Comparative population dynamics of four fiddler crabs (Ocypodidae, genus *Uca*) from a North Brazilian mangrove ecosystem

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ABSTRACT: Abundance, biomass, population structure, growth, mortality and reproduction of 4 fiddler crabs (*Uca cumulanta*, *U. maracoani*, *U. rapax* and *U. vocator*) were studied in the Caeté mangrove estuary, North Brazil, to understand their life history strategies and species distribution in the mangrove forest. Three zones were sampled in the mangrove ecosystem: high intertidal forest (F), small creeks running through the forest (SC), and open mud banks of large tidal creeks (LC). Significant differences between zones were found in silt/clay, water and organic content of the sediment. Species zonation was pronounced: *U. rapax* and *U. vocator* were restricted to the high intertidal forest (differing preferences for organic and water content of the sediment probably allows these 2 species to coexist); *U. cumulanta* and *U. maracoani* were mostly restricted to the mid and low intertidal (the sunny mud banks of large creeks were completely dominated by the latter, probably due to its greater tolerance to high temperatures). Fiddler crab biomass was highest in LC, followed by F and SC (72.9, 19.5, and 10 g m^{-2}, respectively), while abundance was highest in LC, followed by SC and F (79.1, 69.2, and 59.3 ind. m^{-2}, respectively). Population structure of all species was strongly skewed towards the smallest size classes, and sex ratios were 1:1 in *U. maracoani* and *U. vocator*, with significantly more females in *U. cumulanta* and *U. rapax*. All fiddler crabs studied were fast-growing, and had short life spans and high mortality rates. Von Bertalanffy growth parameters, growth performance, and total mortality rates were calculated for all species. L_∞, K, and Munro's ϕ' ranged from 11.1 mm carapace width (CW), 4.24 and 1.7 yr^{-1} in *U. cumulanta* females up to 35.2 mm CW, 2.03 and 3.2 yr^{-1} in *U. maracoani* males. Total mortality rates (Z) varied between 4.9 and 10.1 yr^{-1}, with females having generally 15 to 20% higher mortality rates than males, except for *U. cumulanta*. All species except *U. vocator* reproduced mainly during the dry season, but breeding was always prolonged and sometimes year-round, e.g. in *U. rapax*, 1 of the 2 species occurring in the forest. The second forest species, *U. vocator*, had a clear spawning peak towards the end of the rainy season and temporal separation of reproduction may also promote coexistence of the 2 species.

KEY WORDS: *Uca* spp. · Fiddler crabs · Population dynamics · Growth · Mortality · Reproduction · Zonation · Sympatry · Brazil · Mangrove epibenthos

INTRODUCTION

Fiddler crabs are among the most conspicuous organisms in many intertidal ecosystems including mangrove forests, salt marshes, mud and sand flats. They range from tropical to warm temperate areas, with the highest species diversity found in the Americas (Crane 1975, Montague 1980). Their distribution and zonation in the intertidal mostly depends on abiotic factors such as shore level, salinity, temperature and sediment grain size and organic content (e.g. Gerlach 1958, Macnae 1968, Crane 1975, Icely & Jones 1978, Frith & Brunnenmeister 1980). Although shore level and temperature regime have been considered most influential for the

distribution of intertidal crabs in general (e.g. Macnae 1968, Warner 1969, Jones 1984, Frusher et al. 1994), sediment characteristics such as silt/clay and organic content are especially important for deposit-feeders such as *Uca* spp. (Altevogt 1957, Miller 1961, Icely & Jones 1978, Frith & Brunnenmeister 1980, Robertson & Newell 1982a,b, Jaramillo & Lunecke 1988).

Fiddler crabs are an important link to higher trophic levels in intertidal and shallow water food webs. Koch & Wolff (2002) reported that detritivorous crabs (>95% fiddler crabs) account for almost 90% of total benthic macrofauna production in the Caeté mangroves (intertidal). Wolff et al. (2000) showed that fiddler crabs are among the most important prey in the food web of the Caeté mangroves, where they form part of the diet of many crustaceans, birds, fish and mammals. By converting a substantial part of bacterial production directly into 'bite-sized' food items for larger predators, energy transfer via the 'fiddler crab pathway' is highly efficient.

While the important ecological role of fiddler crabs is evident, few studies (e.g. Shanholtzer 1973, Colby & Fonseca 1984) have focused on their population dynamics (i.e. growth, mortality and recruitment rates). Studies on secondary production of fiddler crabs show that they have high turnover and production rates (Teal 1962, Macintosh 1984, Koch 1999, Koch & Wolff 2002), but there is very little information on the biological processes that determine their population size and productivity. Therefore, the overall objective of this study was to investigate the population dynamics and spatial distribution of the dominant fiddler crabs in the Caeté estuary to better understand their life history strategies and how the species use different zones in the mangrove ecosystem.

Specifically, we asked the following questions: (1) How are the species distributed in the mangrove forest? (2) What is their relative and absolute abundance and biomass in the mangrove ecosystem? (3) How do growth and mortality rates differ between the 4 species? (4) What are the main breeding and recruitment seasons and how do female reproductive traits differ among species?

MATERIALS AND METHODS

Study area. The study area is located on a peninsula on the western shore of the Caeté estuary north of Bragança, about 200 km east of Belém in North Brazil (Fig. 1). The mangrove cover on the peninsula amounts to about 140 km², the tidal range in the area is 3 to 5 m. Numerous channels and creeks cut through the peninsula. The largest part of the mangrove forest is situated above the mean high tide level and is only flooded during spring tide days. Red (*Rhizophora mangle*) and black (*Avicennia germinans*) mangroves dominate, the white mangrove (*Laguncularia racemosa*) is the least common species and can often be found at disturbed sites (Thüllen 1997, Mehlig 2001). The region receives approx. 2500 mm yr⁻¹ of rain, mostly between January and June. Salinity oscillates correspondingly between <10 PSU during the rainy season to 39 PSU at the end of the dry season. Average air (24 to 28°C) and water (27 to 30°C) temperatures vary little over the year, with lowest values occurring after heavy rainfalls (INMET 1992, MADAM unpubl. data). The study site was located at the Furo do Meio, a large creek in the central part of the peninsula. For further details, see Koch (1999), Wolff et al. (2000) and Koch & Wolff (2002).

