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Microhabitat use by foraging white-clawed crayfish (*Austropotamobius pallipes*) in stream pools in the NE Iberian Peninsula

Received: 4 March 2008 / Accepted: 19 August 2008 / Published online: 3 October 2008
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Abstract The white-clawed crayfish (*Austropotamobius pallipes*) is an endangered species across most of its distribution range, and information on its ecological requirements is needed to implement effective conservation measures. Its habitat use has been studied in different areas and at various spatial scales. However, being a nocturnal species, there is scarce information on its habitat selection during foraging periods. In this work we analyse nocturnal habitat use of white-clawed crayfish in pools of a small stream in the northeastern Iberian Peninsula at two different scales: (1) microhabitat selection and (2) pool characteristics. Large crayfish showed a clear positive selection for deeper microhabitats, a selection pattern that was weaker for medium-sized crayfish and absent for small ones. On the other hand, crayfish of all sizes avoided cobble and boulder microhabitats and positively selected fine substrate and more exposed microhabitats. Crayfish abundance in pools was positively influenced by pool area, pool depth

and the availability of fine substrates, especially silt. While studies on white-clawed crayfish habitat use have often stressed the importance of rough substrates as crayfish refuge, our results show that fine substrates are positively selected by foraging crayfish of all size classes and promoted active crayfish abundance in pools. These apparently contradictory results may be due to the differences in microhabitat preferences exhibited by active and inactive crayfish. Thus, our results help to better complete the picture of white-clawed crayfish habitat requirements.

Keywords Freshwater crayfish · Microhabitat selection · Substrate · Nocturnal microhabitat · Iberian Peninsula

Introduction

Crayfish are the largest mobile freshwater invertebrates, being often considered key species in aquatic ecosystems (Holdich 2003). Crayfish populations may reach large densities and display high mobility and omnivorous behaviour, potentially affecting both macroinvertebrate and macrophyte communities (Edgerton et al. 2004; Correia and Anastácio 2008). The knowledge of crayfish habitat use might be therefore important for aquatic ecologists, in order to better understand the effects of crayfish activity on the structure and composition of freshwater communities. The European native freshwater crayfish is a highly threatened group, with all species having suffered sharp declines following habitat alteration and the introduction of several North American crayfish species with their associated pathogens (Souty-Grosset et al. 2006). When dealing with threatened species, the achievement of effective conservation measures should rely on information on their habitat requirements at different spatial scales and during different life-history stages (e.g. Rosenberger and Angermeier 2003).

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The white-clawed crayfish (*Austropotamobius pallipes*) is distributed throughout the western and southern regions of Europe and is the only native freshwater crayfish in the Iberian Peninsula (Gil-Sánchez and Alba-Tercedor 2002; Souty-Grosset et al. 2006). This species is experiencing a drastic decline in natural populations that has been attributed to habitat loss, water pollution and the effects of competition and diseases from introduced crayfish species (Edger-ton et al. 2004; Gouin et al. 2006). As a result, the white-clawed crayfish has been considered as vulnerable on the IUCN Red List and is listed in the Annexes II and IV of European Community Directives for the Conservation of Natural Habitats and Wild Flora and Fauna (92/43/EEC and 97/62/EU). It had been recently suggested that Iberian populations of *Austropotamobius* could have been artificially stocked from NW Italy (Trontelj et al. 2005). However, this hypothesis has been rejected by more extensive genetic works and compilation of historical evidence proving the indigenous status of white-clawed crayfish in the Iberian Peninsula (Diéguez-Uribeondo et al. 2008).

Due to the species' widespread conservation concerns, several studies have analysed white-clawed crayfish distribution and the factors that are involved, both in the Iberian Peninsula (Gil-Sánchez and Alba-Tercedor 2002; Rallo and Garcia-Arberas 2002; Martinez et al. 2003) and in other European regions (e.g. Naura and Robinson 1998; Gallagher et al. 2005; Brusconi et al. 2008). These studies usually compare habitat characteristics of occupied and unoccupied locations or relate habitat characteristics with white-clawed crayfish abundance. Although in some locations within its range it has been shown that white-clawed crayfish can occupy a wide variety of aquatic habitats, Iberian populations are almost exclusively found in unpolluted small mountain streams, where they rarely coexist with introduced crayfish species and fish populations are often scarce (Gil-Sánchez and Alba-Tercedor 2002; Martinez et al. 2003).

