Dominance and population structure of freshwater crabs (*Potamonautes perlatus* Milne Edwards)

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Although freshwater crabs, *Potamonautes* spp, are abundant (up to 23 crabs m^{-2}) in southern African freshwater systems and form a major part of the diet of many vertebrates, little is known about their biology. Understanding crab population dynamics and behaviour, for example, is important to understanding their role in the ecosystem more clearly. In this paper we report on dominance in *Potamonautes perlatus* and test the prediction that larger crabs are dominant to smaller ones, i.e. a linear hierarchy exists and it is size dependent. To understand how this would affect wild populations we also investigated the population structure (sex ratio, size distribution, density and population growth) of a wild population. Using Landau's index of linearity (h) we found three captive groups of *P. perlatus* to show moderate linearity, i.e. h = 0.9; 0.81 and 0.83. In all three groups the largest individual was the most dominant. There was a significant Spearman rank correlation between dominance rank and size of largest chelae in two of the groups, and a significant Spearman rank correlation between dominance rank and carapace width in only one of the three groups. Densities of crabs in the Eerste River, Western Cape Province, ranged from a mean of 2.89 ± 2.11 to 15.57 ± 7.21 crabs m^{-2}. Unexpectedly the size class distribution of the crabs remained unchanged during the year. The lack of a significant increase in the mean size of the crabs can probably be ascribed to a year-round consistency in the availability of refugia for specific/different size classes. Intraspecific aggression, predation and refuge availability are probable strong selection pressures in determining population structures of wild populations of *P. perlatus*.

Keywords: Dominance, linear hierarchy, population structure, refuge availability, rivers, South Africa

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Despite freshwater crabs of the genus *Potamonautes* being locally abundant (up to 23 crabs m^{-2}) in southern African freshwater systems (Turnbull-Kemp 1960; Arkell 1978; King 1983; Räubenheimer 1986; Hill & O'Keeffe 1992), and forming a major part of the diet of many animals, little information is available about their biology. They are eaten by many species of fish (Skelton 1993), birds (Maclean 1985), and mammals such as the Cape clawless otter *Aonyx capensis*, spotted-necked otter *Lutra maculicollis*, and water mongoose *Atilax paludinosus* (Rowe-Rowe 1977; Somers & Purves 1996). Pollutants, e.g. heavy metals (Van Eeden & Schoonbee 1991; Du Preez, Steenkamp & Schoonbee 1993; Steenkamp, du Preez, Schoonbee, Wiid & Bester 1993; Steenkamp, du Preez & Schoonbee 1994; Snyman 1996) can accumulate in crabs and, therefore, in their consumers. Crabs reduce leaf litter particle size, which causes mobilisation of organic material, and contributes significantly to material cycling and energy flow in freshwater systems (Hill & O'Keeffe 1992). They may be important enough in freshwater systems to be termed dominant or even keystone species (Power, Tilman, Estes, Menge, Bond, Mills, Daily, Castilla, Lubchenco, & Paine 1996), but more data are needed.

Turnbull-Kemp (1960) and Räubenheimer (1986) noted that, for *P. perlatus* and *P. sidneyi* respectively, small crabs, with a carapace width of less than 17–30 mm, are not caught with bait. They suggested that larger crabs exclude smaller crabs from bait, or that there is a dominance hierarchy with regard to size. The occurrence of dominance in *P. perlatus*, inducing larger crabs to exclude smaller ones from bait or other resources has, however, remained unstudied. Hierarchical behaviour influences access to food and mates and, therefore, also influences population genetics of groups, and thus individual fitness (Chase 1974). Understanding crab hierarchical behaviour and population dynamics are important, therefore, for understanding crab biology and their role in the ecosystem.

In this paper we report on the influence of dominance on the population structure of freshwater crabs (*Potamonautes perlatus* Milne Edwards). We test the prediction that larger crabs are dominant to smaller ones, i.e. that there is a linear hierarchy and that it is size dependent. For a better understanding of how this would affect wild populations we report on the population structure (sex ratio, size distribution, density and population growth) of, and refuge availability to, a wild population in the Eerste River, Western Cape Province.