Field sampling. The study site was subdivided into 3 zones: high intertidal forest (F), small, shaded creeks within the forest (SC) and the open mud banks of large creeks (LC). The area of each zone varied between 1.5 (SC) and 4 ha (F). At each zone, 8 replicate samples
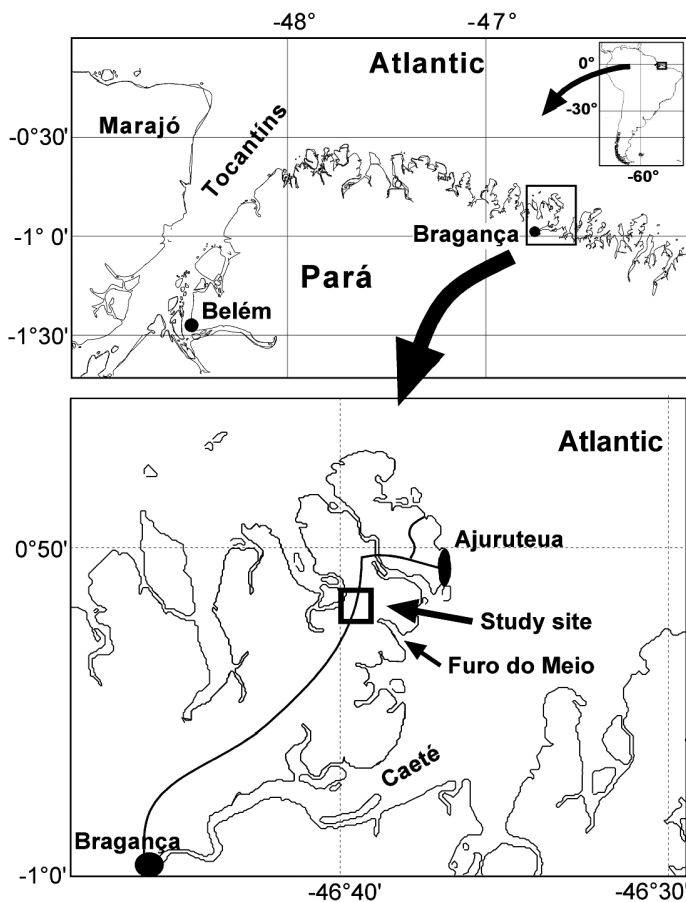

Fig. 1. The study area. The upper part shows the North Brazilian coastline east of the Tocantins, the lower part shows the mangrove peninsula north of Bragança with inset indicating study site at the Furo do Meio

were taken in intervals of 6 wk over a period of 12 mo (10 mo in SC). Enclosure quadrats were made with acrylic glass plates of 70×20 cm that were put together to enclose an area of 70×70 cm (0.49 m^2). The quadrats were set up during spring high tides when the mangrove forest was flooded. This ensured that only specimens that actually inhabited the sampled area were caught, because fiddler crabs retreat to their burrows during tidal inundation. Sampling in all 3 zones started after the tide had receded. Each enclosure quadrat was usually sampled 2 to 3 times to ensure complete removal of crabs. Specimens were removed from the surface and dug up by hand. Crabs were taken to the laboratory, frozen at –20°C and later identified, sexed and checked for presence of eggs. Carapace width (CW) of each specimen was measured to the nearest 0.1 mm under a dissection microscope with a measuring eyepiece (for large individuals, callipers were used) and fresh mass weighed to the nearest 0.01 g.

Growth. The growth of the 4 fiddler crab species was measured in *in situ* cages (Fig. 2) in intervals of 6 wk from July 1997 to February 1998. Cages were built for each species in its preferred zone. When the cages were constructed, special consideration was given to the following: (1) wooden boards reached 60 cm into the sediment to prevent crabs from digging their way out (or in); (2) acrylic glass plates were fixed on top of the cages that also prevented crabs from leaving or entering; (3) a fence of mangrove stems was collocated around each cage (to a depth of about 1 m) to prevent large mangrove crabs *Ucides cordatus* from burrowing into the cages.

Prior to the experiment all animals were removed from the cages in the same way the crabs were sampled in the enclosure quadrats. Two to 3 visits were sufficient to remove all animals and no further crabs were found when checking 2 wk later. Each cage compartment was then stocked with animals of both sexes of 1 size class only (±0.2 mm) at natural densities, thus creating 'artificial cohorts' (for initial sizes, see Fig. 7). Crabs were recaptured and measured to the nearest 0.1 mm CW every 6 to 8 wk and returned to the cages afterwards.

The von Bertalanffy growth function (VBGF) (von Bertalanffy 1934, Ricker 1975) was used to describe the growth of the crabs:

$$L_t \ = \ L_\infty \cdot (1 - e^{-(K \cdot (t - t_0))}) \tag{1}$$

where L_t is the length at time t, t_0 is the age at zero length and K is the curving parameter of the growth function. The parameters were calculated using the Munro plot (Munro 1982):

$$K_{(t_{i+1} - t_i)} \ = \ \ln(L_\infty - L_i) - \ln(L_\infty - L_{i+1}) \tag{2}$$

where L_i and L_{i+1} are the lengths at times t_i and t_{i+1}
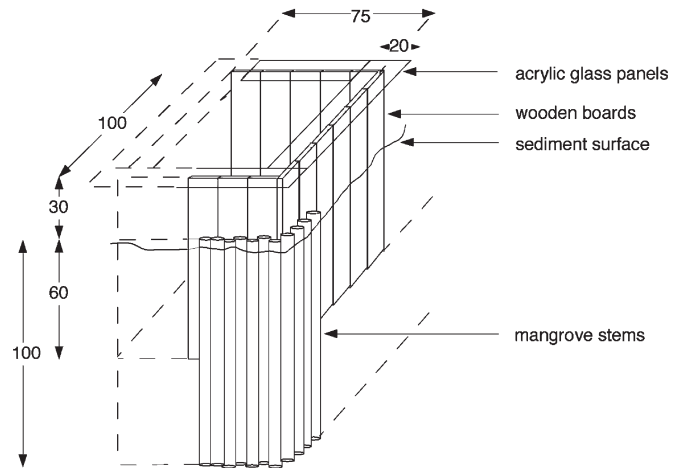

Fig. 2. Cage compartment used for determining growth rates of *Uca* spp. All measurements are given in cm

respectively, and K and L_∞ are as described above. As specimens could not be recognized individually, each pair of lengths represents the arithmetic mean of all males or females of 1 size class in a cage compartment. The optimum combinations of K and L_∞ values were obtained by varying L_∞ until the coefficient of variation for K was minimized. Data analysis was done with FiSAT (Gayanilo et al. 1994). t_0 was set to zero as no data for larval and early postlarval development time was available that would have allowed for the estimation of absolute age for the species under study. Seasonal growth oscillation in all species was small (amplitude of the growth curve: C < 0.1, Pauly & Gaschuetz 1979), therefore the normal VBGF was used. Munro's φ′ (Pauly & Munro 1984) was used to calculate the growth performance of the fiddler crabs:

$$\phi' \ = \ \ln K + 2 \cdot \ln L_\infty \tag{3}$$

This index allows for comparison of the growth potential of different species and thus serves to evaluate patterns along latitudinal gradients and/or among taxonomic groups.

