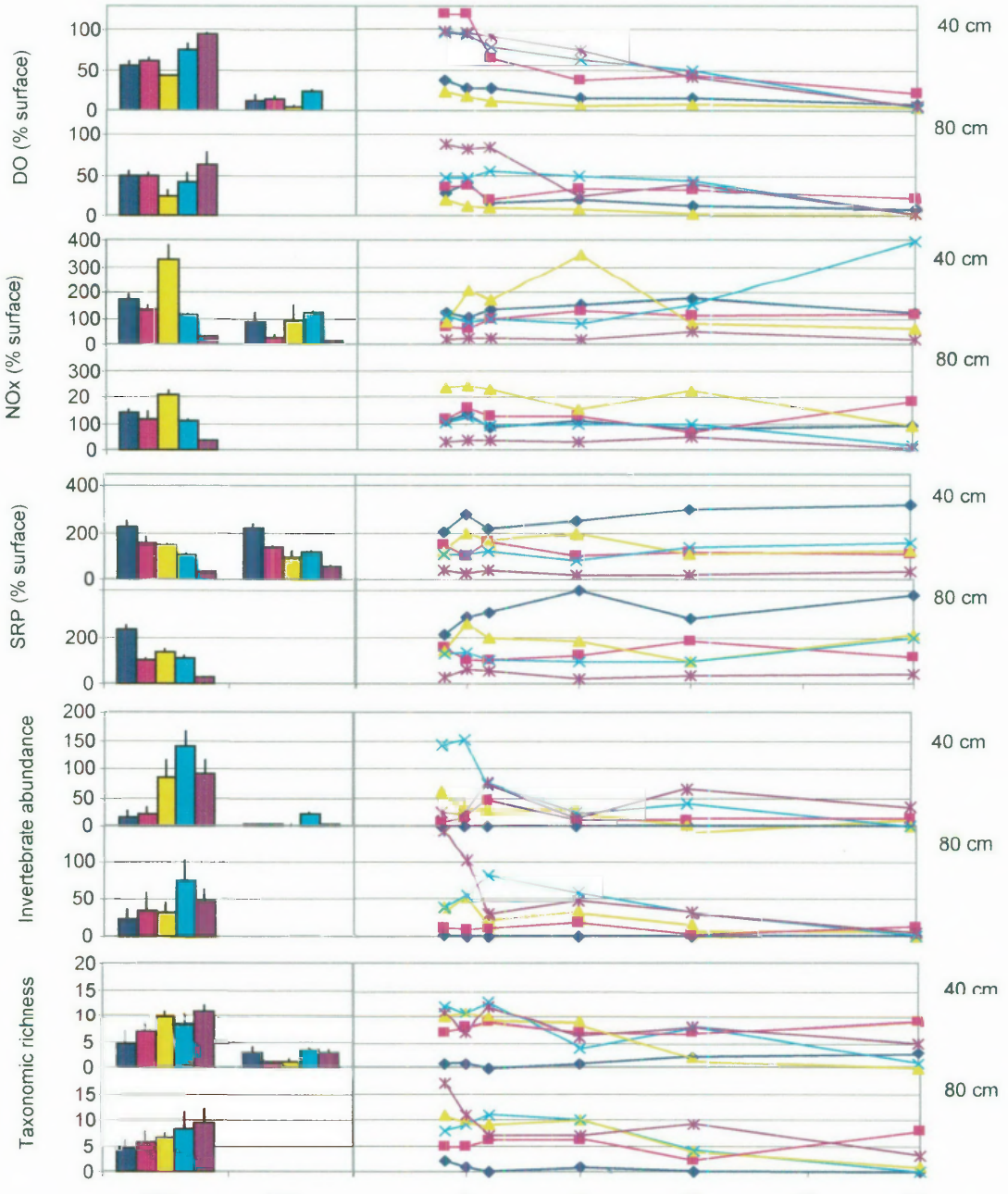
There were more individual invertebrates in the shallow downwelling habitat (70 ± 23, mean ± SE), than in the deep downwelling (42 ± 9) and upwelling (6 ± 4) habitats ($P = 0.001$, Table 3.2, Figure 3.7). The invertebrate community decreased in numbers along the bar at 40 cm (ANCOVA $F_{1,24} = 7.55$, $P = 0.0112$, Figure 3.7) and 80 cm (ANCOVA $F_{1,24} = 29.31$, $P < 0.001$, Figure 3.7). Samples from the head of the bar averaged 93 ± 52 invertebrates (mean ± SE) at 40 cm and 46 ± 25 invertebrates at 80 cm, while after 20 m, mean populations were 18 ± 12, and 3 ± 2 respectively. Highest numbers of invertebrates in all riffle habitats ($P < 0.001$, Table 3.2, Figure 3.7), and at both depths in the bar (ANCOVA $F_{4,24} = 8.48$, $P < 0.001$ for 40 cm; $F_{4,24} = 6.45$, $P = 0.001$ for 80 cm) occurred in summer 2000. Invertebrate abundance correlated positively with DO in the bar ($r_{59} = 0.494$, $P = 0.006$) and in the riffle ($r_{44} = 0.659$, $P < 0.001$).

Taxonomic richness in both downwelling habitats was higher than that of upwelling habitats ($P < 0.001$, Table 3.2, Figure 3.7). The number of taxa decreased along the bar at 40 cm (ANCOVA $F_{1,24} = 10.61$, $P = 0.003$, Figure 3.7) and 80 cm (ANCOVA $F_{1,24} = 15.94$, $P < 0.001$, Figure 3.7). The apparent increase in richness with Time in downwelling habitats (Figure 3.7) was not significant, due to the absence of a corresponding trend in the upwelling habitat ($P = 0.074$, Table 3.2). In the bar, diversity generally increased with Time (Figure 3.7) at 40 cm (ANCOVA $F_{4,24} = 6.45$, $P = 0.001$) and 80 cm (ANCOVA $F_{4,24} = 8.09$, $P < 0.001$). Taxonomic richness correlated with DO in the bar ($r_{59} = 0.515$, $P = 0.004$) and riffle ($r_{44} = 0.667$, $P < 0.001$).

Invertebrate communities in the riffle habitats differed over time (Figure 3.8, Global $R = 0.443$, $P < 0.001$). In autumn 2000 and winter, oligochaete worms and paramelitid amphipods dominated samples. Cyclopoid copepods and oligochaetes were the most abundant taxa in spring and summer, while nematode worms and harpacticoid copepods dominated in autumn 2001. Communities at both depths in the downwelling zones were similar (pairwise ANOSIM $R = 0.159$, $P = 0.091$) but different to the community in the upwelling zone (Figure 3.8, both pairwise $P > 0.001$). Downwelling habitats, dominated by oligochaetes, cyclopoids, and paramelitids, were centrally located in the nMDS plot

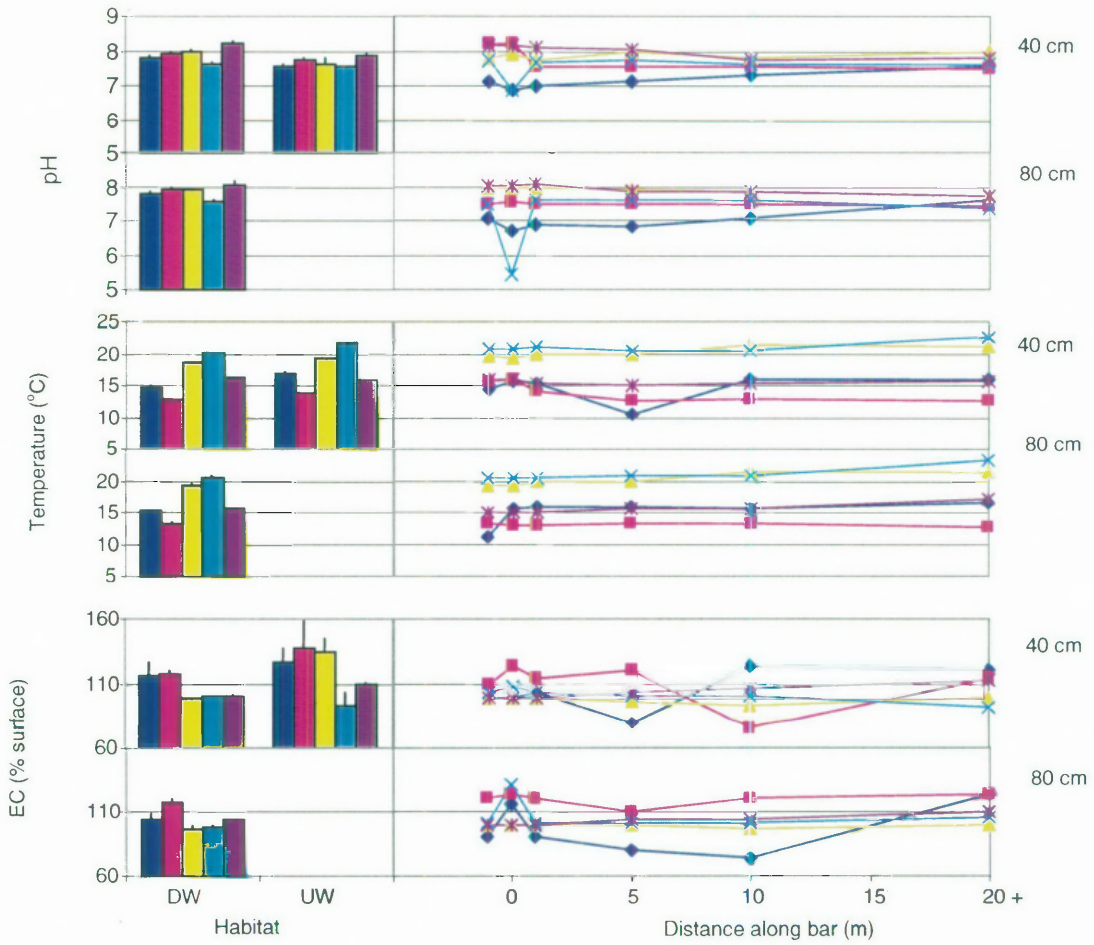
Table 3.2. ANOVA results for Time x Habitat interactions for riffle habitat at Aberdeen. Bold numbers are significant at P = 0.05.

Variable	Source	SS	df	MS	F-Ratio	P
DO						
	T	4462.259	4	1115.565	8.726	**0.000**
	H	22971.364	2	11485.682	24.373	**0.000**
	T*H	3769.991	8	471.249	3.686	**0.004**
	Error	3835.143	30	127.838	127.838	
SRP						
	T	158606.657	4	39651.664	56.218	**0.000**
	H	1681.971	2	840.986	0.657	0.544
	T*H	10243.569	8	1280.446	1.815	0.113
	Error	21159.713	30	705.324		
NOx - Log (x+1)						
	T	4.161	4	1.040	28.017	**0.000**
	H	1.936	2	0.968	8.105	**0.012**
	T*H	0.955	8	0.119	3.217	**0.009**
	Erro	1.114	30	0.037		
EC - Log (x+1)						
	T	0.052	4	0.013	7.220	**0.000**
	H	0.029	2	0.015	4.144	0.058
	T*H	0.028	8	0.004	1.971	0.085
	Error	0.054	30	0.002		
pH - squared						
	T	282.373	4	70.593	20.079	**0.000**
	H	117.419	2	58.709	14.180	**0.002**
	T*H	33.123	8	4.140	1.178	0.345
	Error	105.472	30	3.516		
Temperature						
	T	315.483	4	78.871	1349.500	**0.000**
	H	7.589	2	3.795	64.928	**0.000**
	T*H	6.006	8	0.751	12.846	**0.000**
	Error	1.753	30	0.058		
Invertebrate abundance - Log(x+1)						
	T	4.306	4	1.076	7.940	**0.000**
	H	8.170	2	4.085	18.221	**0.001**
	T*H	1.793	8	0.224	1.654	0.151
	Error	4.067	30	0.136		
Taxonomic richness						
	T	81.022	4	20.256	2.380	0.074
	H	302.400	2	151.200	25.177	**0.000**
	T*H	48.044	8	6.006	0.706	0.684
	Error	255.333	30	8.511		



	Mean DO ± SE % saturation	Mean SRP ± SE mg/L	Mean NOx ± SE mg/L
May-00	93.03 ± 3.97	0.016 ± 0.001	0.082 ± 0.006
Aug-00	88.95 ± 3.25	0.032 ± 0.001	0.123 ± 0.008
Nov-00	97.90 ± 1.70	0.018 ± 0.006	0.028 ± 0.004
Feb-01	83.15 ± 1.65	0.022 ± 0.002	0.149 ± 0.007
May-01	92.50 ± 0.70	0.118 ± 0.094	0.316 ± 0.204

Figure 3.7. Interstitial nitrates (NOx), soluble reactive phosphorus (SRP), invertebrate abundance, taxonomic richness, and measured physico-chemical variables at Aberdeen. Bar graphs on the left are hyporheic data (vertical lines represent standard error), while line bars on the right are parafluvial data. Mean surface measurements are reported in the table below the x-axis.



	Mean pH ± SE	Mean Temp. ± SE (°C)	Mean EC ± SE (mS)
May-00	8.12 ± 0.02	14.0 ± 0.1	0.30 ± 0.02
Aug-00	8.28 ± 0.06	12.2 ± 0.7	0.29 ± 0.05
Nov-00	8.75 ± 0.06	22.6 ± 0.1	0.52 ± 0.01
Feb-01	7.84 ± 0.05	20.1 ± 0.1	0.41 ± 1.65
May-01	8.29 ± 0.01	15.9 ± 0.2	0.31 ± 0.01

Figure 3.7. continued

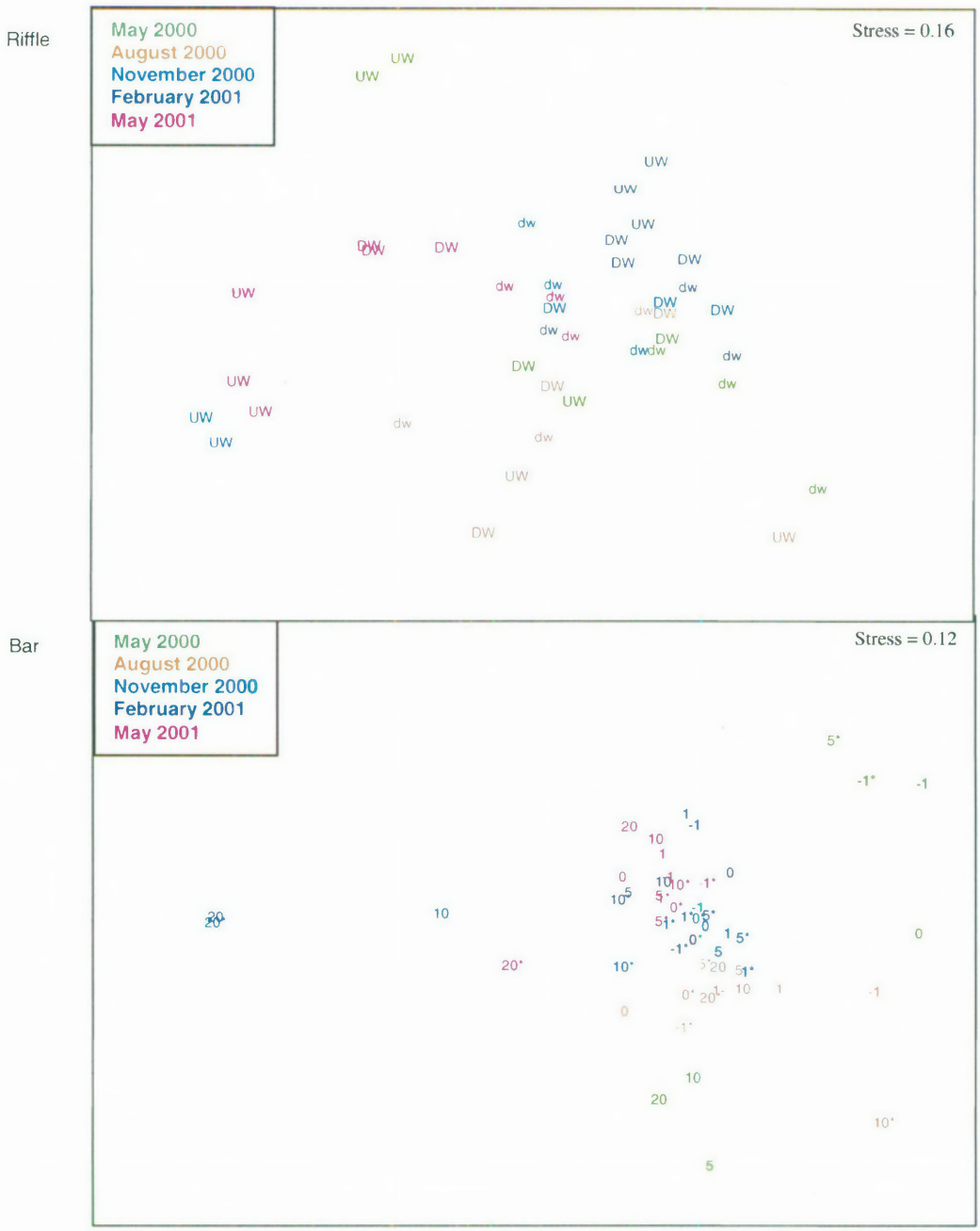


Figure 3.8. Non-metric multi-dimensional scaling diagrams of hyporheic and parafluvial habitats at Aberdeen. Upper-case letters indicate hyporheic samples from 40 cm. Lower-case letters indicate hyporheic samples from 80 cm. DW and dw = downwelling, UW = upwelling. Numerals indicate distance in metres from the leading edge of the bar. Numbers followed by an * were from 80 cm, while those without were from 40 cm.

matched with upwelling habitats, where nematodes, cyclopoids, and microturbellarians were more numerous, occurring on the outer.

In the bar, invertebrate communities differed among Times (Figure 3.8, Global R = 0.537, P < 0.001). Paramelitids dominated autumn and winter 2000 whereas oligochaetes and cyclopoids dominated other seasons. There was no difference in community composition along the bar (Global R = 0.137, P = 0.057), where communities were dominated by oligochaetes, cyclopoids, paramelitids and ostracods. Both depths were dominated by oligochaetes, cyclopoids, and paramelitids but all taxa were more numerous at 40 cm (Global R = 0.411, P < 0.001).

3.4.3 Denman (DENM)

Surface water at DENM was characterised by DO concentrations ranging from 159.7 ± 4.2 % saturation (mean ± SE) in May 2000, to 87.2 ± 0.2 % saturation in May 2001 (Figure 3.9). Along the bar, DO decreased with distance at 40 cm (Figure 3.9, ANCOVA $F_{1,22}$ = 19.16, P < 0.001) and 80 cm (ANCOVA $F_{1,22}$ = 14.51, P = 0.001). Bar DO in November was lower than the other Times (ANCOVA P < 0.001 for both depths, Figure 3.9). In the riffle, DO was higher in the shallow downwelling (65.98 ± 10.11 % surface) than in the deeper downwelling (59.09 ± 12.80 %) and the upwelling (49.81 ± 9.44 %) habitats (P = 0.023, Table 3.3, Figure 3.9). DO in riffle zone-depth habitats in May 2000 and November 2000 were least similar to their respective surface concentrations (P < 0.001, Table 3.3, Figure 3.9).

The pH below the riffle was highest in May 2001, and lowest during November 2000 (P < 0.001, Table 3.3, Figure 3.9). Similar temporal patterns occurred in the parafluvial zone at 40 cm (ANCOVA $F_{3,17}$ = 73.74, P < 0.001) and 80 cm (ANCOVA $F_{3,17}$ = 46.53, P < 0.001). Spatially, pH was higher in the downwelling zone than the upwelling zone (P = 0.032, Table 3.3, Figure 3.9), and decreased with distance along the bar at 80 cm (ANCOVA $F_{1,17}$ = 6.94, P = 0.017, Figure 3.9) , and 40 cm depth (ANCOVA $F_{1,17}$ = 4.66, P = 0.046, Figure 3.9).

Temperature varied seasonally below the riffle (P < 0.001, Table 3.3, Figure 3.9) and the bar (ANCOVA $F_{4,22}$ = 190.90, P < 0.001 for 40 cm; ANCOVA $F_{4,22}$ = 628.48, P < 0.001

for 80 cm). Interstitial temperatures ranged from 12 to 25 ^{0}C throughout the study (Figure 3.9).

Interstitial EC beneath the riffle was more than twice surface EC during May 2000 ($P < 0.001$, Table 3.3, Figure 3.9). In the bar, EC was also high during this month ranging from 100 to 220 % surface (ANCOVA $F_{3,17} = 17.57$, $P < 0.001$ for 40 cm; ANCOVA $F_{3,17} = 7.91$, $P = 0.002$ for 80 cm).