Methods

Dominance

For the test of dominance, we captured crabs during August 1996 in the Eerste River using fish traps (plastic funnel traps: 550 by 250 mm, with a funnel of 100 mm, baited with *ca* 200 g of shallow-water hake *Merluccius capensis*) left overnight in the river. The crabs were removed the following day, transported to the University of Stellenbosch, weighed and sexed. The carapace width and largest chelae (length of the propodite) were measured (Table 1). None of the females had eggs.

If repeated observations of interactions indicate the same hierarchy, then it can be accepted with greater confidence (Martin & Bateson 1986). Three groups of crabs were there-

Table 1 Composition of three captive groups of freshwater crabs *Potamonautes perlatus*. Abbreviations are: M = Male; F = Female

Group number	Crab number	Sex	Carapace width (mm)	Largest chelae length (mm)
1	1	M	33.0	26.5
1	2	M	51.0	41.0
1	3	F	43.3	26.1
1	4	M	46.1	33.6
1	5	F	45.0	26.6
1	6	F	38.3	17.4
1	7	F	37.0	16.9
2	1	M	48.2	41.4
2	2	F	49.2	31.9
2	3	F	36.3	22.4
2	4	M	41.5	31.7
2	5	M	42.6	34.7
2	6	M	50.3	42.5
2	7	F	45.5	28.2
2	8	F	45.7	29.1
3	1	F	42.2	25.0
3	2	F	49.2	29.0
3	3	F	44.2	27.0
3	4	M	36.8	28.1
3	5	M	41.0	31.9
3	6	F	45.0	28.0
3	7	F	42.0	26.5
3	8	F	56.0	35.0
3	9	F	44.6	28.0

fore tested for the existence of a dominance hierarchy. As only data from groups of more than five individuals can be shown to have statistically significant linearity (Appleby 1983), the groups exceeded five, namely: seven in group 1; eight in group 2 and nine in group 3. Each crab was marked on the top of its carapace with a quick-drying, waterproof, chloro-rubber-based (road-marking) paint. Each group was kept in a separate aquarium (613 × 322 mm), with *ca* 50 mm of aerated water. Refuges were provided in the form of plastic objects in the water. The aquaria were kept in a room with a constant temperature of 26°C, and a 12 h light cycle. The crabs were fed *ad lib* with Lopis® rabbit pellets every day. The aquaria were emptied and rinsed *ca* every 48 h. As crab 1 in group 1 was cannibalised before observations began, observations for group 1 were made using six crabs.

Dominance rank was determined from observations of threats (lifted pincers while not eating) and displacements (crab moving away from another threatening individual). Dominance/subordinance as used here, is the relationship between two individuals in which one (the subordinate) defers to the other (the dominant) in contest situations (Kaufmann 1983). Observations were done with the aid of a video recorder in order not to disturb the crabs during observation. Six 60 min observation sessions were conducted, beginning within 1 h of 13h00, on each group. These were done just after feeding the crabs. Refuge objects were removed beforehand. Two types of behaviour were noted: active interactions, in which one crab, the 'initiator', moved towards another crab, which then immediately vacated its position; and passive interactions, where the initiator did not move towards the other crab, but merely showed an action (e.g. lifted pincers) directed towards the other crab which then vacated its spot. Only active interactions were used in order to avoid uncertainties concerning the actions of the crabs.

When threatening occurred, the identities of the crab threatening and threatened, and the eventual winner (the individual which did not retreat) were recorded. A dominance matrix (Martin & Bateson 1986) for each group was constructed and the crabs were ranked according to their position in the group's matrix.

Landau's index of linearity (h) was used to measure the degree to which a dominance hierarchy is linear (Chase 1974).

The index is calculated as

$$h = \frac{12}{n^3 - n} \sum_{a=1}^{n} \left(v_a - \frac{1}{2}(n-1)\right)^2$$

where n is the number of animals in the group and v_a is the number of individuals which individual a has dominated. The index ranges from 0.0 to 1.0, with a value of 1.0 indicating perfect linearity (Chase 1974).