Mortality. Length-converted catch curves (Ricker 1975, Sparre et al. 1989) were used to calculate total mortality rate (Z) for males and females of all 4 species, assuming Type III survivorship (Caddy & Sharp 1986) and single exponential mortality. For the regressions, only the right, descending arm of the catch curve is used, as the left arm represents the smallest animals that were not sampled quantitatively. Z is equal to the negative slope of the resulting regression line. Catch curve analysis was done with the computer package FiSAT (Gayanilo et al. 1994).

Reproduction and recruitment. Size at the onset of maturity of females was calculated from the average of

the 5 smallest ovigerous specimens of each species found over the course of the study. The corresponding age at first maturity for females was estimated using the inverse of the respective VBGF. An estimate for the energy investment per clutch was derived from the ratio of the clutch weight divided by total female weight (both given in g ash free dry mass). The proportion of egg-carrying females (egg-carrying / total number of mature-sized females) of the 4 fiddler crabs at each sampling date was used as an indicator for reproductive activity and peak breeding periods. Sex ratios were calculated by dividing the total number of female crabs (immature and mature) by the total number of crabs whose sex could be identified at each sampling occasion. Sex ratios were tested against an expected frequency of 1:1 using a chi-squared test (Zar 1999). Averages and standard deviations (SD) were calculated over all sampling dates. The number of recruits (defined as the number of early crab stages) entering the populations between 2 sampling dates was estimated as follows: The maximum size a recruit could reach between any 2 sampling dates was estimated using the VBGF for each of the 4 species. All animals found below this size had consequently recruited during that period. The mortality of recruits between sampling dates was not taken into account and our estimates are therefore conservative.

Abiotic parameters (1 sample taken in each replicate quadrat). *Silt/clay content:* Sediment samples were taken with a small corer to a depth of 10 cm. Silt/clay content was determined using the method described by Holme & McIntyre (1984). After drying to constant weight at 100°C, the sample was weighed, placed in a 63 μm sieve, gently broken up after adding hot water and sifted wet until no further sediment could be removed. The remains in the sieve were dried at 100°C, weighed and silt/clay content calculated.

Water content: Samples were taken with a small corer to a depth of 8 to 10 cm, stored in film containers, weighed wet, dried to constant weight in a freeze drier and weighed again. Water content was then calculated from the difference between wet and dry weight. Samples were always taken at the end of a sampling day at low tide.

Organic content: Samples were scraped from the sediment surface with a spoon and frozen at –20°C. In the laboratory, inorganic carbon was removed with 0.02 M HCl, the samples were dried at 100°C to constant weight, homogenized and weighed to the nearest 0.1 mg.

After burning for 6 h at 540°C, the sample was weighed again and organic content was calculated from the weight loss.

Temperature: Air temperature directly above the sediment surface was recorded 2 to 3 times during each sampling day in each replicate (electronic thermometer ama-digit ad 30th, accuracy: ±0.1°C).

Statistical analysis. One-way ANOVA was used to detect differences between environmental parameters in the 3 zones. Heterogeneity of variance was tested with Hartley's F-max test at $p \leq 0.01$, for unequal sample sizes the approximation suggested in Sokal & Rohlf (1995) was used. Unplanned mean comparisons were done using Tukey's HSD test (Sokal & Rohlf 1995). Comparison of environmental parameters in forest quadrats where either *Uca vocator* or *U. rapax* dominated were done with independent *t*-tests. p-values are only given for significant differences in the text. Data analysis was done with the statistical package SYSTAT 5.2 for the Macintosh.

RESULTS

The abiotic environment

Silt/clay content was significantly higher in F and SC than in LC ($p < 0.001$ in both cases) (Fig. 3). Organic matter content in SC was higher than in the other 2 zones ($p < 0.001$ in both cases), water content in F is lower than in SC and LC ($p < 0.001$ in both cases), and air temperature at the sediment surface was higher in LC compared to F and SC ($p < 0.001$ in both cases).

Crab zonation, abundance and biomass

Clear differences in the vertical zonation of the 4 fiddler crab species were found between F (<1 m below
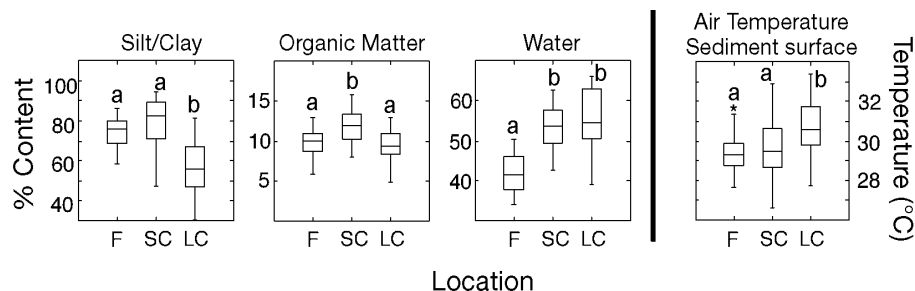

