

Invasion by the exotic crayfish, *Cherax destructor* Clark (Parastacidae), into habitats of local crayfish near Perth, Western Australia.

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ABSTRACT

The yabby, *Cherax destructor* Clark, was introduced into Western Australia in 1932, when ten yabbies were translocated from Victoria to a farm dam near Narembeen. Following subsequent dispersal, this crayfish now co-occurs with two local species *C. quinquecarinatus* and *C. cainii* in river systems in the environs of Perth. Congeneric crayfish may persist in sympatry through microhabitat separation. To elucidate the means for co-existence, microhabitat characteristics of the three species were measured in the Canning River system near Perth. Yabbies were associated with sediments having higher clay content than marron; gilgies occurred in river reaches having higher flow than marron. The distribution of the crayfish within this system displayed a mosaic pattern of sympatric distributions, which would allow for competitive interactions between these species. To investigate one aspect of interactions between the introduced yabby and local crayfish species, laboratory-based sediment competition experiments were performed. Similar-sized yabbies displaced both marron and gilgies from preferred substrates. Superior competitive ability under laboratory conditions was manifested through interference, with yabbies preventing local crayfish species from procuring a limiting resource. This study indicates the potential for the introduced yabby to displace local crayfish species.

Keywords: introduced crayfish, microhabitat separation, competitive exclusion

INTRODUCTION

The parastacid freshwater crayfish of the Canning River system, Perth, Western Australia, constitute a fauna of composite origins. Only the gilgies, *Cherax quinquecarinatus* (Gray), are likely to be native to the system. Marron, *Cherax cainii* Austin & Ryan, are native to more southern rivers and freshwater lakes in south-western Australia (Morrissy 1978, Austin and Ryan 2002). Their occurrence in more northern rivers, including the Canning River system, therefore represents an extension in geographical range of the species, presumably resulting from human influence. The natural range of the yabby, however, is in eastern and central Australia (Riek 1969, Austin 1996). In 1932, ten specimens were translocated from western Victoria to a farm dam in the Narembeen district of the central wheatbelt of Western Australia (Morrissy & Cassells 1992). By the 1990s, the geographical range of yabbies in Western Australia had extended westwards into streams on the Darling Range and Swan Coastal Plain (Lynas *et al.* 2004).

This study assessed the potential for competitive exclusion of local species by the introduced yabby. When a crayfish species is translocated outside its natural range and is introduced into a region in which niches are already occupied, there is the potential for competition with native species for limiting resources (Pianka 1974). The potential for interspecific competition may be exacerbated when congeneric species are introduced, due to the increased chance of ecological similarities that may lead to a substantial overlap in the use of resources between native and introduced species (Pianka 1974, Franke and Janke 1998). In this situation, the species with the competitive advantage will eventually dominate. Alternatively, species in sympatry may be maintained by microhabitat separation (e.g. Suter and Richardson 1977, Rabeni 1985, Lachat and Laurent 1987). Therefore, this study addressed the question: Are the species *C. quinquecarinatus*, *C. cainii* and *C. destructor*, in the Canning River system, ecologically separated?

Given apparent overlap in the ecological niches of the three crayfish species then high competition for substrate would be expected owing to its importance for shelter. In fact, Capelli and Magnuson (1983), in a study of the distribution of crayfish in northern Wisconsin, USA, found that substrate type was the single most important variable related to total crayfish abundance. In sympatry, the effective use of habitat and substrate may be particularly important. It would be anticipated that competition for substrates affording reasonable protection (i.e. rocky sites) would be high. The species less able to utilise this resource would experience a considerably increased susceptibility to predation (Butler and Stein 1985).

MATERIALS AND METHODS

Study sites

Preliminary sampling using baited collapsible box traps was undertaken to locate sites where each species occurred exclusively, and where two species occurred in sympatry, following which final sampling stations (Figure 1) were selected; sites 1 and 2 (Roleystone, Kelmscott) of exclusive marron occurrence; sites 3 and 4 (Gosnells, Martin) of exclusive gilgie occurrence; and, site 5 (Westfield) where marron and yabbies co-occurred.

Microhabitat sampling

At each site, crayfish from a 25 m stretch of river were sampled using a Smith-Root Model 12B backpack electrofisher. Specimens were identified on site then returned to the river. The following microhabitat characteristics were recorded at the location where each animal was collected, using instrumentation described in Lynas (2002): water velocity (cm s^{-1}) at 0.6 m depth; pH; electrical conductivity (mS cm^{-1}); and dissolved oxygen (% saturation). Turbidity (NTUs) was measured on water samples transported to the laboratory.

Percent moisture content and particle size of 10 g sediment samples from the point of capture of the crayfish were analysed in the laboratory as described in Lynas (2002). Organic material was removed by oxidation using 6% H_2O_2 following which sediment particles were dispersed in water using the dispersal agent sodium hexametaphosphate + NaOH and violent disaggregation. Amounts of clay ($<2 \mu\text{m}$) and silt (2-20 μm) were determined using the pipette method of Bowman and Hutka (2002). The sand (20 μm – 2mm) content was estimated as the difference between 100% and the total silt plus clay. Particle sizes were assigned on the basis of the international code for size fractions (McDonald *et al.* 1990).