Population structure

To determine population structure of the crabs, we sampled two sites in the Eerste River near Stellenbosch. Site 1 was located just below Kleinplaas Dam (33°58'33"S, 18°56'35" E), and site 2 in the Assegaaisbos Nature Reserve (33°58'0" S, 18°55'33"E). The river at site 1 was *ca* 5 m wide and 50 mm deep, and 10–20 m below the dam wall. At site 2 the river was *ca* 2 m wide and 400 mm deep and 600 m downstream from the dam. Crabs were collected from both sites on 22 October 1993 and 28 October 1994. Site 1 was also sampled on 18 January and 4 June 1995. Quadrats of 1 m^2 were sampled randomly by removing all the crabs from the water by hand. All the substrate particles large enough to conceal a crab were removed to ensure that all crabs in the quadrat were removed. The crabs were weighed and their carapace widths measured. Care was taken to ensure no crabs escaped out of the quadrat while sampling. Crabs ≥ 20 mm carapace width were sexed.

To determine refuge size and availability for the crabs, we determined the number of substrate particles and their sizes at sites 1 and 2. Particle size, as used here, is the width of the smallest square or diameter of the smallest circular opening through which a particle can pass (Goudie 1990). The intermediate axes of all gravel (20–60 mm), cobbles (60–200 mm) and boulders (> 200 mm) in six 1 m^2 quadrats were measured, to the nearest 5 mm, at each site. The size class distributions of substrate particles at the two sites were also determined by placing each particle in one of the three particle size classes.

Statistical tests were done using Siegel (1956) or the computer programme SigmaStat for Windows version 1.0, Jandel Corporation©.

Results

Dominance

In all three groups (Table 1) the largest crab was the most dominant. The dominance hierarchies are given in interaction matrices for each group (Table 2). Landau's index of linearity for group 1 is $h = 0.9$; group 2, $h = 0.81$ and for group 3, $h = 0.83$. Combining dominance rank of all three groups, males and females did not rank significantly different (Mann-Whitney U test, $p = 0.361$, two-tailed for this and all subsequent Mann-Whitney U tests).

There was a significant Spearman rank correlation between dominance rank and size of the largest chelae, in two of the groups, and a significant Spearman rank correlation between dominance rank and carapace width only in one of the three groups (Table 3).

Table 2 Dominance matrix of *Potamonautes perlatus* in group 1–3. Dominance decreases from left to right across the table. The figures in the table are the number of interactions won by crabs in the left-hand column

Group 1

Crab No.	4	3	2	5	6	7
4	–	16	8	14	1	1
3	1	–	6	17	1	0
2			–	2	1	0
5				–	1	1
6					–	1
7						–

Group 2

Crab No.	6	2	8	5	4	1	3	7
6	–	7	8	13	2	2	1	4
2		–	8	9	2	0	2	19
8			–	2	1	1	4	1
5				–	2	0	6	9
4				1	–	0	1	4
1						–	1	2
3							–	1
7			2	9	4			–

Group 3

Crab No.	8	2	6	5	9	7	3	1	4
8	–	0	2	1	4	6	11	2	4
2		–	8	2	1	1	3	1	2
6			–	6	4	0	1	4	7
5				–	6	0	2	8	0
9				1	–	2	1	2	2
7						–	1	2	12
3							–	4	3
1								–	6
4									–

Table 3 Correlations between dominance rank and size (carapace width and chelae length) of three captive groups of freshwater crabs

Group No.	Crab characteristic compared to dominance rank	Spearman rank correlation
1	Carapace width	$r_s = 0.714$; $p = 0.136$
1	Chelae length	$r_s = 0.714$; $p = 0.136$
2	Carapace width	$r_s = 0.857$; $p = 0.002$
2	Chelae length	$r_s = 0.857$; $p = 0.002$
3	Carapace width	$r_s = 0.619$; $p = 0.672$
3	Chelae length	$r_s = 0.746$; $p = 0.016$