Fig. 3. Box plots of sediment parameters and temperature measured at the sediment surface from the sampling quadrats F (forest), SC (small creek) and LC (large creek). The horizontal line dividing the box is the median, the size of the box denotes the 25% quartiles (interquartile range), the whiskers delimit ±1.5 interquartile ranges from the edges of the box (∗ = value outside this range). Letters denote homogeneous groups defined by ANOVA and Tukey's HSD post hoc comparison
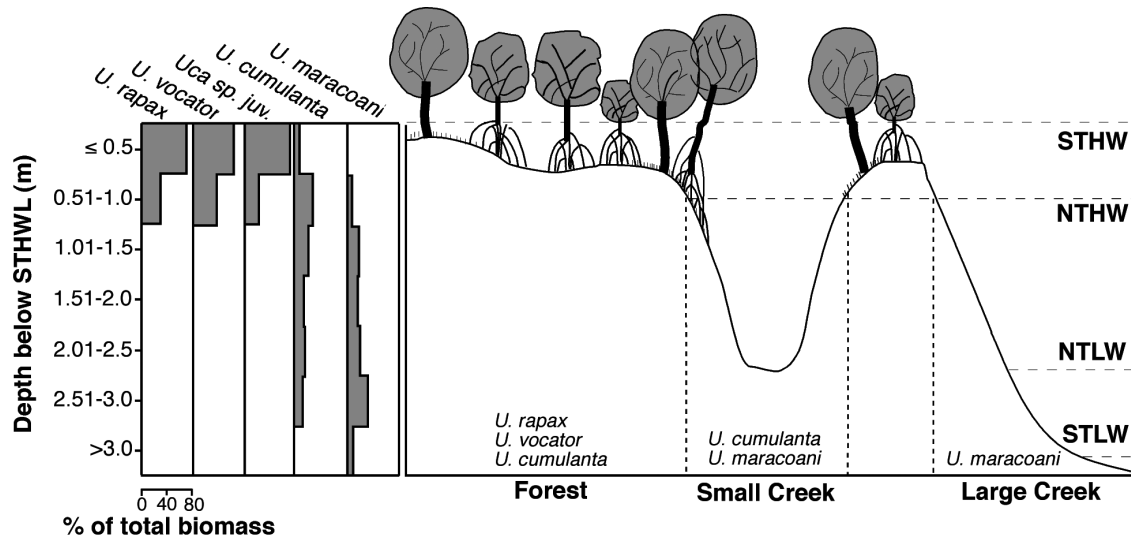
Fig. 4. Vertical zonation of *Uca* spp. Bar height indicates the percentage of the total biomass of each species found on a certain shore level. The right part of the graph gives a schematic view of the 3 zones sampled, and the dominant species found in each. ST = spring tide; NT = neap tide; HW = high water level; LW = low water level

STHWL), SC (1 to 2.5 m below STHWL) and LC (1 to >3 m below STHWL) (Fig. 4). *Uca vocator* and *U. rapax* and their juveniles (*Uca* sp. juv.) occurred only in F, whereas *U. cumulanta* was mostly found in the mid intertidal of SC, but also close to the creek margins in F. *U. maracoani* occurred at lower tidal levels in SC and was the only species found on the mud banks of LC. None of the species occurred in all 3 zones.

Biomass and abundance of each species in its preferred forest zone varied throughout the sampling period without a clear trend (Table 1). *Uca maracoani* completely dominated the epifauna in LC and also had the highest biomass in SC. *U. cumulanta* was by far the most abundant species in SC and contributed over 10% to the forest biomass (>6% abundance) where *U.*

vocator and *U. rapax* were dominant. Highest biomass values were found in LC, followed by F and SC. Abundance was also highest in LC, followed by SC and F. The 4 fiddler crab species made up a large part of total epifaunal abundance (65.8 to 96.5%) and biomass (11.3 to 99.4%) in the 3 zones (data in last row of Table 1 taken from Koch & Wolff 2002). The low % contribution in F resulted from the dominance of another ocypodid crab, the leaf-eating *Ucides cordatus*.

To test if and how the distribution of *Uca rapax* and *U. vocator* in the forest was related to temperature, grain size, organic matter and water content, the dominance of each species was used as a grouping variable for the environmental parameters measured. Only those sampling quadrats were used where either of the 2 species accounted for at least 75% of their combined biomass (*U. vocator*: n = 14; *U. rapax*: n = 11). *U. vocator* was dominant in areas with higher organic (independent *t*-test: p = 0.014) and water content (p = 0.027) when compared to areas were *U. rapax* was dominant. Although *U. vocator* was generally found in sediments with higher silt/clay content, the differences were not significant (p = 0.086). No preferences were found regarding the air temperature at the sediment surface (p = 0.477).

Table 1. Average biomass (fresh wt, g m^{-2}) and density (no. m^{-2}) ± standard error of *Uca* spp. in the 3 zones sampled: F (forest), SC (small creek) and LC (large creek). Bold numbers indicate where each species is most abundant. The % contribution to total epifaunal biomass and abundance in the 3 zones was calculated using values from Koch & Wolff (2002)

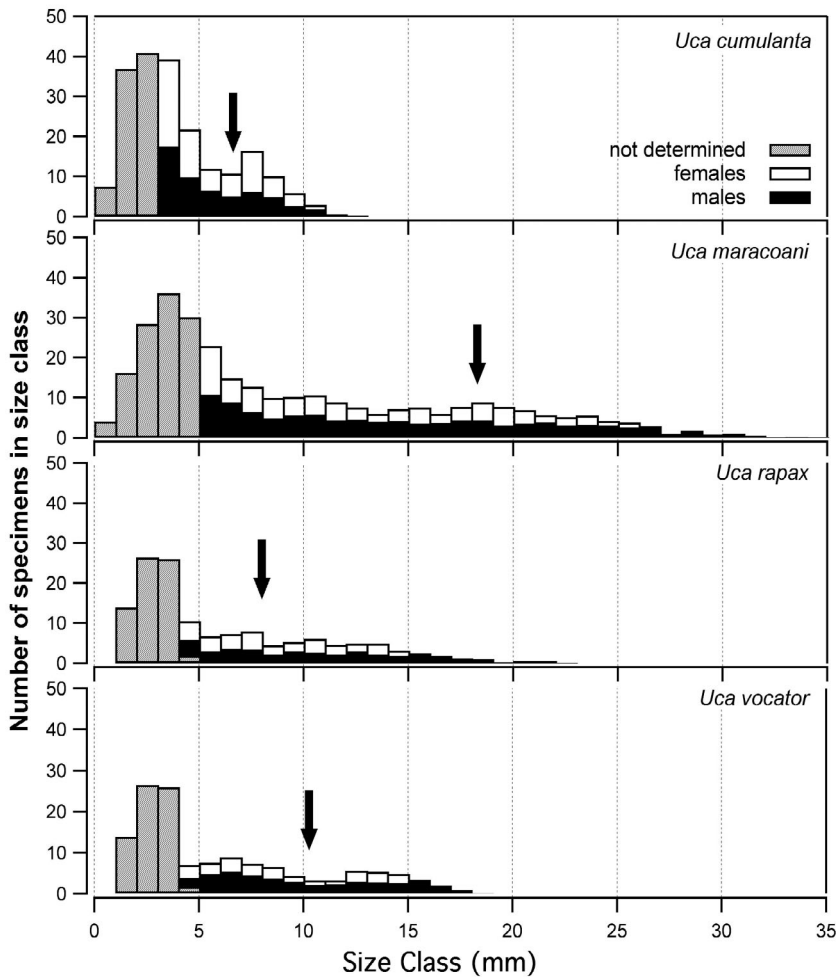| Species	F		SC		LC	
	Biomass	Density	Biomass	Density	Biomass	Density
U. cumulanta	1.1 ± 1.2	6.7 ± 6.9	**2.6 ± 1.1**	**56.3 ± 22.1**	–	–
U. maracoani	–	–	6.4 ± 4.4	12.9 ± 10.7	**72.9 ± 12.7**	**79.1 ± 9.6**
U. rapax	**8.9 ± 2.8**	**19.4 ± 5.7**	–	–	–	–
U. vocator	**9.4 ± 2.1**	**18.3 ± 8.7**	–	–	–	–
Uca sp. juv.	**0.1 ± 0.1**	**14.9 ± 13.9**	–	–	–	–
% of total epifauna	11.3	65.8	49.5	68.7	99.4	96.5