Analysis

The nine microhabitat variables were analysed by principal components analysis (PCA) using SuperANOVA. The factor scores contributing most to the overall variation are displayed graphically with samples identified by species and site. Two-tailed t-tests (given no prior prediction of directions of any differences) on the factor scores were used to test for significance of microhabitat separations of crayfish species.

Competition for sediment

Competition trials were undertaken at night under a red lamp in a round tank divided into four areas of 700 cm^2 . Substrates with a range of particle sizes representative of those likely to be encountered by crayfish in natural environments filled each section to a depth of 5 cm: sand (20 μm -2 mm); clay ($<2 \mu\text{m}$); pea-gravel (1-3 cm); and rocks (3-5 cm). Turbidity, which initially restricted visibility, was reduced by application of pool water clarifier ('Drop Out') which assisted flocculation. A preliminary trial was undertaken to determine the preferred substrate for each species in isolation. An individual was left in the experimental tank overnight and its location with respect to substrate type was noted the following morning. This was replicated for both marron and gilgies. Both the marron and the gilgie were recovered from the clay sector.

Two treatments were designed with differing densities and combinations of crayfish and were run simultaneously to facilitate analysis by paired t-tests (Table 1).

For each treatment the release point for crayfish was the centre of the tank which intersected all quadrants. Each trial lasted for 2 hours, at the completion of which the location of each crayfish with respect to substrate was recorded. Agonistic behaviour was continuously recorded during each trial.

Analysis

To ascertain the preferred substrate for both marron and gilgies in isolation, a block ANOVA test was conducted on the number of crayfish on each sediment type at the completion of trials. A paired t-test was used to determine whether marron or gilgies were displaced from the preferred substrate when in the presence of yabbies. The data were paired, with tank one run simultaneously with tank two. In order to separate species from density effects, intra- and inter-specific tension contacts in both tanks were also analysed by two-way paired t-tests. A block ANOVA was utilised to compare the number of tension contacts on each sediment type relative to the final number of marron or gilgies on the preferred substrate.

RESULTS

Microhabitat separation

Sampling of the 25 m long reaches yielded: 13 marron, site 1; 20 marron, site 2; 13 gilgies, site 3; 19 gilgies, site 4; and two marron and two yabbies, site 5. Values of the microhabitat parameters measured are summarised in Table 2. Stream bed water velocity varied considerably within and between sites. Water flow values ranged from 0-10 cm s⁻¹ at most sites but water flow was particularly slow (0-1 cm s⁻¹) at site 5; mean water velocity was highest at site 4. Mean pH varied from circumneutral (6.65 at site 2) to moderately alkaline (8.37 at site 5). Minimal variation in pH, for example 6.4-6.9 at site 2, is likely to occur diurnally due to changes in DO and NH₃ concentrations. Electrical conductivity (Ec) values ranged among sites from 0.41-0.65 mS cm⁻¹, well within the range of fresh water (<3 mS cm⁻¹). The highest mean Ec value of 0.65 mS cm⁻¹, equivalent to 0.325 g L⁻¹ salinity, was recorded at site 4. Turbidity varied significantly within and among sites (Table 2). Over all sites, turbidity ranged from 2.83-72.4 NTUs; at site 3, turbidity ranged from 7.81-72.4 NTUs. Sediment at all sites was dominated by larger particle sizes (Tables 2 and 3). However, some sites contained sediment with higher percentages of clay. The mean sediment at site 5 comprised over 26% clay and therefore was classified as a clay soil. In contrast, the mean sediment surrounding marron from this same site contained considerably less clay (11%) and was classified as loamy sand. Gravel content varied widely within and between sites, ranging from 0-100%. Mean gravel content ranged from 0 (sites 3 and 5) to 36%, site 2.

Principal components analysis yielded three factors with eigenvalues which together accounted for >60% of the variance in the original samples (Table 4). The highest weightings assigned to Factor 1 were sand (0.61) and gravel (0.54). Dissolved oxygen (0.51) and pH (0.55) contributed the most to Factor 2. Factor 3 was explained predominantly by water flow (0.65) and electrical conductivity (i.e. salinity; 0.54). Although turbidity had the highest weighting in Factor 4 (0.86), the eigenvalue suggests that this Factor did not contribute substantially to the overall variation. Factor 5, the percentage of clay (0.55) and silt (0.67) content of the sediment, contributed least to the overall variation.