There are, however, few studies analysing white-clawed crayfish habitat use at the microhabitat scale. Most studies on white-clawed crayfish microhabitat use (and other *Austropotamobius* species) have been centred in refuge characteristics, either through telemetry techniques (Bubb et al. 2006) or stone turning (Streissl and Hodl 2002). However, only a few studies have examined *Austropotamobius* microhabitat habitat selection at night time (Gherardi et al. 2001; Benvenuto et al. 2008), when more foraging activity is displayed (Barbaresi and Gherardi 2001; Holdich 2003). The combination of information for foraging and refuge microhabitat selection is necessary to get a more complete picture of white-clawed crayfish conservation needs.

In this work we assess nocturnal microhabitat selection by white-clawed crayfish in stream pools at two different scales (pools and microhabitats within pools). Our main objectives were: (1) to characterise foraging microhabitat use in pools accounting for its

availability, (2) to analyse possible size-related variations in the species microhabitat selection, and (3) to study which, if any, pool habitat characteristics influence species abundance and size structure.

Study area

The study was carried out on a 300-m stretch in the Cros Stream, a small tributary of La Muga River (north-eastern Iberian Peninsula, 42°23'N, 2°42'E). The climate in the study area is Mediterranean with mean annual temperatures ranging from 14.9 to 16.2°C and a mean annual rainfall around 900 mm, concentrated mostly between October and May. The Cros stream was selected for the study because it was known to support a stable and relatively abundant crayfish population (Benejam et al. 2005). It is 4-km long and runs from 900 to 450 m above sea level, draining a mostly siliceous area. Water flow is usually low during summer and autumn (June–October), but stream pools usually remain connected, and they rarely dry up. The studied stream stretch is composed by a succession of pools and narrow riffles (usually 1–3 m width), with occasional runs and small waterfalls. Dominant substrates are boulders, cobbles and fine gravels. Riparian vegetation, dominated by alder (*Alnus glutinosa*) and hazel tree (*Corylus avellana*), is dense and continuous. Vegetation in the stream's basin is mixed forest including cork oak (*Quercus suber*), chestnut tree (*Castanea sativa*) and European beech (*Fagus sylvatica*). The Cros stream fish fauna is very poor, including only small populations of Mediterranean barbel (*Barbus meridionalis*). No fish was observed in the studied stretch during the field work. The Cros stream can be used as a typical example of low-order mountain Mediterranean stream, mostly unpolluted and free of important human modifications affecting basin land uses or stream flow regime, which are the main refuges for crayfish populations in the Iberian Peninsula (e.g. Martinez et al. 2003).

Fifteen consecutive pools were selected and numbered in the studied stream stretch. Riffles and runs were not surveyed, since water turbulence would not allow an accurate crayfish detection, and *Austropotamobius* crayfish have been showed to display a preferential use of slow flow microhabitats (Benvenuto et al. 2008).

Methods

Crayfish abundance and microhabitat measurements

Crayfish observations were conducted in all 15 pools for 2 nights in early October 2006. Observations started about 1 h after dusk, in order to coincide with crayfish main foraging activity periods according to Robinson et al. (2000) and Barbaresi and Gherardi (2001). Two observers followed a transect in each pool by visually

screening on foot along in an upstream direction axis, using flashlights to detect crayfish. Observers tried to minimise the time spent at each pool, never exceeding 5 min. Whenever a crayfish was detected, its position was immediately marked with a numbered metal plate, and its total length was estimated to the nearest centimetre. Crayfish were not captured in order to avoid disturbance (e.g. Benvenuto et al. 2008). We made 464 crayfish observations during the 2 survey nights. Due to the loss of some metal plates, we recorded microhabitat measurements of 436 crayfish individuals.

