

# Application of the functional habitat concept to the regulated Lower Ord River, Western Australia, Part I, macroinvertebrate assemblages

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**Abstract** This paper tests the applicability of the Functional Habitat Concept (FHC) to a lowland tropical river in Australia. The underlying tenet of the FHC is that in-stream hydrological and physical processes form distinct habitats, and where these habitats support distinct macroinvertebrate assemblages they are considered ‘functional’ habitats. This concept has been employed in the northern hemisphere as a tool for river restoration and management, especially where habitats are easier to manage than species, but the FHC has yet to be tested in Australia. This study reports the application of the FHC to the regulated Lower Ord River (LOR) in the remote far north of Western Australia. Seven ‘potential’ in-stream habitat units were identified on the basis of their physical properties. Multivariate and species preference analysis of macroinvertebrate data indicated that these habitats supported six distinct macroinvertebrate assemblages, provid-

ing six ‘functional’ habitats (gravel runs and rock rapids, sand margins, mud/silt margins, flooded riparian vegetation, emergent vegetation, and submerged macrophyte beds). Macroinvertebrate preferences for particular habitats reflected the broad ecology and life-history characteristics of the species, which in turn reflected the physical attributes of the habitats. We argue that in a region where the fauna has been little studied, and for which there is little ecological information, the FHC is a valuable approach. For a river that is facing increased water abstraction, the FHC potentially aids in the preservation of macroinvertebrate diversity as it identifies critical functional habitats for managers to maintain.

**Keywords** Functional habitats · Macroinvertebrates · River management · Physico-chemistry · Mesohabitats

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## Introduction

Rivers in the remote north of Australia are relatively free from the pressures of development affecting those in the south of the continent (i.e. impoundment, regulation, abstraction and diversion) (WRC, 1997). However, in a drying climate (CSIRO, 2001), there is mounting pressure to develop these rivers, particularly for irrigated agriculture (Storey & Trayler, 2006). The tyranny

of distance from major population centres also means that these northern systems have been seldom studied, with relatively little known of their ecologies. As a result, river managers have a poor knowledge base on which to make decisions, such as determining environmental flows (Trayler et al., 2002; Storey & Trayler, 2006). Gathering the necessary ecological information can be a time consuming exercise, and in the face of development, an alternative approach is required. Working at the habitat level may be such an approach.

The process of dividing streams into habitat types is widely used in restoration ecology, biological monitoring and fishery management, and this practice is based on the acceptance of the assumption that habitats have some consistent biological meaning, and working at the habitat level will “make [the system] easier to study, understand or manage” (Rabeni et al., 2002). The acceptance of the linkage between habitat and biota is well entrenched in theoretical ecology (see Rabeni et al., 2002 and references therein), to the point where habitat is used as a surrogate for the biota; with management of habitats being the ultimate goal. As reported by Kemp et al. (2000), mesohabitats are proving useful for river survey, management and rehabilitation, as they provide a rapid and effective source of information of sufficient detail to assess the ecosystem without the need for painstaking identification of macroinvertebrates or complex hydraulic modelling.

As noted by Kemp et al. (2002), biological communities of rivers have been well studied over many years by ecologists, as have the processes and dynamics of channel morphology and hydraulics by hydrologists and geomorphologists. But, it is only in recent years that these parallel fields in stream ecology and geomorphology have been linked, especially in relation to habitats (Pardo & Armitage, 1997; Harper & Everard, 1998; Kemp et al., 1999; Buffagni et al., 2000; Kemp et al., 2002; Sullivan et al., 2004).

The role physical river processes have in shaping in-channel habitats, and in turn, affecting macroinvertebrate communities is also well studied (Pardo & Armitage, 1997; Buffagni et al., 2000; Kemp et al., 2000; Newson & Newson, 2000;

Tickner et al., 2000; Brunke et al., 2001; Sullivan et al., 2004; Brooks et al., 2005). The distribution and diversity of aquatic invertebrates, for instance, can be influenced by water depth, water velocity, and substrate type (i.e. Wetmore et al., 1990; Gore & Judy, 1981; Orth & Maughan, 1983; Pardo & Armitage, 1997; Statzner et al., 1988; Harper et al., 2000; Kemp et al., 2000; Rempel et al., 2000; Brunke et al., 2001; Brooks et al., 2005). Furthermore, Newson & Newson (2000) suggest that physical aspects of in-stream habitat dominate biotic responses in regulated rivers and those modified by engineering design. This is possibly because regulated rivers are subject to changes in flow regime, and, of the physical aspects of in-stream habitat, flow velocity, in particular, has been found to determine the spatial distribution and abundance of macroinvertebrates (i.e. Barmuta, 1990; Pardo & Armitage, 1997; Statzner et al., 1988; Kemp et al., 2000; Newson & Newson, 2000; Jowett, 2003; Brooks et al., 2005). Since river habitats are influenced by geomorphological processes (Harper & Everard, 1998), they are sensitive also to anthropogenic disturbance, such as flow regulation, and thus are an important focus for river management (Armitage et al., 2001).

One of the products of the collaboration between ecologists and hydrologists has been the Functional Habitat Concept (FHC), which grew out of the known association between the quality of in-stream habitats and the diversity of species they support (Harper & Everard, 1998; Newson & Newson, 2000). The concept is based on the assumption that conserving habitats ultimately conserves biodiversity (Tickner et al., 2000; Rabeni et al., 2002). As summarised by Buffagni et al. (2000), habitats that are recognisable from simple visual survey are termed ‘potential habitats’. Where the numerical analysis of the faunal assemblages of these habitats produces an objective classification of habitats which support different assemblages of invertebrates, these are then regarded as ‘functional habitats’. Although their definition is based on structural aspects of the benthic community, the term functional habitats recognises how important, for river processes, ecological ‘health’ and diversity of biota, the presence or absence of the various

functional habitats might be (Buffagni et al., 2000).