The scatter plot of Factor 2 on Factor 1 showed some microhabitat separation of the three species (Figure 2), notably that marron and gilgies were separated in part on the basis of Factor 2: gilgies were found in microhabitats with higher DO concentration and pH than marron. The differences in factor scores were significant (two-tailed t-test; $p < 0.001$, $df = 63$). Factor 1 discriminated significantly (two-tailed t-test, $p = 0.019$; $df = 2$) between marron and yabbies in sympatry, with marron associated with sediment comprising higher percentages of sand (Figures 2 and 3). When classified by sites, there was overlap amongst sites 1, 2 and 3 on both Factor 1 and 2, but with progressive separation of sites 4 and 5 on Factor 2 scores (Figure 3).

The scatter plot of Factor 3 on Factor 2 also provided evidence for microhabitat separation of species. Marron and gilgies separated on the basis of Factor 3, with gilgies being associated with higher flow rates and salinity levels than marron (Figure 4). The difference between the factor scores of marron and gilgies was significant (two-tailed t-test; $p < 0.001$; $df = 63$). Yabbies and marron from different sites (Figures 4 and 5) were separated by Factor 2. The microhabitats of yabbies had higher DO and pH levels than marron. However, the marron and yabbies in sympatry were not separated by this same factor (Figures 4 and 5). Sites showed some clustering with respect to Factors 2 and 3, with overlap between sites 1, 2 and 3, and progressive separation of sites 4 and 5 (Figure 5).

Competition for sediment

Gilgies and yabbies

In isolation, the number of gilgies on clay was significantly higher than the number on all other sediment types (Figure 6 and Table 5; least significant range test, $p < 0.05$; $df = 3, 9$). However, their numbers on clay decreased significantly when in the presence of yabbies (two-tailed paired t-test; $p < 0.05$; $df = 3$; $t\text{-stat} = 2.449$; alone mean = 2.25; with yabbies mean = 1.25).

Agonistic behaviour in the form of tension contacts (fight, strike, threat and avoidance) was common during the trials. The number of tension contacts recorded on each substrate for both gilgies and yabbies, corrected for the final number of animals on each substrate, were significantly different (Table 6). Interspecific aggression was most commonly observed on the clay substrate (Figure 7).

Intraspecific aggression in gilgies, determined by the number of tension contacts, was not significantly different when alone (mean = 3.75) than when with yabbies (Table 7; mean = 2.5). Levels of interspecific aggressive behaviour were similar in gilgies and yabbies when together. The number of tension contacts 'won' by each species was not significantly different (Table 7; mean gilgies = 3.5; mean yabbies = 3.75). Gilgies were more commonly involved in tension contacts with yabbies (mean = 7.25) than other gilgies (mean = 2.5) when both species were together (Table 7).

Marron and yabbies

In isolation, the number of marron on the clay sector was significantly higher than on all other substrates (Figure 8; Table 8; least significant range test, $p < 0.05$; $df = 3, 9$). However, the number of marron on the clay was significantly lower when in the presence of yabbies (mean = 1) than when alone (mean = 2; two-tailed paired t-test; $p < 0.05$; $df = 3$; $t\text{-stat} = 6.003$).

The number of intraspecific tension contacts by marron was not significantly different when they were alone than with yabbies (Table 9; mean alone = 5.25; mean with yabbies = 4.5). When in tanks together, there was no significant difference between the number of tension contacts 'won' by marron (mean = 4.75) and those 'won' by yabbies (mean = 7; Table 9). Intra- and inter-specific levels of aggression displayed by marron when in the presence of yabbies were significantly different (Table 9). When in tanks together, marron were most commonly involved in contests with yabbies (interspecific contacts mean = 11.75) than with marron when in the presence of yabbies (intraspecific contacts mean = 4.5).

DISCUSSION

Microhabitats

Field sampling supported previous observations that gilgies occur more commonly than marron in areas of higher water flow velocity, and marron are most commonly found in deeper pools where water current is reduced (Morrissey 1978, Storey unpublished data). In addition, salinity, dissolved oxygen concentrations and pH generally were higher for gilgies than marron, although DO concentrations and pH values vary diurnally and are

positively correlated due to variations in the rate of photosynthesis, particularly in the presence of macrophytes. Indeed, several parameters, notably water flow and electrical conductivity, may define separate microhabitats for the two Western Australian species in the Canning River. Sediment differences, particularly in the percentage composition of sand and gravel, were evident between marron and yabbies in sympatry (site 5), with the yabbies occupying areas with less sand and higher clay content. This probably reflects the strong burrowing behaviour of yabbies and the requirement for finer sediments in soils to contribute to maintenance of burrow integrity. However, due to the low number of sampled yabbies at site 5, results on microhabitat usage should be interpreted with caution. It remains to confirm the microhabitat definitions for each species through preference experiments.

Richardson and Horwitz (1987), in reviewing case studies of habitat partitioning by Australian burrowing crayfish, noted that fine-scale partitioning of habitat on the basis of local topography maintains species in sympatry. Richardson and Horwitz (1987) distinguished between transverse partitioning – across stream gullies – and longitudinal partitioning – along the length of the watercourse. For example, along streams in rainforests in north western Tasmania, *Engaeus fossor* (Erichson) burrow into the stream margins while *Engaeus cisternarius* Suter burrow in the gully slopes just above the streams. The burrows of the two species may have as little as 1 m separation from each other (Suter and Richardson 1977). Richardson and Horwitz (1987) also recorded instances of the occurrence of more than one species of crayfish at a site but with no habitat partitioning being readily discernable: for example, the co-occurrence of *Parastacoides tasmanicus* (Erichson) and *Parastacoides inermis* Clark on flats at the base of hill-slopes in south western Tasmania (Richardson and Swain 1980).