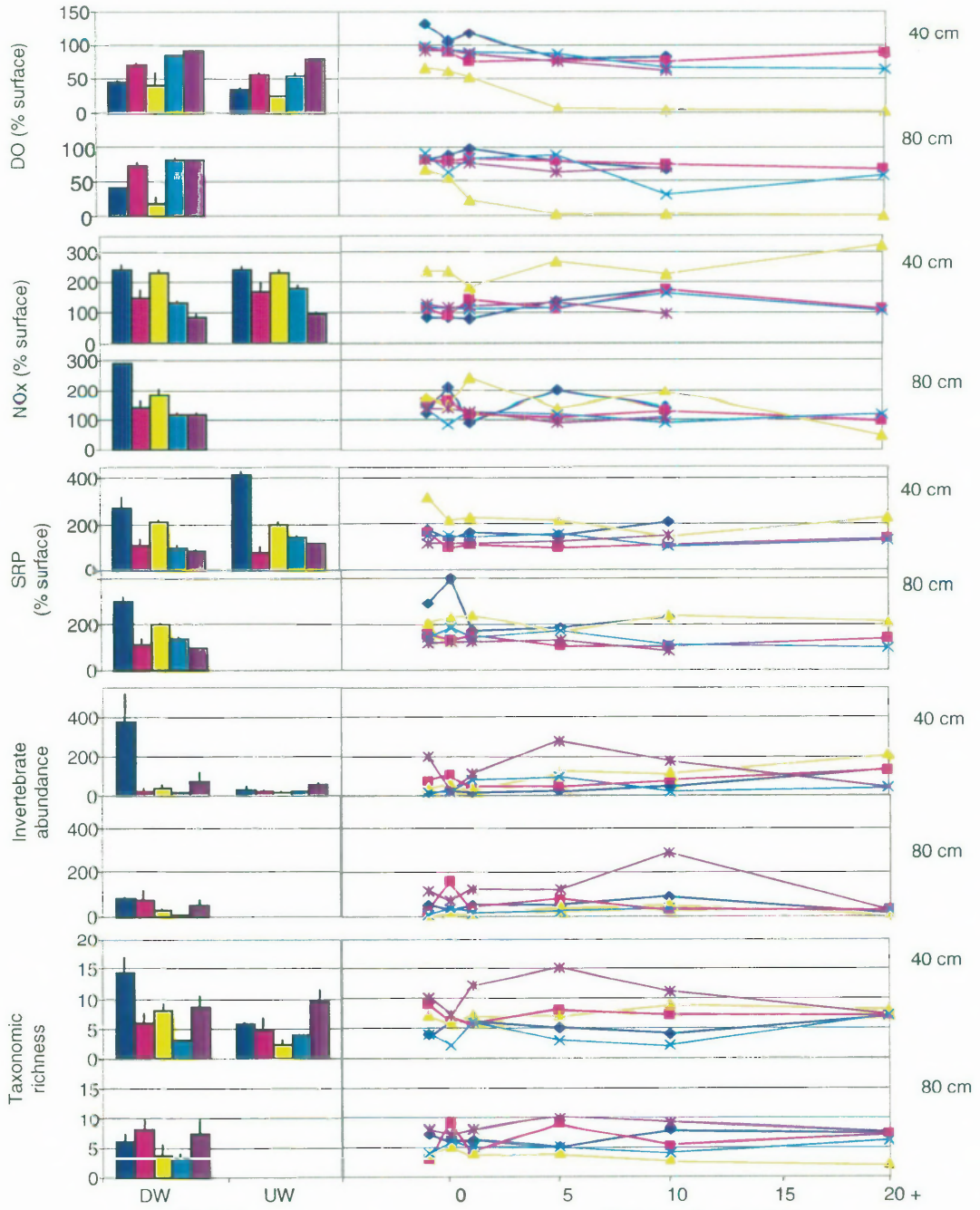
Surface NOx ranged from 0.057 ± 0.001 mg/L in May 2000 to 0.230 ± 0.017 mg/L in May 2001 (Figure 3.9). NOx was higher in the bar during November at 40 cm (ANCOVA $F_{4,22} = 14.11$, $P < 0.001$, Figure 3.9) but not at 80 cm. NOx concentrations in the riffle habitats decreased consecutively with each time except for spring ($P < 0.001$, Table 3.3, Figure 3.9). NOx decreased along the flow path in the deep bar habitat (ANCOVA $F_{1,22} = 6.56$, $P = 0.018$, Figure 3.9) but not at 40 cm. There was no difference in NOx among the riffle zone-depth habitats ($P = 0.57$, Table 3.3, Figure 3.9). NOx correlated negatively with DO in bar ($r_{55} = -0.834$, $P = 0.008$) and in the riffle ($r_{44} = -0.746$, $P < 0.001$).

The surface water SRP concentrations at DENM ranged between 0.013 ± 0.001 mg/L in May 2000, and 0.058 ± 0.004 mg/L in May 2001 (Figure 3.9). Concentration differed with distance along the bar at 80 cm only (ANCOVA $F_{1,22} = 4.36$, $P = 0.049$, Figure 3.9), mainly due to high concentrations at –1 and 0 m in May 2000. These samples also contributed to the variation observed with Time (ANCOVA $F_{4,22} = 13.23$, $P < 0.001$, Figure 3.9). Generally, concentrations at 40 cm in the bar were higher in spring 2000 (ANCOVA $F_{4,22} = 10.18$, $P < 0.001$, Figure 3.9). In the riffle, SRP concentrations were homogenous among habitats ($P = 0.605$, Table 3.3, Figure 3.9). Riffle concentrations, however, did vary among sample times, with May and November 2000 being highest ($P < 0.001$, Table 3.3, Figure 3.9). SRP correlated negatively with dissolved oxygen in the hyporheic zone of the riffle ($r_{44} = -0.600$, $P < 0.001$).

Invertebrate abundance in the deeper part of the bar did not differ with distance along the flowpath. At 40 cm, invertebrate abundance increased with distance (ANCOVA $F_{1,22} = 6.78$, $P = 0.016$, coefficient = 0.021, Figure 3.9). Invertebrate abundance did not differ among riffle habitats ($P = 0.431$, Table 3.3, Figure 3.9). A strong Time-Site interaction

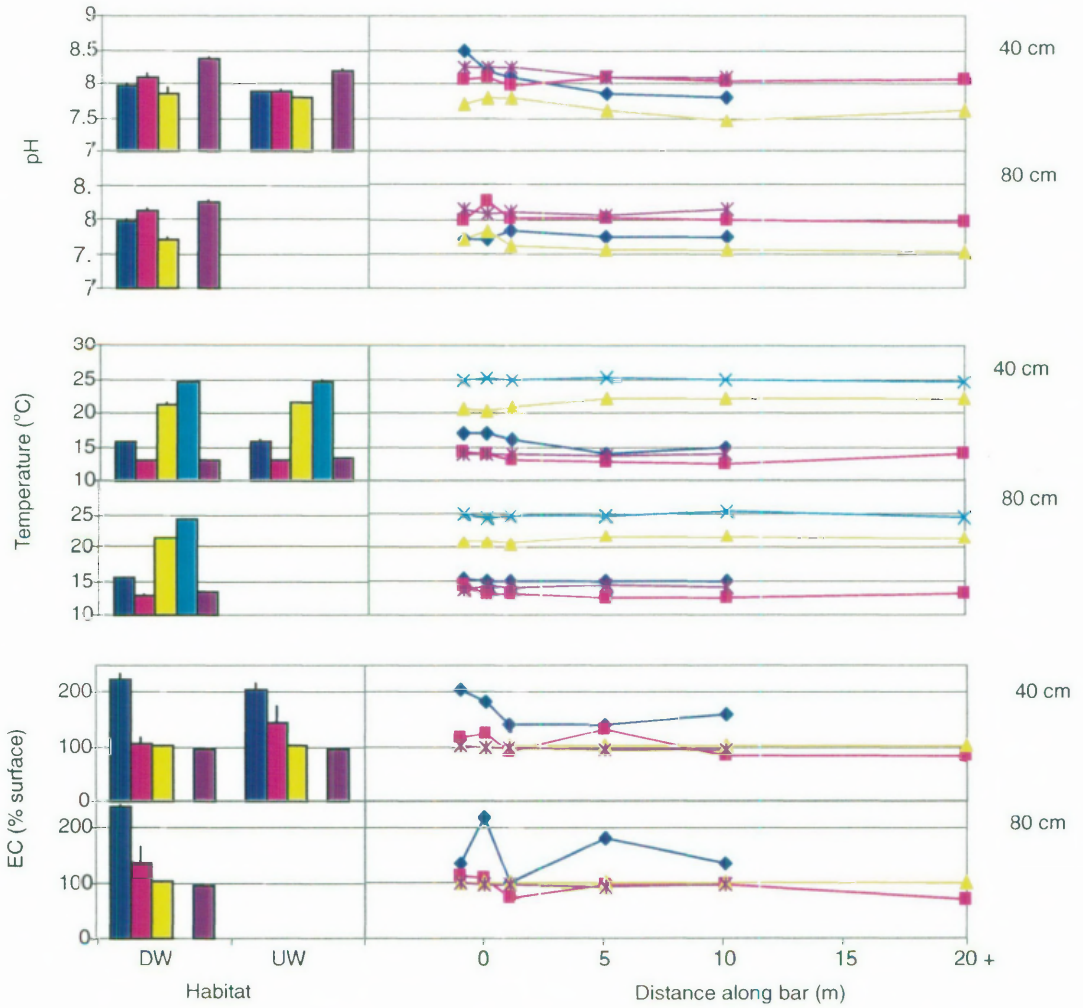
Table 3.3. ANOVA results for Time x Habitat interactions for riffle habitat at Denman. Bold numbers are significant at P = 0.05.

Variable	Source	SS	df	MS	F-Ratio	P
DO						
	T	20049.636	4	5012.409	52.154	**0.000**
	H	1976.788	2	988.394	6.231	**0.023**
	T*H	1268.932	8	158.617	1.650	0.152
	Error	2883.259	30	96.109		
SRP - Log (x+1)						
	T	2.063	4	0.516	25.754	**0.000**
	H	0.030	2	0.015	0.535	0.605
	T*H	0.224	8	0.028	1.401	0.236
	Error	0.601	30	0.020		
NOx - Log (x+1)						
	T	0.988	4	0.247	38.124	**0.000**
	H	0.015	2	0.008	0.589	0.577
	T*H	0.105	8	0.013	2.022	0.078
	Error	0.194	30	0.006		
EC - Log (x+1)						
	T	0.744	3	0.248	52.234	**0.000**
	H	0.003	2	0.001	0.309	0.745
	T*H	0.029	6	0.005	1.019	0.437
	Error	0.114	24	0.005		
pH - squared						
	T	284.906	3	94.969	86.091	**0.000**
	H	23.615	1	23.615	7.117	**0.032**
	T*H	23.226	7	3.318	3.008	**0.020**
	Error	26.475	24	1.103		
Temperature						
	T	802.023	4	200.506	5738.856	**0.000**
	H	0.230	2	0.115	1.460	0.288
	T*H	0.630	8	0.079	2.252	0.055
	Error	0.943	27	0.035		
Invertebrate abundance - Log (x+1)						
	T	3.617	4	0.904	7.795	**0.000**
	H	0.581	2	0.290	0.938	0.431
	T*H	2.478	8	0.310	2.670	**0.024**
	Error	3.480	30	0.116		
Taxonomic richness						
	T	0.783	4	0.196	7.076	**0.000**
	H	0.221	2	0.111	1.787	0.228
	T*H	0.496	8	0.062	2.239	0.053
	Error	0.830	30	0.028		



	Mean DO ± SE (% saturation)	Mean SRP ± SE (mg/L)	Mean NOx ± SE (mg/L)
May-00	159.65 ± 4.10	0.013 ± 0.000	0.057 ± 0.000
Aug-00	103.70 ± 2.40	0.016 ± 0.002	0.122 ± 0.027
Nov-00	88.85 ± 1.25	0.024 ± 0.004	0.067 ± 0.030
Feb-01	89.71 ± 0.121	0.030 ± 0.001	0.228 ± 0.060
May-01	87.25 ± 0.15	0.058 ± 0.004	0.230 ± 0.017

Figure 3.9. Interstitial nitrates (NOx), soluble reactive phosphorus (SRP), invertebrate abundance, taxonomic richness, and measured physico-chemical variables at Denman. Bar graphs on the left are hyporheic data (vertical lines represent standard error), while line bars on the right are parafluvial data. Mean surface measurements are reported in the table below the x-axis.



			Mean pH ± SE	Mean Temp. ± SE (°C)	Mean ± EC (mS)
May 00	May 00	May-00	8.05 ± 0.00	16.0 ± 0.0	0.17 ± 0.01
Aug 00	Aug 00	Aug-00	8.50 ± 0.01	13.8 ± 0.0	0.27 ± 0.06
Nov 00	Nov 00	Nov-00	8.24 ± 0.05	20.7 ± 0.2	0.65 ± 0.01
Feb 01	Feb 01	Feb-01		24.9 ± 0.1	
May 01	May 01	May-01	8.37 ± 0.08	12.6 ± 0.1	0.44 ± 0.01

Figure 3.9. continued

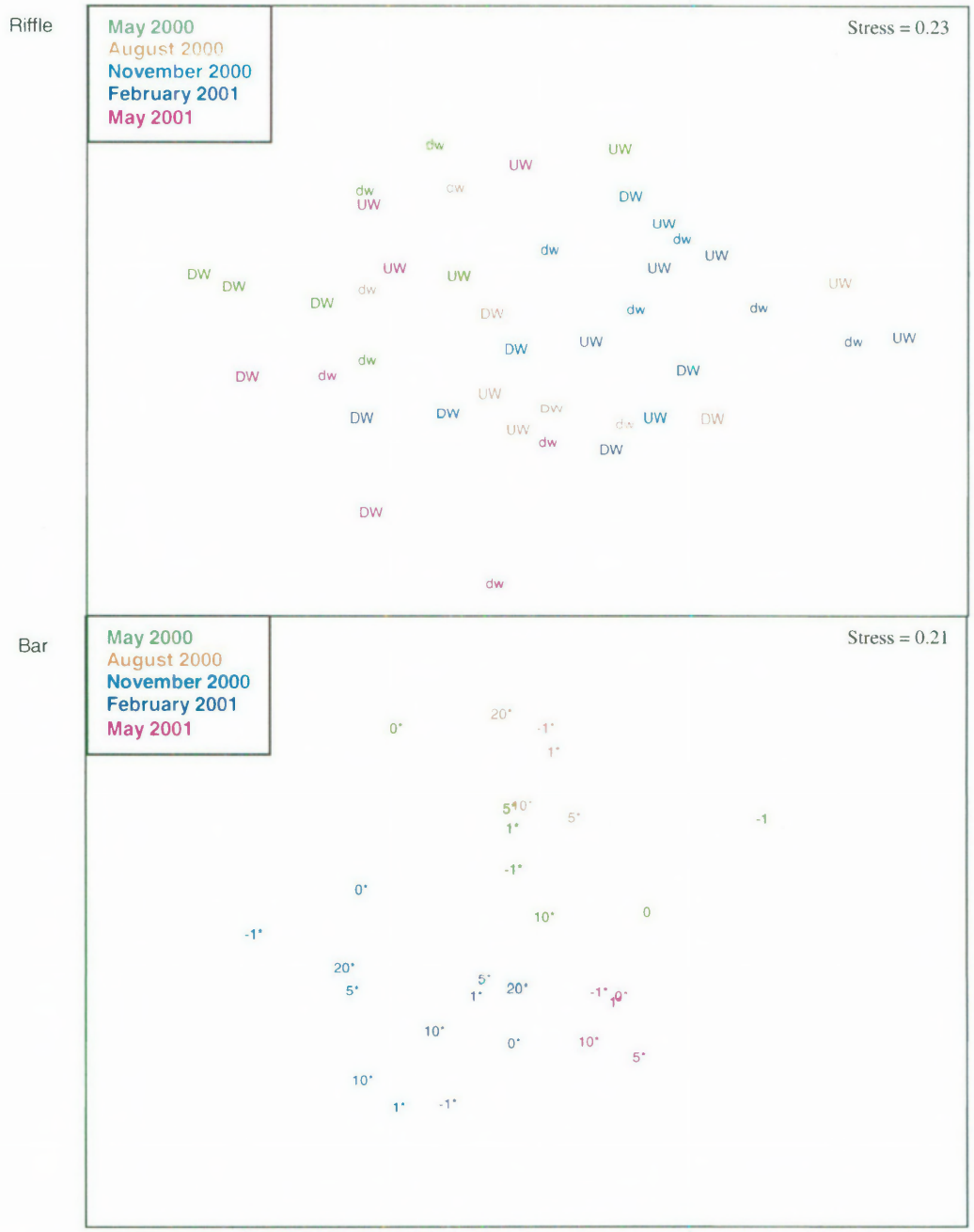


Figure 3.10. Non-metric multi-dimensional scaling diagrams of hyporheic and parafluvial habitats at Denman. Upper-case letters indicate hyporheic samples from 40 cm. Lower-case letters indicate hyporheic samples from 80 cm. DW and dw = downwelling, UW = upwelling. Numerals indicate distance in metres from the leading edge of the bar. Numbers followed by an * were from 80 cm, while those without were from 40 cm.

(P = 0.024, Table 3.3) occurred because of the high abundance at May 2000 in the shallow downwelling habitat (Figure 3.9). Invertebrates in the shallow bar were more numerous in May 2001 than at other times (ANCOVA $F_{4,22} = 5.72$, P = 0.003, Figure 3.9). This was also the case for 80 cm (ANCOVA $F_{4,22} = 6.73$, P = 0.001, Figure 3.9). There was a strong negative correlation between invertebrate abundance and DO for bar samples ($r_{55} = -0.489$, P = 0.008).

Taxonomic richness was highest in the bar during May 2001 (ANCOVA P < 0.001 for both depths, Figure 3.9) and it did not differ with distance from the upstream edge. The number of taxa in the riffle habitats did not differ from each other (P = 0.023, Table 3.3, Figure 3.9). More taxa occurred in the riffle habitats during May 2000 and 2001 than at other times (P < 0.001, Table 3.3, Figure 3.9), yielding an average of 6-14 and 7–10 taxa respectively.

Community assemblages in the riffle habitats varied significantly over time (Global R = 0.642, P < 0.001, Figure 3.10). Oligochaetes dominated the fauna at all Times, comprising between 21 and 88 % of the community. Winter and spring community assemblages were similar to each other (pair-wise R = 0.148, P = 0.194), with their fauna consisting mostly of oligochaetes and cyclopoids. Other common taxa were ostracods (autumn 2000), microturbellarians (summer), and harpacticoids (autumn 2001). Community structure differed among riffle habitats (Global R = 0.398, P < 0.001), with high numbers of oligochaetes and cyclopoids occurring with harpacticoids in the shallow downwelling zone. Oligochaetes and cyclopoids also dominated the deeper downwelling and the upwelling habitats, but they were not as abundant there. Microturbellarians made up a large proportion of the community at deep downwelling habitat, while nematodes contributed significantly to community assemblages of the upwelling zone.

Denman bar communities displayed marked temporal differences (Global R = 0.635, P < 0.001, Figure 3.10). From August 2000 temporal groupings move anticlock-wise in MDS space. Oligochaetes and cyclopoids dominated the fauna in autumn 2000, winter, summer, and autumn 2001. Spatially, community structure did not change with distance along flow path (Global R = 0.074, P = 0.773), and cyclopoids and oligochates dominated the entire length of the bar. Cyclopoids, oligochaetes, and *Heterias* sp. dominated samples from both

depths, but there were more *Heterias* sp. at 40 cm than at 80 cm (average = 13 and 4 animals per sample respectively, Global R = 0.309, P < 0.001)

3.4.4 Bowmans Crossing (BOWM)

The highest and lowest surface dissolved oxygen concentrations occurred in November 2000 and February 2001 respectively and were 85.00 ± 3.50 and 121.75 ± 0.75 % saturation (Figure 3.11). These two times corresponded to the lowest bar DO measurements for 40 cm in the bar (ANCOVA $F_{4,22} = 6.48$, P = 0.001, Figure 3.11). There was no significant difference among Time in the concentration of DO at 80 cm (ANCOVA $F_{4,22} = 1.95$, P = 0.137). DO concentrations decreased as interstitial water moved along the bar (ANCOVA $F_{1,22} = 35.61$, P < 0.001 for 40 cm, and ANCOVA $F_{1,22} = 25.36$, P < 0.001 for 80 cm, Figure 3.11). In the riffle, DO was higher in the shallow downwelling zone, than the deep downwelling and upwelling habitats (P = 0.018, Table 3.4, Figure 3.11). There was a decrease in DO for each time in both downwelling habitats, except for autumn 2001 at 40 cm (P < 0.001, Table 3.4, Figure 3.11). In the upwelling habitat autumn 2000, spring, and autumn 2001 had higher dissolved oxygen than the other seasons (Figure 3.11).

At BOWM, hyporheic pH was higher in the downwelling zone than the upwelling zone (P = 0.026, Table 3.4, Figure 3.11). There was also temporal variation in pH, with averages of over 8 in all riffles during November 2000 (P < 0.001, Table 3.4, Figure 3.11). In the parafluvial zone, pH generally declined with Distance at 40 cm (ANCOVA $F_{1,23} = 4.51$, P = 0.045) and 80 cm (ANCOVA $F_{1,23} = 14.12$, P = 0.001). The pH of the bar was also highest during November 2000 (ANCOVA $F_{4,23} = 5.42$, P = 0.003 for 40 cm; ANCOVA $F_{4,23} = 9.36$, P < 0.001 for 80 cm).

Temperature displayed seasonal trends in the hyporheic zone (P < 0.001, Table 3.4) and parafluvial zone (ANCOVA $F_{4,23} = 190.52$, P < 0.001 for 40 cm; ANCOVA $F_{4,23} = 82.17$, P < 0.001 for 80 cm), with maxima occurring in November 2000. Temperature generally increased along the bar at 40 cm (ANCOVA $F_{1,23} = 190.52$, P < 0.001) and 80 cm (ANCOVA $F_{1,23} = 4.58$, P = 0.043, Figure 3.11).

In the hyporheic zone, EC was high in May 2000, but otherwise remained relatively stable ($P < 0.001$, Table 3.4). EC in the parafluvial zone did not differ with Distance (ANCOVA $F_{1,23} = 0.42$, $P = 0.524$ for 40 cm; ANCOVA $F_{1,23} = 0.08$, $P = 0.783$ for 80 cm) or Time (ANCOVA $F_{4,23} = 0.94$, $P = 0.459$ for 40 cm, ANCOVA $F_{4,23} = 1.55$, $P = 0.220$ for 80 cm).