The FHC is based on the premise that it is possible to manage habitats in rivers far more easily than it is to manage species (Armitage & Pardo, 1995; Kemp et al., 2000; Buffagni et al., 2000; Tickner et al., 2000), particularly in species rich systems, and those where little is known of the life history or ecological requirements of individual species (Armitage & Pardo, 1995). Since its development, the FHC has gained acceptance and is being employed in the northern hemisphere to more clearly detect the effects of lowland river regulation over more conventional biological assessment techniques (Armitage & Pardo, 1995). It has been used as a basis to establish cost-effective monitoring programs for improved river management (Buffagni et al., 2000), to maximise habitat heterogeneity and therefore biodiversity in river rehabilitation projects (Kemp et al., 2000), and in the assessment of the impact of flow reduction on lotic fauna (Brunke et al., 2001).

To date, however, the FHC has not been applied in Australia. The efficacy of this tool in river management in Australia will largely depend on the presence of discrete, easily recognisable physical habitats that support distinct suites of macroinvertebrates (*sensu* functional habitats; Armitage & Pardo, 1995; Pardo & Armitage, 1997; Kemp et al., 1999, 2000; Buffagni et al., 2000; White & Irvine, 2003).

The Ord River, in the remote north of Western Australia presented an opportunity to trial the FHC. Currently, approximately 90% of the catchment area is impounded to provide water for irrigated agriculture and for the generation of hydroelectric power. There are plans to more than double the area under irrigation, which could triple water demand. If this increased demand were to be met, it would mean a reduction in the amount of water for the environment (Storey & Trayler, 2006). The State agency responsible for river management was tasked with developing an environmental flow for the river, but with little understanding of its ecology (Trayler et al., 2002, Storey & Trayler, 2006). Preliminary surveys revealed a diverse macroinvertebrate fauna, but with many undescribed species, and a paucity of ecological or life history information (Storey & Trayler, 2006).

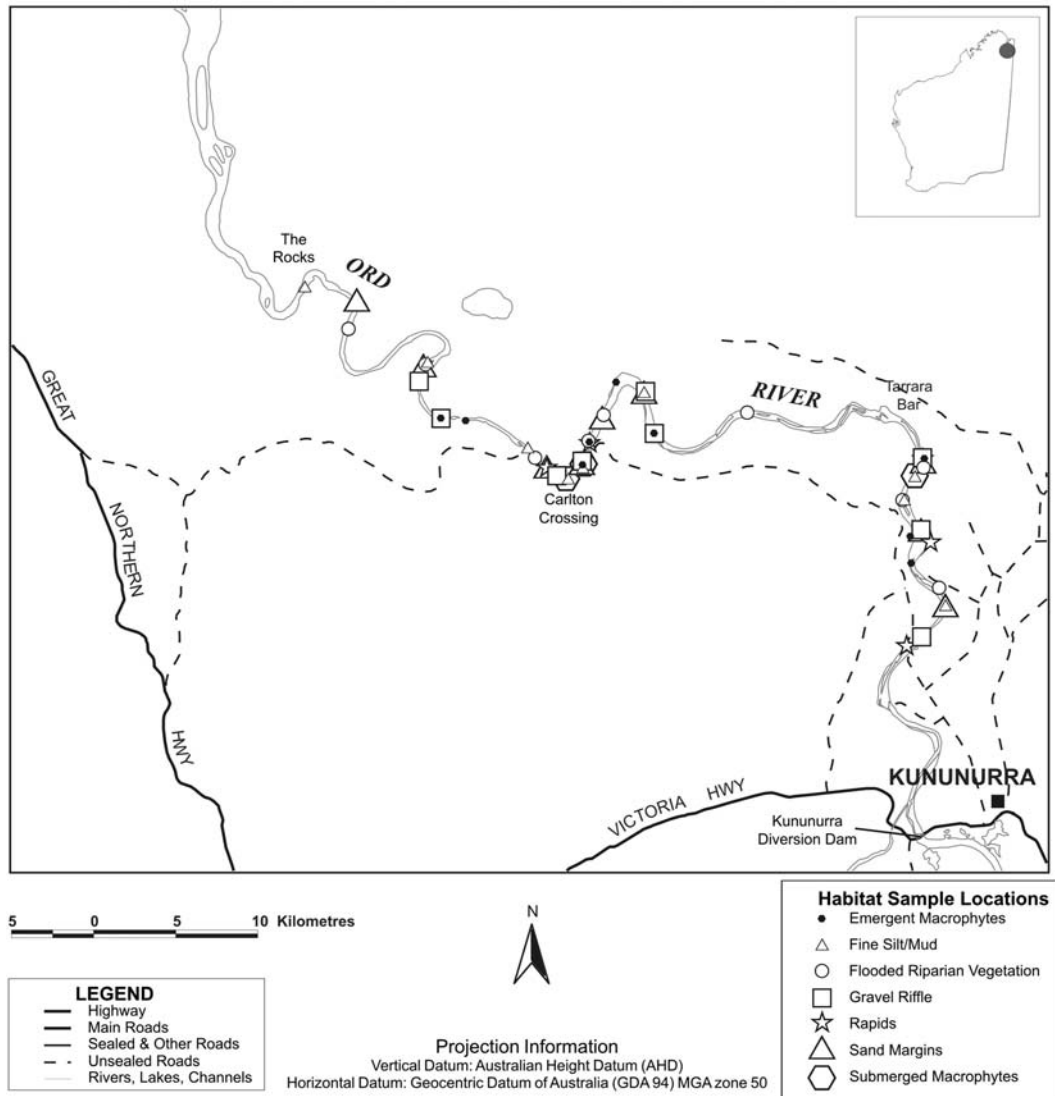
Therefore, the FHC was seen as a means to manage this system. Prior to applying the FHC to the Lower Ord River (LOR), it was necessary to test the underlying tenets of the approach; to determine the existence of easily recognisable habitats within the system and the extent to which they support distinct macroinvertebrate assemblages.