Although the data are not sufficient to show unambiguous microhabitat separations by species, they do show trends which should be examined further in a subsequent more comprehensive study. Overlap in microhabitat variables was evident between sites 1, 2 and 3 with separation of characteristics from sites 4 and 5. This demonstrates the typically heterogenous nature of rivers with respect to microhabitat structure, and may in fact suggest a third kind of partitioning of crayfish in streams, mosaic partitioning.

In any case, it would be difficult to determine whether a resource is in short supply relative to species' needs since it is highly likely that freshwater crayfish utilise different resources at different maturation and reproductive stages. A juvenile, moulted individual or gravid female, for example, is more likely to require substrates affording high levels of protection than adults. Therefore, microhabitat separation or overlap may be influenced by age and/or reproductive cycles. In addition, the energy budgets of competing species would also vary depending on the season, age of individuals, reproductive demands and weather conditions (Jaeger 1974). Ultimately, the extent to which these crayfish compete for limiting resources would be temporally and spatially variable. It is likely that some degree of overlap in the use of limiting resources would occur between the introduced yabby and local species of crayfish at certain stages.

Competition for sediment

This experiment demonstrated a preference by gilgies and marron for clay substrate. Marron were never observed on the rocks at observation times, despite the hypothesis that this substrate would offer the highest amount of protection. The spaces between the pea-gravel and rocks possibly were not large enough to provide a refuge whereas the clay perhaps provided protection because the crayfish could bury themselves in the sediment. In fact, marron, gilgies and yabbies were all frequently observed pushing the clay around with their chelae and were, on occasion, half submerged in the sediment.

In the presence of yabbies, however, the number of both gilgies and marron found on the clay was significantly reduced. This provides evidence for competitive exclusion because species effects can be removed from density effects. Intraspecific aggression in gilgies and marron did not increase in the presence of yabbies, despite the increase in density of crayfish. Also, in the presence of yabbies, both marron and gilgies were more commonly involved in interspecific than intraspecific contests, implying that interspecific competition for limiting substrate was more fierce than intraspecific competition. Further, interspecific aggression in the form of tension contacts was more frequently observed on clay than on the other substrates, suggesting gilgies and marron were engaging in aggressive behaviour with yabbies in competition for this limiting resource. Thus, under laboratory conditions, yabbies were able to exclude gilgies and marron from the use of preferred substrate.

The predominance of infertile sandy soils in the study area along the foot of the Darling Ranges is indicative of a dearth of clay soils available to freshwater crayfish. It is not clear whether a preferred substrate in the laboratory correlates with a preference for the same substrate in natural environments. However, this experiment clearly showed that yabbies are capable of excluding both marron and gilgies from the use of a shared resource which is in limiting supply. Further evidence for such a hypothesis was provided by Henryon (1989) who found that in laboratory-based trials, similar-sized yabbies occupied limiting shelter sites to the exclusion of marron.

Competitive exclusion from suitable substrates has also been documented in some northern hemisphere crayfish (e.g. Bovberg 1952, 1970). Bovberg (1970) observed sympatric field populations of two crayfish species and found *O. virilis* occupied the rock and gravel areas, while *O. immunis* was restricted to the muddy and soft substrates. Laboratory studies on substrate choice, however, revealed that, when alone, both species displayed a marked 'preference' for rock substrates. In interspecific trials, *O. virilis* occupied the rock to the exclusion of *O. immunis*, which was displaced to the soft substrate sector. During these interspecific experiments, a marked increase in aggressive interactions was also observed.

Yabbies excluded similar-sized marron and gilgies from preferred substrates. Yet, as has been found in aggressive behaviour studies (Lynas 2002) similar-sized gilgies and marron exhibited comparable levels of aggressive behaviour to yabbies, with neither species 'winning' significantly more tension contacts than the other. This suggests that aggression might be displayed in ways other than the tactile aggression measured by these experiments. For example, chemical and visual communication may also influence aggressive dominance in freshwater crayfish. Bovberg (1956) concluded that both visual and tactile senses, particularly using the antennae, are important in crayfish social contacts. Behaviours such as antennal waving and entwining were commonly observed in all interspecific trials in the present study and would have enabled crayfish to monitor the actions of nearby opponents. Horwitz (1980) noted similar behaviours in aggression experiments with *Cherax quinquecarinatus* and *C. preissi* (Erichson).

In summary, the introduced yabby is able to out-compete similar-sized gilgies and marron for preferred limiting substrate under laboratory conditions. Given a degree of overlap in the use of limiting resources in natural environments, the spread of yabbies in south-west Western Australia poses a serious threat to local and endemic species.