Table 4 Sex ratio of crabs *Potamonautes perlatus*

Date	Locality	Males : Females	n	Binomial test
22 October 1993	Site 1	64.9 : 35.1	77	$p = 0.006$
28 October 1994	Site 1	51.2 : 48.8	41	$p = 0.5$
22 October 1993	Site 2	57.1 : 42.9	7	$p = 0.5$
28 October 1994	Site 2	50 : 50	26	$p = 0.578$

Population structure

The density of crabs at site 1 was significantly higher than at site 2 in 1993 (site 1: mean = 15.57 ± 7.21; range = 6–36 crabs m^{-2}; $n = 14$; site 2: mean = 3.0 ± 1.31; range = 1–5 crabs m^{-2}; $n = 8$) (Mann-Whitney U test, $p < 0.001$), and 1994 (site 1: mean = 9.40 ± 8,09; range = 2–26 crabs m^{-2}; $n = 10$; site 2: mean = 2.89 ± 2.11; range = 0–9 crabs m^{-2}; $n = 18$) (Mann-Whitney U test, $p = 0.008$). There was no significant difference in crab density between years for site 2 (Mann-Whitney U test, $p = 0.697$), but there was for site 1 (Mann-Whitney U test, $p = 0.028$).

In 1993 the crabs at site 1 showed a significant male bias in the sex ratio. This did not apply to the other samples (Table 4).

There was no difference in size of the crabs collected at site 1 between October 1993 (mean carapace width = 18.8 ± 6.95 mm; n = 175) and October 1994 (mean carapace width = 19.5 ± 8.39 mm; n = 104) (Mann-Whitney U test, $p = 0.865$). There was, however, a significant difference in this parameter between site 1 and 2 (mean carapace width = 16.8 ± 7.85 mm; $n = 79$) in October 1994 (mean carapace width = 19.5 ± 8.39 mm; $n = 104$) Mann-Whitney U test, $p = 0.015$). No significant increase in crab size (carapace width) at site 1 from October 1994 to January 1995 (mean carapace width = 16.7 ± 6.17 mm; $n = 40$) Mann-Whitney U test, $p = 0.072$) and from January 1995 to June 1995 (mean carapace width = 17.5 ± 6.7 mm; $n = 70$) (Mann-Whitney U test, $p = 0.48$) was recorded (Figure 1). Although not significant, there is a shift in the size class distribution and mean size of the crabs from January to June and from June to October (Figure 1).

The mean particle size (> 20 mm) of the substrate at site 1 (mean = 67.9 ± 37.5 mm; $n = 494$) was significantly smaller than at site 2 (mean = 117.4 ± 84.7 mm; $n = 204$) (Mann-Whitney U test, $p < 0.001$). Site 1 had significantly more substrate particles m^{-2} (mean = 82.3 ± 29.05 particles m^{-2}; $n = 6$) than site 2 (mean = 34.0 ± 9.63 particles m^{-2}; $n = 6$) (Mann-Whitney U test, $p = 0.002$). The size class distribution of substrate particles at site 1 and 2 is given in Figure 2.