## Methods

### Study area

The Ord River, located in the East Kimberley region of Western Australia (Fig. 1), is one of the state's major river systems, around 650 km long, with a catchment area of 46,100 km<sup>2</sup>. Pre-dam, it had a mean annual discharge of 4 500 GL, and the largest recorded instantaneous flow was approximately 30,800 m<sup>3</sup>/s (1956). The climate is semi-arid to arid monsoonal with two distinct seasons: a warm, dry season (May to October) and a hot, wet season (November to April). Monsoonal depressions and tropical cyclones are responsible for the vast majority of annual rainfall (approx, 870 mm p.a. at Kununurra), with 90% falling during the 'wet' (Trayler et al., 2002).

The Ord River is impounded by the 13.7 m high Kununurra Diversion Dam (KDD), which forms Lake Kununurra, and the 98.5 m high Ord River Dam (ORD) 55 km upstream, which forms the much larger Lake Argyle (surface area 74,000 ha and storage of 10,700 GL). Water is released via the ORD into Lake Kununurra to provide a hydraulic head to feed water to irrigation paddocks. Water is also released from the KDD to maintain flows in the LOR. Regulation has so altered the flow regime that the system has effectively been transformed from a seasonally-flowing to a permanent river. There is now constant flow in the LOR during the dry season, and this security of water in a seasonally dry landscape means the system supports a greater abundance and diversity of fish and bird species than would historically have been present (Storey & Trayler, 2006). Small but important recreational and commercial fisheries have developed subsequent to regulation, as has the listing of two Ramsar wetlands of international importance.



**Fig. 1** Location of the study sites along the Ord River, northwestern Australia

The area is also an important tourist destination for wilderness and wildlife experience. An increased allocation for irrigation will decrease mean dry season flows from the current  $\sim 80 \text{ m}^3/\text{sec}$  to approx  $40\text{--}45 \text{ m}^3/\text{sec}$ . This will result in an approximately 50 cm drop in current late dry season water levels. Modelling indicates that reduced discharge is likely to change the proportion of shallow and deep water habitats in the low-flow dry season, particularly the area of habitats along margins and shallows. However, there will be little effect on current wet season flows which are determined by high intensity

monsoonal and cyclonic rains and the seasonally flowing, but unregulated Dunham River which enters the LOR below the KDD, providing wet season high flows (Trayler et al., 2002).

The current study focused on the LOR, a meandering 70 km long lowland section between the KDD and the Ord River estuary. The channel is approximately 150 m wide and up to 5 m deep. Approximately 80% of the LOR consists of long (2–3 km), deep pools, interspersed by rock bar/boulder rapids and gravel/cobble runs. The pools are lined by a diversity of habitats, including shallow submerged macrophyte beds (predomi-

nantly *Vallisneria americana* Michaux), beds of emergent reeds/rushes (*Phragmites australis* (Cav) Trin. Ex Steud, *Typha domingensis* Pers), shallow backwaters, and shorelines of sand and silt. Riparian vegetation along the shoreline includes various riparian trees including silver cadjeput, *Melaleuca argentea* W. Fitz., cadjeput *Melaleuca leucadendra* (L.) L., river gum *Eucalyptus camaldulensis* Denh, freshwater mangroves *Barringtonia angulata* (L.) Gaertn., white dragon tree *Sesbania formosa* F. Muell., and pandanus palms *Pandanus aquaticus* R. Br (Doupé & Pettit, 2002). The river supports diverse fish (~30 species) (Storey & Trayler, 2006) and waterbird fauna (115 species of resident and migratory waterbirds and shorebirds) (Burbidge et al., 1991; Halse et al., 1996). It also supports large populations of freshwater *Crocodylus johnstoni* Krefft and estuarine crocodile *Crocodylus porosus* Schneider, both of which are protected. Due to the high risk of attack from the latter, all sampling was conducted from a boat and in relatively shallow areas (< ~70 cm). However, sampling intentionally targeted shallow habitats which were seen to be at risk from the anticipated changes in dry season flows as opposed to the deep pools.

### Field sampling

Sampling was undertaken during the late dry season (16–26th October) 2001, when conditions were hot (39–43°C) and humid, with occasional isolated thunderstorms, as is typical in the lead-up to the wet season. Although not gauged, discharge was very constant over the period, with depth changing <10 cm, as is typical for the end of the dry season. Seven visually discernible habitat types were identified: emergent macrophyte beds, submerged macrophyte beds, gravel runs, turbulent rock rapids, edges of coarse sand, edges of unconsolidated silts and muds (defined as inorganic material <250 µm), and flooded riparian vegetation along margins. Together, these mesohabitats dominated the wetted area of the main channel. Pools *per se* were not sampled as a distinct habitat, rather habitats within and between pools were sampled. Macroinvertebrate sampling was conducted using a standard 250 µm mesh net to kick/sweep over a discontinuous 10 m

area within each mesohabitat. Nine replicate samples were taken from each habitat type, with the exception of rapids ( $n = 5$ ) and submerged macrophyte beds ( $n = 8$ ), to make a total of 58 samples. Each replicate was taken from a distinct and separate occurrence of each habitat spatially stratified over approximately 25 km of river. Macroinvertebrate samples were preserved in formalin (30% w/w) and freighted to the Aquatic Research Laboratory at the University of Western Australia where specimens were removed, identified to species level (where possible) and enumerated to  $\log_{10}$  abundance classes.