Microhabitat measurements were recorded in the morning after each survey night. Using crayfish positions as the centre of a 30-cm-diameter circle, seven microhabitat measurements were taken: (1) depth (cm), (2) distance to the shore (cm), (3) dominant substrate size, (4) subdominant substrate size, (5) availability of refuge in stones, (6) availability of refuge in roots or other woody materials, and (7) abundance of leaves. Substrate size was coded (1–7) using a modified Wentworth scale: 1, silt (<1/8 mm diameter; i.e. materials able to be in suspension in water, including fine organic detritus); 2, sand (1/8–2 mm); 3, fine gravel (2–4 mm); 4, rough gravel (4–64 mm); 5, cobble (64–256 mm); 6, boulders (>256 mm); 7, bedrock. Availability of refuge (whether in stones or in wood) was coded (1–3) as follows: 1, without available refuge; 2, with refuge for 1 or few crayfish individuals; 3, with refuge for many crayfish individuals (based on the estimated availability of holes and substrate embeddedness). Finally, abundance of submerged leaves was also coded (1–3) as follows: 1, without leaves; 2, some leaves (i.e. few disaggregated leaves or aggregated leaves cover <25%); 3, abundant leaves (aggregated leaves cover >25%).

Available microhabitat measurements were taken at daytime, after all crayfish observations and crayfish microhabitat measurements had finished. Transversal transects were established at each pool every 50 cm, in a perpendicular direction in respect to the pool's maximal length. At each transect the seven microhabitat measurements listed above were recoded every 50 cm, and transect length was also noted. Measurements started at the centre of each transect, in order to avoid taking initial measurements at a constant distance from the shore. Overall, 617 points were used for the characterisation of microhabitat availability, with a mean of 41 (± 22.9 SD) points per pool.

Crayfish abundance and habitat in pools

At each survey date, we counted the number of crayfish observed at each pool. The number of crayfish counted in the different pools during each of the two survey dates were highly correlated (Pearson's correlation; $r = 0.90$; $n = 15$; $P < 0.001$). Thus, we used the average number of crayfish observed in the two survey nights to characterise crayfish abundance at each pool (expressed as number of crayfish detected per pool). Mean size of

crayfish at each pool was also recorded. Pool area (in m^2) was estimated by approximation to a rectangle, i.e. multiplying pool length by the mean perpendicular transects length (mean width) (Magoulick 2004). Pool habitat was characterised by: (1) mean depth; (2) maximum depth; (3) mean dominant substrate size; (4) mean subdominant substrate size; (5) proportion of silt; (6) proportion of sand; (7) proportion of fine gravel; (8) proportion of rough gravel; (9) proportion of cobbles; (10) proportion of boulders; (11) proportion of bedrock; (12) substrate diversity; (13) mean availability of refuge in stones; (14) mean availability of refuge in roots or other woody materials; (15) mean abundance of leaves. The proportion of the different substrate sizes (5–11) was calculated as the times that a certain substrate size had been recorded as dominant or subdominant in a pool divided by the total amount of dominant and subdominant substrate records in that pool. Substrate diversity (13) was calculated by applying the Shannon–Wiener index (H') to the proportions of the different substrate sizes ($H' = -\sum p_i \times \ln(p_i)$, where p_i is the proportion of substrate size i).

Data analyses

To analyse possible size-related variations in microhabitat use, crayfish were classified in three size classes: small (<5 cm total length, $n = 156$), medium (5–7 cm, $n = 244$) and large crayfish (≥ 8 cm, $n = 35$).

The complex nature of microhabitat structure must be taken into account in microhabitat selection studies, since many interacting variables can be simultaneously implied. This situation is best analysed through the use of multivariate statistics, since direct univariate tests would overlook the covariation of many microhabitat variables.

In a first analysis, a factorial MANOVA was performed on microhabitat variables using available-used (2 levels) and pool (15 levels) as factor, to test for differences between microhabitat availability and use accounting for microhabitat variability among pools. Correlations among microhabitat variables were checked prior to the MANOVA, in order to avoid the inclusion of highly correlated dependent variables in the analysis. However, although many of the 21 possible pair-wise correlations were statistically significant due to large sample size ($N = 1,053$), Pearson coefficients were in general low ($r < 0.50$ in all cases), and thus all variables were kept for the analysis. Univariate factorial ANOVAs were also run on individual microhabitat variables to interpret MANOVA results.