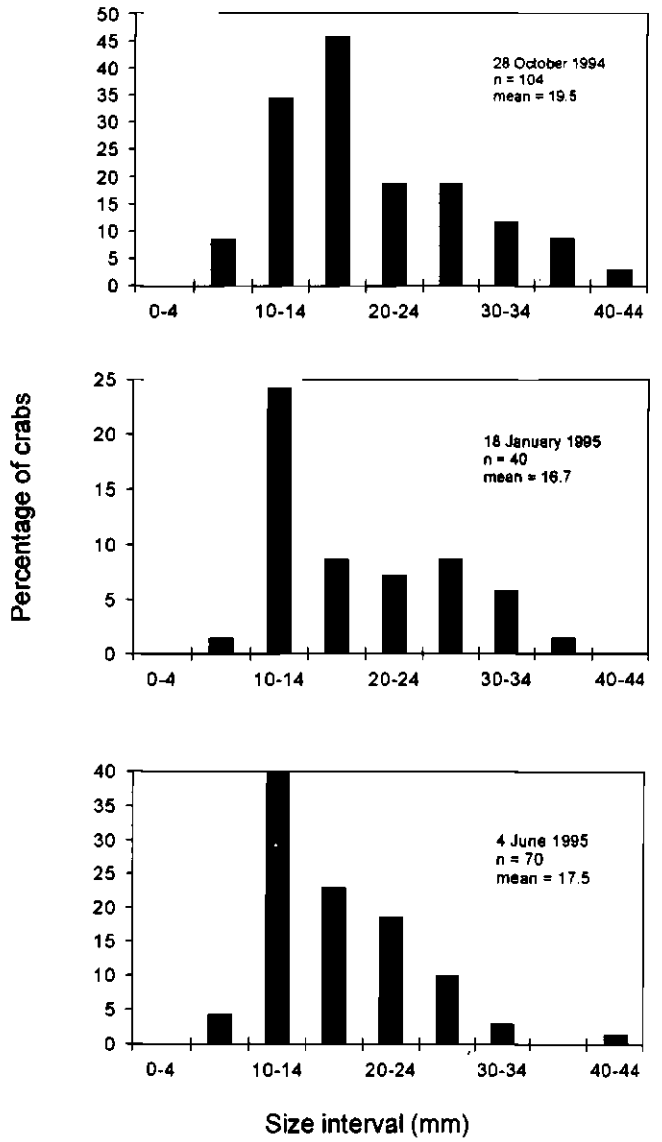

Figure 1 Carapace length-frequency data of *Potamonautes perlatus* from site 1, Eerste River, Western Cape Province.

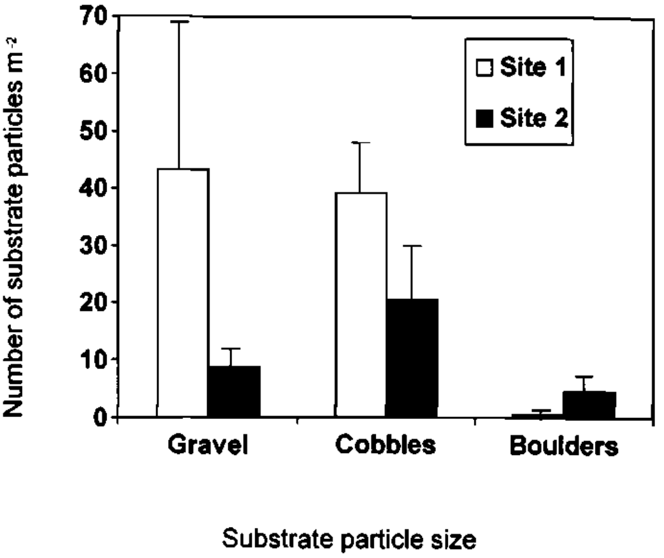

Figure 2 The size class distribution of substrate particles (gravel, 20–60 mm; cobbles, 60–200 mm; boulders, > 200 mm) at two sites in the Eerste River, Western Cape Province.

Discussion

Dominance

Linear hierarchies have been observed in birds (e.g. Keys & Rothstein 1991), fishes (e.g. Oliveira & Almada 1996), insects (e.g. Wilson 1971) and mammals (e.g. Schwarz-Weig & Sachser 1996). Chase (1974) defines a strong hierarchy, although somewhat arbitrarily, as a hierarchy giving an h measure of 0.9 or higher. The results of this study show that dominance hierarchies, although only moderately strong (h = 0.9; 0.81 and 0.83), also exist in captive *P. perlatus*. As densities of up to 36 crabs m^{-2} were found in this study and even 41 crabs m^{-2} have been found just below Kleinplaas Dam (Somers, unpublished data), a similar hierarchy could be expected in some natural situations. In areas of low density, high densities may also form when feeding on food items such as fish (Somers pers. obs.). In a group of animals, it is expected that some individuals have qualities, e.g. total size or size of chelae in the case of crabs, that would give them a high probability of being successful in pairwise competitions (Chase 1974). In this study the larger individuals of both sexes, especially those with larger chelae, were more dominant in two of the three groups. Here dominance occurred in aggressive interactions involving food, but it may also occur when procuring mates or shelter.