To test how accurately the visually defined mesohabitats represented discrete habitat types, a range of environmental parameters were measured at each replicate site (Table 1). Water temperature, pH, dissolved oxygen, redox potential, electrical conductivity, salinity and turbidity were measured in situ using a Yeo-kal Model 611 multiprobe water quality analyser. Measurements were taken at the top (10 cm below the water surface) and bottom (10 cm above the river bed) of the water column and then averaged. Water velocity was measured with a Marsh-McBirney velocity meter, with velocity recorded at approximately 0.6 of water depth. Water depth was measured at ten randomly selected locations at each site with a graduated staff (<1.5 m) or a Garmin Model 135 GPSMAP sounder (>1.5 m) and location of sites recorded with the Garmin GPS. The percent cover at each site of different substrate particle size classes (silt =  $\phi$  6.5, sand =  $\phi$  2.0, gravel =  $\phi$  - 2.0, pebbles =  $\phi$  - 4.5, cobbles =  $\phi$  - 6.5, boulders =  $\phi$  - 9.0), and vegetation types (submerged, flooded riparian and emergent) were estimated visually. Mean particle size was calculated as the mean  $\phi$  value weighted by the percentage cover of each mineral substrate type following the method described by Storey et al. (1991). As an indication of habitat heterogeneity, the number of organic and inorganic substrate types represented at each site was totalled.

### Data analysis

Amongst habitat differences in measured environmental parameters were tested by one-way ANOVA. Prior to analysis, appropriate transformations

**Table 1** Measured and derived physico-chemical parameters, giving names and units of measurement

Type	Parameters	Unit
Phys/Chem parameters	pH top	#
	pH bottom	#
	Mean pH	#
	Conductivity	μS/cm
	Salinity	mg/l
	Turbidity top	ntu
	Turbidity bottom	ntu
	Mean turbidity	ntu
	Temperature top	°C
	Temperature bottom	°C
	Mean temperature	°C
	Redox top	#
	Redox bottom	#
	Mean redox	#
	Mean velocity	cm/s
	Mean depth	cm
	Variance in depth <sup>a</sup>	cm
	Dissolved oxygen top	%
	Dissolved oxygen bottom	%
	Mean dissolved oxygen	%
Inorganic substrate <sup>b</sup>	Oxygen concentration top	mg/l
	Oxygen concentration bottom	mg/l
	Mean oxygen concentration	mg/l
	Bedrock	%
	Boulders	%
	Cobbles	%
	Pebbles	%
	Gravel	%
	Sand	%
	Silt	%
	Clay	%
	Mean particle size <sup>c</sup>	
	Organic substrate <sup>b</sup>	Mineral
Emergent macrophyte		%
Submerged macrophyte		%
Algae		%
Detritus		%
Riparian vegetation		%
Large woody debris		%
Other (i.e. root mats etc)		%
Description	Habitat diversity <sup>d</sup>	#
	Riparian cover	%
	Substrate compaction	1–5

<sup>a</sup> Variance in depth was taken as the variance in multiple depth measurements ( $n = 10$ ) taken at each site, averaged across sites

<sup>b</sup> Percent cover of each site by inorganic and organic substrates were estimated visually

<sup>c</sup> Mean particle size calculated as the mean phi value weighted by the percentage cover of each mineral substrate type (clay = phi 9.5, silt = phi 6.5, sand = phi 2.0, gravel = phi - 2.0, pebbles = phi - 4.5, cobbles = phi - 6.5, boulders = phi - 9.0). Where bedrock was present, it was given the same phi value as boulders

<sup>d</sup> Habitat diversity calculated as the total number of organic and inorganic substrate types present

were applied to conform with the assumptions of the test (equality of sample variances). Tukey's HSD multiple range test was applied to locate between-habitat differences where there was a significant main effect. Where multiple tests were performed, a Bonferroni correction was applied to minimise the chance of Type I errors, whereby critical  $P = (0.05/n)$ , where  $n =$  number of tests performed. The same analyses were used to test for amongst habitat differences in macroinvertebrate species richness.

Environmental and macroinvertebrate community data were then analysed using multivariate procedures from the PRIMER (v5) software package (Clarke & Gorley, 2001). Replicate samples were ordinated using Multi-Dimensional Scaling (MDS) (Clarke & Warwick, 2001). Environmental data were standardised within the program so all parameters were on the same scale. Macroinvertebrate data were analysed using log<sub>10</sub> abundance classes with infrequently occurring species (i.e. species occurring in <10%

of samples) omitted from the ordination analysis to avoid ‘low-occurrence’ taxa having a disproportionate effect on the results (Gaugh, 1982; Belbin, 1995). The Bray-Curtis similarity coefficient was used to produce the similarity matrix for both datasets. Samples within each ordination were labelled according to *a priori* habitat types. The ANOSIM routine within PRIMER was used to test the significance ( $P < 0.05$ ) of the separation of habitat types in MDS ordination space. Unless indicated, default values or procedures otherwise recommended in the PRIMER (v5) User Manual (Clarke & Gorley, 2001) were employed. Species habitat preferences were examined using both Chi-squared contingency table analysis and the SIMPER (similarity percentage) routine within PRIMER. Chi-square was applied at the species level, but only to those species with sufficient levels of occurrence within and across habitats to allow valid analysis, as determined by the SAS statistical package (SAS, 1999). Deviation of the observed from the expected frequency (i.e. the preference of a species for a habitat type) was taken as significant if  $P < 0.05$ , and when significant, those species occurring in  $\geq 75\%$  of samples from a habitat type were considered to show a preference for that habitat. The relationship between the environmental and biotic data was then assessed using the BIOENV routine within PRIMER to calculate the smallest subset of environmental variables that explained the greatest percentage of variation in the taxa ordination pattern.