Then, a principal components analysis (PCA) was applied to a matrix including both available and used records (1,053 rows) of the microhabitat variables (7 columns). The resulting gradients of microhabitat variation (henceforth PC_{mic}) were selected for further analyses when the eigenvalues were larger than 1 (McGarigal et al. 2000). The scores of the selected PC_{mic} were

divided in six segments of equal length, in each of which the number of available microhabitat records and the number of small, medium and large crayfish records were counted. We chose to divide PC_{mic} in six segments in order to maximise a regular repartition of records among segments (more segments would imply an important number of them with few records) and the possibility of describing patterns of preference along gradients of variation in microhabitat characteristics (which would have been worse with less segments). Selection of certain microhabitat characteristics was analysed by applying the Ivlev's electivity index (D) with Jacobs' modification (Jacobs 1974) to each of the segments defined in the different PC_{mic} . This index ranges from -1 (total avoidance) to 1 (absolute positive selection) and is formulated as:

$$D = (r - p) / (r + p - 2rp),$$

where " D " is the electivity measure, " r " is the percentage use of the resource (i.e. proportion of crayfish of a certain size class included in a PC_{mic} segment), and " p " is the percentage of the resource in the environment (i.e. proportion of available microhabitat records in a PC_{mic} segment). Following Sempeski and Gaudin (1995), D values between 0.25 and 0.5 were considered moderate positive selection, and those > 0.5 were considered positive selection (negative selection in case of negative D values).

To characterise variation in habitat characteristics among pools, a second PCA was applied to a matrix of habitat variables of each pool (i.e. 15 rows \times 15 columns), and PCs with eigenvalues larger than 1 were kept for further analyses (henceforth PC_{pool}). Factors influencing crayfish abundance in pools were analysed through stepwise multiple regression. Minimum adequate models (MAMs) were selected both by forward and backward stepwise procedures in order to check for coincidences in selected models that would reinforce results. Selection of independent variables relied on statistical significance ($P < 0.05$). We did not use information criteria (i.e. AICs) for model building, since AICs tend to be more generous in leaving explanatory variables in the model than the more conservative F test (Crawley 2002). Independent variables included in the analysis were pool area and the extracted PC_{pool} . An analogous procedure was used to analyse variation in mean crayfish size among pools. Both pool area and crayfish abundance were $\log_{10}(X)$ transformed prior to analyses, to improve the assumptions of parametric statistics.

Results

Microhabitat availability and use

The microhabitat characteristics of crayfish locations differed from those of the microhabitat available in the

field, as shown by the MANOVA (Wilks' $\lambda = 0.90$; $P < 0.001$). There were also significant differences in microhabitat variables among pools (Wilks' $\lambda = 0.46$; $P < 0.001$), but this variation differed between available and used microhabitats (available-used \times pool interaction Wilks' $\lambda = 0.85$; $P < 0.001$). The main differences between available and used microhabitats were observed for depth, dominant substrates and stone refuges (Fig. 1). Crayfish selected deeper positions within pools and with finer substrates than those available.

The PCA on microhabitat characteristics of used and available locations produced two gradients of variation ($PC1_{mic}$ and $PC2_{mic}$) that explained 45% of the original variation within the data set. $PC1_{mic}$ had towards its negative extreme shallow locations placed near the stream's shore, while at its positive extreme locations were characterised by large depths and high availability of leaves and woody refuges. $PC2_{mic}$ described a gradient running from locations with rough substrates and abundant stone refuges to locations dominated by fine substrates (Table 1).

Crayfish by size classes showed distinct microhabitat use along the gradient defined by $PC1_{mic}$ (Fig. 2). Small individuals seemed to use randomly the available microhabitats in relation to depth, distance to the shore, leaf debris and woody refuges, showing only an avoidance of positions very close to the stream's shore. In contrast, large crayfish showed a strong to moderate avoidance of shallow positions near the shore and a strong selection for deep locations with abundant leaves and woody refuges. This pattern of microhabitat use was similar to that of medium-sized crayfish, but in this case both positive and negative selections were to a lesser degree than those displayed by large individuals. In contrast with these size-related patterns, all crayfish size classes showed a similar microhabitat selection in relation to $PC2_{mic}$ (Fig. 2). Rough substrate microhabitats were strongly avoided by crayfish of all three size classes, which positively selected fine substrate positions. However, the microhabitat selection was weaker towards the extreme of the gradient defined by $PC2_{mic}$ (i.e. finest substrates), especially in the case of large individuals.

Pool characteristics and crayfish abundance

The PCA applied to the matrix of pools' habitat characteristics produced four main gradients of variation (PC_{pool} 1–4), which accounted for 80% of the variation contained in the original data set. The first of these gradients ($PC1_{pool}$) showed a significant relationship with pool area, but the other three did not (Table 2).