Fig. 5. Population size structure of *Uca* spp. As juveniles of *U. rapax* and *U. vocator* could not be distinguished, the total amount of *Uca* sp. juv. is shown in the graphs for the species. Black arrows give the size at maturity for females, estimated as the average of the 5 smallest egg-carrying females in the sample. Numbers in each size class represent the average number of specimens found per sampling occasion (3.92 m²)

Growth

Growth measurements in the cage experiments included almost the whole size range >6 mm for all species. SD was generally small and never exceeded 15% of the average value (Fig. 6). This ensured a good coverage of most of the calculated growth curve with actual measurements. The growth parameters calculated with the Munro-plot (Table 2) show a good fit, with the standard error of K being around 10% of the mean. Munro's ϕ' was highest in *Uca maracoani* and lowest in *U. cumulanta*. Variation between sexes was small, except for *U. cumulanta*, where ϕ' of females was 15% lower than that of males.

Mortality

The total mortality rates (Z) as calculated from the length-converted catch curves (Fig. 7) were highest in *Uca cumulanta*, followed by *U. vocator*, *U. maracoani* and *U. rapax*. Generally, females had about 20% higher mortality rates than males, except for *U. cumulanta*, where the value of males was approx. 10% higher. The mortality estimate for *U. vocator* had wide confidence intervals and the graph indicates that this species might not quite follow the single exponential mortality. However, the Z-value resulting from the single exponential model was used as an estimate to be able to compare mortality rates among species.

Population size structure

The size frequencies of each species during the sampling period (Fig. 5) show a strong peak at the smallest size classes in all 4 species. A second, and much smaller, peak was present in *Uca cumulanta*, *U. maracoani* and also in *U. vocator* that coincides closely with the size at which females first reach sexual maturity (arrows in Fig. 5). Sex ratios were significantly different from 1:1 only in *U. cumulanta* and *U. rapax*, with females being more abundant in both cases (see Table 3).

Table 2. Parameters of the von Bertalanffy growth function (L_∞, $K \pm$ SE) for males and females of *Uca* spp. as calculated with the Munro plot. Size range over which growth was measured is shown. Maximum age is defined as the age where 95% of L_∞ is reached; ϕ' is Munro's growth performance index

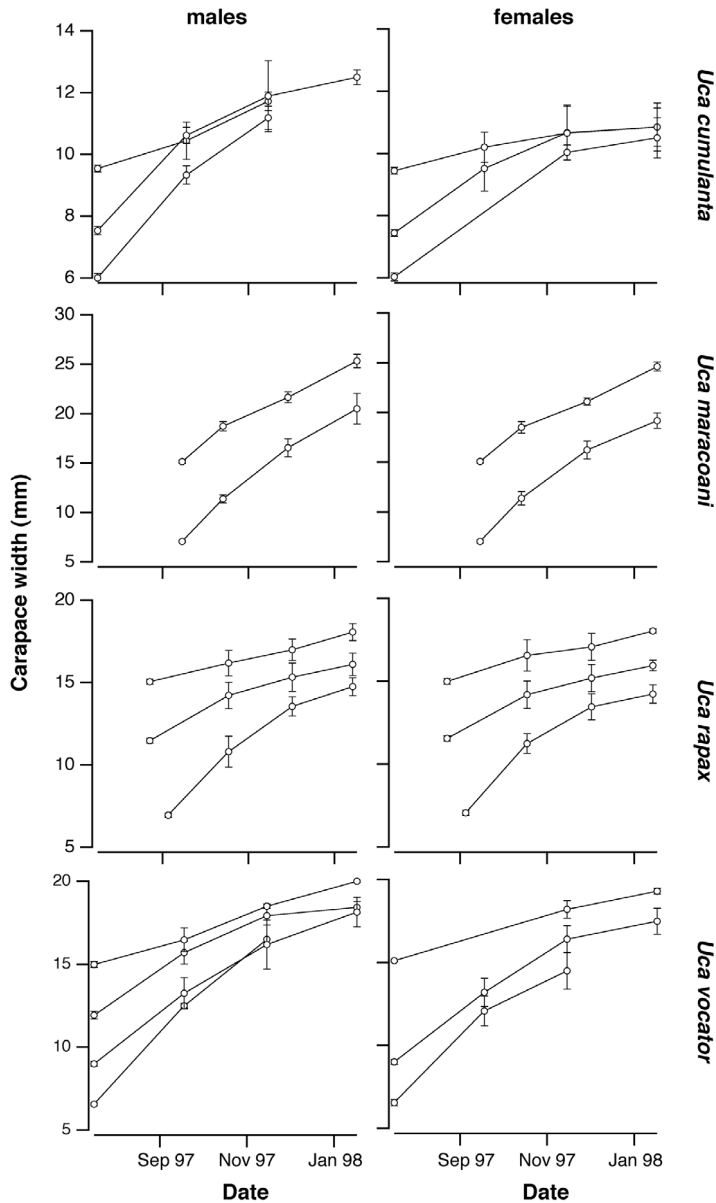| Species	Sex	Size range used (mm)	L_∞ (mm)	$K \pm$ SE (yr^{-1})	Max. age (yr)	ϕ'
U. cumulanta	Males	6.0 – 12.5	13.1	4.22 ± 0.14	0.71	2.0
	Females	6.0 – 10.9	11.1	4.24 ± 0.49	0.70	1.7
U. maracoani	Males	7.0 – 24.6	35.2	2.03 ± 0.14	1.47	3.2
	Females	7.0 – 25.3	31.0	2.44 ± 0.29	1.23	3.0
U. rapax	Males	6.9 – 18.0	20.5	2.08 ± 0.22	1.44	2.2
	females	7.1 – 18.0	20.0	2.15 ± 0.28	1.40	2.2
U. vocator	Males	6.6 – 20.0	21.6	2.71 ± 0.27	1.10	2.5
	Females	6.5 – 19.3	20.6	2.97 ± 0.28	1.01	2.5