## Results

### Environmental descriptors of habitats

Significant between-habitat differences were detected for 19 of the 42 measured and derived environmental variables after application of a Bonferroni correction (Table 2). These included the physical attributes of water depth, stream velocity, sediment composition, cover by organic substrates (viz. submerged and emergent vegetation, detritus, woody debris etc) and degree of sediment compaction. No significant differences were recorded for any of the measured

chemical parameters generally indicative of water quality (i.e. pH, conductivity, turbidity, temperature, redox and dissolved oxygen). This suggested that waters were well mixed across habitat types. Many of the between-habitat differences were intuitive and reflected the readily observed physical differences that were used to characterise habitat types in the first instance. For example, percentages of boulder and cobble substrates were highest in rapid habitat, pebble and gravel substrate was greatest in gravel habitat, sand in sand habitat, and silt in mud/silt habitat (Table 2).

MDS ordination of samples on environmental parameters separated the seven mesohabitats into six groups, with gravel runs and rapids not significantly different from each other (Fig. 2; ANOSIM Global  $R = 0.408$ ; significance level of sample statistic = 0.1%, i.e.  $P = 0.001$ ).

### Macroinvertebrate assemblages within habitats

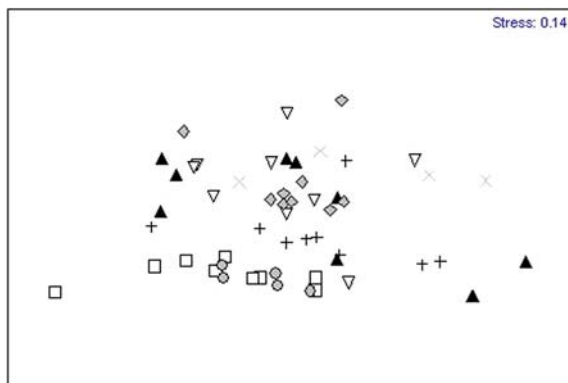
A total of 171 taxa of macroinvertebrates were recorded from the samples collected across all habitat types. Insecta comprised 80% of the taxa recorded, with the remaining 20% consisting of Mollusca, Annelida, Crustacea and Arachnida. The Insecta were dominated by Coleoptera (48 taxa), Chironomidae larvae (30 taxa) and Hemiptera (18 taxa). Generally, most taxa were distributed along the length of the LOR, with the exception of nereid polychaetes and the freshwater crab *Austrothelphusa* sp (family Parathelphusidae), which were only occasionally recorded from the most downstream freshwater, but tidally-influenced reach.

Taxa richness differed significantly among mesohabitats (Table 3 and Fig. 3). Emergent macrophyte, submerged macrophyte and rapid habitats supported the greatest number of taxa, while sand and mud habitats supported the fewest. MDS ordination on macroinvertebrate abundance data also showed a strong grouping of samples according to mesohabitat (Fig. 4). Analyses indicated distinct macroinvertebrate assemblages amongst all mesohabitats (ANOSIM, Global  $R = 0.575$ ; significance level of sample statistic = 0.1%), with the exception, once again, of gravel runs and rapids. Spatial variation in community structure was most strongly correlated

**Table 2** One-way ANOVA comparing differences in physico-chemical parameters amongst habitat types

Parameter	<i>P</i>	Tukey's HSD multiple range test						
Mean velocity (log10)	<0.0001	R (60.44)	G (57.30)	S (10.29)	E (9.65)	F (7.18)	M (2.65)	SM (1.71)
Mean depth (log10)	<0.0001	F (1.92)	E (1.33)	SM (0.38)	G (0.24)	S (0.23)	R (0.22)	M (0.20)
Variance in depth (log10)	0.0011	F (0.56)	E (0.21)	SM (0.02)	G (0.003)	S (0.002)	R (0.002)	M (0.002)
Boulders (log10)	<0.0001	R (56.6)	E (6)	F (1.10)	M (0)	G (0)	S (0)	SM (0)
Cobbles (log10)	<0.0001	R (27.70)	G (15.55)	E (7.67)	F (1.67)	M (0)	S (0)	SM (0)
Pebbles	<0.0001	G (56.56)	R (10.50)	E (4.78)	F (3.33)	SM (1.25)	S (1.11)	M (0)
Gravel	<0.0001	G (18.44)	E (4.78)	R (3.80)	F (3.33)	SM (1.87)	S (1.11)	M (0)
Sand (log10)	<0.0001	S (90)	E (32.22)	F (30)	G (6.33)	M (4.67)	SM (2.50)	R (1.40)
Silt (log10)	<0.0001	M (95.33)	SM (94.37)	F (60.56)	E (44.44)	S (7.78)	G (0.78)	R (0)
Mean phi	<0.0001	M (6.29)	SM (6.09)	F (4.11)	S (2.23)	E (2.18)	G (-3.84)	R (-7.41)
Mineral (log10)	<0.0001	S (99.11)	G (98.11)	R (90.8)	M (86.33)	SM (32.50)	F (29.44)	E (14.11)
Emergent (log10)	<0.0001	E (84.44)	SM (6.25)	F (0)	M (0)	R (0)	S (0)	G (0)
Submerged (log10)	<0.0001	SM (55)	M (0.56)	E (0)	F (0)	R (0)	S (0)	G (0)
Detritus (log10)	<0.0001	M (12.22)	SM (6.25)	F (2.78)	R (2.60)	S (0.89)	E (0.67)	G (0.22)
Riparian vegetation surface area (log10)	<0.0001	F (4.44)	E (0.11)	G (0)	M (0)	R (0)	S (0)	SM (0)
Large woody debris (log10)	<0.0001	F (63.33)	M (1)	E (0.56)	G (0)	R (0)	S (0)	SM (0)
Habitat diversity (log10)	<0.0001	SM (3.12)	F (3.11)	M (2.44)	E (2.44)	R (2.4)	S (1.44)	G (1.33)
Riparian vegetation cover (log10)	<0.0001	F (25)	R (8)	M (8.89)	E (1.33)	G (1.11)	S (0.56)	SM (0)
Compaction	<0.0001	R (3.40)	G (3.33)	E (1.78)	F (1.44)	M (1)	S (1)	SM (1)

(E = emergent macrophyte, F = flooded riparian, G = gravel run, M = mud/silt, R = rapids, S = sand, SM = submerged macrophyte) (degrees of freedom = 6, 51). Only significant parameters are shown. Data transformations are indicated where applied. Habitat types joined by a common line are not significantly different. Habitats are arranged in descending order of mean values for the respective parameter, and means for each habitat are presented in parentheses for each parameter



**Fig. 2** MDS ordination of samples on physico-chemical parameters with samples grouped by habitat type (emergent macrophyte = ▲, flooded riparian = ▽, gravel run = □, mud/silt = ◆, rapids = ●, sand = +, submerged macrophyte = X). Stress in two dimensions was 0.14

to percentage cover of cobble substrate, percent emergent macrophyte and percent riparian vegetation (BIOENV, correlation = 44%).