The multiple regression analysis showed that crayfish abundance was positively influenced by pool area (i.e. larger pools had more crayfish). However, the most important variable influencing crayfish abundance was

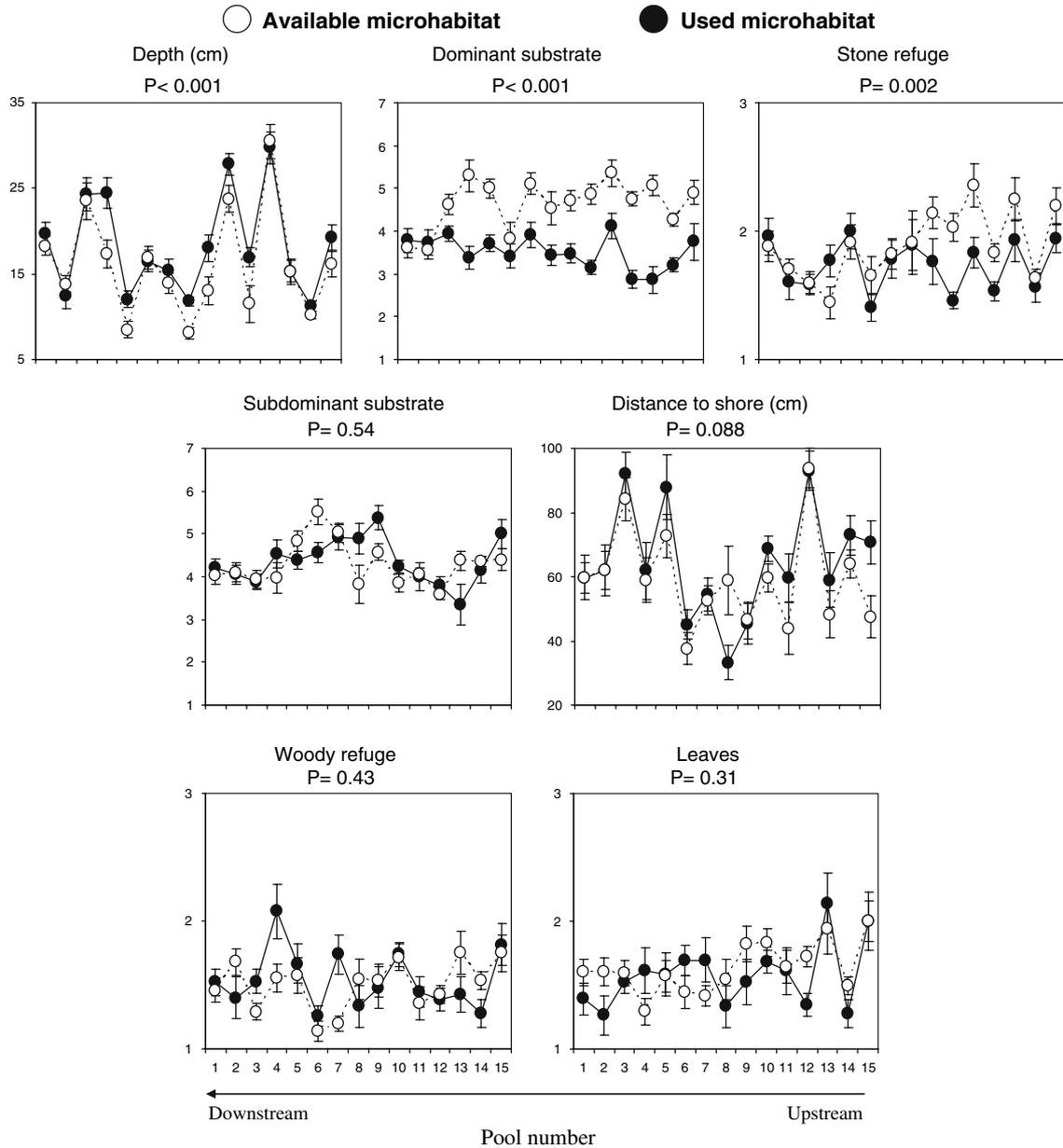


Fig. 1 Mean (\pm SE) values of the seven microhabitat variables recorded, shown separately for available and used locations and for the 15 studied pools. Shown *P* values are the significance of the factor “available-used” in an univariate factorial ANOVA. Other

factors included in these analyses were “pool” and the “available-used \times pool” interaction. See “Methods” for the explanation substrate, refuge and leaves variables