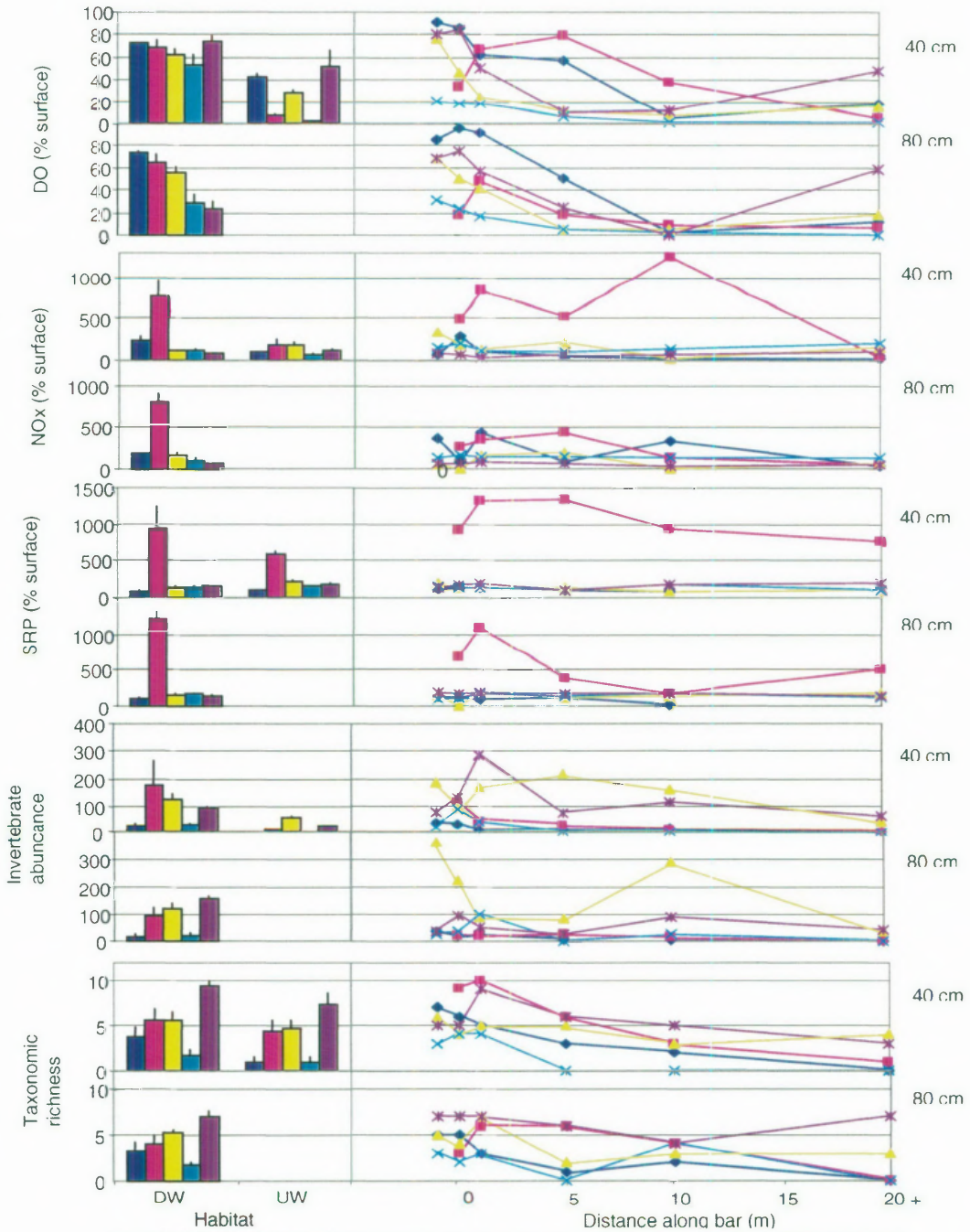
Surface concentrations of NOx ranged from 0.027 ± 0.013 mg/L in August 2000, to 0.144 ± 0.018 mg/L in February (Figure 3.11). August had the highest hyporheic NOx concentrations in the riffle ($P < 0.001$, Table 3.4, Figure 3.11) and in the bar (ANCOVA $F_{4,22} = 3.42$, $P = 0.026$ for 40 cm, and ANCOVA $F_{4,23} = 3.87$, $P = 0.015$ for 80 cm). NOx concentration in the bar decreased with Distance at 40 cm (ANCOVA $F_{1,22} = 6.05$, $P = 0.022$) and 80 cm (ANCOVA $F_{1,23} = 4.34$, $P = 0.049$). All three riffle habitats did not differ ($P = 0.328$, Table 3.4). NOx correlated with DO in the riffle ($r_{44} = 0.453$, $P = 0.018$) but not in the bar.

Mean SRP in surface waters at BOWM was lowest in August 2000 (0.008 ± 0.001 mg/L) and highest in May 2000 (0.066 ± 0.005 mg/L, Figure 3.11). As with NOx, interstitial SRP concentrations were higher in winter than the other times for the riffle ($P < 0.001$, Table 3.4, Figure 3.11), and the bar (ANCOVA $F_{4,23} = 9.03$, $P < 0.001$ for 40 cm, and ANCOVA $F_{4,23} = 9.57$, $P < 0.001$ for 80 cm). There were no differences in SRP among hyporheic habitats in the riffle ($P = 0.395$, Table 3.4, Figure 3.11), nor was there any difference in concentration along the bar at either depth (ANCOVA $F_{1,23} = 3.77$, $P = 0.065$ for 40 cm, and ANCOVA $F_{4,23} = 1.31$, $P = 0.264$ for 80 cm).

Invertebrate abundance in the bar was highest during November 2000 (ANCOVA $F_{4,23} = 11.78$, $P < 0.001$ for 40 cm, and ANCOVA $F_{4,23} = 7.57$, $P < 0.001$ for 80 cm, Figure 3.11). Riffle habitats contained more invertebrates during autumn 2000, winter, and autumn 2001 ($P < 0.001$, Table 3.4, Figure 3.11). Invertebrates were more numerous in the shallow and deep downwelling, than in the upwelling habitat of the riffle ($P < 0.001$, Table 3.4, Figure 3.11). Faunal numbers declined along the bar at 40 cm (ANCOVA $F_{1,23} = 25.70$, $P < 0.001$) and 80 cm (ANCOVA $F_{1,23} = 19.18$, $P < 0.001$, Figure 3.11). A correlation existed between invertebrate abundance and DO in the bar ($r_{57} = 0.525$, $P = 0.005$) and the riffle ($r_{44} = 0.391$, $P = 0.008$).

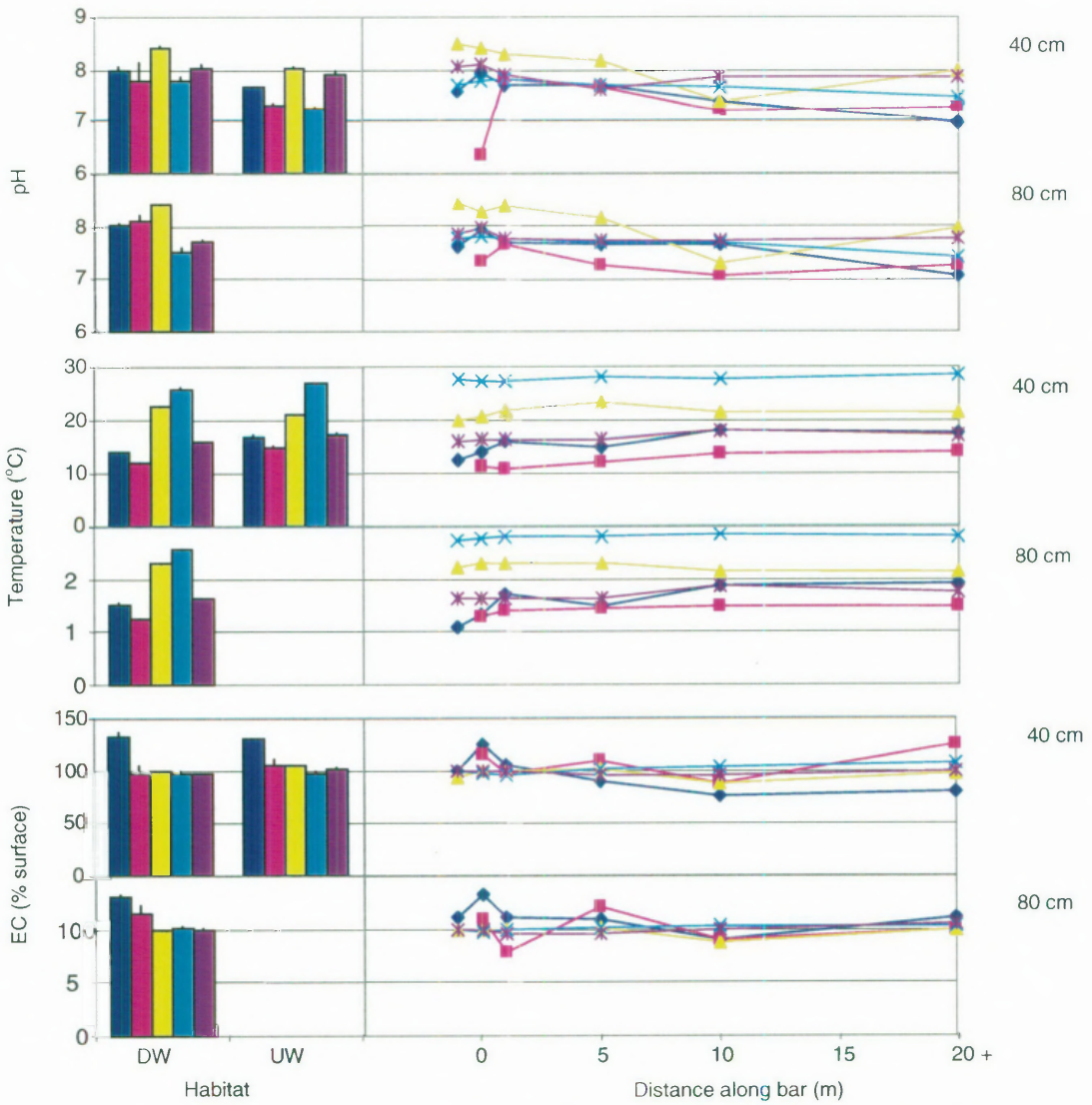
Table 3.4. ANOVA results for Time x Habitat interactions for riffle habitat at Bowmans Crossing. Bold numbers are significant at P = 0.05.

Variable	Source	SS	df	MS	F-Ratio	P
DO						
	T	5676.81	4	1419.205	11.970	**0.000**
	H	11727.000	2	5863.542	6.995	**0.018**
	T*H	6706.393	8	838.299	7.070	**0.000**
	Error	3557.021	30	118.567		
SRP - Log (x+1)						
	T	4.823	4	1.206	84.281	**0.000**
	H	0.059	2	0.030	1.045	0.395
	T*H	0.226	8	0.028	1.974	0.085
	Error	0.429	30	0.014		
NOx - Log (x+1)						
	T	3.021	4	0.755	26.495	**0.000**
	H	0.368	2	0.184	1.286	0.328
	T*H	1.144	8	0.143	5.018	**0.001**
	Error	0.855	30	0.029		
EC - Log (x+1)						
	T	0.092	4	0.023	30.760	**0.000**
	H	0.003	2	0.001	1.697	0.243
	T*H	0.007	8	0.001	1.158	0.356
	Error	0.022	30	0.001		
pH - squared						
	T	674.318	4	168.580	20.115	**0.000**
	H	291.872	2	145.936	5.966	**0.026**
	T*H	195.677	8	24.460	2.919	**0.016**
	Error	251.419	30	8.381		
Temperature						
	T	1031.424	4	257.856	1365.121	**0.000**
	H	13.803	2	6.902	2.145	0.180
	T*H	25.744	8	3.218	17.036	**0.000**
	Error	5.667	30	0.189		
Invertebrate abundance - Log (x+1)						
	T	8.949	4	2.237	35.456	**0.000**
	H	6.450	2	3.225	23.748	**0.000**
	T*H	1.086	8	0.136	2.152	0.061
	Error	1.893	30	0.063		
Taxonomic richness						
	T	221.911	4	55.478	24.718	**0.000**
	H	17.911	2	8.956	6.272	**0.023**
	T*H	11.422	8	1.428	0.636	0.741
	Error	67.333	30	2.244		



	Mean DO ± SE (% saturation)	Mean SRP ± SE (mg/L)	Mean NOx ± SE (mg/L)
May-00	111.74 ± 14.56	0.066 ± 0.005	0.107 ± 0.015
Aug-00	88.10 ± 2.10	0.008 ± 0.001	0.027 ± 0.013
Nov-00	85.00 ± 3.50	0.022 ± 0.002	0.036 ± 0.000
Feb-01	121.75 ± 0.75	0.023 ± 0.001	0.144 ± 0.018
May-01	93.85 ± 1.15	0.028 ± 0.005	0.088 ± 0.005

Figure 3.11. Interstitial nitrates (NOx), soluble reactive phosphorus (SRP), invertebrate abundance, taxonomic richness, and measured physico-chemical variables at Bowmans Crossing Bar graphs on the left are hyporheic data (vertical lines represent standard error), while line bars on the right are parafluvial data. Mean surface measurements are reported in the table below the x-axis.



	Mean pH ± SE	Mean Temp. ± SE (°C)	Mean ± EC (mS)
May-00	8.67 ± 0.02	17.7 ± 1.5	0.43 ± 0.03
Aug-00	8.30 ± 0.05	12.0 ± 1.0	0.47 ± 0.12
Nov-00	8.55 ± 0.06	21.4 ± 0.1	0.86 ± 0.00
Feb-01	8.18 ± 0.70	26.8 ± 0.0	0.81 ± 0.75
May-01	8.35 ± 0.00	16.6 ± 0.1	0.40 ± 0.00

Figure 3.11. continued

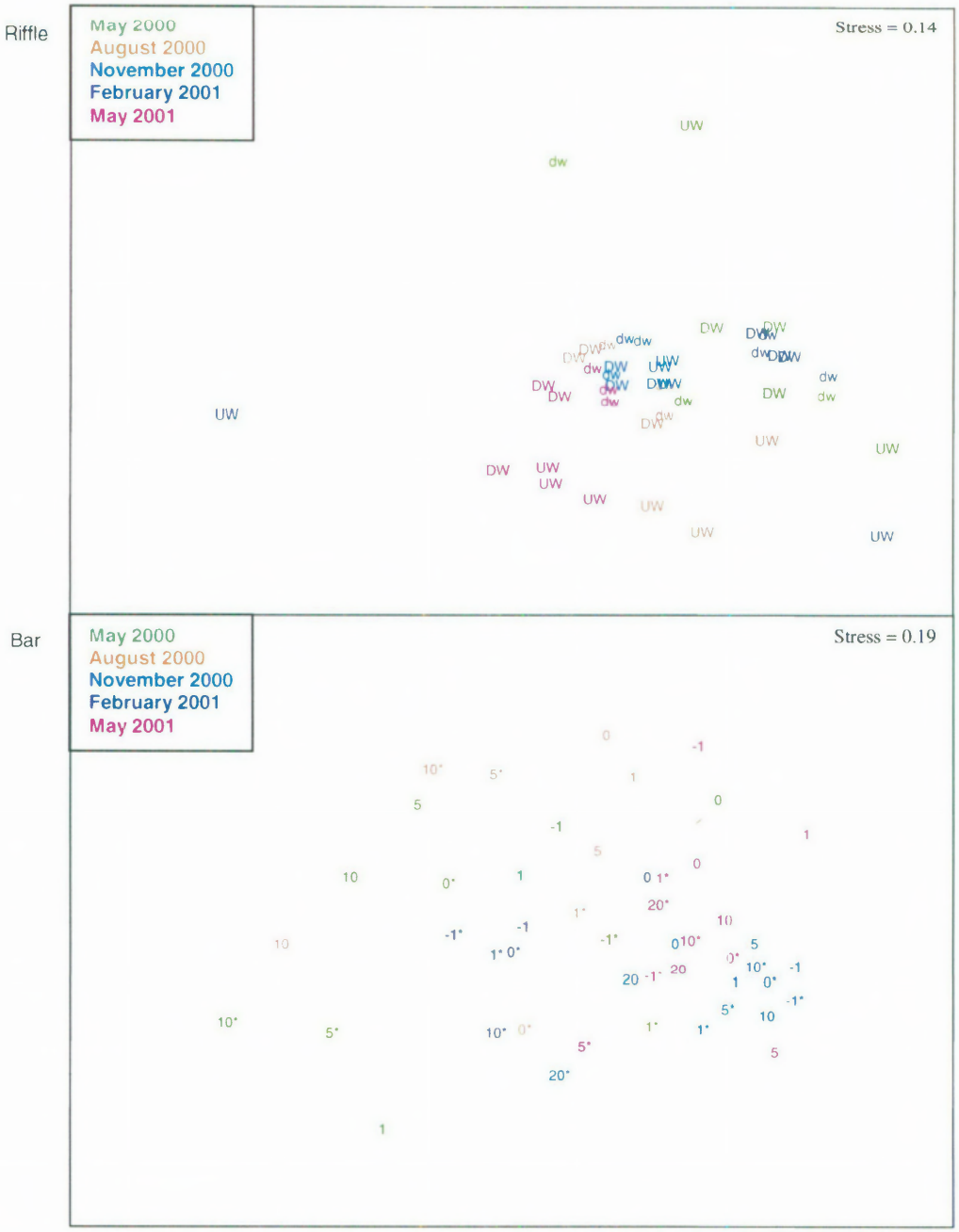


Figure 3.12. Non-metric multi-dimensional scaling diagrams of hyporheic and parafluvial habitats at Bowmans Crossing. Upper-case letters indicate hyporheic samples from 40 cm. Lower-case letters indicate hyporheic samples from 80 cm. DW and dw = downwelling, UW = upwelling. Numerals indicate distance in metres from the leading edge of the bar. Numbers followed by an * were from 80 cm, while those without were from 40 cm.

There were more taxa at the head of the bar than at its tail, both at 40 cm (ANCOVA $F_{1,23}$ = 31.31, P < 0.001) and 80 cm depths (ANCOVA $F_{1,23}$ = 11.94, P = 0.002, Table 3.4). Likewise, taxonomic richness was higher in the downwelling habitats than the upwelling zone (P = 0.023, Table 3.4). Spring and autumn had the richest fauna in the bar (ANCOVA $F_{4,23}$ = 6.19, P = 0.001 for 40 cm, and ANCOVA $F_{4,23}$ = 6.91, P < 0.001 for 80 cm, Table 3.10). Taxonomic richness in all riffle habitats increased with each season, with the exception of summer (P < 0.001, Table 3.4, Figure 3.11).

Hyporheic community assemblages differed with Time (Global R = 0.657, P < 0.001, Figure 3.12). Oligochaetes and cyclopoids dominated autumn 2000, while the harpacticoid family Parastenocarididae, and oligochaetes were most common in winter, spring, and autumn 2001. During summer, oligochaetes were the most common invertebrates. Differences were also present among riffle zone-depth habitats (Global R = 0.416, P < 0.001) with both downwelling habitats being similar to each other (pairwise P = 0.266) but different to the upwelling habitat (pairwise P < 0.001). Downwelling habitat communities were characterised by high numbers of parastenocarids and harpacticoids (more than 35 of each taxa per sample), while the upwelling zone was dominated by lower numbers (< 10) of these taxa.

Parafluvial community composition differed with Time (Global R = 0.508, P < 0.001, Figure 3.12). May and August 2000, and February 2001 had similar communities (pairwise P = 0.568), with two dominant taxa – oligochaetes and microturbellarians. For both other times oligochaetes and parastenocarids were more common. Communities along the bar remained similar to each other with distance (Global R = 0.171, P = 0.054) and were dominated by oligochaetes, microturbellarians, and parastenocarids. These three taxa were common at both depths, which were similar (Global R = 0.055, P = 0.182).

3.4.5 Downstream of Macquarie Generation (DSMG)

DO in the surface water at DSMG was 96.50 ± 0.49, 126.00 ± 4.00, and 84.80 ± 0.50 % saturation for May 2000, November 2000, and February 2001 respectively (Figure 3.13). In the bar, DO showed noticeable trends with both Time and Distance (Figure 3.13). At 40 cm, DO was lower for each consecutive sampling period (ANCOVA $F_{2,14}$ = 12.66, P < 0.001) and decreased along the flowpath (ANCOVA $F_{1,14}$ = 12.06, P = 0.004). Similar

patterns were apparent in the bar sediments at 80 cm (ANCOVA $F_{2,14} = 19.37$, $P < 0.001$, and ANCOVA $F_{1,14} = 11.37$, $P = 0.005$). At both downwelling depths, DO concentrations did not differ (Figure 3.13), but decreased with time ($P < 0.001$, Table 3.5). The difference between downwelling and upwelling habitats (Figure 3.13) may not have been detected by the ANOVA model used in the analysis ($P = 0.054$, Table 3.5) because of the similarity of the downwelling habitats.

Hyporheic pH was higher during November 2000 than at any other Time ($P < 0.001$, Table 3.5, Figure 3.13) and was highest in the downwelling zone ($P = 0.046$, Table 3.5, Figure 3.13). Parafluvial pH did not differ significantly with Time for both Depths, but did decrease along the flowpath at 80 cm (ANCOVA $F_{1,14} = 11.42$, $P = 0.005$).

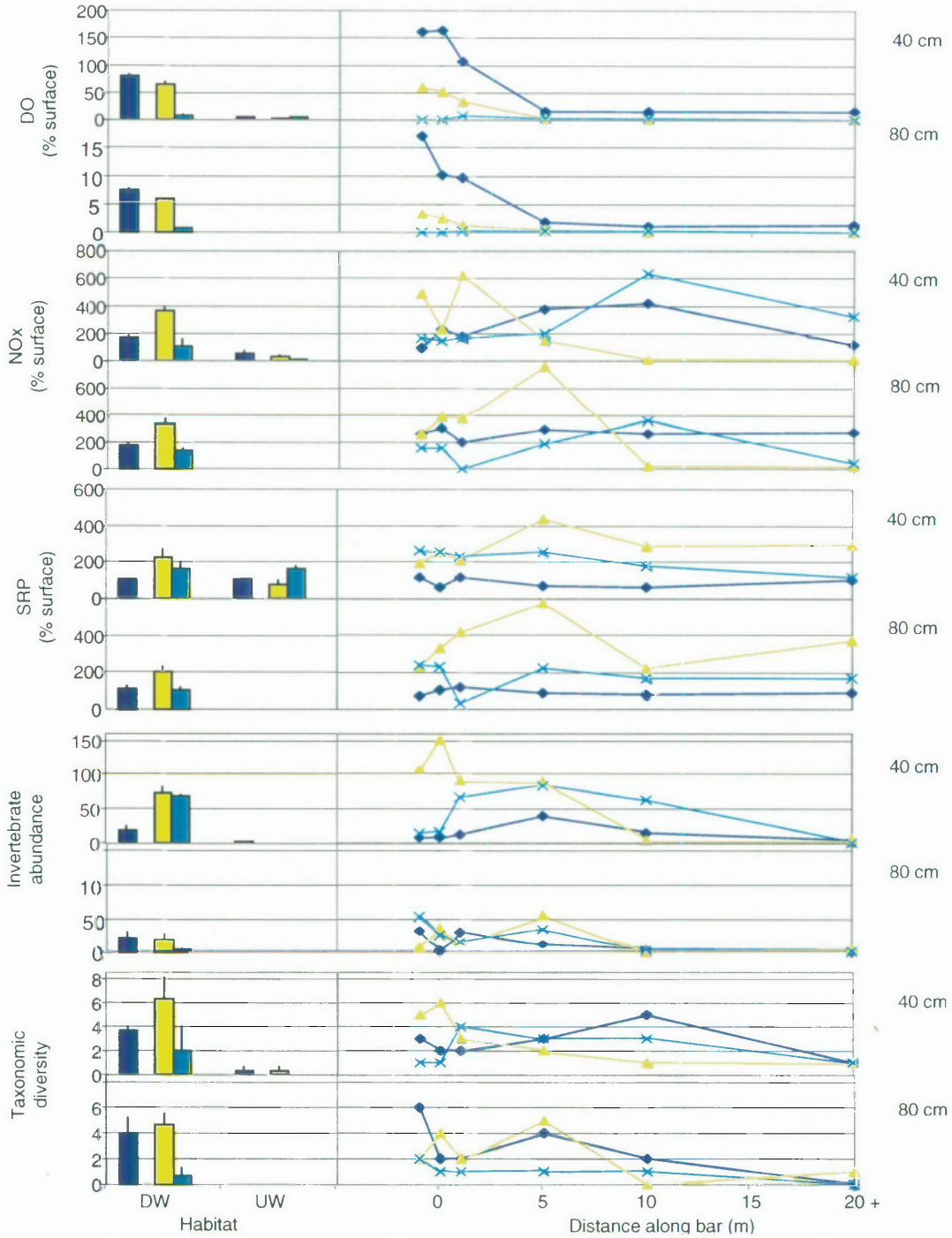
Interstitial temperature did not change significantly with distance along the bar, but did display a seasonal pattern, being highest in February 2001 (ANCOVA $F_{2,14} = 87.97$, $P < 0.001$ for 40 cm; ANCOVA $F_{2,14} = 9.59$, $P = 0.002$ for 80 cm). Seasonal trends in temperature were also evident in the riffle ($P < 0.001$, Table 3.5, Figure 3.13). Hyporheic temperature increased from downwelling to upwelling in May 2000 and February 2001 ($P= 0.001$, Table 3.5, Figure 3.13).