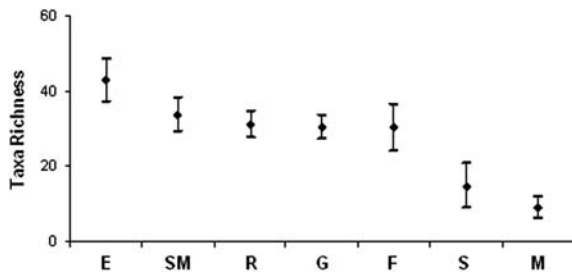
Species found at consistently high abundances within samples from a particular mesohabitat were considered indicator species for that habitat. Emergent macrophyte was typified by eight such species: two mayflies (*Tasmanocoenis arcuata* Alba-Tercedor & Suter and Baetidae Genus 1 WA Sp.1), two hemipterans (*Micronecta* sp UK1 and *Plea brunni* Kirkaldy), two coleopterans (*Paracymus pygmaeus* Macleay and *Hydrochus* sp.) and two chironomids [(*Cricotopus* sp. and *Larsia albiceps* (Johannsen)]. Communities within flooded riparian vegetation were dominated by seven taxa: five chironomids (*L. albiceps*, *Cricotopus* sp., *Dicrotendipes* sp., *Nilotanytus* sp. nov. and *Cladotanytarsus* sp.), the Hemiptera *Micronecta* sp UK1 and Ceratopogoninae larvae. Indicators for submerged macrophyte included four chironomids (*L. albiceps*, *Harnischia* sp., *Tanytarsus* sp. and *Cladotanytarsus* sp.), the mayfly larva *Cloeon* sp., moth larvae of the Pyralidae family, and two damselflies (*Pseudagrion*



**Table 3** One-way ANOVA to test for differences in taxa richness amongst habitat types

Parameter	F	P	Df	Tukey's HSD multiple range test						
				E	SM	R	G	F	S	M
Taxa richness	22.9	<0.0001	6, 51	(42.8)	(33.8)	(31.0)	(30.3)	(30.2)	(14.8)	(9.0)

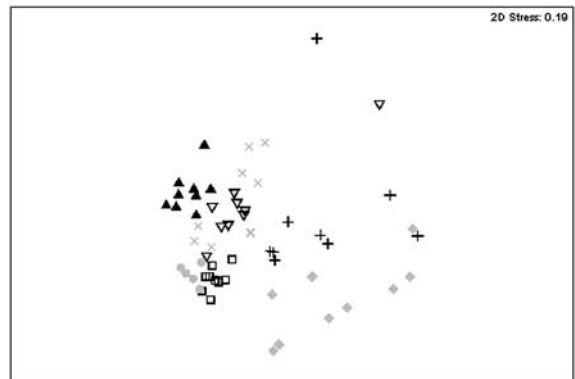
Tukeys HSD multiple comparison test was applied to locate differences between habitats where there was a significant main effect. Habitat types joined by a common line are not significantly different, habitats are arranged in descending order of taxa richness and mean number of taxa is in parenthesis for each habitat. (E = emergent macrophyte, F = flooded riparian, G = gravel run, M = mud/silt, R = rapids, S = sand, SM = submerged macrophyte)



**Fig. 3** Mean taxa richness ( $\pm$  95% CI) for each habitat type with habitats ranked in descending order of taxa richness (E = emergent macrophyte, SM = submerged macrophyte, R = rapids, G = gravel run, F = flooded riparian, S = sand, M = mud/silt)

*microcephalum* Rambur and *Austroagrion cyane* Selys). The mud/silt habitat was characterised by three chironomids (*Cladotanytarsus* sp., *Tanytarsus* sp. and *Harnischia* sp.), Oligochaete species, Ceratopogoninae larvae and Nematoda. Sand habitat was typified by Diptera including Ceratopogoninae larvae and the chironomids *Paracladopelma* sp., *Cricotopus* sp., *Cladotanytarsus* sp., and *Cryptochironomus griseidorsum* Kieffer. Communities within gravel/rapid habitat were dominated by the simuliid *Simulium ornatipes* Skuse, the Trichoptera *Cheumatopsyche* sp. and the chironomid *Cricotopus* sp. Average pair-wise dissimilarity between habitat types was high, with the exception of gravel runs and rapids (SIMPER, 38.3%; see Table 4).