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TABLES

Table 1. Treatments details.

TREATMENT	TANK ONE	TANK TWO	REPLICATION
1	3 Marron	3 Marron + 3 Yabbies	4
2	3 Gilgies	3 Gilgies + 3 Yabbies	4

Table 2. Microhabitat characteristics of each site (M = marron; G = gilgies; 5 M and 5 Y refer to data for marron and yabbies from the sympatric site, respectively).

MICROHABITAT CHARACTERISTIC	SITE	MEAN \pm SE	RANGE
Water flow (cm/s)	1 (M)	0.77 \pm 0.12	0 - 1
	2 (M)	3.65 \pm 0.60	0 - 10
	3 (G)	3.77 \pm 0.67	1 - 10
	4 (G)	3.89 \pm 0.52	1 - 10
	5 M	1 \pm 0	1 - 1
	5 Y	0 \pm 0	0 - 0
pH	1	6.85 \pm 0.02	6.8 – 7.0
	2	6.65 \pm 0.03	6.4 – 6.9
	3	7.05 \pm 0.02	6.9 - 7.2
	4	7.17 \pm 0.01	7.0 – 7.2
	5 M	8.37 \pm 0.19	8.2 – 8.5
	5 Y	7.43 \pm 0.19	7.2 – 7.6
Electrical conductivity (mS/cm)	1	0.41 \pm 0.001	0.41 – 0.42
	2	0.43 \pm 0.001	0.42 – 0.44
	3	0.59 \pm 0.001	0.59 – 0.60
	4	0.64 \pm 0.001	0.62 – 0.65
	5 M	0.51 \pm 0.005	0.50 – 0.51
	5 Y	0.52 \pm 0.005	0.51 – 0.52
Turbidity (NTUs)	1	9.38 \pm 1.96	2.83 - 27.3
	2	10.89 \pm 3.17	4.04 - 34.5
	3	19.74 \pm 5.43	7.81 - 72.4
	4	7.74 \pm 1.57	5.09 - 35.9
	5 M	5.35 \pm 1.34	4.01 – 6.7
	5 Y	5.13 \pm 0.89	4.24 – 6.03
Dissolved oxygen (%)	1	78.31 \pm 0.73	74 - 81
	2	90.6 \pm 0.54	87 - 93
	3	78.61 \pm 0.72	72 - 82
	4	89.53 \pm 0.70	80 - 92
	5 M	152.5 \pm 14.5	138 - 167
	5 Y	95.5 \pm 14.5	81 - 110
% Clay in sediment (<2 μ m)	1	7.63 \pm 2.33	1.04 - 18.41
	2	6.24 \pm 1.39	0 - 16.14
	3	8.28 \pm 2.16	0 - 22.57
	4	6.13 \pm 2.29	0.24 - 14.74
	5 M	11.27 \pm 0.61	10.67 - 11.88
	5 Y	26.33 \pm 0	
% Silt in sediment (2-20 μ m)	1	3.84 \pm 1.09	0.34 - 7.08
	2	5.84 \pm 0.64	0.63 - 10.54
	3	4.64 \pm 1.07	0.57 - 11.1
	4	6.53 \pm 2.34	0.19 - 27.11
	5 M	5.26 \pm 1.55	3.71 - 6.81
	5 Y	11.42 \pm 0	
% Sand in sediment (20 μ m -2 mm)	1	88.53 \pm 3.27	75.09 - 98.62
	2	88.22 \pm 1.32	76.95 - 95.12
	3	87.44 \pm 2.81	69.03 - 95.67
	4	87.33 \pm 4.01	45 - 99.24
	5 M	83.46 \pm 0.94	82.52 - 84.41
	5 Y	62.25 \pm 0	
Gravel (>2 mm)	1	30.77 \pm 13.32	0 - 100

	2	35.71 ± 11.12	0 – 100
	3	0	0
	4	21.05 ± 9.61	0 – 100
	5 M	0	0
	5 Y	0	0

Table 3. Soil types found at each site (M = marron; G = gilgies; 5 M and 5 Y refer to data for marron and yabbies from the sympatric site, respectively).

SITE	SOIL TYPES FOUND	MOST COMMON SOIL TYPE
1 (M)	Sand, sandy loam, loamy sand, gravel	Sand
2 (M)	Sand, loamy sand, sandy loam, gravel	Sand
3 (G)	Sand, sandy clay, loamy sand, sandy loam	Sand
4 (G)	Sand, sandy loam, loamy sand, gravel, clay loam	Sand
5 M	Loamy sand	Loamy sand
5 Y	Clay	-

Table 4. Eigenvalues obtained by PCA for microhabitat data.

FACTOR	MAGNITUDE	VARIANCE PROPORTION
1	2.6154	0.2906
2	1.697	0.1886
3	1.3352	0.1484
4	1.005	0.1117
5	0.8386	0.0932

Table 5. Block design ANOVA statistics for the number of gilgies on each sediment type when alone.