Table 1 Factor loadings and eigenvalues resulting from the PCA applied to a matrix of microhabitat variables recorded for available ($N = 617$) and used ($N = 436$) locations

	PC1 _{mic}	PC2 _{mic}
Depth	0.73	-0.21
Distance to shore	0.61	-0.16
Dominant substrate	-0.36	-0.71
Subdominant substrate	-0.26	0.10
Stone refuge	-0.29	-0.74
Woody refuge	0.65	-0.05
Leaves	0.58	-0.28
Eigenvalue	1.95	1.21
Prop. explained variance	0.28	0.17

the gradient defined by PC3_{pool} (Table 3), an influence that was independent from that of pool area. Thus, crayfish tended to be more abundant in deep pools with a high proportion of silty substrates than in shallow pools dominated by fine gravel substrates (see Table 2). In fact, PC4_{pool}, which was also related to the proportion of silt in the pools, also had a significant, though minor, influence on crayfish abundance (Table 3).

The only independent variable that had a significant effect on mean crayfish size in pools was pool area (Table 3). Thus, larger pools not only had more crayfish, but also were inhabited by larger crayfish individuals.

Fig. 2 White-clawed crayfish electivity (Ivlev's index, D) for each of the six sections in which the gradients of variation of microhabitat characteristics were divided ($PC1_{mic}$ and $PC2_{mic}$). Results are represented separately for each of the three crayfish size classes defined for this study. The interpretation of PCs is based in the original variables' loadings (see Table 1), using only those with loadings larger than 0.5 (in absolute value)