Fig. 6. Growth increments of *Uca* spp. obtained from the cage experiments. Average CW ± SD are given for males and females separately. Each line corresponds to the specimens in 1 cage compartment ('artificial cohort'). Note that the *y*-axes have different scales

Reproduction and recruitment

The proportion of egg-carrying females and the number of juveniles recruited between any 2 sampling dates is shown in Fig. 8, together with salinity and precipitation values for the study period. Most precipitation occurred between January and June and salinity was below 15 PSU during this time (in 1998, values almost approached 0 PSU during times of heavy rainfall). Ovigerous *Uca maracoani* females were mostly found

in the drier season, when recruitment was highest (up to 50 recruits m^{-2} in 6 wk). However, fairly high levels of recruitment occurred also during the wet season when none or few egg-carrying females were found. Reproductive activity of *U. cumulanta* also seemed to be more concentrated during the drier season, when the proportion of egg-carrying females peaked at 0.3 to 0.4 from September 1997 to January 1998. Peak recruitment however, was found at the end of the rainy season in June with about 60 recruits m^{-2} in 7 wk. Egg-carrying females of *U. rapax* were found throughout the study period with a small peak from October to December at the end of the dry season. *U. vocator*, on the other hand, had a very pronounced reproductive peak from March to June. Generally, recruitment levels of *Uca* sp. juv. were highest at the end of the rainy and beginning of the dry season from May to September (up to 50 recruits m^{-2} per 6 wk), and were lower during the rest of the year (10 to 15 recruits m^{-2} per 6 wk)

The age at onset of maturity was very similar (0.20 to 0.23 yr) in all species except for the largest species, *Uca maracoani*, with 0.36 yr (Table 3). Size at onset of maturity was around or a little over half the maximum size (L_∞) in all species except for *U. rapax* where females reached reproductive size at just over $\frac{1}{3}$ of their maximum size. Energy investment per clutch was similar in all species (not measured in *U. rapax*) with 11 to 13% of the ash-free dry mass of the organism.

DISCUSSION

Crab zonation, abundance and biomass

Zonation of the 4 fiddler crab species was characterized by *Uca rapax* and *U. vocator* being restricted to the high intertidal forest, while *U. cumulanta* and *U. maracoani* were found in the mid and low intertidal. The distribution limit between the 2 groups coincided well with the neap high tide level (NHTL) and the observed zonation is consistent with the findings of Crane (1975).

The spatial distribution of the 4 fiddler crab species was strongly related to sediment characteristics and correlated with the number, size and form of setae on their feeding appendages. Species possessing abundant spoon-tipped setae (sturdy setae with little spoon-shaped tips) on their second maxillipeds are best adapted to feeding on sandy sediments with low organic content, while species feeding on muddy sediments with high organic content primarily have plumose setae (more flexible, featherlike setae) (Altevogt 1957, Miller 1961, Crane 1975, Icely & Jones 1978, Robertson & Newell 1982b). Microscopical examination showed that the number of spoon-tipped
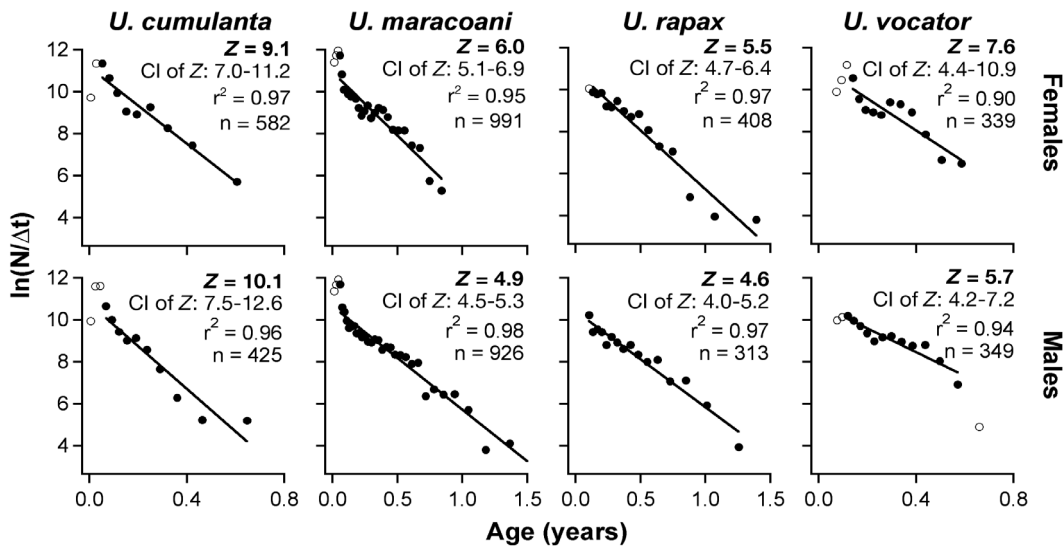
Fig. 7. Length-converted catch curves for males and females of *Uca* spp. Total *Z* with confidence intervals (CI) and goodness of fit (r^2) of the regression are given in each graph. Only data points represented by filled circles (●) were used to calculate the regression line

setae was highest in *Uca maracoani*, followed by *U. rapax* and *U. cumulanta*, while *U. vocator* possessed only plumose setae (Koch 1999). Accordingly, in the mid and low intertidal *U. maracoani* was found in areas with high sand and low organic content while *U. cumulanta* was most abundant in SC, the zone with the highest silt/clay and organic content.

In F, *Uca vocator* was dominant in sediments with higher organic content, while *U. rapax* was most abundant in areas with low organic content as predicted by the setae types found. No direct dependence on sediment grain size was found (*t*-test, p = 0.086), but silt/clay content in the area had a comparably narrow range (55 to 85%). The distribution of *U. rapax* and *U. vocator* in the upper part of the forest could also have been influenced by differing tolerance against desiccation: while the former predominated in dry and sunny areas (Wessels 1999, V. Koch pers. obs.), the latter was found to prefer shaded areas with higher water content of the sediment. However, no experiments were done to test for desiccation tolerance of the 2 species.