In May and November, EC was more than 100 % surface (Figure 3.13). Parafluvial EC showed no spatial patterns, but decreased with Time from May 2000 to February 2001 (ANCOVA $F_{1,14} = 1.15$, $P = 0.302$ for 40 cm; ANCOVA $F_{1,14} = 0.01$, $P = 0.917$ for 80 cm). EC in the riffle increased from downwelling to upwelling ($P = 0.021$, Table 3.5) and was higher in May and November than in February ($P < 0.001$, Table 3.5, Figure 3.13).

Surface NOx concentrations ranged from 0.020 ± 0.006 to 0.348 ± 0.010 mg/L throughout the study (Figure 3.13). November 2000 had the highest NOx concentrations in the riffle habitat ($P < 0.001$, Table 3.5, Figure 3.13). Downwelling riffle habitats had higher NOx concentrations than the upwelling habitat ($P = 0.05$, Table 3.5, Figure 3.13). At 40 cm, NOx concentrations did not differ with distance (ANCOVA $F_{1,14} = 0.22$, $P = 0.647$) or time (ANCOVA $F_{2,14} = 0.05$, $P = 0.949$). NOx at 80 cm in the parafluvial zone did not change along the flowpath (ANCOVA $F_{1,14} = 1.18$, $P = 0.296$), or with time (ANCOVA

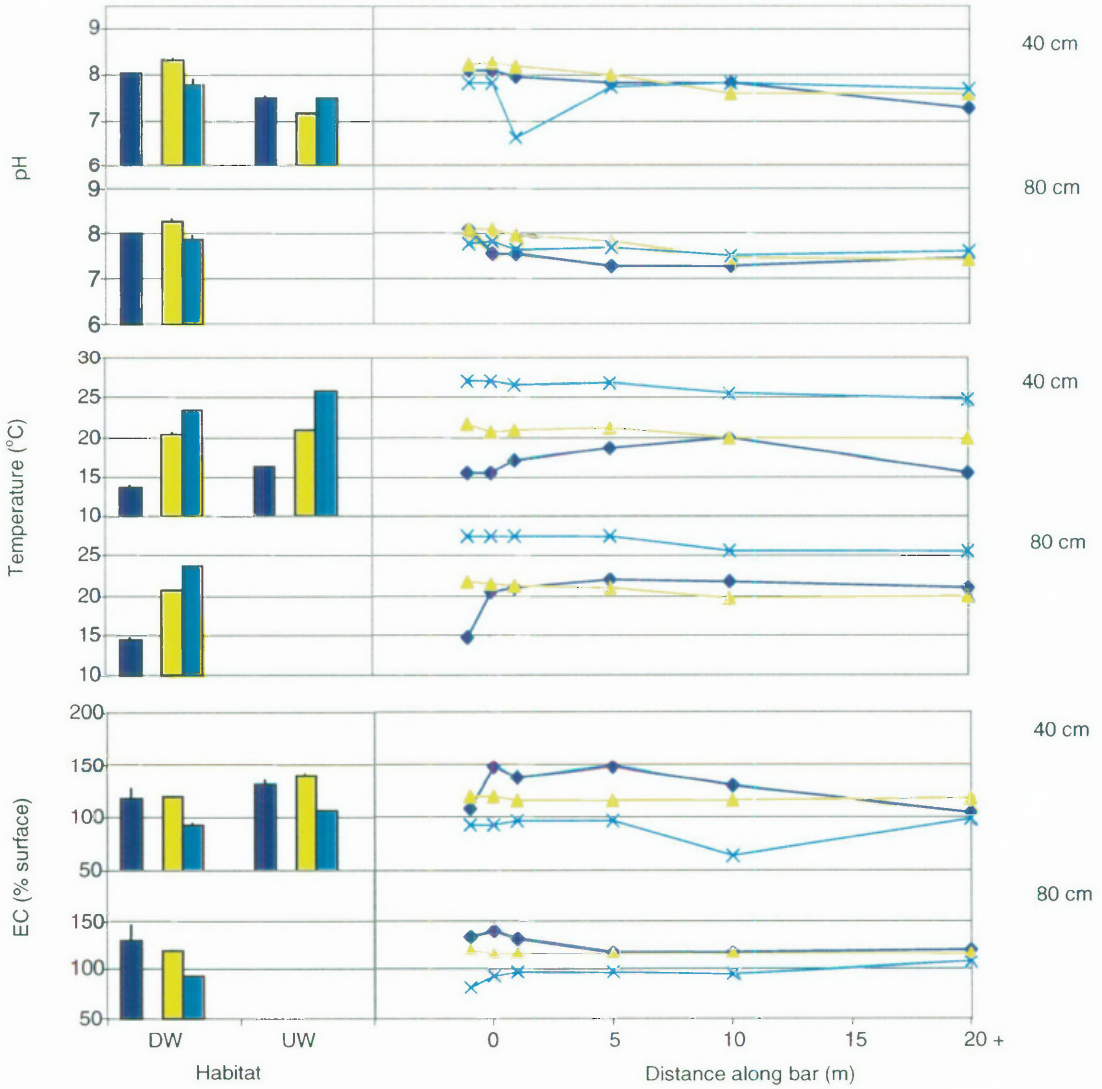
Table 3.5. ANOVA results for Time x Habitat interactions for riffle habitat at Downstream of Macquarie Generation. Bold numbers are significant at P = 0.05

Variable	Source	SS	df	MS	F-Ratio	P
DO - Log (x+1)						
	T	2.205	2	1.102	157.573	**0.000**
	H	4.708	2	2.354	6.590	0.054
	T*H	1.429	4	0.357	51.063	**0.000**
	Error	0.126	18	0.007		
SRP - Log (x+1)						
	T	0.075	2	0.037	2.754	0.091
	H	0.113	2	0.057	0.583	0.599
	T*H	0.388	4	0.097	7.135	**0.001**
	Error	0.245	18	0.014		
NOx - Log (x+1)						
	T	119251.814	2	59625.907	34.080	**0.000**
	H	197669.356	2	98834.678	6.926	0.050
	T*H	57084.488	4	14271.220	8.157	**0.001**
	Error	31492.270	18	1749.571		
EC - Log (x+1)						
	T	0.057	2	0.029	14.165	**0.000**
	H	0.014	2	0.007	11.780	**0.021**
	T*H	0.002	4	0.001	0.304	0.871
	Error	0.030	15	0.002		
pH - squared						
	T	48.227	2	24.113	17.461	**0.000**
	H	543.247	2	271.624	7.311	**0.046**
	T*H	148.615	4	37.154	26.903	**0.000**
	Error	20.715	15	1.381		
Temperature						
	T	353.067	2	176.533	1336.249	**0.000**
	H	13.110	2	6.555	5.869	0.065
	T*H	4.468	4	1.117	8.455	**0.001**
	Error	1.982	15	0.132		
Invertebrate abundance - Log (x+1)						
	T	0.830	2	0.415	1.522	0.245
	H	8.711	2	4.256	15.746	**0.013**
	T*H	1.106	4	0.277	1.014	0.426
	Error	4.910	18	0.273		
Taxonomic richness						
	T	26.963	2	13.481	4.550	**0.025**
	H	81.407	2	40.704	10.990	**0.024**
	T*H	14.815	4	3.704	1.250	0.326
	Error	53.333	18	2.963		



	Mean DO ± SE (% saturation)	Mean SRP ± SE (mg/L	Mean NOx ± SE (mg/L)
May-00	96.50 ± 0.49	0.064 ± 0.000	0.094 ± 0.026
Nov-00	126.00 ± 4.00	0.023 ± 0.001	0.020 ± 0.006
Feb-01	84.80 ± 0.50	0.047 ± 0.000	0.348 ± 0.010

Figure 3.13. Interstitial nitrates (NOx), soluble reactive phosphorus (SRP), invertebrate abundance, taxonomic richness, and measured physico-chemical variables Downstream of Macquarie Generation. Bar graphs on the left are hyporheic data (vertical lines represent standard error), while line bars on the right are parafluvial data. Mean surface measurements are reported in the table below the x-axis.



	Mean pH ± SE	Mean Temp. ± SE (°C)	Mean ± EC (mS)
May-00	8.16 ± 0.01	14.0 ± 0.0	0.38 ± 0.06
Nov-00	8.46 ± 0.06	23.4 ± 0.4	0.77 ± 0.16
Feb-01	7.72 ± 0.05	22.9 ± 0.0	0.81 ± 0.50

Figure 3.13. continued

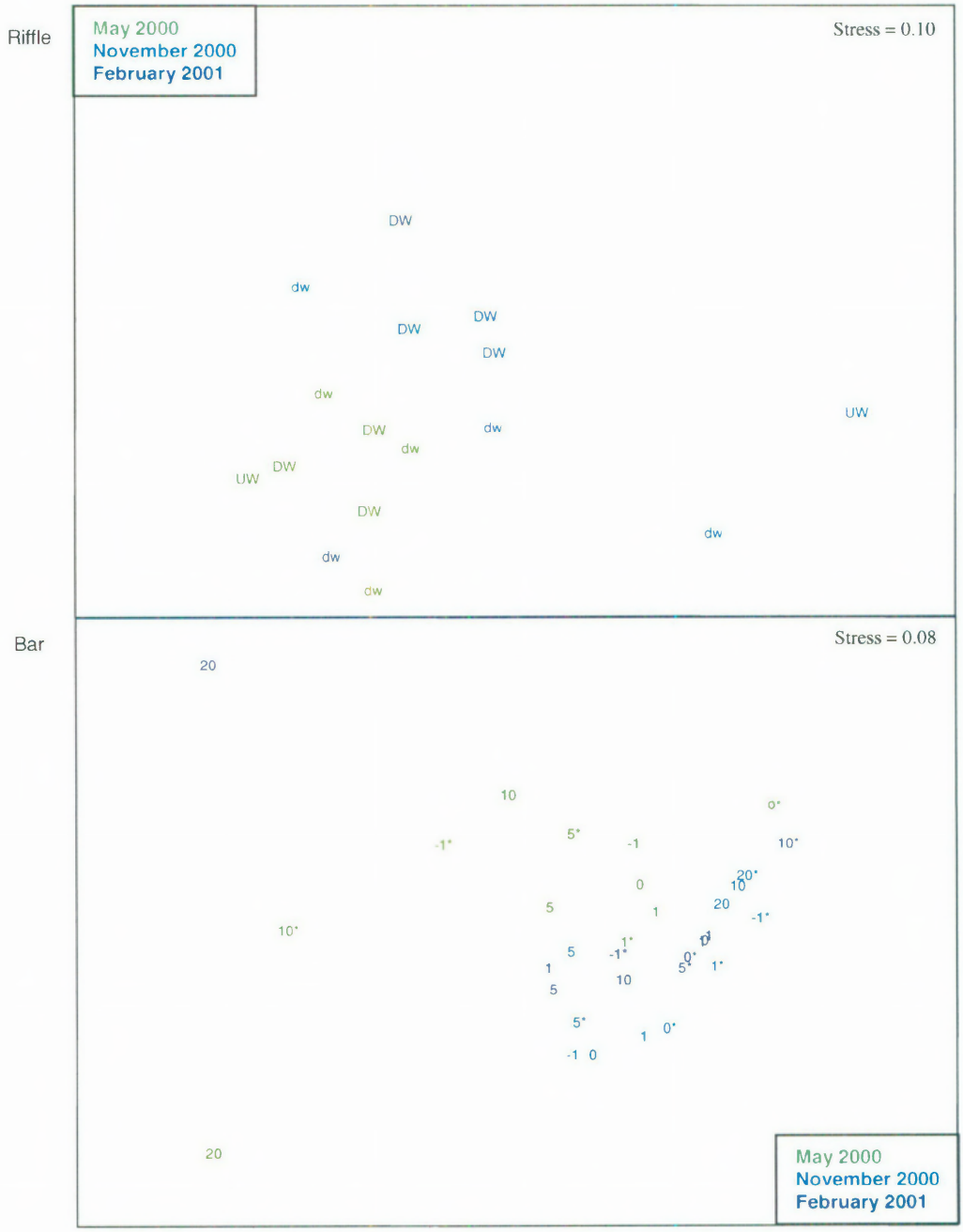


Figure 3.14. Non-metric multi-dimensional scaling diagrams of hyporheic and parafluvial habitats at Downstream of Macquarie Generation. Upper-case letters indicate hyporheic samples from 40 cm. Lower-case letters indicate hyporheic samples from 80 cm. DW and dw = downwelling, UW = upwelling. Numerals indicate distance in metres from the leading edge of the bar. Numbers followed by an * were from 80 cm, while those without were from 40 cm.

$F_{2,14} = 1.22$, $P = 0.325$). In the bar, NOx corresponded negatively with DO ($r_{35} = -0.333$, $P = 0.047$), while in the riffle, the correlation was positive ($r_{26} = 0.712$, $P < 0.001$).

In the main stream at DSMG, SRP concentration ranged between 0.023 ± 0.001 and 0.064 ± 0.000 mg/L (Figure 3.13). Concentrations were highest in the bar at 40 cm (ANCOVA $F_{2,14} = 14.70$, $P < 0.001$) and at 80 cm (ANCOVA $F_{2,14} = 13.52$, $P < 0.001$) during November 2000 (Figure 3.13). In the riffle there was no temporal variation in SRP ($P = 0.091$, Table 3.5, Figure 3.13). SRP concentrations did not vary significantly along the bar at 40 cm (ANCOVA $F_{1,14} = 0.32$, $P = 0.581$) or 80 cm (ANCOVA $F_{1,14} = 0.01$, $P = 0.926$, Figure 3.13). Among habitats in the riffle, SRP remained homogenous ($P = 0.599$, Table 3.5, Figure 3.13). There was a negative correlation between SRP and DO in the bar ($r_{35} = -0.551$, $P = 0.0178$).

Invertebrate abundance did not vary with Time in the riffle ($P = 0.245$, Table 3.5) but was higher in the shallow downwelling habitat than in the other areas ($P = 0.013$, Table 3.5, Figure 3.13). Invertebrates became less numerous with distance along the bar at 40 cm (ANCOVA $F_{1,14} = 11.37$, $P = 0.005$) and at 80 cm (ANCOVA $F_{1,14} = 17.62$, $P < 0.001$, Figure 3.13). The number of invertebrates correlated with DO concentration in the riffle ($r_{26} = 0.691$, $P < 0.001$).

A similar number of taxa was present in the bar for the three times that DSMG was sampled (ANCOVA $F_{2,14} = 0.38$, $P = 0.688$ for 40 cm , and ANCOVA $F_{2,14} = 2.34$, $P = 0.133$). However, in the riffle there were more taxa in May and November 2000, than in February 2001 ($P = 0.025$, Table 3.5, Figure 3.13). The downwelling zone had more taxa than the upwelling zone ($P = 0.024$, Table 3.5, Figure 3.13). There was no difference in diversity along the bar at 40 cm (ANCOVA $F_{1,14} = 4.04$, $P = 0.064$), but at 80 cm the number of taxa declined with distance (ANCOVA $F_{1,14} = 13.46$, $P = 0.003$, Figure 3.13). The number of taxa correlated with DO in the bar ($r_{35} = 0.5347$, $P = 0.022$) and riffle ($r_{26} = 0.753$, $P < 0.001$).

Many of the samples collected from the riffle habitats contained no invertebrates, so were excluded from multivariate analysis. Only two samples each from the upwelling habitat and from summer actually contained any invertebrates. Therefore, the only solid

conclusion that can be drawn here is that the fauna was fairly depauperate. Nevertheless, multivariate comparisons were made, though often with only 4900 permutations, and the results in regard to these two variables were interpreted with caution. The riffle community at DSMG did differ among season (Global R = 0.567, P = 0.006, Figure 3.14), with low numbers of oligochaetes and microturbellarians making up the fauna in autumn 2000 and spring, and high numbers of these taxa occurring during summer. There was no difference among habitats in the riffle (Global R = 0.067, P = 0.36). Downwelling zones were dominated by oligochaetes, cyclopoids, and microturbellarians. Upwelling habitats contained only oligochaetes and low numbers of ostracods.

Bar community composition differed with time (Global R = 0.213, P = 0.029, Figure 3.14) with oligochaetes and microturbellarians dominating in May, and oligochaetes alone dominating in November and February. Invertebrate assemblage changed along the bar (Global R = .0213. P = 0.044) from one dominated by oligochaetes to one where microturbellarians and oligochaetes were common. Oligochaetes dominated both depths (Global R = -0.045, P = 0.721).

3.4.6 Moses Crossing (MOSE)

Surface DO ranged from 84.75 ± 2.15 to 114.63 ± 11.27 % saturation at MOSE during this study (Figure 3.15). DO decreased along the bar at 40 cm (ANCOVA $F_{1,22} = 21.55$, $P < 0.001$, Figure 3.15) and 80 cm (ANCOVA $F_{1,20} = 22.58$, $P < 0.001$, Figure 3.15). Both depths also displayed temporal variation (ANCOVA $F_{4,22} = 8.31$, $P < 0.001$ for 40 cm and $F_{4,20} = 11.73$, $P < 0.001$ for 80 cm) with November having lowest DO. In the riffle there were no differences between habitats (P = 0.133, Table 3.6). Changes in DO occurred with each Time, where concentration was highest in August, then both Mays, November, and February ($P < 0.001$, Figure 3.15).

Riffle pH decreased from downwelling to upwelling (P = 0.026, Table 3.6), and was highest during November ($P < 0.001$, Table 3.6, Figure 3.15). In the bar, pH generally decreased with distance at 40 cm (ANCOVA $F_{1,22} = 18.97$, $P < 0.001$) and 80 cm (ANCOVA $F_{1,20} = 7.32$, P = 0.014, Figure 3.15) but displayed no significant temporal variation.

Hyporheic temperatures followed seasonal trends, ranging from 13 °C in August 2000 to 26 °C in February 2001 ($P < 0.001$, Table 3.6). Temperature in the parafluvial zone at both 40 cm (ANCOVA $F_{4,22} = 222.75$, $P < 0.001$) and 80 cm (ANCOVA $F_{4,20} = 1356.08$, $P < 0.001$) also varied seasonally as would be expected (Figure 3.15). At 80 cm in the bar, EC increased with Distance (ANCOVA $F_{4,20} = 5.26$, $P = 0.033$).

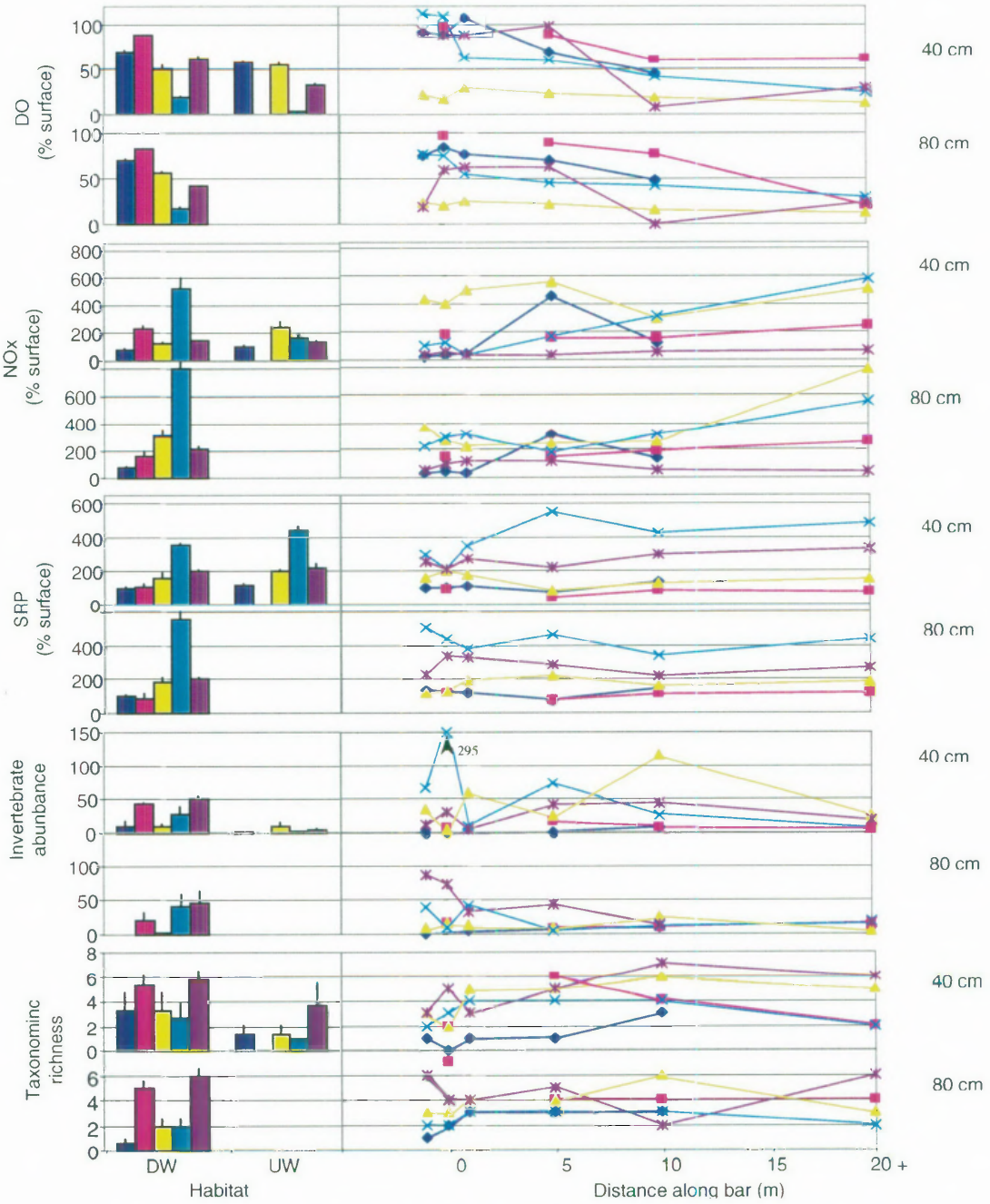
During August, hyporheic EC was 46 % that of the surface in the downwelling zone, while at other times it was between 85 % and 120 % ($P < 0.001$, Table 3.6, Figure 3.15). Similar temporal differences were also evident in the bar at 40 cm (ANCOVA $F_{4,22} = 46.51$, $P < 0.001$) and 80 cm (ANCOVA $F_{4,20} = 45.84$, $P < 0.001$).