Analysis of the frequency of occurrence and preference of each taxon for different habitat types with Chi-square analysis was possible for 142 of the 171 taxa recorded. Analysis demonstrated that emergent macrophyte was the most preferred habitat type, with sand and mud habitats being preferred by the fewest number of taxa (Fig. 5). Fifteen percent of taxa (13 taxa) showed



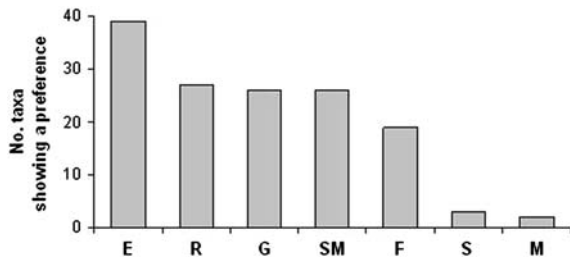
**Fig. 4** MDS ordination of samples on macroinvertebrate abundance with samples grouped by habitat type (emergent macrophyte =  $\blacktriangle$ , flooded riparian =  $\nabla$ , gravel run =  $\square$ , mud/silt =  $\blacklozenge$ , rapids =  $\bullet$ , sand =  $+$ , submerged macrophyte =  $\times$ ). Stress in two dimensions was 0.19

no preference for any habitat type, 67% (59 taxa) had a significant preference for one or two habitat types, and 18% of taxa (16 taxa) had a preference for three or more habitats. Most taxa occurred across two or more habitat types, with only seven taxa restricted to only one habitat type, predominantly submerged macrophyte (Electronic Supplementary Material—Appendix 1).

Across broad taxonomic levels, there was evidence of a full spectrum of habitat profiles, from generalists to taxa having preferences for specific habitats (Electronic Supplementary Material—Appendix 1). Diptera tended to occur across all habitat types with no single habitat preferred or avoided, probably reflecting the broad range in tolerances within this diverse group. The filter-feeding simuliid *S. ornatipes*, however, showed a preference for gravel runs/rock rapids, as did most Trichoptera species. Odonata, Acarina and Gastropoda species showed a strong preference for submerged and/or emergent macrophyte

**Table 4** Pair-wise between group average dissimilarity (%) determined by SIMPER (E = emergent macrophyte, F = flooded riparian, G = gravel run, M = mud/silt, R = rapids, S = sand, SM = submerged macrophyte)

	G	S	F	M	E	R
S	75.27					
F	64.83	76.30				
M	77.58	78.29	79.72			
E	68.36	80.44	57.58	88.58		
R	38.29	80.60	64.38	81.76	66.38	
SM	66.85	76.64	66.08	81.11	66.30	68.38

**Fig. 5** Number of taxa showing a preference for each habitat type, with habitats ranked in descending order of total taxa preferences (E = emergent macrophyte, R = rapids, G = gravel run, SM = submerged macrophyte, F = flooded riparian, S = sand, M = mud/silt)

habitats. Lepidoptera, Ephemeroptera and the palaemonid prawns occurred across most habitats except sand and mud/silt. Coleoptera similarly avoided sand and mud/silt habitats.

## Discussion

Distinct mesohabitats within the LOR could be distinguished on the basis of their physical properties and these habitats supported different macroinvertebrate assemblages, making them 'functional habitats' *sensu* Armitage & Pardo (1995), Kemp et al. (2000), Buffagni et al. (2000) and Tickner et al. (2000). Although seven habitats were originally classified by visual appraisal, only six were considered functionally distinct on the basis of their physical characteristics and macroinvertebrate assemblages: emergent macrophyte beds, submerged macrophyte beds, flooded riparian vegetation, sand, mud/silt, and with gravel runs/rock rapids combining to form one

habitat. These habitats broadly concord with habitats identified in other studies. For example, Pardo & Armitage (1997) found macrophyte beds, sand, silt and gravel were discrete habitat units in a lowland chalk stream in England. In the River Frome, England, Armitage & Cannan (1998) recognised six mesohabitats; silt, sand, main channel gravel, riffle gravel, *Ranunculus* and emergent vegetation. Buffagni et al. (2000) reported on five functional habitats, including margin with macrophytes, margin without macrophytes, backwater, run-riffle, and macrophytes in the flow for a lowland river in Italy. Finally, Brunke et al. (2001) identified eight mesohabitats in a lowland river in Germany; *Dreissena*-bank, unionid mussel bed, rip-rap, coarse woody debris, alder roots, stable sand, shifting sand and mud.

Distribution and abundance of macroinvertebrates across habitats were influenced primarily by physical attributes of percent cobble substrate and macrophyte and riparian vegetation cover, rather than water quality parameters. Emergent and submerged macrophyte beds and gravel/rapid runs supported greatest taxa richness and abundance. These results support those of numerous northern hemisphere studies where macrophyte and riffle-run habitats have been found to contain the greatest diversity, biomass and richness of fauna (i.e. O'Connell & Campbell, 1953; Gaufin et al., 1956; Gregg & Rose, 1985; Brown & Brussock, 1991; Lombardo, 1997; Armitage & Cannan, 1998; Barbour et al., 1999; Phillips, 2003). It has been suggested that such habitats provide greater refuge from predation (O'Connell & Campbell, 1953; Gregg & Rose, 1985; Lombardo, 1997). Diversity of aquatic fauna can also be maintained by complex macrophyte habitats due to their high surface area and spatial

heterogeneity (Gregg & Rose, 1985; Lombardo, 1997; Linhart et al., 2002). Bella et al. (2005) found that, in particular, Coleoptera species richness was driven by macrophyte cover within ponds in Italy. In riffles, the variety of particle size likely provides a stable habitat (Barbour et al., 1999), while the increased flows provide the food, oxygen and silt-free substrate required by many taxa (Brown & Brussock, 1991). Results from the current study suggest that the loss of key macrophyte and gravel/cobble rapid habitats would likely result in a loss of biodiversity from the LOR since a number of taxa were essentially restricted to these habitat types.