In LC, temperature tolerance appears as a major factor influencing species distribution. Temperatures on the sunny creek banks often exceeded 35 to 38°C while they remained 3 to 5°C lower in the other zones where tree cover provided shade. *Uca maracoani* seems best adapted to cope with these conditions. Oxygen consumption measured in water at different temperatures by Koch (1999) revealed that O_2-consumption of *U. maracoani* increased up to a temperature of 35°C, while all other species showed highly reduced O_2-consumption at temperatures above 30 to 32°C, indicating physiological stress due to overheating. If crabs have to retreat to their burrows to avoid heat stress, foraging time would be reduced, putting them at a disadvantage.

Biomass and abundance values for the 4 species were within the range reported for fiddler crabs (e.g. Teal 1958, 1962, Warner 1969, Wolf et al. 1975, Cammen et al. 1980, Colby & Fonseca 1984, Jones 1984). While abundance was rather similar, marked differences in biomass were found between zones. Highest

Table 3. Reproductive parameters of female *Uca* spp. (average ± SD). Age and size at first maturity was calculated as the average of the 5 smallest egg-carrying females of each species. p-values for the chi-squared test are given in parentheses below the proportion of females in each species

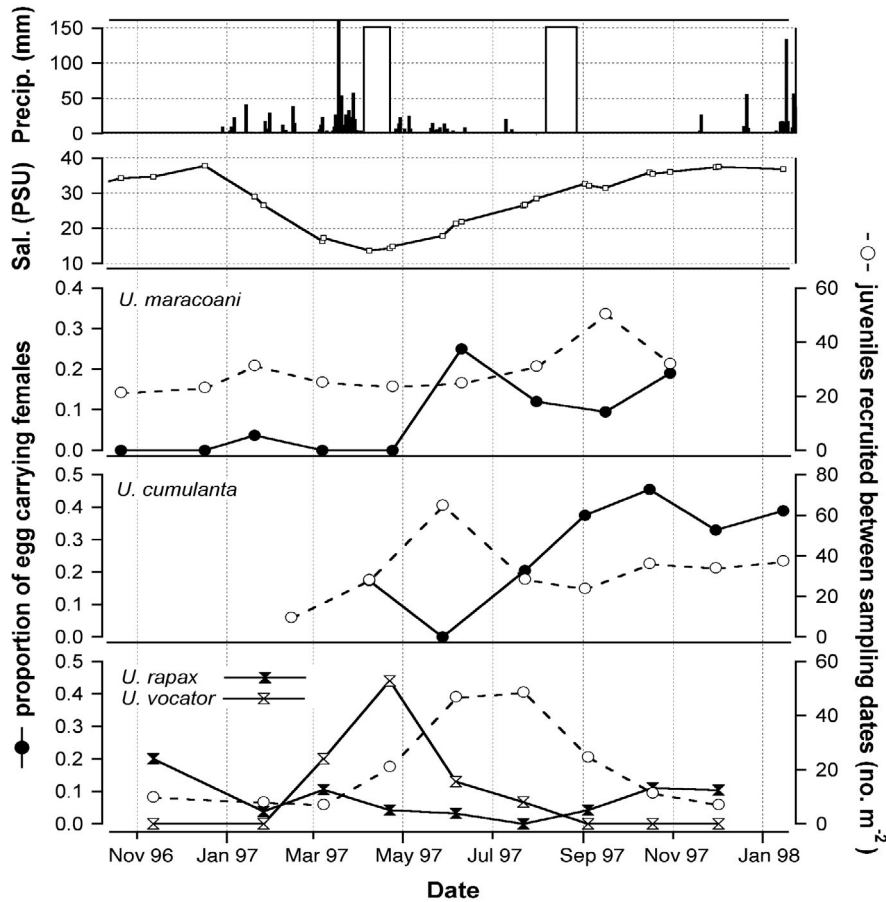| Species	Age at first maturity (yr)	Size at first maturity (mm)	Clutch weight in % of female ash-free dry mass	% females in population (p, χ^2 test)	Reproductive season (peak mo)
U. cumulanta	0.20 ± 0.01	6.2 ± 0.1	10.9 ± 4.6 (n = 23)	58.6 ± 5.9 (p < 0.001)	Sep–Jan
U. maracoani	0.36 ± 0.01	18.0 ± 0.3	11.2 ± 1.3 (n = 5)	49.5 ± 5.8 (p > 0.05)	Jun–Nov
U. rapax	0.22 ± 0.01	7.4 ± 0.2	–	56.3 ± 3.3 (p < 0.001)	Oct–Dec
U. vocator	0.23 ± 0.03	9.9 ± 1.0	12.9 ± 2.5 (n = 5)	48.1 ± 10.2 (p > 0.05)	Mar–Jun

Fig. 8. Proportion of egg-carrying females (●, except for *Uca rapax* and *U. vocator*, which are represented by filled and open double triangles, respectively) and number of recruits of each fiddler crab species (○) throughout the study period. Precipitation and salinity fluctuations over the same time period are given in the upper 2 graphs for comparison. White bars in the precipitation graph indicate periods where no rainfall data were available

values were found in LC dominated by *Uca maracoani*, where secondary production was also found to be highest by Koch & Wolff (2002), possibly because food production by bacteria and microalgae exceeded that of the other zones. The 4 fiddler crabs accounted together for about 11.2% of the total faunal biomass in the Caeté mangrove ecosystem (Wolff et al. 2000), but for almost 90% of total epibenthic production (Koch & Wolff 2002), indicating fast growth and turnover rates.

Population structure, growth and mortality

The population structure of all 4 species is typical for fast-growing, short-lived species where juveniles dominate the population (Hartnoll 1982, Hartnoll & Bryant 1990). *Uca rapax* had the highest proportion of adult-sized individuals (40.9%), followed by *U. vocator* (28.8%), *U. cumulanta* (26.5%) and *U. maracoani* (16.6%). No clear cohorts were visible in any of the size frequency histograms, although small, secondary peaks are present. However, as fiddler crabs in general (with the possible exception of *U. vocator*, see below) have rather prolonged breeding seasons, no attempt was made to relate these secondary peaks to different

cohorts. Sex ratios of *U. maracoani* and *U. vocator* were close to 1, corresponding to Fisher's theory (Fisher 1930). The significantly higher proportion of females in *U. cumulanta* and *U. rapax* contradict several studies on fiddler crabs that reported much higher proportions of males as a rule (for a review, see Montague 1980). Considering, however, that the mating system of *Uca* spp. is promiscuous with territorial males competing for females, deviations from Fisher's 1:1 ratio should favor females (Willson & Pianka 1963, Emlen 1973), as found in our study. It remains unclear however, how this fits in with the higher mortality rates measured in females of all species except *U. cumulanta* (see below).