NOx concentration in the surface water was between 0.020 ± 0.008 and 0.122 ± 0.004 mg/L for the times sampled (Figure 3.15). In the riffle, NOx concentrations changed with Time at each Habitat ($P < 0.001$, Table 3.6, Figure 3.15). In February, NOx concentration in the deep downwelling zone was 8 times higher than the surface. There was no difference in NOx among the riffle habitats ($P = 0.503$, Table 3.6). NOx concentrations increased with distance along the bar at 40 cm (ANCOVA $F_{1,22} = 8.09$, $P = 0.009$) and 80 cm (ANCOVA $F_{1,20} = 4.62$, $P = 0.044$, Figure 3.15). November and February had the highest NOx concentrations for both depths in the bar (ANCOVA $F_{4,22} = 10.93$, $P < 0.001$ for 40 cm, $F_{4,22} = 8.45$, $P < 0.001$).

In-stream SRP concentration was 0.010 ± 0.001 mg/L in February 2001 and 0.076 ± 0.000 mg/L in May 2000 (Figure 3.15). In February, the maximum SRP concentration was 558 % of the surface concentration in the deep downwelling site, while in the bar the maximum SRP for this time was 545 %. Strong temporal trends existed for SRP in the bar at 40 cm (ANCOVA $F_{4,22} = 29.73$, $P < 0.001$) and 80 cm (ANCOVA $F_{4,20} = 38.51$, $P < 0.001$), but concentrations were not significantly different throughout the length of the bar (ANCOVA $F_{1,22} = 2.81$, $P = 0.108$ for 40 cm, and $F_{1,20} = 0.00$, $P = 0.968$ for 80 cm). The high SRP in February was probably responsible for the difference among seasons at the riffle ($P < 0.001$, Table 3.6). There was no difference between SRP concentrations in the downwelling and upwelling habitats ($P = 0.881$, Table 3.6, Figure 3.15). SRP corresponded negatively with DO in the bar ($r_{54} = -0.0207$, $P < 0.001$), and in the riffle ($r_{43} = -0.793$, $P < 0.001$).

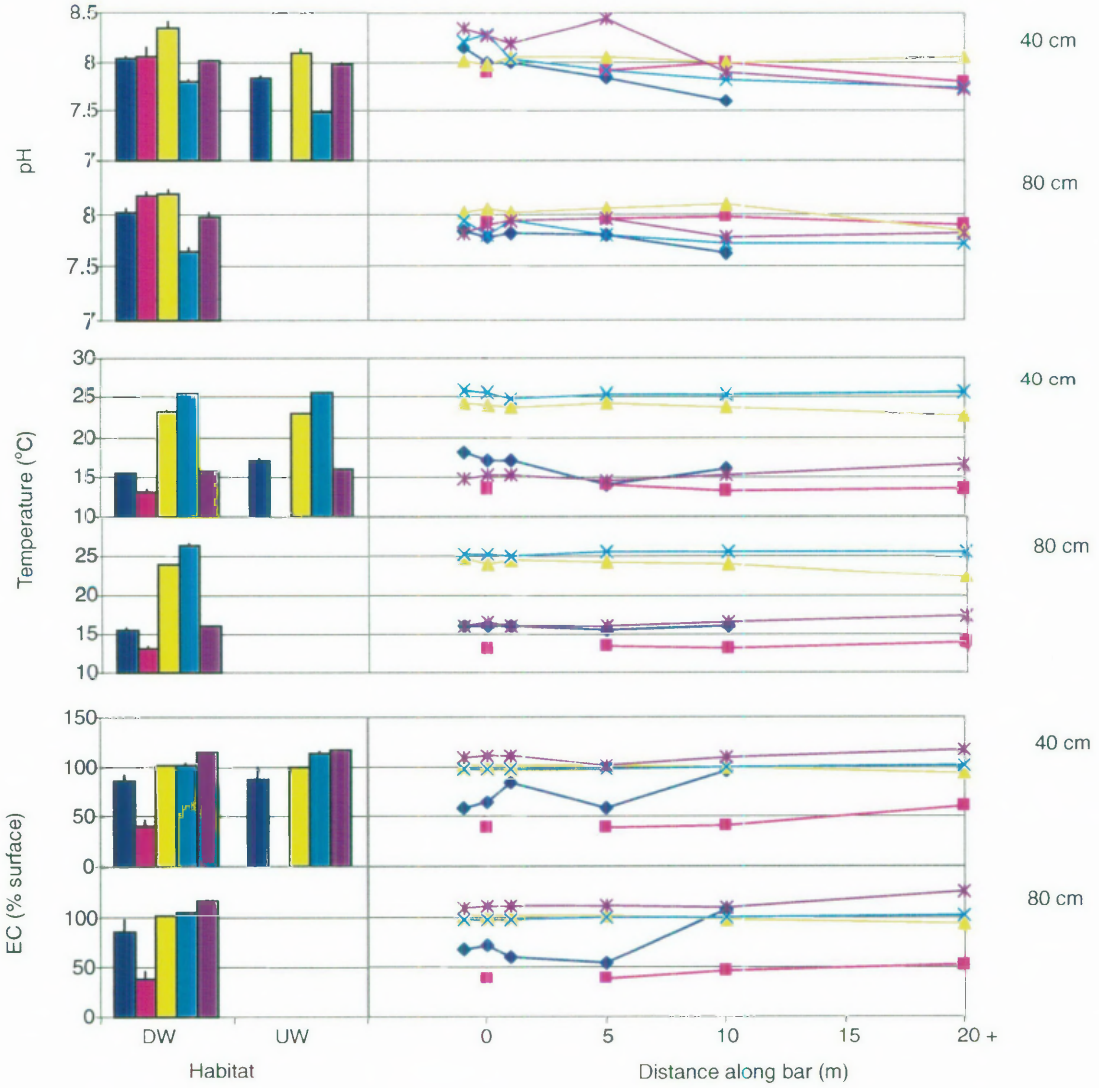
Table 3.6. ANOVA results for Time x Habitat interactions for riffle habitat at Moses Crossing. Bold numbers are significant at P = 0.05.

Variable	Source	SS	df	MS	F-Ratio	P
DO - Log (x+1)						
	T	17006.442	4	4251.611	29.643	**0.000**
	H	878.832	2	439.416	2.726	0.133
	T*H	1128.530	7	161.219	1.124	0.376
	Error	4015.932	28	143.426		
SRP - Log (x+1)						
	T	1.728	4	0.432	42.9.8	**0.000**
	H	0.005	2	0.002	0.129	0.881
	T*H	0.124	7	0.018	1.762	0.135
	Error	0.282	28	0.010		
NOx - Log (x+1)						
	T	2.181	3	0.727	56.673	**0.000**
	H	0.185	2	0.093	0.749	0.503
	T*H	0.989	8	0.124	9.635	**0.000**
	Error	0.359	28	0.013		
EC - Log (x+1)						
	T	0.446	4	0.112	24.064	**0.000**
	H	0.004	2	0.002	2.345	0.166
	T*H	0.007	7	0.001	0.203	0.982
	Error	0.130	28	0.005		
pH - squared						
	T	358.943	4	89.736	69.864	**0.000**
	H	64.205	2	32.102	6.394	**0.026**
	T*H	35.142	7	5.020	3.909	**0.004**
	Error	35.964	28	1.284		
Temperature						
	T	720.386	4	180.097	2231.285	**0.000**
	H	1.146	2	0.573	0.595	0.577
	T*H	6.738	7	0.963	11.926	**0.000**
	Error	2.260	28	28.000	0.081	
Invertebrate abundance - Log (x+1)						
	T	3.951	4	0.988	8.121	**0.000**
	H	2.088	2	1.044	3.132	0.107
	T*H	2.334	7	0.330	2.741	**0.027**
	Error	3.406	28	0.122		
Taxonomic richness - Log (x+1)						
	T	0.847	4	0.212	5.958	**0.001**
	H	0.334	2	0.167	5.969	**0.031**
	T*H	0.196	7	0.028	0.788	0.603
	Error	0.995	28	0.036		



	Mean DO ± SE (% saturation)	Mean SRP ± SE (mg/L)	Mean NOx ± SE (mg/L)
May-00	114.63 ± 11.27	0.076 ± 0.000	0.108 ± 0.017
Aug-00	100.72 ± 4.88	0.025 ± 0.004	0.122 ± 0.004
Nov-00	85.55 ± 4.05	0.019 ± 0.005	0.020 ± 0.008
Feb-01	84.75 ± 2.15	0.010 ± 0.001	0.022 ± 0.009
May-01	97.35 ± 1.05	0.032 ± 0.004	0.114 ± 0.023

Figure 3.15. Interstitial nitrates (NOx), soluble reactive phosphorus (SRP), invertebrate abundance, taxonomic richness and measured physico-chemical variables at Moses Crossing. Bar graphs on the left are hyporheic data (vertical lines represent standard error), while line bars on the right are parafluvial data. Mean surface measurements are reported in the table below the x-axis.



		Mean pH ± SE	Mean Temp. ± SE (°C)	Mean ± EC (mS)
May 00	May-00	8.15 ± 0.15	17.3 ± 0.8	0.44 ± 0.02
Aug 00	Aug-00	8.41 ± 0.14	13.4 ± 0.2	0.47 ± 0.01
Nov 00	Nov-00	8.54 ± 0.00	22.8 ± 0.3	0.91 ± 0.01
Feb 01	Feb-01	8.36 ± 0.00	25.0 ± 0.0	0.82 ± 0.01
May 01	May-01	8.38 ± 0.04	14.5 ± 0.0	0.38 ± 0.02

Figure 3.15. continued

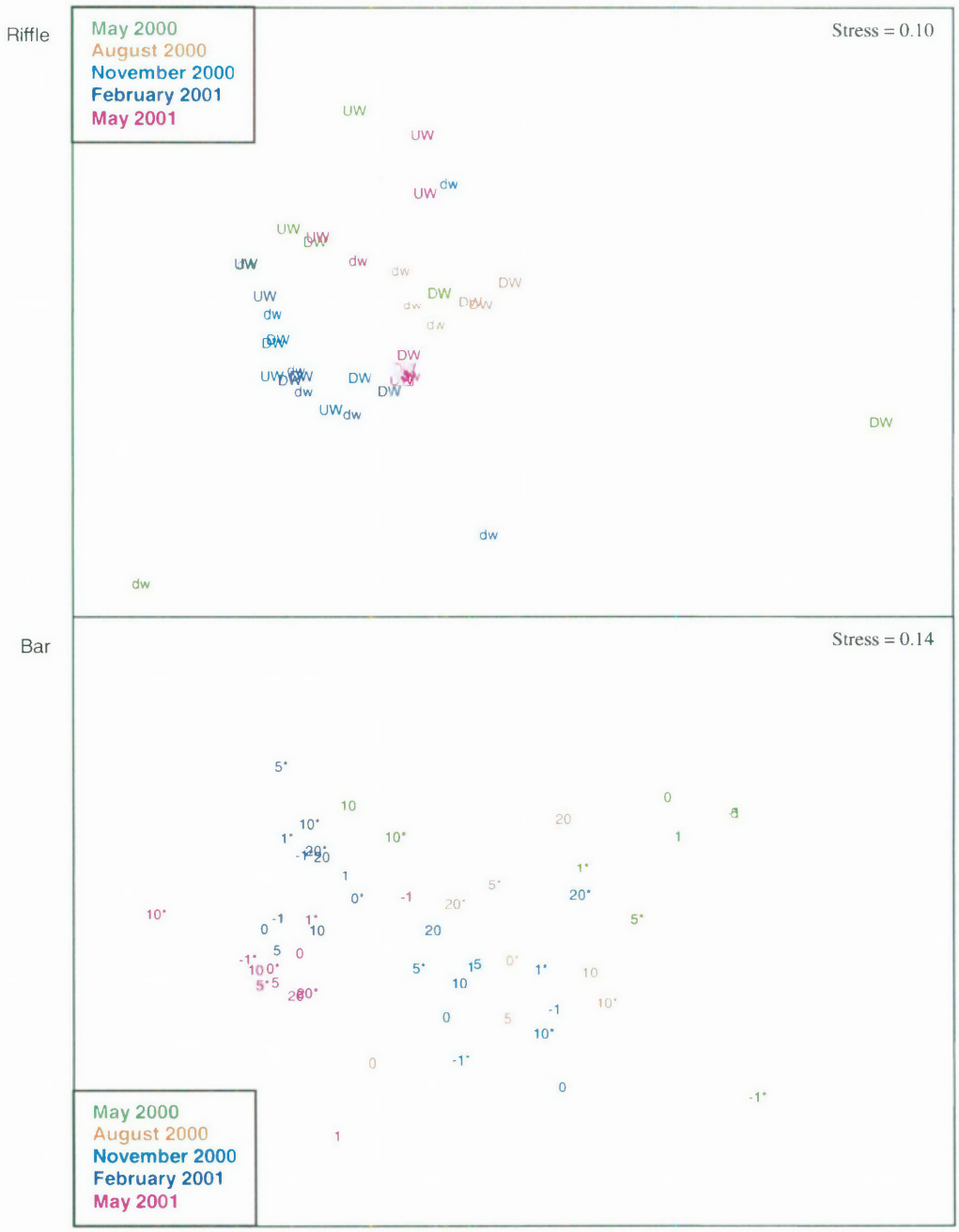


Figure 3.16. Non-metric multi-dimensional scaling diagrams of hyporheic and parafluvial habitats at Moses Crossing. Upper-case letters indicate hyporheic samples from 40 cm. Lower-case letters indicate hyporheic samples from 80 cm. DW and dw = downwelling, UW = upwelling. Numerals indicate distance in metres from the leading edge of the bar. Numbers followed by an * were from 80 cm, while those without were from 40 cm.

Invertebrate abundance varied between times at each of the riffle habitats ($P = 0.027$, Table 3.6, Figure 3.15). Invertebrate abundance was consistent among habitats ($P = 0.107$, Table 3.6) but not times ($P < 0.001$, Table 3.6). During February, 295 invertebrates were collected from 0 m along the bar at 40 cm depth. Analysis with and without this outlier did not affect the significance of the analyses, so it was included for the results discussed here. There were no less invertebrates at the end of the bar than at the beginning (ANCOVA $F_{1,25} = 0.05$, $P = 0.818$ for 40 cm, and $F_{1,23} = 0.10$, $P = 0.757$ for 80 cm). Invertebrates were most abundant in the bar at 40 cm during February (ANCOVA $F_{4,25} = 8.91$, $P < 0.001$). At 80 cm the highers poputation of invertebrates occurred in May 2001 (ANCOVA $F_{4,23} = 5.87$, $P = 0.002$, Figure 3.15).

Taxonomic diversity did not change with distance along the bar at 40 cm (ANCOVA $F_{1,25} = 1.67$, $P = 0.208$, Figure 3.16) and 80 cm (ANCOVA $F_{1,23} = 0.26$, $P = 0.617$, Figure 3.16). There was variation with time in the number of taxa present in the bar at 40 cm (ANCOVA $F_{4,25} = 5.66$, $P = 0.002$), with higher numbers occurring in May 2001, and the lowest numbers occurring in May 2000 (Figure 3.16). There was no temporal variation at 80 cm in the bar (ANCOVA $F_{4,23} = 2.31$, $P = 0.089$, Figure 3.16). Downwelling riffle habitats were more diverse than the upwelling habitat ($P = 0.031$, Table 3.6, Figure 3.16), and temporal variation was characterised by diverse faunas in August 2000 and May 2001 ($P = 0.001$, Table 3.6, Figure 3.16).

Fauna communities in the riffle habitats changed over time (Global $R = 0.502$, $P < 0.001$, Figure 3.16), with oligochaetes dominating spring and summer, and oligochaetes and paramelitid amphipods dominating autumn 2000. Cyclopoids and paramelitids dominated in winter, while cyclopoids and oligochaetes were most numerous during autumn 2001. The upwelling zone differed from downwelling habitats (Global $R = 0.279$, $P = 0.004$), with the former being dominated by oligochaetes and cyclopoids, and the latter being dominated solely by oligochaetes.

In the bar, invertebrate community assemblages changed with time (Global $R = 0.658$, $P < 0.001$, Figure 3.16). Paramelitid's dominated May 2000, which also dominated in August with cyclopoids and microturbellarians. *Heterias sp.*, cyclopoids, and paramelitids dominated November, and oligochaetes and microturbellarians dominated February. In

May 2000 cyclopoids, oligochaetes, and parastenocarids were the most numerous taxa. Communities were similar along the bar (Global R = 0.105, P = 0.125) and didn't change with depth (Global R = -0.009, P = 0.542). These communities were dominated by cyclopoids and oligochaetes.

3.4.7 Maison Dieu (MASO)

DO in the surface water ranged from 96.13 ± 23.67 to 119.10 ± 4.40 % saturation during this study. DO was highest in the riffle during November (P = 0.001, Table 3.7), where concentrations at both depths in the downwelling zone exceeded the surface water (Figure 3.17). This was probably due to photosynthesising benthic algae at the downwelling zone. The shallow downwelling zone contained more oxygen than the deeper downwelling and upwelling habitats (P = 0.001, Table 3.7, Figure 3.17). There was a decrease in oxygen with distance along the bar at 40 cm (ANCOVA $F_{1,22}$ = 8.57, P = 0.008) but not at 80 cm (ANCOVA $F_{1,22}$ = 0.32, P = 0.576). Oxygen concentration in the bar was highest in November and August at 40 cm (ANCOVA $F_{4,22}$ = 11.21, P < 0.001) and 80 cm (ANCOVA $F_{4,22}$ = 16.26, P < 0.001, Figure 3.17).

In the hyporheic zone, pH was highest in November 2000 (P < 0.001, Table 3.7, Figure 3.17). pH was also highest during this month in the bar at 40 cm (ANCOVA $F_{3,18}$ = 11.97, P < 0.001) and 80 cm (ANCOVA $F_{3,16}$ = 22.56, P < 0.001, Figure 3.17).

As with the other sites, temperature in the hyporheic (P < 0.001, Table 3.7) and parafluvial (ANCOVA $F_{4,22}$ = 439.26, P < 0.001 for 40 cm; ANCOVA $F_{3,22}$ = 290.42, P < 0.001 for 80 cm; Figure 3.17) zone at MASO fluctuated seasonally, having summer highs of 24 °C. Temperature at 80 cm in the bar increased with Distance (ANCOVA $F_{1,22}$ = 8.73, P = 0.007) but no change was observed at 40 cm (ANCOVA $F_{1,22}$ = 4.17, P = 0.053, Figure 3.17).

EC in the hyporheic zone was between 120 and 130 % of the surface during May 2000, significantly higher than it was in any of the other month (P < 0.001, Table 3.7, Figure 3.17). In the parafluvial zone, EC also fluctuated temporally (ANCOVA $F_{3,18}$ = 14.71, P < 0.001 for 40 cm; ANCOVA $F_{3,16}$ = 13.64, P < 0.001 for 80 cm, Figure 3.17).

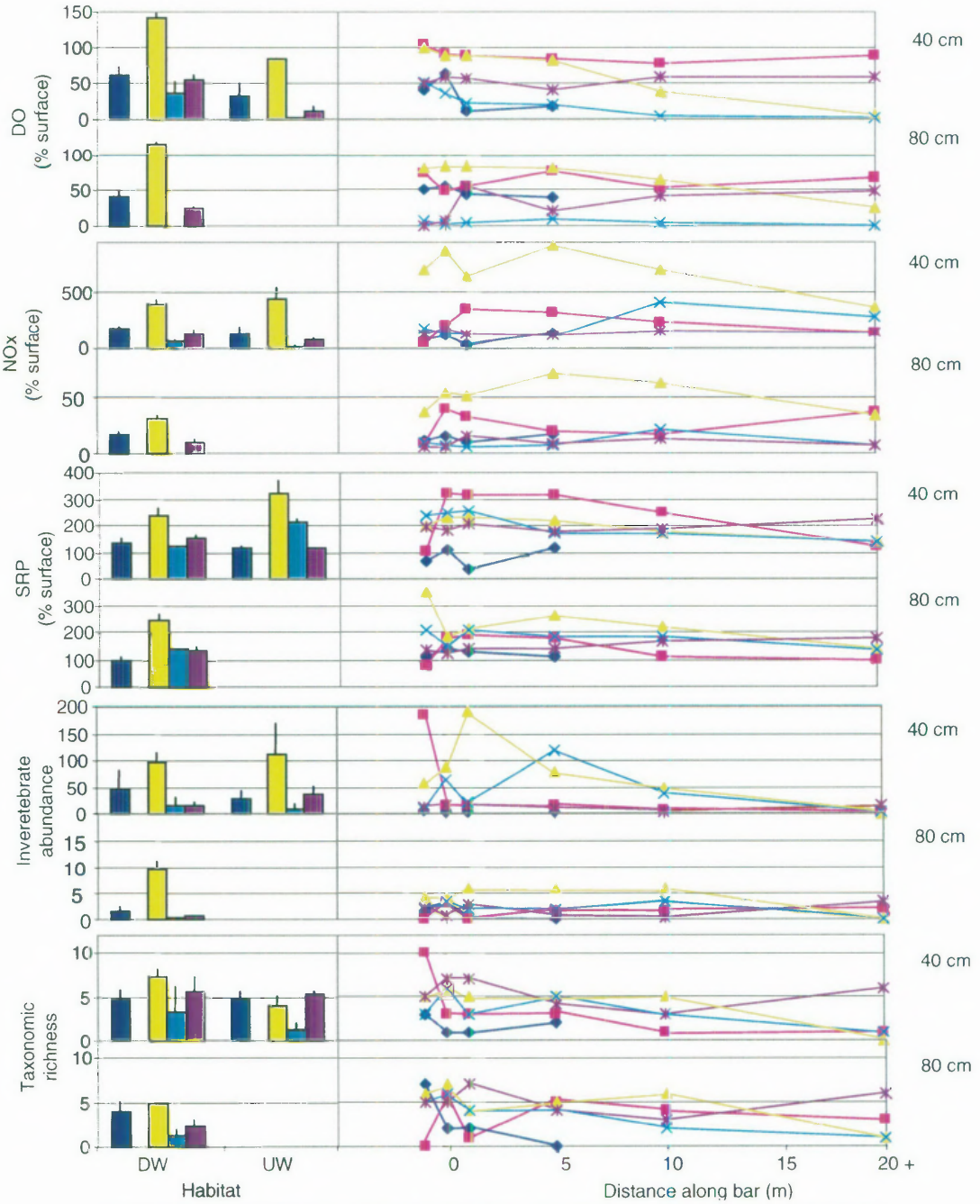
Surface NOx concentrations ranged from 0.011 ± 0.001 to 0.238 ± 0.016 mg/L (Figure 3.17). There was no difference in the NOx concentration among riffle habitats ($P = 0.047$, Table 3.7), but concentrations were different with Time ($P < 0.001$, Table 3.7) because of the high concentration in November. NOx was also higher in the bar during November than at other times (ANCOVA $F_{4,22} = 10.72$, $P < 0.001$ for 40 cm, $F_{4,22} = 17.10$, $P < 0.001$ for 80 cm, Figure 3.17). Neither the 40 cm (ANCOVA $F_{1,22} = 0.040$, $P = 0.836$) or 80 cm (ANCOVA $F_{1,22} = 1.13$, $P = 0.300$) depths changed along the bar (Figure 3.17). NOx corresponded to DO in the riffle hyporheic zone ($r_{26} = 0.795$, $P < 0.001$).