Hill & O'Keeffe (1992) showed that crabs of 21–30 mm ate a significantly higher percentage of aquatic invertebrates than larger crabs. In crabs in the 61–70 and 71–80 mm size classes, vertebrate tissue and crab remains, in small amounts, were present. Crab remains were also found in female crabs in these two size classes indicating cannibalism. In the Eerste River a small crab of *ca* 20 mm was seen to be cannibalised by a larger crab of *ca* 40 mm after it had been displaced from its refuge (Somers pers. obs.). These observations, and the cannibalising of crab 1 (the smallest crab in group 1), suggest that the existence of a dominance hierarchy may be responsible for the skewed size-class representation when sampling crab populations using bait.

Population structure

Owing to their possible key role in freshwater ecosystems, it is important to have an understanding of crab population parameters such as density. The densities of *P. perlatus* found at site 1, just below the dam wall in the Eerste River (9.40 ± 8.09 and 15.57 ± 7.21 crabs m^{-2}, in 1993 and 1994 respectively) are much higher than anywhere else recorded for a *Potamonautes* sp. The densities found at site 2 (3.0 ± 1.31 and 2.89 ± 2.11 crabs m^{-2}, in 1993 and 1994 respectively) are more similar to those found by Arkell (1978) in the Eerste River during February 1975 (2.0 ± 1.5 crabs m^{-2}). Hill & O'Keeffe (1992) gave densities (3.69 ± 0.36 and 2.47 ± 0.24 crabs m^{-2}) for all sizes of *P. perlatus* at two sites in the upper Buffalo River, Eastern Cape Province. King (1983) sampled the same locality as site 1 along with another locality further upstream between March 1975 and April 1976 while Kleinplaas Dam was being built. King (1983) found a density of 0.7 crabs m^{-2} combining both sites but pointed out that densities of invertebrates below the construction site were kept low by increased turbidity caused by construction activities. In other sites in the Eerste River, King (1983) found densities ranging from 0.3–2.7 crabs m^{-2}.

Turnbull-Kemp (1960) estimated that densities of *P. perlatus* in Zimbabwean trout streams range from 0.75–1.29 crabs m^{-2}. Butler & du Toit (1994) estimated densities of *P. perlatus* at two sites in the Kairezi River, Zimbabwe, to range between 2.18 and 0.11 crabs m^{-2}. These authors, however, used a mark recapture method of crabs caught in funnel traps, so the results are not directly comparable. The high densities reported for one of the sites in this study emphasise the possible importance of crabs in freshwater systems. The results also show localised differences in densities within a system which could be important for crab populations, and their predators.

As refuge size and availability are important in determining population structure of many aquatic organisms (Beck 1995 and references therein), size distribution of the crab population may be determined by the availability of refuges created by the number and size of substrate particles. The results presented here show that where there are fewer, larger substrate particles, there are fewer but larger crabs. The lack of more data from more sites and the uncertainty whether or not refuges are limited precludes further speculation at this stage.

As dominance hierarchies exist and densities are the result of each individual maximising its fitness considering the decisions of all other individuals (Maynard Smith & Price 1973; Parker & Sutherland 1986), it is unlikely that an ideal free distribution (Fretwell 1972) occurs in the crab population. Interactions between individuals in conjunction with refuge availability (Figure 2), therefore, may be a very strong selection pressure for determining population structure of *P. perlatus* in various microhabitats. This may explain the apparent lack of a discrete breeding season as found at site 1.

The findings of this study support the earlier suggestions by Turnbull-Kemp (1960) and Räubenheimer (1986) that larger crabs exclude smaller crabs from bait (locality of temporary high crab density), and that there is a dominance hierarchy with regard to size.

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