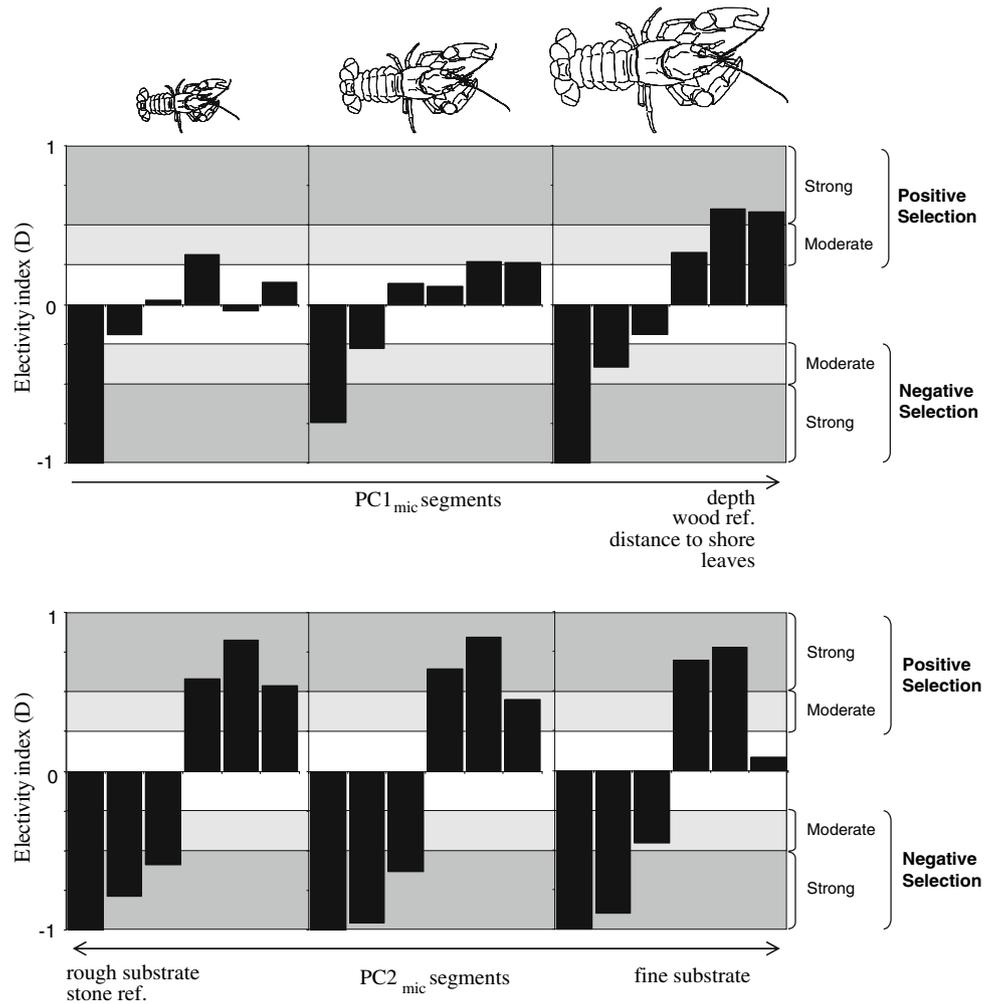


Table 2 Factor loadings and eigenvalues resulting from the PCA applied to a matrix of habitat characteristics of the 15 studied pools results

	$PC1_{pool}$	$PC2_{pool}$	$PC3_{pool}$	$PC4_{pool}$
Mean depth	0.47	-0.43	0.67	0.18
Maximum depth	0.55	-0.36	0.60	-0.01
Mean dominant substrate	-0.37	0.07	0.44	-0.53
Mean subdominant substrate	-0.08	0.89	-0.11	0.18
Prop. of silt	0.13	0.27	0.55	0.55
Prop. of sand	0.74	-0.38	-0.34	-0.04
Prop. of fine gravel	0.44	-0.61	-0.53	0.05
Prop. of rough gravel	-0.77	-0.06	0.30	-0.44
Prop. of cobbles	-0.87	-0.36	0.06	-0.05
Prop. of boulders	-0.49	0.53	-0.16	0.43
Prop. of bedrock	0.64	0.63	0.27	-0.11
Substrate diversity	0.75	-0.19	0.30	0.10
Stone refuge	-0.87	-0.10	0.24	0.08
Woody refuge	-0.51	-0.54	-0.24	0.33
Leaves	-0.66	-0.45	0.29	0.40
Eigenvalue	5.42	3.06	2.19	1.34
Prop. explained variance	0.36	0.20	0.15	0.09
Correlation with pool area	0.54	-0.23	0.21	0.13
P	0.04	0.42	0.46	0.66

The correlation of each pool score with pool area (\log_{10} transformed) and its associated P value are also shown for each of the principal components

Discussion

White-clawed crayfish showed a non-random pattern of microhabitat use in the studied stream stretch for all sizes. Active crayfish positively selected fine-grained substrates independent of their size, but large- and medium-sized individuals avoided shallow areas, selecting deeper positions with abundant plant debris within stream pools.

The observed size-related differences in depth selection could be explained by the ontogenetic changes in the feeding behaviour of white-clawed crayfish (Benvenuto et al. 2008). The species has been shown to be chiefly detritivorous although it behaves as an opportunistic consumer of both animals and plants (Gherardi et al. 2004). However, it has been noted that juvenile individuals include higher proportions of animal prey in their diets than do adults, which rely more on plant detritus (Reynolds and O'Keeffe 2005), a pattern that has been also observed in other crayfish species (e.g. Correia and Anastácio 2008). In our study stretch increasing depth positions held also more plant debris (both in terms of leaves and woody material, see Table 1). Larger and more

Table 3 Minimum adequate models (MAM) resumming the effects of pool area and the four PC_{pool} (shown in Table 2) on crayfish abundance and crayfish mean size for 15 stream pools

	<i>b</i>	<i>t</i>	<i>P</i>
Crayfish abundance			
PC _{3pool}	0.164	5.2	< 0.001
Log ₁₀ area	0.502	4.6	0.001
PC _{4pool}	0.075	2.4	0.033
<i>F</i> _{3,11}	23.8		< 0.001
Adj. <i>R</i> ²	0.83		
Crayfish size			
Log ₁₀ area	1.103	2.7	0.018
<i>F</i> _{1,13}	7.3		0.018
<i>R</i> ²	0.36		

Shown MAMs are coincident results obtained through both forward and backward stepwise selection procedures of independent variables

detrivorous individuals could then be using deeper positions due to the higher food availability.