SOURCE	df	SUM OF SQUARES	MEAN SQUARE	F-VALUE	P-VALUE
Subject	3	0.000	0.000		
Substrate	3	12.500	4.167	15.00	0.001
Substrate*Subject	9	2.500	0.278		

Table 6. Block design ANOVA comparing the number of tension contacts recorded on each substrate relative to the final number of gilgies on that substrate.

SOURCE	df	SUM OF SQUARES	MEAN SQUARE	F-VALUE	P-VALUE
Subject	3	4.672	1.557		
Substrate	2	51.672	17.224	4.842	0.028
Substrate*Substrate	9	32.016	3.557		

Table 7. Two-tailed paired t-test results examining aggression levels in the form of tension contacts.

TEST (# of tension contacts)	df	T-STAT	P-VALUE
Gilgies (alone v with yabbies)	3	1.321	0.278
Yabbies vs gilgies	3	-0.181	0.867
Intra- vs inter- specific contacts (gilgies)	3	-5.563	0.011

Table 8. Block design ANOVA statistics for the number of marron on each sediment type when alone.

SOURCE	df	SUM OF SQUARES	MEAN SQUARE	F-VALUE	P-VALUE
Subject	3	0.000	0.000		
Substrate	3	9.000	3.000	6.750	0.011
Substrate*Subject	9	4.000	0.444		

Table 9. Two-tailed paired t-test on results of aggression levels in the form of tension contacts.

TEST (# of tension contacts)	df	T-STAT	P-VALUE
Intraspecific contacts by marron (alone vs with yabbies)	3	1.192	0.319
Yabbies vs marron	3	-0.615	0.582
Intra- vs inter- specific contacts (marron)	3	-7.660	<0.005