Surface water at MASO had SRP concentrations between 0.018 ± 0.000 and 0.042 ± 0.032 mg/L (Figure 3.17). SRP was not significantly different among riffle habitats ($P = 0.466$, Table 3.7), but did differ with Time ($P < 0.001$, Table 3.7, Figure 3.17). In November, hyporheic SRP concentration was more than 200 % of that in surface water in all habitats. In both November and February, SRP was higher in the upwelling riffle habitat ($P = 0.003$, Table 3.7). In the bar at 40 cm, there was more SRP in August than at other times (ANCOVA $F_{4,22} = 3.59$, $P = 0.021$), while at 80 cm November had the highest SRP concentrations (ANCOVA $F_{4,22} = 6.94$, $P < 0.001$, Figure 3.17). SRP in the bar decreased with distance at 80 cm (ANCOVA $F_{1,22} = 7.12$, $P = 0.014$, Figure 3.17) but not at 40 cm (ANCOVA $F_{1,22} = 0.91$, 0.350). SRP correlated with DO in the riffle habitats ($r_{26} = 0.546$, $P < 0.001$).

Invertebrates were as common in the upwelling zone of the riffle as in the downwelling zones ($P = 0.126$, Table 3.7, Figure 3.17). However, there were more invertebrates in the riffle in November than any other time ($P < 0.001$, Table 3.7, Figure 3.17). November invertebrate numbers were highest in the bar too, both at 40 cm (ANCOVA $F_{4,24} = 5.38$, $P = 0.003$, Figure 3.17) and 80 cm (ANCOVA $F_{4,22} = 4.26$, $P = 0.010$, Figure 3.17). Invertebrate abundance decreased with distance at 40 cm (ANCOVA $F_{1,24} = 7.28$, $P = 0.013$, Figure 3.17) but remained relatively constant at 80 cm (ANCOVA $F_{1,22} = 3.14$, $P = 0.090$). There was a strong correlation of invertebrate abundance with DO in the riffle ($r = 0.718$, $P < 0.001$).

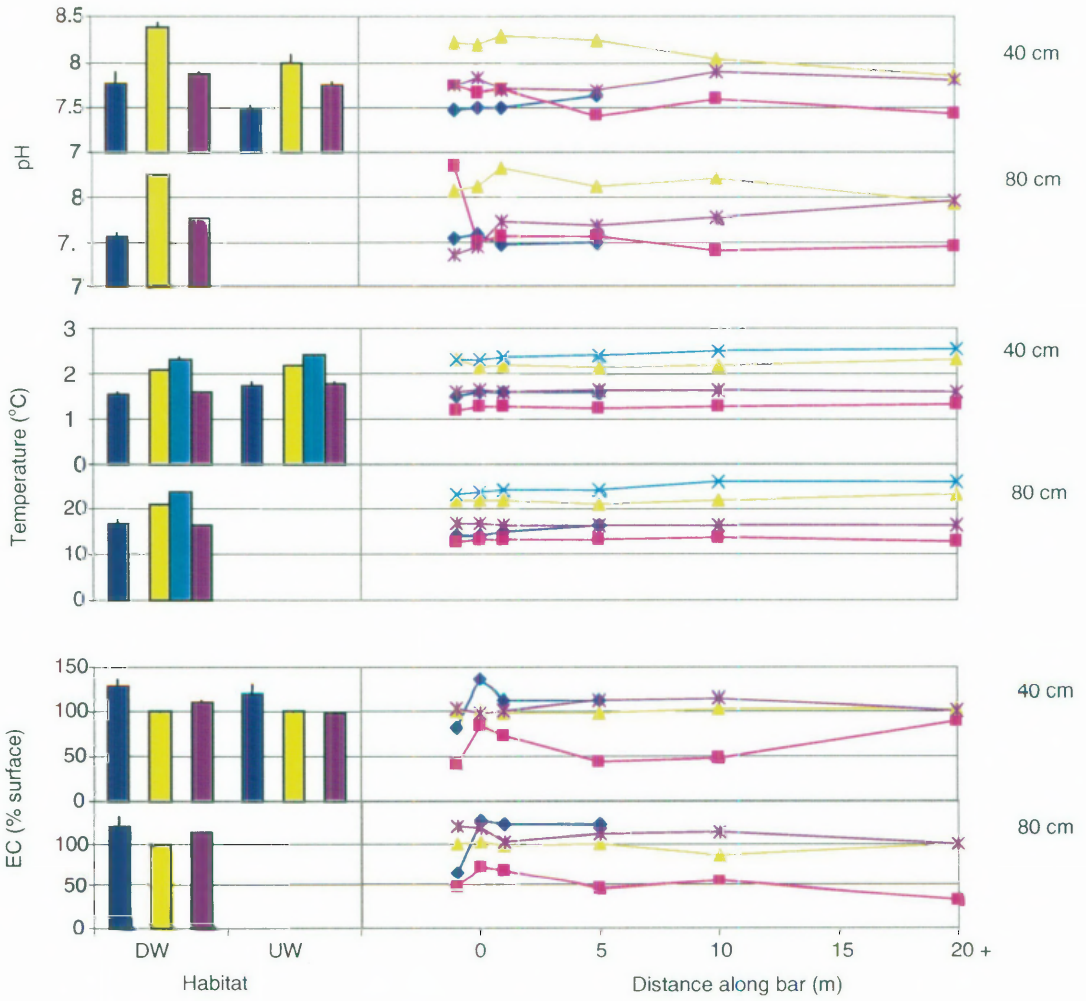
Table 3.7. ANOVA results for Time x Habitat interactions for riffle habitat at Maison Dieu. Bold numbers are significant at P = 0.05.

Variable	Source	SS	df	MS	F-Ratio	P
DO						
	T	51817.293	3	17272.431	90.949	**0.000**
	H	10736.219	2	5368.109	27.129	**0.001**
	T*H	1187.255	6	197.109	27.129	**0.001**
	Error	4227.944	24	189.914		
SRP - Log (x+1)						
	T	0.655	3	0.218	45.744	**0.000**
	H	0.039	2	0.019	0.870	0.466
	T*H	0.133	6	0.022	4.659	**0.003**
	Error	0.115	24	0.005		
NOx - Log (x+1)						
	T	7.649	3	2.550	45.210	**0.000**
	H	0.578	2	0.289	2.003	0.216
	T*H	0.865	6	0.144	2.557	**0.047**
	Error	1.354	24	0.056		
EC - Log (x+1)						
	T	0.032	2	0.016	12.366	**0.000**
	H	0.002	1	0.002	1.240	0.316
	T*H	0.006	5	0.001	0.969	0.463
	Error	0.023	18	0.001		
pH - squared						
	T	442.697	2	221.348	83.820	**0.000**
	H	32.929	2	16.464	3.938	0.113
	T*H	16.722	4	4.181	1.583	0.222
	Error	47.533	18	2.641		
Temperature						
	T	272.020	3	90.673	222.186	**0.000**
	H	0.521	1	0.521	1.551	0.253
	T*H	2.351	7	0.336	0.823	0.579
	Error	8.570	21	0.408		
Invertebrate abundance - Log (x+1)						
	T	5.364	3	1.788	10.377	**0.000**
	H	0.805	2	0.402	2.979	0.126
	T*H	0.810	6	0.135	0.784	0.591
	Error	4.135	24	0.172		
Taxonomic richness - Log (x+1)						
	T	0.282	3	0.094	4.113	**0.017**
	H	0.189	2	0.095	3.337	0.106
	T*H	0.170	6	0.028	1.241	0.321
	Error	0.549	24	0.023		



	Mean DO ± SE (% saturation)	Mean SRP ± SE (mg/L)	Mean NOx ± SE (mg/L)
May-00	96.13 ± 23.67	0.042 ± 0.032	0.079 ± 0.012
Aug-00	97.10 ± 2.90	0.020 ± 0.009	0.103 ± 0.046
Nov-00	119.10 ± 4.40	0.018 ± 0.000	0.011 ± 0.000
Feb-01	102.55 ± 0.65	0.029 ± 0.010	0.238 ± 0.016
May-01	97.55 ± 1.95	0.031 ± 0.003	0.118 ± 0.037

Figure 3.17. Interstitial nitrates (NOx), soluble reactive phosphorus (SRP), invertebrate abundance, taxonomic richness, and measured physico-chemical variables at Maison Dieu. Bar graphs on the left are hyporheic data (vertical lines represent standard error), while line bars on the right are parafluvial data. Mean surface measurements are reported in the table below the x-axis.



			Mean pH ± SE	Mean Temp. ± SE (°C)	Mean ± EC (mS)
May 00	May 00	May-00	7.96 ± 0.29	18.5 ± 0.5	0.38 ± 0.03
Aug 00	Aug 00	Aug-00	8.23 ± 0.02	12.0 ± 0.1	0.74 ± 0.14
Nov 00	Nov 00	Nov-00	8.68 ± 0.02	24.1 ± 0.7	0.83 ± 0.00
Feb 01	Feb 01	Feb-01		24.8 ± 0.4	
May 01	May 01	May-01	8.30 ± 0.05	16.6 ± 0.1	0.56 ± 0.01

Figure 3.17. continued

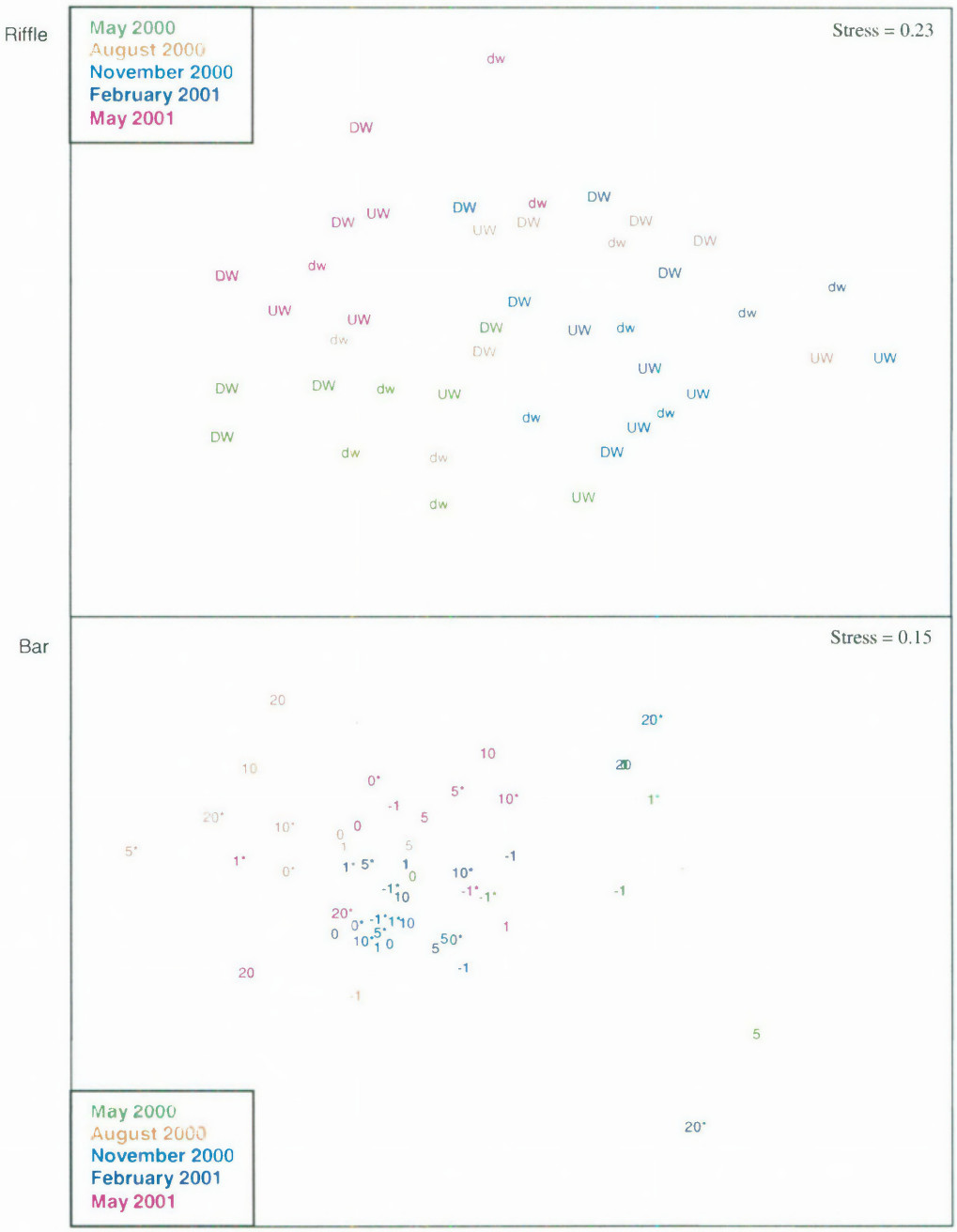


Figure 3.18. Non-metric multi-dimensional scaling diagrams of hyporheic and parafluvial habitats at Maison Dieu. Upper-case letters indicate hyporheic samples from 40 cm. Lower-case letters indicate hyporheic samples from 80 cm. DW and dw = downwelling, UW = upwelling. Numerals indicate distance in metres from the leading edge of the bar. Numbers followed by an * were from 80 cm, while those without were from 40 cm.

There were more taxa at the head of the bar than at its tail (ANCOVA $F_{1,24} = 6.96$, $P = 0.014$ for 40 cm, $F_{1,22} = 8.88$, $P = 0.007$ for 80 cm, Figure 3.17). Bar diversity remained consistent with Time at 40 cm (ANCOVA $F_{4,22} = 1.99$, $P = 0.131$). Less taxa were collected from 80 cm during May 2000 and August (ANCOVA $F_{4,24} = 3.62$, $P = 0.019$, Figure 3.17) than in any other month. Taxonomic diversity in the riffle didn't change among habitats ($P = 0.106$) but differed with Time ($P = 0.017$), with February 2001 having the fewest species (Figure 3.17).

The riffle invertebrate community changed with Time (Global $R = 0.642$, $P < 0.001$, Figure 3.18). Oligochaetes, ostracods, and cyclopoids dominated May 2000, while nematodes, oligochaetes and cyclopoids dominated in August. Oligochaetes controlled invertebrate assemblages in November and February, with oligochaetes, cyclopoids, and harpacticoids dominating in May 2001. Oligochaetes and cyclopoids were common in all riffle habitats, but populations of harpacticoids in the shallow downwelling, microturbellearians in the deeper downwelling, and nematodes in the upwelling, contributed to differences among Habitats (Global $R = 0.398$, $P < 0.001$).

In the bar, community assemblage varied with Time (Global $R = 0.442$, $P < 0.001$, Figure 3.18). Cyclopoids and oligochaetes, made up the majority of the fauna in August and February. Microturbellarians, cyclopoids, oligochaetes and parastenocarids dominated in November 2000 and May 2001. In May 2000 oligochaetes were the sole dominant group. The community was relatively homogenous for the length of the bar (Global $R = 0.112$, $P < 0.001$) but differed with depth (Global $R = 0.322$, $P < 0.001$). Oligochaetes and cyclopoids at 40 cm were more numerous than they were at 80 cm.

3.4.8 Dights Crossing (DIGH)

Surface DO concentrations were between 76.65 ± 1.25 and 97.75 ± 1.92 % saturation at DIGH. There was no difference in DO among the three times that riffles were sampled ($P = 0.323$, Table 3.8, Figure 3.19). DO was higher in the downwelling zone than the upwelling zone ($P = 0.004$, Table 3.8, Figure 3.19). DO concentration declined with distance along the bar at 40 cm (ANCOVA $F_{1,24} = 7.58$, $P = 0.011$) and 80 cm (ANCOVA $F_{1,24} = 4.61$, $P = 0.042$, Figure 3.19). May 2001 and November had the highest DO concentrations at 80 cm depth (ANCOVA $F_{1,24} = 4.61$, $P = 0.042$), while May 2001 and

August had the highest oxygen concentration at 40 cm (ANCOVA $F_{1,24} = 7.58$, $P = 0.011$, Figure 3.19).

There was no discernable difference in the pH of the downwelling and upwelling hyporheic zones, but pH did differ with Time, being higher in November 2000 ($P < 0.001$, Table 3.8, Figure 3.19). There was no significant change in pH with distance along the bar (ANCOVA $F_{1,19} = 0.32$, $P = 0.579$ for 40 cm and ANCOVA $F_{1,19} = 0.11$, $P = 0.745$ for 80 cm, Figure 3.19). Parafluvial pH changed with Time, having highest concentrations in November at 40 cm (ANCOVA $F_{3,19} = 11.67$, $P < 0.001$) and 80 cm (ANCOVA $F_{3,19} = 19.53$, $P < 0.001$).

Water in the upwelling zone was slightly warmer than that of the downwelling zone ($P = 0.003$, Table 3.8, Figure 3.19). Temperature fluctuated seasonally in the hyporheic zone ($P < 0.001$, Table 3.8) and parafluvial zone (ANCOVA $F_{4,24} = 66.68$, $P < 0.001$ for 40 cm and ANCOVA $F_{4,24} = 122.73$, $P < 0.001$ for 80 cm, Figure 3.19).With the exception of May 2000, parafluval water temperature increased with distance along the flow path (ANCOVA $F_{1,24} = 7.67$, $P = 0.011$ for 40 cm and ANCOVA $F_{1,24} = 6.68$, $P = 0.016$ for 80 cm, Figure 3.19).

EC did not change with Time ($P = 0.540$) or between sub-habitats in the hyporheic zone ($P = 0.929$, Table 3.8, Figure 3.19). In the bar, EC was significantly higher in May 2000 than at other times at 40 cm (ANCOVA $F_{3,19} = 13.98$, $P < 0.001$) and 80 cm (ANCOVA $F_{3,19} = 06.88$, $P = 0.003$, Figure 3.19).

In the surface, NOx concentration ranged between 0.003 ± 0.002 to 0.144 ± 0.058 mg/L (Figure 3.19). November riffle samples were characterised by NOx concentrations of more than 10 times that of the surface (Figure 3.19), and this led to a significant temporal difference ($P < 0.001$, Table 3.8). NOx was similar among riffle habitats ($P = 0.542$, Table 3.8, Figure 3.19). NOx was highest in the bar at 40 cm during November and February (ANCOVA $F_{4,24} = 5.40$, $P = 0.003$, Figure 3.19). There was no significant temporal difference at 80 cm (ANCOVA $F_{4,24} = 1.14$, $P = 0.362$). No significant variation occurred with distance at 40 cm (ANCOVA $F_{1,24} = 0.01$, $P = 0.911$), but NOx declined with distance at 80 cm (ANCOVA $F_{1,24} = 5.44$, $P = 0.028$, Figure 3.19).