The FHC considers distinct habitats as functional units if they support different suites of macroinvertebrates, but these studies tend not to describe the functional role of these habitats. This in part reflects the aim of the concept, being to replace the need for this detailed ecological knowledge. However, as can be seen from the current study, macroinvertebrate preference for distinct habitat units generally reflected the ecology and life-history of the species. For example, filter-feeding macroinvertebrates, such as the simuliid *S. ornatipes* and the hydropsychid Trichoptera *Cheumatopsyche* sp., showed distinct preferences for the shallow, faster-flowing gravel run/rock rapid habitat. Hydropsychids build fixed retreats on the upper surface of stable substrates such as rocks or boulders and construct silken capture nets to filter food particles from fast-flowing water (Gooderham & Tsyrlin, 2002; Brooks et al., 2005). Simuliids also attach themselves to solid objects in fast-flowing water and use their feathered mouthparts to filter food particles from the water column (Gooderham & Tsyrlin, 2002). In contrast, the predatory Odonata preferred emergent and submergent macrophyte habitats within the LOR. Odonate nymphs are commonly found in association with vegetation within the littoral zone of freshwater systems (Bergey et al., 1992; Lombardo, 1997). Since odonate nymphs are generalist feeders, their colonisation of macrophyte habitat is not likely due to the presence of particular prey species, but rather increased predation success resulting from the high diversity of prey species within the habitat (see Lombardo, 1997). Four species of

chironomids were found to typify sand habitat in the current study, including *Paracladopelma* sp., *Cricotopus* sp., *Cladotanytarsus* sp., and *Cryptochironomus griseidorsum*. This probably reflects the burrowing/case-building habit of these collectors. Similarly, Pardo & Armitage (1997) found indicator taxa for sand habitats in an English chalk stream included species of midge and oligochaeta which are known to burrow into sandy sediments where they feed on detritus and small prey. It is likely that further comment on the 'functional roles' of macroinvertebrates from each habitat would be possible were there greater knowledge of their individual ecologies and life histories. Nevertheless, the FHC is promoted as a solution for this exact situation.

The concept of functional habitats has been mainly tested in northern Europe, especially in upper and middle-order streams and small, lowland rivers where the habitats are, for the most part, distinguished by the in-channel vegetation (i.e. Pardo & Armitage, 1997; Buffagni et al., 2000). However, there are few examples of its application to large lowland rivers, likely because of the difficulties in defining physical habitats and sampling aquatic invertebrate fauna in these systems (Humphries et al., 1996). When applied to lowland rivers the functional habitat approach was found to be highly effective. Armitage & Pardo (1995) assessed the environmental effects of stream regulation using the habitat approach compared with more conventional biotic scores and indices that are often used to summarise data on faunal community structure and richness. They observed that the conventional approaches were unable to detect the subtle changes associated with regulation, because the changes along the reach were not associated with change in scores and indices based on family richness, but were associated with altered physical habitat, as reflected in the proportion of habitats above and below sluice gates. They concluded that the habitat approach was more sensitive than conventional approaches. Similarly, Rabeni et al. (2002) concluded that habitats were distinct and useful in understanding the distribution and abundance of stream invertebrates. They also noted that spatially, habitats had consistent fauna, providing biological meaning throughout a stream

(Rabeni et al., 2002). The consolidation of species lists into commonly used indices of community structure were not found to relate in a consistent manner to habitat units, indicating loss of relevant biological information (Rabeni et al., 2002). Finally, Rabeni et al. (2002) noted that the use of habitats will assist in differentiating between water quality and physical habitat deterioration, two of the main sources of stream degradation in the Missouri Ozark ecoregion. Buffagni et al. (2000) promoted the use of the functional habitat approach in water quality monitoring in the Po River, Italy. They suggested the FHC enabled a more standardised application of biotic indices to assess biological quality by identifying appropriate habitats to sample. They conclude that “the use of the FHC as a basis to establish monitoring programs can be a cost-effective tool and can increase reproducibility and comparability of field results and indices application”. In discussing the practical uses of functional habitats, Buffagni et al. (2000) commented that with knowledge of the ecological importance of habitats, it is possible to maintain specific functional habitats to protect endangered or rare species or to increase hydraulic and habitat heterogeneity by modification of channel morphology. Such applications have commenced in the UK (Kemp et al., 1999). In northern Italy, to define benthic habitat availability, flow was related to functional habitat occurrences, not to taxa preferences for water depth and velocity (Buffagni, 2001). Overall, these studies support the use of the FHC in river management.

Given the lack of detailed knowledge of the biology of individual species, but the presence of distinct ‘functional habitats’, the application of the FHC to the LOR seems an appropriate choice to assist in development of environmental flows and for future river management. This study targeted shallow and marginal habitats because modelling indicated that these areas were most likely to be affected by further abstraction from this already heavily regulated system (Trayler et al., 2002). Although the hydrology of the system is highly modified, it still supports substantial ecological value, a reflection of establishing a secure water source throughout the year in a seasonally dry region. Whilst reviewing a draft

environmental water provision for the LOR (WRC, 1999), the Western Australian Environmental Protection Authority recommended that any environmental flow should maintain the riverine environmental values established *since* the construction of the ORD (Trayler et al., 2002; Storey & Trayler, 2006). Although controversial, this pragmatic decision acknowledged the current, arguably high values of the system, and that the dams were not going to be removed (see Storey & Trayler, 2006). Our inference is that maintenance of the current array of habitats will help support the current values. Environmental flows for the LOR must be designed to protect and maintain the current distribution and area of these key habitat types to maintain their dependent faunas (*sensu* Buffagni et al., 2000). The challenge for hydrologists/geomorphologists is to predict how the distribution of these habitats may change under a new flow regime, a generic issue discussed by Tickner et al. (2000).

Given the physically distinct nature of the identified functional habitats, it was considered possible to monitor their extent over time. In 2003, Storey & Marshall (2005) developed a monitoring program using high resolution (0.25 m), low level (4,000 ft) digital aerial photography of the channel to quantify the area of each functional habitat as identified for macroinvertebrates (this study) and fish assemblages (see Storey & Creagh, *in press*). In late 2006 the recommended approach was applied to three 5 km reaches on the LOR. It is intended that monitoring be conducted in late dry season over 3 years prior to and 3 years after a new flow regime is implemented, to detect changes. The environmental flow regime for the LOR, which is currently being finalised is being designed to maintain these functional habitats, and their associated faunas.

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