FIGURES

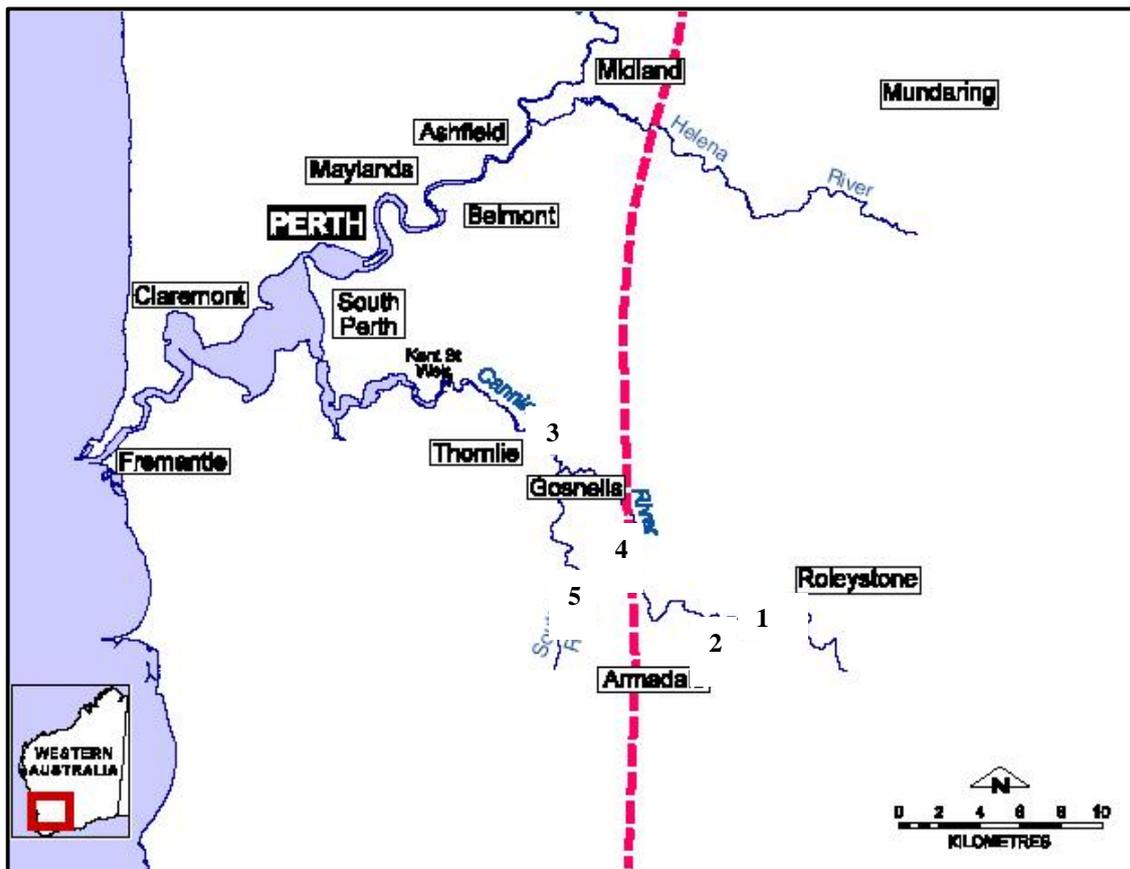


Figure 1. The locations of sites used in the microhabitat study

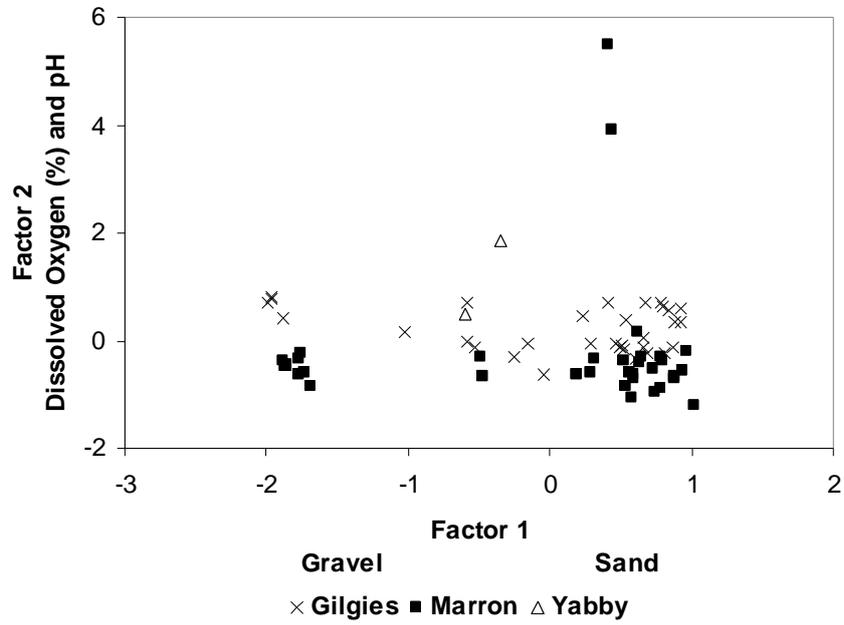


Figure 2. Scatter plot of Factor 1 v Factor 2 on the basis of species.

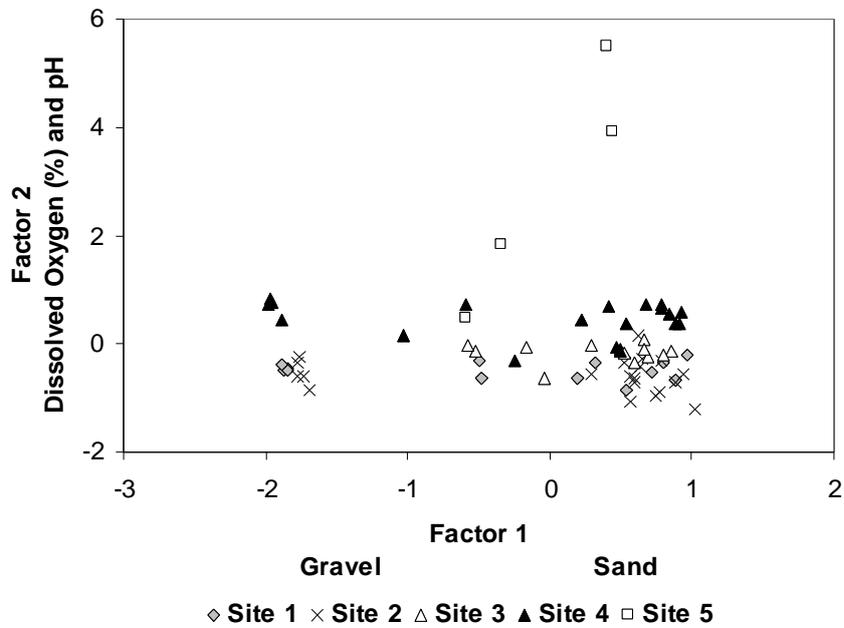


Figure 3. Scatter plot of Factor 1 v Factor 2 on the basis of site.