However, the risk of predation could also play a role in the use of depths exhibited by the different crayfish size classes. The selection of deeper areas displayed by larger individuals is a pattern that has been repeatedly documented both for crayfish (e.g. Rabeni 1985; Creed 1994) and for fish (e.g. Power 1987; Harvey and Stewart 1991), and has been related to the differential predation risk posed by terrestrial (birds and mammals) and aquatic (fish) predators (Power 1987). In our study location, the apparent lack of selection of small crayfish in relation to depth and distance to the shore, except for the avoidance of the shallowest zones (see Fig. 2), could be due to the absence of predatory fish. Englund and Krupa (2000) showed that in the presence of predatory fish, small crayfish clearly shifted towards shallow habitats, while in their absence they displayed no clear depth selection. On the other hand, the presence of terrestrial predators, to which large individuals are more vulnerable (Power 1987), often results in the use of deeper microhabitats by these large individuals (e.g. Clavero et al. 2007). In our study area avian predators of aquatic organisms (e.g. herons, kingfishers) are absent. Additionally, signs of semi-aquatic mammals such as the otter (*Lutra lutra*) or the American mink (*Mustela vison*), which are known to inhabit the region, were not detected in the field. However, terrestrial predators not specialised in capturing aquatic prey, such as the genet (*Genetta genetta*) or the fox (*Vulpes vulpes*), can include a significant quantity of crayfish in their diets (Correia 2001). The threat posed by these terrestrial predators, which correspondingly have nocturnal habits, could be related to the avoidance of shallow positions near the stream shore exhibited by medium-sized and, especially, large crayfish.

White-clawed crayfish of all size classes positively selected fine-grained bottoms, a clear pattern maintained both across pools and size classes (see Fig. 1), and the presence of silt in pools was an important factor

determining crayfish abundance in pools (see Table 3). This is an interesting result of this work, differing from previously reported daytime observations on the species' habitat requirements. In concordance with our results, Gherardi et al. (2001) found that during foraging excursions white-clawed crayfish positively selected substrates composed by plant detritus, which were the ones bearing the highest concentrations of organic carbon and nitrogen. Benvenuto et al. (2008), based also on night time direct observations, described a positive, though slight, selection of fine-grained substrates. These patterns of microhabitat use at night contrast with results obtained in daytime studies. In a telemetry study, Bubb et al. (2006) found white-clawed crayfish exclusively in locations with boulders and large cobbles, substrates that, in addition, were relatively rare in their study area. Concerning ecologically similar species, Streissl and Hodl (2002) also stressed the importance of large stones as refuge for *A. torrentium*, and similar preferences for rough substrates have been reported for the signal crayfish (*Pacifastacus leniusculus*) by Bubb et al. (2006).

The apparent contradiction between these and our results may be due to the fact that most studies on *Austropotamobius* species (and, in general, on crayfish) habitat use are based on daytime data, when most individuals are inactive and using refuges and not foraging microhabitats. DiStefano et al. (2003) advised against generalising about crayfish habitat use from crayfish survey results performed during daytime. Our results show that white-clawed crayfish microhabitat selection patterns during activity periods in terms of substrate composition clearly differ from those previously reported for inactive crayfish (i.e. refuge selection). Smily and Dibble (2000), using passive capture methods (which rely on crayfish activity), also found that rusty crayfish (*Orconectes rusticus*) from northern USA consistently preferred fine-grain bottoms.

The habitat requirements of white-clawed crayfish have been analysed by several previous works. Many of these compare sites with crayfish populations and sites without them or relate crayfish abundance to habitat features and, in general, conclude that the presence of effective refuges (mostly boulders and tree roots) is a crucial factor allowing the presence and controlling the abundance of the species (e.g. Smith et al. 1996; Broquet et al. 2002; Kemp et al. 2003; Holdich 2003; Gallagher et al. 2005). However, the importance of fine depositional substrates for crayfish populations have been rarely stressed (Gherardi et al. 2001). Our results show the clear differences in habitat selection between inactive and active individuals, suggesting that optimal white-clawed crayfish habitat should include large boulders serving as effective refuges and fine-grained substrates used as profitable foraging microhabitats.

Acknowledgments We greatly acknowledge the important help and stimulating company provided during the field work by Sandra Saura, Eva Garangou, Raul Gavira and Mercè Berga. Ana Filipa

Filipe and Adrew Gascho Landis made useful suggestions that helped us to improve this manuscript.

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