Growth of all fiddler crabs examined was fast and the calculated maximum life spans short (0.7 to 1.47 yr). Individual growth rates varied little as indicated by the small SD within the 'artificial cohorts'. Temperate fiddler crabs grow slower and have longer maximum life spans (up to 4 yr) but their growing season lasts only 7 to 9 mo and the crabs spend the coldest months hibernating in their burrows (Shanholtzer 1973, Montague 1980, Colby & Fonseca 1984). The geographical distribution of the genus *Uca* at higher latitudes is mainly limited by low temperatures and length of growing season (Crane 1975); longer life

spans and slower growth rates can thus be expected towards the distribution limits.

Growth rates of males and females were quite similar in all 4 species, as is reported by Shanholtzer (1973) for *Uca pugnax*. Higher K-values of female fiddler crabs were compensated for by larger L_∞ values of males, and growth performance indices for both sexes are similar. Only in *U. cumulanta* was growth performance about 17% higher in males. Possibly, females of this species invest comparably more in reproduction than the other species, or males have lower energy investments in territory defense and courtship behavior, a time- and energy-consuming activity for male fiddler crabs (Crane 1975). Growth performance was highest in *U. maracoani* and lowest in *U. cumulanta*. Values for *U. rapax* and *U. vocator*, the 2 species co-occurring in F, differed considerably, with the latter having >20% higher values. Niche separation of these 2 fiddler crabs could therefore partly be achieved by their different growth strategies.

The use of cages built in the natural environment was considered the best possible choice to measure growth as individual crabs were too small to be tagged reliably without risking damage and reducing growth and survivorship (Cobb & Caddy 1989). Effects of the experimental setup on growth rates were minimized by ensuring that (1) density and biomass in the cages were within the range encountered in the field; (2) cages were built only in areas were crabs were observed to live and feed; (3) sediment disturbance was kept minimal during sampling. Also, measurements of sediment organic content showed similar values inside and outside the cages. However, possible bias (and reduction of growth rates) introduced by differing foraging area size of each species was not tested for, and the growth estimates presented here are probably conservative.

Mortality rates (*Z*) were high for all species (4.6 and 7.6 yr^{-1}), with the highest values found in male and female *Uca cumulanta* (9.1 and 10.6 yr^{-1}, respectively). This is consistent with their much smaller size and faster growth rate compared to the other species. Turnover rates of temperate fiddler crabs from the southern United States were much lower (2.2 to 3.3 yr^{-1}) than those found in the present study (Teal 1962, Cammen et al. 1980). Alongi (1989) attributed this pattern to a lack of temperature compensation in metabolic processes and to higher predation pressure in the tropics. Except for *U. cumulanta*, mortality rates of males were consistently 10 to 20% lower, which can be expected as male fiddlers can shed their large claw when attacked and have a higher chance to escape a predator (Wolf et al. 1975, Lee & Kneib 1994). Predation is the most important source of mortality in fiddler crabs in the Caeté estuary (Wolff et al. 2000, Koch & Wolff 2002) and the crabs make up a substantial part of the diet of many birds, fish, predatory crabs and mammals (Montague 1980, Montague et al. 1981, Jones 1984, Wiedemeyer 1997, Keuthen 1998, Wolff et al. 2000). The mortality rates found in this study were close to those found in many shrimp populations (3 to 11 yr^{-1}) (e.g. Devi 1987, Caddy 1989, Gracia 1989, D'Incao 1990, Jayawickrema & Jayakody 1992, Gabche & Hockey 1995, Xu et al. 1995) that are also fast-growing, highly productive and feed partly on detritus. From a functional point of view, both groups are similar and occupy important positions in the food webs of their respective environments (Caddy & Sharp 1986, Caddy 1989, Wolff et al. 1998, Wolff et al. 2000).

Reproduction and recruitment

Females of all species (except *Uca rapax*, not measured) invested similar amounts of energy in each clutch (11 to 13%), but it remains unclear whether the species differ in total reproductive investment as the number of clutches over a female's life span was not determined. All fiddler crabs showed prolonged breeding seasons, as can be expected for tropical species (Ahmed 1976, Sastry 1983). While *U. cumulanta* and *U. maracoani* bred mostly during the drier season (June to December), *U. rapax* seemed to breed almost year-round with only a small peak between October and December (see also Ahmed 1976). Reproduction in *U. vocator*, however, showed a pronounced peak during the end of the rainy season. The differences in reproductive timing of the 2 forest species can provide a temporal niche separation as has been suggested for sympatric portunid swimming crabs with broad dietary and habitat overlap (Paul 1982, Negreiros-Franzoso & Franzoso 1995, Pinheiro et al. 1997).

Peak recruitment was remarkably constant for all species, with 50 to 60 recruits m^{-2} in 6 wk. True numbers of recruits must have been higher as mortality was not considered in the calculations. The number of juvenile crabs recruiting to the study area did not coincide well with the occurrence of egg-carrying females found on the previous sampling date. Recruits were found even when no ovigerous females had been recorded previously. Low sampling efficiencies of egg-carrying females can be excluded, as high proportions of ovigerous females were found on other occasions and the removal efficiency of the sampling technique was 88% in LC and >95% in F and SC (Koch & Wolff 2002). However, recruits could have originated from other locations, as larvae of many *Uca* sp. are exported from estuaries and can be dispersed over considerable distances (e.g. Christy & Stancyk 1982, Epifanio et al. 1988, Rodriguez et al. 1997, Drake et al. 1998). Diele (2000) showed that occurrence of ovigerous females of

the ocypodid crab *Ucides cordatus* varied widely among different locations in the Caeté estuary. Therefore, the sampled area might have been too small to adequately describe reproductive activities of the fiddler crab populations for the whole study area.

In conclusion, the overall theme of fiddler crab life history strategy appears to be: 'live fast, die young, and reproduce early'. In comparison to their temperate relatives, growth and mortality rates were higher, as can be expected. The high population turnover and productivity explains why fiddler crabs occupy a key position in the intertidal food web, where they efficiently convert microbial production into energy available to higher trophic levels (e.g. Teal 1962, Montague 1980, Koch & Wolff 2002).

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