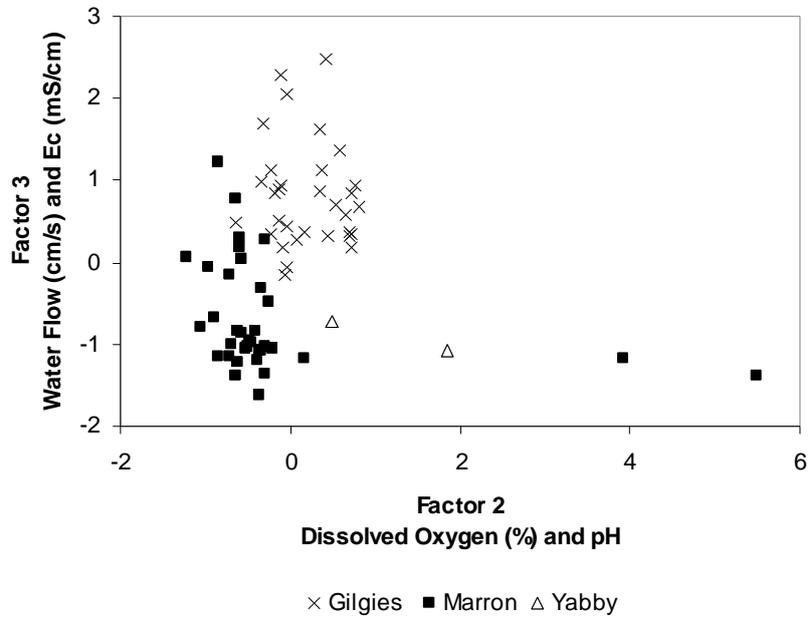


Figure 4. Scatter plot of Factor 2 v Factor 3 on the basis of species.

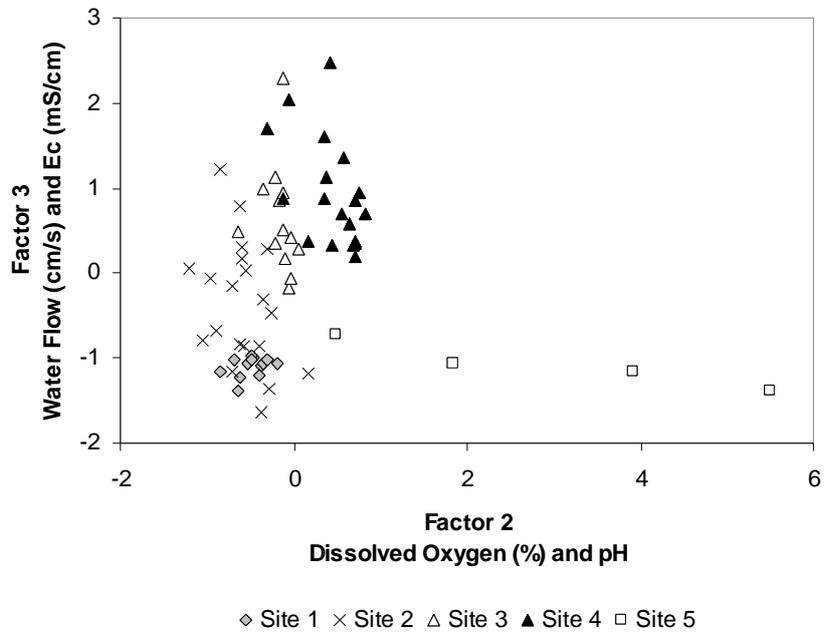


Figure 5. Scatter plot of Factor 2 v Factor 3 on the basis of site.

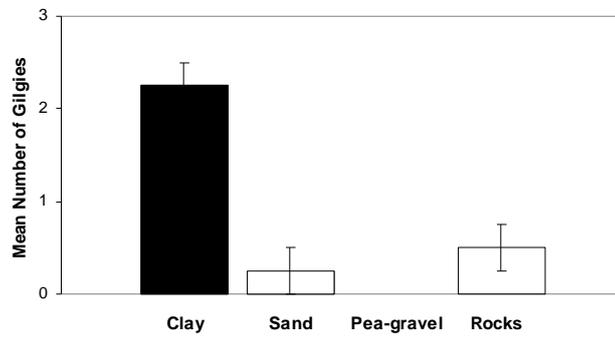


Figure 6. Mean number of gilgies on each sediment when alone

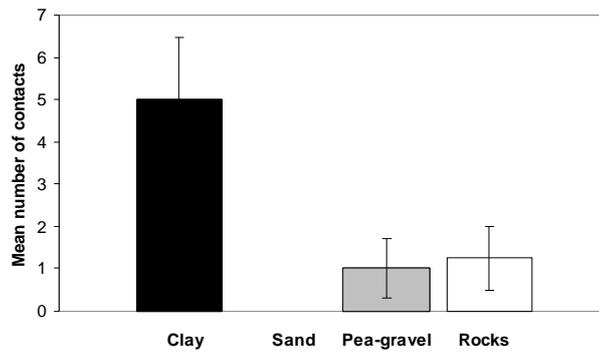


Figure 7. Mean number of tension contacts (\pm se) by gilgies and yabbies observed on each sediment type.

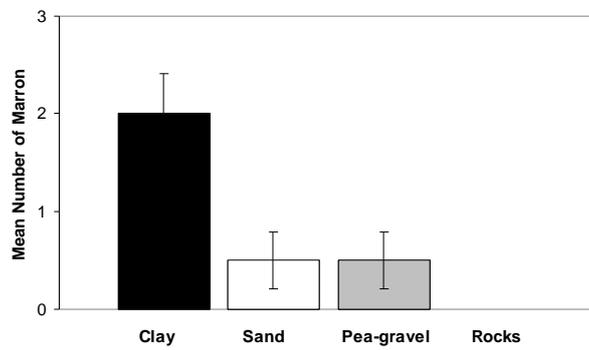


Figure 8. Mean number of marron on each sediment when alone