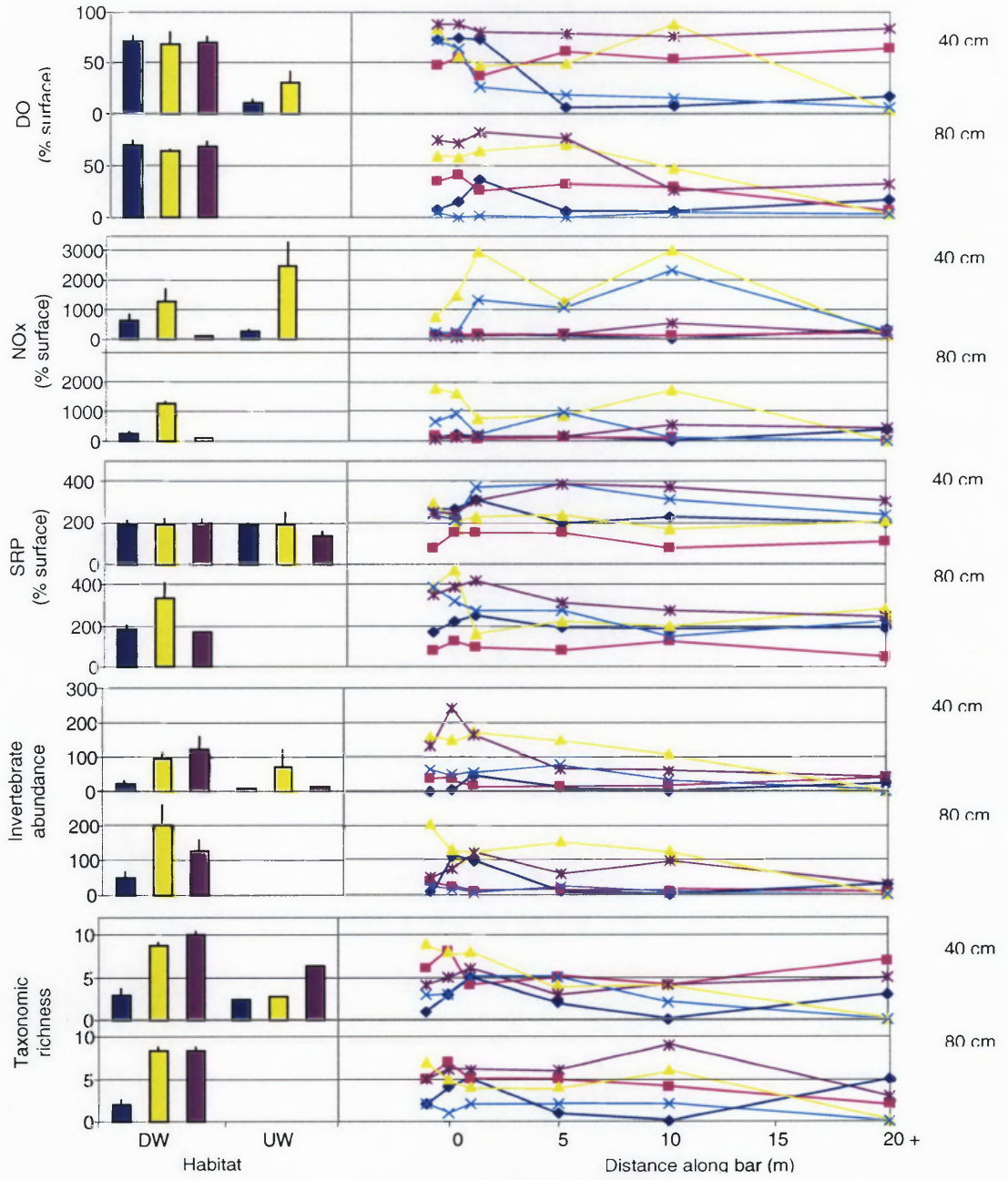
Surface SRP measured 0.018 ± 0.002 to 0.037 ± 0.018 mg/L (Figure 3.19). SRP concentrations differed among times (P = 0.050, Table 3.8) and habitats (P = 0.050, Table 3.8) in the riffle. The significance in both these factors was probably due the high SRP recorded in November from the deep downwelling habitat (Figure 3.19). SRP concentration declined with distance at 80 cm (ANCOVA $F_{1,24} = 8.23$, P = 0.009, Figure 3.19), but not at 40 cm (ANCOVA $F_{1,24} = 3.85$, P = 0.061). The significant temporal variation in the bar at 40 cm was due to high SRP in February and May 2001 (ANCOVA $F_{4,24} = 13.60$, P < 0.001, Figure 3.19). At 80 cm, February and May 2001 were also the highest (ANCOVA $F_{4,24} = 27.36$, P < 0.001, Figure 3.19). There was no correlation between DO and SRP in the riffle ($r_{26} = 0.102$, P = 0.612) or bar ($r_{59} = -0.056$, P = 0.672).

There were more invertebrates in the leading edge of the bar than at the end (ANCOVA $F_{1,24} = 9.56$, P = 0.005 for 40 cm, $F_{1,24} = 15.08$, P = 0.001 for 80 cm, Figure 3.19). Invertebrate abundance at 40 cm in the bar was highest during November (ANCOVA $F_{4,24} = 3.82$, P = 0.015, Figure 3.19). It was also highest during November at 80 cm (ANCOVA $F_{4,24} = 4.37$, P = 0.009, Figure 3.19). Both downwelling riffle habitats had more invertebrates than the upwelling habitat (P = 0.010, Table 3.8). There were fewer invertebrates in the riffle in May 2000 than other times (P = 0.001, Table 3.8, Figure 3.19). Invertebrate numbers correlated with DO in the riffle ($r_{26} = 0.613$, P < 0.001) and bar ($r_{59} = 0.636$, P < 0.001).

There were more taxa in May 2001 and November in the downwelling habitats, but this pattern was not maintained for the upwelling zone (P = 0.002, Table 3.8, Figure 3.19). When averaged over all times, taxonomic richness was similar among habitats in the riffle (P = 0.138, Figure 3.19, Table 3.8). There were more species in the riffle during May 2001 than in any of the other months (P < 0.001, Table 3.8, Figure 3.19). The number of taxa declined along the bar at 40 cm (ANCOVA $F_{1,24} = 6.42$, P = 0.018) and at 80 cm (ANCOVA $F_{1,24} = 6.13$, P = 0.021, Figure 3.19). There were also temporal differences at each depth (ANCOVA $F_{4,24} = 3.62$, P = 0.019 for 40 cm, ANCOVA $F_{4,24} = 6.13$, P = 0.021 for 80 cm, Figure 3.19).

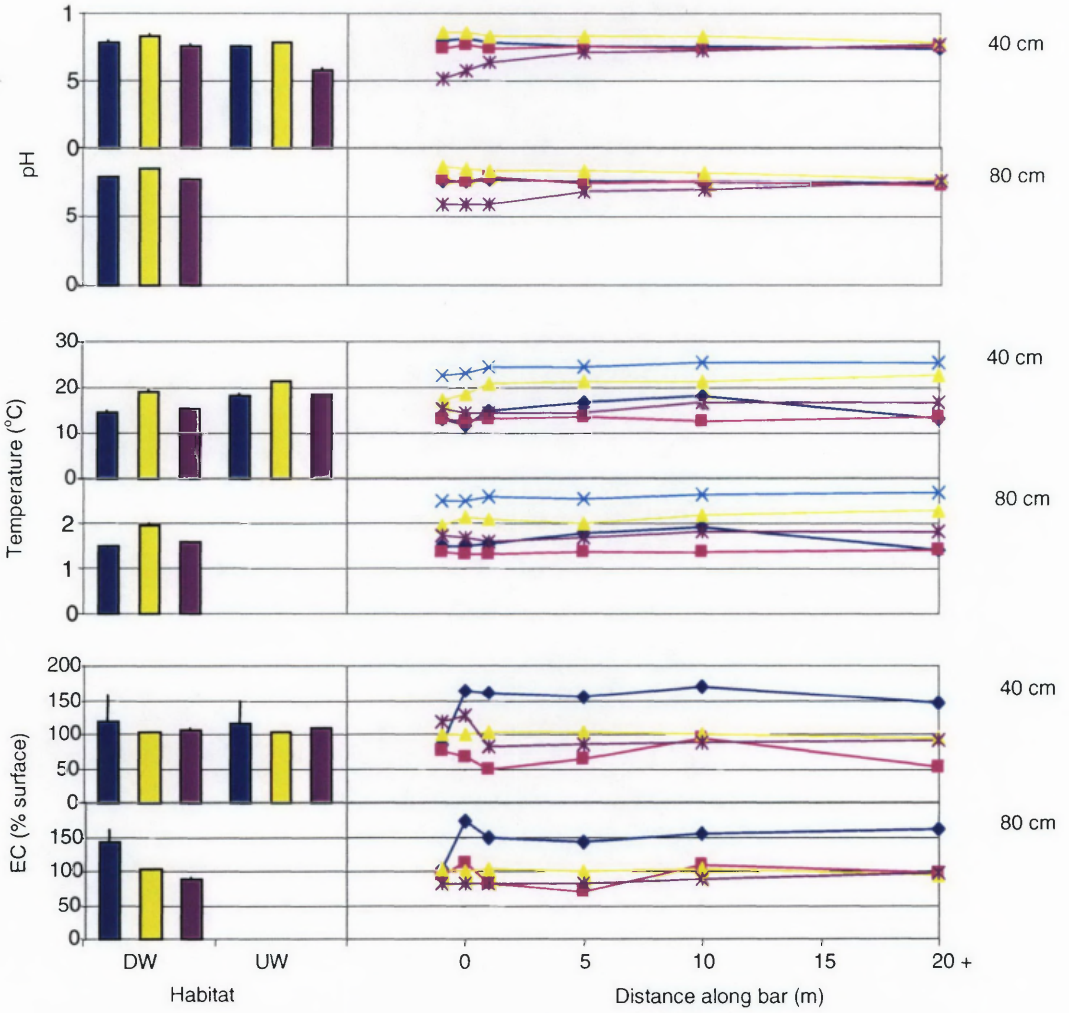
Table 3.8. ANOVA results for Time x Habitat interactions for riffle habitat at Dights Crossing. Bold numbers are significant at P = 0.05.

Variable	Source	SS	df	MS	F-Ratio	P
DO						
	T	289.123	2	144.561	1.204	0.323
	H	18096.887	2	9048.443	29.626	**0.004**
	T*H	1221.684	4	305.421	2.543	0.075
	Error	2161.960	18	120.109		
SRP - rank transformed						
	T	382.889	2	191.444	3.567	0.050
	H	382.889	2	191.444	3.567	0.050
	T*H	239.111	4	59.778	1.114	0.381
	Error	966.000	18	53.667		
NOx - Log (x+1)						
	T	9.833	2	4.916	115.030	**0.000**
	H	0.609	2	0.304	0.717	0.542
	T*H	1.698	4	0.424	9.932	**0.000**
	Error	0.769	18	0.043		
EC - Log (x+1)						
	T	0.027	2	0.014	0.639	0.540
	H	0.002	2	0.001	0.075	0.929
	T*H	0.060	4	0.015	0.702	0.601
	Error	0.382	18	0.021		
pH - squared						
	T	1473.010	2	736.505	133.500	**0.000**
	H	1042.256	2	521.128	4.362	0.099
	T*H	477.896	4	119.474	21.656	**0.000**
	Error	99.304	18	5.517		
Temperature						
	T	88.179	2	44.089	189.254	**0.000**
	H	46.716	2	23.358	34.358	**0.003**
	T*H	2.681	4	0.670	2.787	0.053
	Error	4.193	18	0.233		
Invertebrate abundance - Log (x+1)						
	T	2.227	2	1.113	10.578	**0.001**
	H	2.952	2	1.476	18.020	**0.010**
	T*H	0.328	4	0.082	0.778	0.554
	Error	1.894	18	0.105		
Taxonomic richness						
	T	159.185	2	79.593	59.694	**0.000**
	H	56.519	2	28.259	3.376	0.138
	T*H	33.481	4	8.370	6.278	**0.002**
	Error	24.000	18	1.333		



	Mean DO ± SE (% saturation)	Mean SRP ± SE (mg/L)	Mean NOx ± SE (mg/L)
May-00	97.75 ± 1.92	0.037 ± 0.018	0.070 ± 0.003
Aug-00	97.20 ± 2.10	0.027 ± 0.015	0.098 ± 0.039
Nov-00	76.65 ± 1.25	0.018 ± 0.002	0.003 ± 0.002
Feb-01	80.75 ± 1.05	0.021 ± 0.005	0.144 ± 0.058
May-01	95.75 ± 1.65	0.021 ± 0.002	0.113 ± 0.001

Figure 3.19. Interstitial nitrates (NOx), soluble reactive phosphorus (SRP), invertebrate abundance, taxonomic richness, and measured physico-chemical variables at Dights Crossing. Bar graphs on the left are hyporheic data (vertical lines represent standard error), while line bars on the right are parafluvial data. Mean surface measurements are reported in the table below the x-axis.



	Mean pH ± SE	Mean Temp. ± SE (°C)	Mean ± EC (mS)
May-00	8.06 ± 0.01	13.0 ± 0.0	0.32 ± 0.01
Aug-00	8.36 ± 0.09	13.1 ± 0.1	0.48 ± 0.04
Nov-00	8.55 ± 0.01	18.2 ± 0.5	0.83 ± 0.00
Feb-01		22.0 ± 0.2	
May-01	6.43 ± 0.32	15.7 ± 0.1	0.57 ± 0.02

Figure 3.19. continued

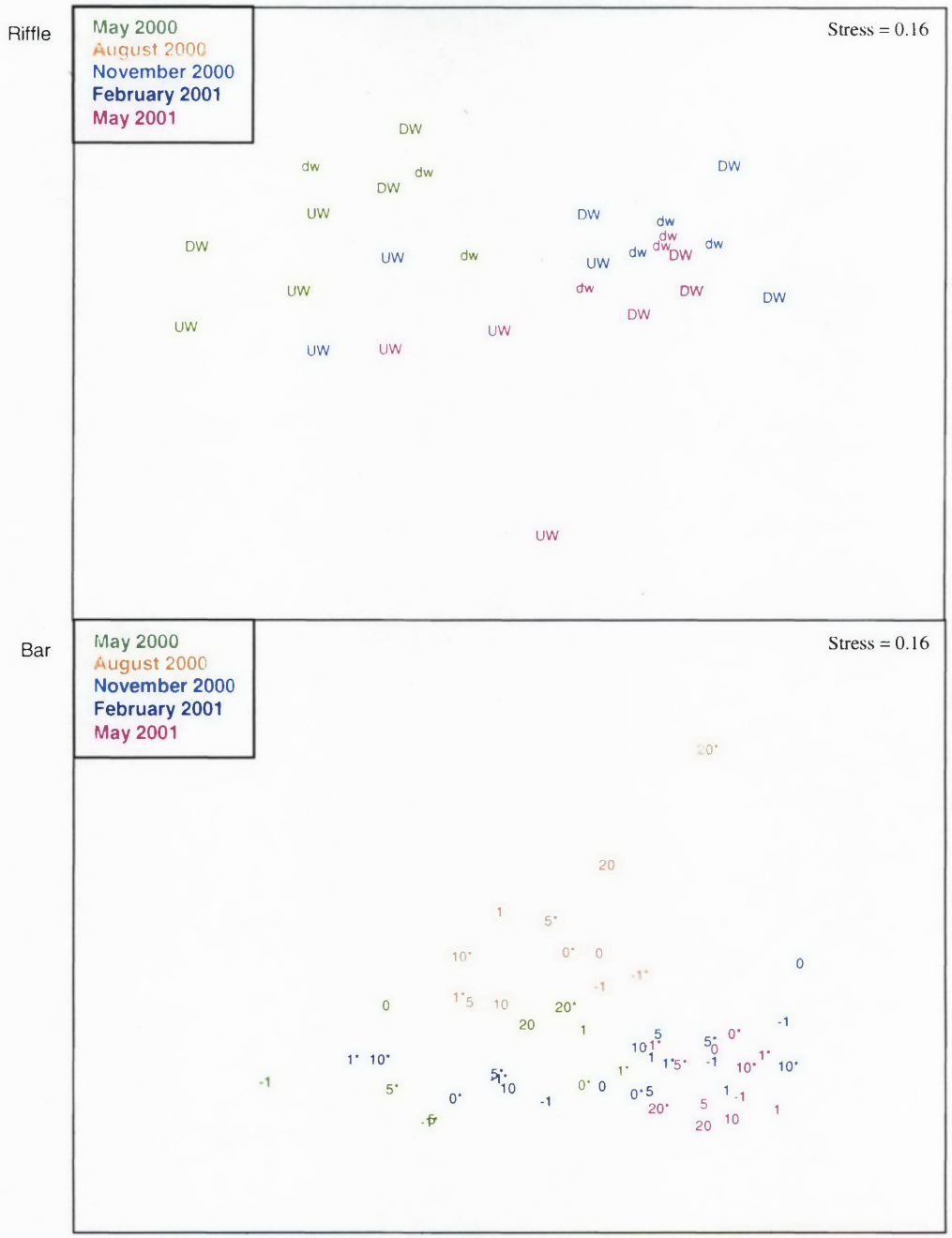


Figure 3.20. Non-metric multi-dimensional scaling diagrams of hyporheic and parafluvial habitats at Dights Crossing. Upper-case letters indicate hyporheic samples from 40 cm. Lower-case letters indicate hyporheic samples from 80 cm. DW and dw = downwelling, UW = upwelling. Numerals indicate distance in metres from the leading edge of the bar. Numbers followed by an * were from 80 cm, while those without were from 40 cm.

Invertebrate community assemblages were distinctly different for each of the three times that riffle habitats were sampled (Global R = 0.509, P < 0.001, Figure 3.20). The fauna in May 2000 was characterised solely by oligochaetes, while in November oligochaetes, nematodes, and parastenocarids dominated. These three taxa were also common in May 2001, but so were microturbellarians and cyclopoids. Oligochaetes, parastenocarids, and cyclopoids were the dominant taxa in the shallow downwelling habitat of the riffle, while oligochaetes, parastenocarids, and nematodes were most common in the deeper sediments. Downwelling habitat communities differed to those in the upwelling zone (Global R = 0.292, P = 0.005), which had higher populations of oligochaetes and nematodes.

Bar community assemblages displayed distinct groupings for each time (Global R = 0.678, P < 0.001, Figure 3.20). Oligochaetes remained dominant in the samples throughout the study, but contributions from other taxa distinguished temporal groups. Microturbellarians separated autumn 2001 from summer, while parastenocarids characterised spring and autumn 2001. In winter oligochaetes, cyclopoids, harpacticoids, and members of the syncarid family Psammaspididae were the most numerous invertebrates. Communities along the bar did not differ, (Global R = 0.111, P = 0.125) and were dominated by oligochaetes and parastenocarids. The community at 40 cm depth differed to that of 80 cm (Global R = 0.199, P = 0.002), being dominated by oligochaetes, parastenocarids, and microturbellarians.

3.5 Discussion

3.5.1 Longitudinal patterns

River scale

Neither the abundance nor taxa richness declined along the length of the Hunter River. However, the parafluvial habitats in ABER and DENM contained higher numbers of taxa than downstream sites. A higher proportion of cobble-size particles dominated both of these sites (Chapter 5). This provided a more stable matrix than the downstream sites, allowing higher hydraulic gradients and therefore a stronger connection with the stream. Both sites also maintained strong linkages to groundwater, as evidenced by populations of stygofaunal syncarids, harpacticoids, and amphipods. While links with stygofaunal communities and surface communities in the other sites were also moderately high, perhaps pore-space stability in the sand-dominated substrate was lower, limiting the

numbers of epigean taxa able to inhabit the parafluvial zone in the sites downstream of the Goulburn River confluence. In three upstream tributaries of the Elklick Run (West Virginia), and on the Elklick Run itself, the hyporheic fauna resembled the benthic epigean fauna less at downstream sites than at upstream sites (Angradi *et al.* 2001). Here, invertebrate abundance and taxonomic richness correlated positively with interstitial flow, decreasing with distance downstream (Angradi *et al.* 2001). On the other hand, taxa richness of the hyporheos of the glacial Roseg River increased downstream, displaying affinities to temperature, the influence of groundwater, and the amount of organic matter (Malard *et al.* 2003). While displaying distinct, though contrasting, longitudinal patterns in their faunal distribution, both studies indicated that spates were also significant in shaping hyporheic communities (Angradi *et al.* 2001, Malard *et al.* 2003).

Over the 138-km stretch of the Hunter River surveyed, there were discernable longitudinal river-scale patterns for some physico-chemical variables. The most distinct trend in the Hunter River was that of temperature, which generally increased with distance downstream. In the glacial Roseg River, there was a similar trend of increasing temperature over an 11-km length of river (Malard *et al.* 2003). In the Roseg, upwelling groundwater was the dominant influence on these temperature changes (Malard *et al.* 2001, 2003). Upwelling groundwater may still be an important buffer in the temperature dynamics of the hyporheic zone of the Hunter River, and could explain the decline in temperature at DIGH. However, travel distance downstream of Glenbawn Dam is probably the main factor, with in-stream water possibly being warmed by direct solar radiation, or as it passes through successive parafluvial zones.

There were no longitudinal trends in nutrient concentrations at the scale of the river. The role that hyporheic and parafluvial zones play in nutrient spiralling has been well documented (Grimm and Fisher 1984, Duff and Triska 2000). In Sycamore Creek, an Arizonan desert stream, it was postulated that net nutrient concentrations would increase downstream as a cumulative result of site-scale interstitial nitrification and organic matter mineralisation (Fisher *et al.* 1998). Upwelling water from the subsurface of Sycamore Creek influenced surface water nutrient patterns at scales from meters to several kilometres (Dent *et al.* 2001), highlighting the possibility for cumulative effects of hyporheic nutrient transformations. In the Hunter River the absence of a noticeable

longitudinal increase or decrease in either SRP or NOx, despite significant bar-scale transformations, suggests that the net nutrient balance is maintained along the stream. It is possible that in-stream algal and macrophyte nutrient uptake is significant. However, the occurrence of both reducing and oxidising conditions in interstitial habitats is essential in ameliorating the effects of high nutrient loads (particularly nitrogen) in streams (Triska *et al.* 1993, Findlay 1995). The balance in the Hunter River further emphasises the importance of the hyporheic zone in maintaining an overall nutrient balance at the river scale. However, a more comprehensive understanding of nutrient dynamics in the Hunter River will be obtained from research investigating the role of other ecosystem components (e.g., algae, bar and riparian vegetation, macrophytes).

Site and habitat scales

Hyporheic NOx in the Hunter River displayed no spatial pattern that was consistent between all sites. Five riffles displayed no net change in NOx concentration, while in the other two, ABER and DSMG, NOx declined (refer to Table 3.9). However, within the upper 40 cm of sediment of the Hunter River, there was substantial nitrification, with hyporheic NOx increasing to concentrations often 200 % that of the surface. Similarly, NOx concentrations of Sycamore Creek were almost twice as high in the downwelling zone at 10 cm, than the surface (Jones *et al.* 1995). In the East Branch of the Maple River, Michigan, hyporheic physico-chemical parameters displayed noticeable patterns of variation along a 10-m riffle (Hendricks and White 1991). Hyporheic NOx generally increased along the riffle, while conductivity, DO, and SRP decreased (Hendricks and White 1991). Similar patterns for nitrate have been observed over a 400 m run in Sycamore Creek, Arizona (Fisher *et al.* 1998), and in a 500-m riffle of the Rhône River in France (Fauvet *et al.* 2001). The decline of NOx concentration in the ABER and DSMG hyporheic zones is most likely due to the dominance of denitrifying bacterial activity.

Along the parafluvial zones, NOx concentrations did not change at 40 cm depth for five of the sites (ABER, DENM, DSMG, MASO, DIGH). Parafluvial NOx concentrations in Sycamore Creek increased with distance along the bar and summer concentrations doubled travelling 10 m in the parafluvial zone (Holmes et al. 1994b). At 40 cm in the Hunter River, interstitial NOx was often 2 – 4 times surface concentrations, indicating a

Table 3.9. Dominant spatial trends in nutrient and invertebrate patterns at each site. Upward arrows indicate that variable increased with distance along parfluvial or hyporheic flow paths. Downward arrows indicate a decrease with distance. NC denotes no change.

		Bar					Riffle				
Site		DO	NOx	SRP	Invertebrate abundance	Taxonomic richness	DO	NOx	SRP	Invertebrate abundance	Taxonomic richness
ABER	40	↓	NC	NC	↓	↓	↓	↓	NC	↓	↓
	80	↓	↓	NC	↓	↓					
DENM	40	↓	NC	NC	↑	NC	↓	NC	NC	NC	NC
	80	↓	↓	NC	NC	NC					
BOWM	40	↓	NC	NC	↓	↓	↓	NC	NC	↑	↓
	80	↓	NC	NC	↓	↓					
DSMG	40	↓	NC	NC	↓	NC	↓	↓	NC	↓	↓
	80	↓	NC	NC	↓	↓					
MOSE	40	↓	↑	NC	NC	NC	NC	NC	NC	NC	↓
	80	↓	↑	NC	NC	NC					
MASO	40	↓	NC	NC	NC	↓	↓	NC	NC	NC	NC
	80	NC	NC	NC	NC	↓					
DIGH	40	↓	NC	NC	↓	↓	↓	NC	NC	↓	NC
	80	↓	↓	↓	↓	↓					

similar pattern of significant nitrification in upper sediments as observed in the riffles. Nutrient-enriched waters were also present in the interstitial environments of Maple River, where they were 3 - 4 times higher than surface concentrations (Hendricks and White 1991), and Sycamore Creek (2 – 3 times surface, Valett *et al.* 1990). Concentrations did not change much between 40 cm and 80 cm in the Hunter River, confirming the view that the majority of nutrient transformations occur in the shallow, near-stream sediments (Fisher *et al.* 1998, Jones *et al.* 1995). In all but three of the bars (DSMG, MOSE, and MASO), dissolved NOx concentrations at 80 cm declined with horizontal travel distance through the bar. Interstitial sediments with low oxygen are often areas of denitrification, and thus regulate the nitrogen loads of some streams (Triska *et al.* 1993, Findlay 1995). Interstitial flow paths in the Hunter River were much longer than the 10-m flow path studied in Maple River (Hendricks and White 1991), giving more time for anaerobic conditions to develop, and for denitrification to become dominant.

SRP concentrations remained relatively constant with distance in the parafluvial and hyporheic habitats at all sites along the Hunter River (refer to Table 3.9). Like NOx, concentrations were often higher in the sediments than in the surface stream. This has also been observed in other streams, with concentrations in the hyporheic zone of Maple River almost triple those of the surface (Hendricks and White 1995), and Walker Branch and Panther Creek in Tennessee having nearly twice the SRP of surface waters (Hendricks and White 2000). The lack of any longitudinal trends with SRP in the Hunter River, may reflect the complex nature of this nutrient, which is affected by oxygen distribution, redox conditions, and the presence or absence of various ions such as iron or manganese (Boulton *et al.* 1998).

An alternative explanation for the observed lack of nutrient gradients could be a balance between bacterial production or mineralisation, and vegetative uptake, since all of the bars where NOx and SRP remained constant were well-vegetated during the study. Uptake by plant roots can substantially affect nutrient concentrations in hyporheic and parafluvial sediments (White and Hendricks 2000). Even in anoxic sediments, plant roots can provide enough oxygen to stimulate nitrification (Reddy *et al.* 1989). In the shallow sediments, where NOx and SRP concentration does not change with distance, plant use could be as rapid as bacterial production. In sediments that are high in nitrate and low in oxygen,

denitrifying bacteria allow the hyporheic zone to be a significant nitrate sink (Bradley *et al.* 1995). Parafluvial NOx at ABER, DENM, BOWM, and DIGH appear to have experienced a combination of plant and microbial absorption in the shallower sediments, allowing nitrification to continue at a fairly constant rate, whereas, in the deeper sediments, denitrification occurred. The role of vegetation in nutrient processes of regulated rivers is further complicated, since these rivers often have different vegetative patterns than unregulated streams (Jannson *et al.* 2000). Therefore, future research on the dynamics of Hunter River bar and riparian vegetation, with response to flow fluctuations and their nutrient demands, would further improve our understanding of hyporheic and parafluvial nutrient dynamics.

3.5.2 Seasonal patterns

Due to the intrinsic links between the stream and its interstitial surrounds, the seasonal patterns that influence surface water and terrestrial ecology affect hyporheic and parafluvial zones. In the Hunter River, hyporheic dissolved oxygen concentration was low in November at all sites except BOWM, MASO, and DIGH. Following the November flood, hyporheic dissolved oxygen at all sites except DSMG became more similar to that of the surface water. This may be a consequence of several factors resulting from the flood. Reduced biological consumption possibly occurred because of the abrasion of biofilm. In both a sand and gravel/pebble section of the Breitenbach, Germany, bacterial carbon production declined following a spate, probably from abrasion (Marxsen 2001). However, bacterial activity in the mobile upper sediments of the River Spree, where significant friction between particle surfaces presumably occurred, was higher than that of less mobile, deeper sediments (Fischer *et al.* 2003). These contrasting observations indicate that bacterial activity in hyporheic zones differs between streams, but they also raise the point that an additional factor, other than abrasion, might be contributing to decline in DO consumption in the Hunter River sediments.

Surface flow in November was low before the flood, so exchange between the surface and hyporheic zone would have been minimal, whereas after the flood, higher hydraulic head enhanced the exchange with surface water. Additionally, following the flood, new gravel was deposited over the bed of the stream at all sites. It is likely that the loose packing of this gravel allowed the oxygen-rich water to pass through it more readily.

In the Rhône River, hyporheic bacterial activity was highest in the warmer months, and this led to decreases in DO and to DOC immobilisation (Claret *et al.* 1998). During summer, the increased activity led to anoxic conditions and promoted denitrification (Claret *et al.* 1998). Since many metabolic processes in the hyporheic zone rely on inputs of organic matter from external sources, seasonal inputs of deciduous leaves can also influence the interstitial environment. The addition of leaves to the hyporheic zone of Hugh White Creek, North Carolina, stimulated respiration in the sediments, increasing the retention rates of many solutes (Crenshaw *et al.* 2002). Net nitrate fluxes from a gravel bar in McRae Creek were lowest in summer, and highest in autumn, especially following a spate (Wondzell and Swanson 1996).

In Sycamore Creek, microbial nitrification re-established 60 days after a flash flood (Holmes *et al.* 1998). All parafluvial NOx concentrations in the Hunter River were high in November, except at BOWM. Flow remained high for two months after the November 2000 flood, and for the remainder of the study parafluvial NOx concentrations remained lower than they were in November. However, at all sites except BOWM, concentrations after the November flood resembled those before it, so in the long term at least, nitrifying bacteria appeared neither to be stimulated by the flood, nor impaired by it. The absence of any stimulation of nitrification contrasts with the observations of Jones *et al.* (1995), who observed nitrification rates immediately following the flood had increased more than ten-fold later in succession. Apart from BOWM and MOSE, NOx concentrations in the hyporheic zone mirrored the parafluvial patterns. High river stage prevented sampling sooner after the flood, so short term NOx responses to the flood could not be assessed. NOx concentrations may have declined immediately following the flood, then recovered as the sediment matrix stabilised and allowed the microbiota to re-colonise.

NOx at BOWM peaked in autumn with concentrations approximately 7 times the surface water concentration in the downwelling area of the riffle, and more than 10 times surface concentration at 10 m along the bar. This may be due to an increase in allochtonous carbon in the sediments, which could have stimulated bacterial activity. Hyporheic nitrogen was also highest during autumn in McRae Creek, Oregon (Wondzell and Swanson 1996).

The strong hydrothermal gradients that occurred between the surface stream and the hyporheic zone of Maple River during winter and summer contributed to increases in interstitial SRP concentration (Hendricks and White 1995). However, in the Hunter River there were no observable temporal patterns in SRP consistent across all sites with season. The two sites with coarse sediments, ABER and DENM, had high SRP concentrations in May 2000. SRP usually declined with each sampling occasion, except for November before the flood. High phosphate concentrations are often found when DO is low (Hendricks and White 2000), so in the Hunter River we might expect higher concentrations in November. Of the other sites, DSMG, MASO, and DIGH all had highest SRP concentrations in November. Thus, SRP appears to accumulate in the sediments at these sites as surface flow decreases. Contrary to all other sites, SRP concentration at MOSE peaked in February, following the flood. NOx concentration was also high, so perhaps this was due to the flood burying large amounts of organic matter, which subsequently decomposed in the sediments. This would also explain the low DO content here.

3.5.3 Invertebrate community structure

The results of this study supported previous findings (Boulton 2000a) that sites along the Hunter River have hyporheic zones that are both microbially active and rich in invertebrate taxa. The Hunter River has a diverse hyporheic fauna of 71 invertebrate taxa. Flathead River in Montana had a comparable number of species, with more than 70 taxa collected from the hyporheic zone (Stanford *et al.* 1994). Of the hyporheic invertebrates found in the Hunter River, 10 crustacean taxa (including members of three syncarid families – Parabathynellidae, Psammaspididae, and Bathynellidae) were hypogean. This is fewer than the 38 hypogean taxa recorded from the regulated Rhône River in France (Dole-Olivier *et al.* 1994). However, the taxonomy of Australian hypogean invertebrates

is much less well known than those of other areas (Hahn 2002), and the broad groupings used in the current study are likely to envelope several species, possibly bringing the hypogean fauna of the Hunter River to a similar richness as the Rhône.

Perhaps one of the reasons why there is such a taxonomically diverse hyporheic zone in the Hunter River is because, despite the presence of Glenbawn Dam, the river level is still able to fluctuate regularly. Although it stops much of the flow in the higher reaches of the Hunter River, Glenbawn Dam is upstream of the confluence with the Pages River, Rouchel Brook, and several other tributaries. These tributaries supply a variety of sediment and fluctuating flows. During the period of this study a large flood occurred that scoured much of the bed of the river and then subsequently re-deposited sediment. As well, irrigation flows, and water releases for power stations provide regular fluctuations. As will be seen in Chapter 6, only small fluctuations in flow are required to stimulate hyporheic and parafluvial microbial activity, so perhaps these flows, combined with less frequent medium to large events have enabled the hyporheic community of the Hunter River to maintain some of its original biota, though it is impossible to know how diverse this was.

Generally, all of the sites contained a diverse hyporheic fauna made up of both stygophiles (species which occur in surface and groundwaters but have no adaptations to subterranean life – Marmonier *et al.* 1993), and stygobites. The presence of stygofauna in the hyporheic zone signifies the linkages between the stream and groundwater. Along bars and riffles, taxonomic richness was highest in the shallow downwelling zone of the riffle because of high numbers of insect larvae. By far, the most abundant taxa in all habitats were oligochaetes and cyclopoids, which dominated samples at all sites. Parastenocarid harpacticoids were also abundant in sites upstream of DSMG, but became less dominant at sites downstream. The three syncarid families of the Hunter River were most common at ABER and DENM. This may be in part due to the relative coarseness of the substrate, since members of the family Psammaspididae, which were found in the Hunter River, are often found in coarse sediments (Coineau 2000). The small Parabathynellidae occurred in moderate numbers at Sandy Hollow on the Goulburn River, a tributary of the Hunter River, but this is not surprising since members of this family occur mostly in fine substrates (Coineau 2000).

Following the November flood, hyporheic habitats at all sites had high invertebrate abundance and high taxonomic richness. At all sites in the Hunter River, the taxa responsible for the increased invertebrate numbers were all copepods; harpacticoids at ABER and DENM, parastenocarids at BOWM, cyclopoids and parastenocarids at MOSE and DIGH, and harpacticoids and cyclopoids at MASO. Similarly, higher discharges in the Acheron River in Victoria during winter and spring encouraged vertical migration of epigean taxa deeper into the hyporheic zone (Marchant 1995). Small-scale (1.5 – 3.5 cm) downward movements of copepods were observed in response to increased flow velocity during a test of the hyporheic refuge hypothesis in a sand-bed stream in Virginia, USA (Palmer *et al.* 1992). The authors concluded that such small-scale migrations were not significant enough to prevent substantial losses of fauna during floods. Similar loss of fauna was observed following a flood in the Elklick Run (Angradi *et al.* 2001). However, the current study suggests that the hyporheic zone may provide at least some refuge to copepods. It is uncertain whether the copepods actively migrated in search of shelter, or food, or were passively transported by water. Because populations were still elevated two months after the flood, it can be postulated that the copepods moved actively into the sediments and that conditions there were more favourable than on the surface. However, during February, stream level was still receding from the November flood, so invertebrates might have been using the interstitial habitat as a refuge from flow.

Hyporheic zones with coarse substrate and larger pore-spaces often contain more invertebrates than fine sediments (Hakenkamp and Palmer 2000, Gayraud and Philippe 2001). In 14 hyporheic sites scattered along the eastern United States, invertebrate densities of some taxa were higher in corse sediments than in fine sediments, with most taxa occurring less frequently in fine sediments (Strayer *et al.* 1997). This was the case in the Hunter River, with ABER and DENM commonly yielding 10 or more taxa and being richer than the other sites. Except for DIGH, taxonomic richness decreased with distance downstream. This may have been a product of the substrate becoming increasingly sand-dominated downstream of the Goulburn River confluence, with smaller pore-spaces for invertebrates to inhabit, or it may be that sandy sediments are less stable than coarser sediments, and more prone to scouring.

The number of invertebrates correlated positively with DO concentration in all of the bars except BOWM. Oxygen is an important factor in influencing hyporheic communities, with oxygen-rich sediments often having more epigean fauna than anoxic sediments. Strayer *et al.* (1997) found that some taxa, mostly epigean insect larvae, rarely occurred in sediments with low dissolved oxygen. However, in the hyporheic zones below riffles in the Hunter River, only invertebrate abundances at MOSE, DIGH, DSMG and DENM were correlated to oxygen concentration. Despite being important for epigean hyporheic taxa, low oxygen concentration does not appear to be a factor that limits the distribution of some stygofaunal species (Strayer 1994), so this may explain why oxygen concentration did not always correlate with invertebrate abundance.

3.5.4 Hyporheic ecosystem services

Filtration efficiency is a measure of the rate at which dissolved nutrients and physico-chemical variables of a parcel of water are transformed during a period of interstitial flow. To assess filtration efficiency, key indicators, such as DO and NOx concentrations can be measured along subsurface flow-paths. Rapidly declining oxygen concentrations, indicate the presence of interstitial microbial activity, a key component of hyporheic filtration. Similarly, a corresponding increase in nitrogen oxides (NOx) to a point where oxygen becomes limiting, then a subsequent drop in NOx concentration as anaerobic bacteria dominate, can also be indicative of efficient hyporheic filtration.

This study indicates that filtration efficiency appears to be strongly linked to sediment size, with the sites dominated by coarse sediments (ABER and DENM) having the most efficient filters. A reason for this is that larger sediments are more stable than sandy sediments. This makes them less susceptible to the loss of bacteria by abrasion. The abrasion of bacteria from a sand-bed stream in Arizona temporarily reduced bacterial numbers in the parafluvial zone following a flash flood (Holmes *et al.* 1998). Stability in gravel beds also means that they are able to maintain a steeper grade than sand-bed streams (Matthai and Townsend 2000), and therefore allow water to pass through the sediment interstices rather than moving the sediments. However, the analysis of frozen sediment cores showed a higher amount of fine sand at ABER than at MOSE and BOWM (Chapter 5) so the coarseness of the sediments may not be the sole reason for the high filtration ability.

Although small in comparison to the bars at the other sites, the bars at ABER and DENM showed the best potential for hyporheic filtration. Parafluvial and hyporheic nutrient levels were higher than those of surface waters but they never reached concentrations above 400% as they did at other sites. There was extensive microbial transformation to NOx and SRP, but these nutrients did not accumulate in the sediments. There are three likely explanations for this. First, anaerobic processes such as ammonification, denitrification or mineralisation could be removing the nutrients from the water. The potential for nitrogen removal by the hyporheic and parafluvial habitats can moderate the effects of high nitrogen in some streams (Triska *et al.* 1993). Denitrification is an important process in stream nitrogen budgets, and in oxygen-rich streams the hyporheic and parafluvial habitats play important roles here (Findlay 1995). Second, both bars supported extensive herbaceous vegetation, and both riffles contained growths of macrophyte. To aquatic plant species that rely on these roots to obtain the majority of their food, interstitial water can be an important source of nutrients (White *et al.* 1992). Therefore, vegetative use by plants in the Hunter River could have offset nutrient accumulation in the interstitial water.

However, a third explanation could be due to a combination of the geomorphological structure of the bar, sediment heterogeneity, and bacterial activity. Because it had a high proportion of fine sediments, the bed at ABER was less porous than that of BOWM and MOSE (averaging 14.8 to 16.3 % compared to 16.6 to 21.7 % - Chapter 5). However, the bars at ABER and DENM were short in comparison to the bars at other sites, and water and nutrients would have spent less time travelling through the interstices so that nutrients, once transformed, were readily removed. Additionally, the coarser substrate provided a more stable bed, allowing a higher degree of hydraulic sheer stress before bed-movement. This allowed water to infiltrate and move through the sediments with more force. The high proportion of fine sediments would also have increased the overall surface area that was available for microbial activity, further increasing the filtration efficiency.

Findlay (1995) recognised that contact time between interstitial water and the sediment surface area was an important factor in determining the hyporheic contribution to stream metabolism. Water moving through active sediments, where biogeochemical processes are high, will contribute more to stream metabolism than water moving through inactive

sediments. Additionally, for sediments with low flow velocities and long flow paths, even moderate activities can result in marked changes in water chemistry (Findlay 1995). Bar size and shape are crucial to subsurface nutrient processing. More nitrate will be generated by a short, compact bar than a long, thin one of the same area because a greater proportion of the bar occurs in the head (Fisher *et al.* 1998). The filtration efficiency at DENM and ABER was higher than at other sites. However, all of these sites, with the exception of DSMG, had extensive parafluvial habitats with a much greater stream/parafluvial margin, so although not as efficient as DENM and ABER, these sites had larger contact areas, where oxygen-rich surface water was available for bacterial transformation in shallow sediments. Behind the active area of these large parafluvial bars were large transient storage areas where anaerobic processes like denitrification, ammonification, or mineralisation possibly occurred. This physical bar structure may allow for a larger volume of water to be filtered, and for the hyporheic and parafluvial zones at these sites to still contribute significantly to in-stream metabolism.

At BOWM and MOSE, filtration in the riffle hyporheic zone was limited. There was little transformation of nitrogen or phosphorus with depth or distance in the riffle at all times, except in August at BOWM, and February at MOSE. In contrast to this, NOx concentrations along the bars did change. Apart from the high concentrations in August at BOWM, NOx concentration at both sites initially increased and then fell, before increasing steadily with distance. The first 20 m of these bars were moderately efficient filters, but both bars were more than 700 m long and 110 m wide, so their potential to affect stream metabolism is substantially large as long as water exchange is maintained or enhanced by fluctuating flows.

Nutrient concentrations in the riffle at DSMG also remained constant with depth but declined with distance, indicating that the majority of microbial activity occurred in the upper sediments supporting the findings of Battin (2000) and Deal *et al.*(2000). The hyporheic sediments at DSMG were more effective at transforming NOx than SRP. Parafluvial filtration at DSMG was moderate, with nutrient patterns consistent with those in the model proposed in section 3.1.1 (i.e., NOx and SRP increase in oxygenated sediments, and decrease as oxygen is consumed). Nitrification and SRP accumulation along the first 5 m of this small bar appear to have been significant and these findings

contrast with the initial conclusion of poor filtration at this site (Boulton 2000a).

MASO and DIGH both had high interstitial concentrations of NOx and SRP. However, neither of these sites displayed any significant change in nutrient concentration with distance along flow paths in either the riffle or the bar. Therefore, the majority of filtration appears to have occurred in the initial 20 – 30 cm. At DIGH, extremely high NOx concentrations occurred in the bar during November, reflecting the accumulation of the nutrient in the sediments, perhaps due to a slowing of the denitrification process. However, concentrations were only slightly less in February so the flood appears to have had little flushing effect here despite there being obvious bed-movement due to the flood. Alternatively, the flood may have flushed NOx from the bar, stimulated nitrifying microbial activity, and concentrations may have recovered before the first post-flood sampling. MASO also had accumulated high NOx in the parafluvial zone in November, but this was probably flushed by the November flood. Nitrogen fluxes from a gravel bar into McRae Creek, Oregon were highest during storms when flow was at its peak (Wondzell and Swanson 1996).

3.6 Summary and conclusions

Studies on hyporheic contributions to whole-stream nutrient budgets should consider a number of hierarchical scales. This study showed that while significant nutrient transformations occur at the site scale, it is not until the cumulative effect of several bars along a river is considered, that the net impact of interstitial nutrient retention or transformation can be appreciated. Temporal variation is also an important consideration here, since hyporheic zones can at one time be a net nutrient producer, and at another a net nutrient sink. All of the sites sampled for this study had active and dynamic hyporheic and parafluvial zones, and individually contributed to the overall nutrient budget of the river. Because the hyporheic processes varied among sites and among seasons, it is important that a range of temporal and spatial scales be sampled when attempting to obtain a picture of whole-stream hyporheic activity.

Seventy-one invertebrate taxa were collected from the sediments, comprising temporary hyporheic, permanent hyporheic, and true groundwater species. Of these, at lease two species of syncarid, and three species of mites are new to science. The occurrence of

stygobitic species at all seven sites indicates that the Hunter River is intrinsically linked to groundwater aquifers.

Generally, parafluvial zones were better transient storage areas for nutrients than hyporheic zones, probably because water percolated through the sediments at a slower rate. Declining concentrations of dissolved oxygen indicated an active microbial community that effectively filtered NOx and SRP from the water. Although filtration efficiency decreased, the potential for hyporheic and parafluvial zones to influence stream nutrient dynamics at a river scale generally increased with distance downstream. Consistent with the model (Figure 3.1), the upper 40 cm of sediments appeared to be the most active area of SRP and NOx transformation. ABER and DENM were the most efficient filters, with a relatively stable bed and potentially high through-flow of water. Next were BOWM and MOSE, which, despite having only limited nutrient transformation in the riffles, had moderate filtration in large bars. Changing nutrient concentrations in the hyporheic and parafluvial habitats at DSMG indicated that this site was an effective filter with an active microbiota. The hyporheic and parafluvial habitats at DIGH and MASO had higher SRP and NOx concentrations than the surface water, but these did not change with distance along the bar, or between downwelling and upwelling habitats of the riffle. Therefore the majority of nutrient transformation occurred in the upper 40 cm. A combination of large (to provide stability) and small (to increase surface area and contact time between water and bacteria) sediments in the hyporheic or parafluvial zones appeared to increase the hyporheic filtration ability of a site.

This chapter established the presence of diverse hyporheic ecology and highlighted the importance of hydrological exchange between the river and hyporheic zone. It also accentuated the importance of sediment grain size on many hyporheic biological and chemical processes. In the next chapter, the hyporheic zones of two sand-bed tributaries of the Hunter River are investigated and compared to those of some sites with coarser substrates.