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Field experiments on feeding of European fiddler crab *Uca tangeri*

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ABSTRACT: The quality of the food, especially origin and size, of the only European fiddler crab, *Uca tangeri* (Eydoux, 1835), was studied over a 2 yr period. In experiments with fluorescent microparticles, all particles smaller than 250 µm were ingested regardless of their chemical composition. Comparisons of sediment, feeding pellets and faeces showed that *U. tangeri* feeds primarily on microalgae which are completely extracted from the sediment. It also consumes vascular macrophytes (*Arthrocnemum* spp.), macroalgae, detritus and fish carcasses.

INTRODUCTION

The fiddler crab *Uca tangeri* (Eydoux, 1835) is a dominant species in the intertidal zone of the Ria Formosa in southern Portugal. Like all fiddler crabs it is semiterrestrial; social life and feeding activity only take place during low tide, and during high tide crabs stay in their burrows.

Uca tangeri also shows a clear annual cycle of activity. Crabs need a sediment temperature of at least 18 °C to become active at the surface. Hence their annual activity in the Ria Formosa starts in March and ceases at the end of October. During winter, from November to the end of February, crabs stay inside their burrows.

The food uptake and sorting mechanisms were first described by Altevogt (1957). Miller (1961) studied adaption of the mouth extremities of different *Uca* species to their particular food sources. Primarily, *Uca* spp. are sediment eaters. The sediment is taken up with the minor chela and carried to the buccal cavity. There the material is sorted and either selected for ingestion or passed to the bottom of the buccal cavity from where the material drops to the sediment surface, forming feeding pellets. In addition, crabs feed on macroalgae, salt marsh plants and animal carcasses (Altevogt 1957, Miller 1961).

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Previous studies with *Uca tangeri* did not deal with feeding (Altevogt 1959). This study investigates the food of *U. tangeri* with special regard to its origin and particle size. The influence of *U. tangeri* feeding activity on the environment of the Ria Formosa is also discussed.

MATERIAL AND METHODS

All investigations were carried out on a mudflat near Ramalhete Creek in the Ria Formosa on the Portuguese Algarve coast near the city of Faro. The study area had a size of 2 × 3 m and rose about 0.5 m above water level at low tide. It merged into a salt marsh zone of *Arthrocnemum* spp. that is also inhabited by *Uca tangeri*. The mudflat becomes dry twice a day for about 6 h, leading to very high temperatures in the upper 2 to 3 mm of the sediment, especially in summer (in August up to 32 °C). During the winter months (from November to February) all mudflats are covered with a thick layer of long filamentous green algae. This layer begins to disappear at the end of January and has completely gone by the beginning of April. More detailed information on the biotope of the Ria Formosa and the occurrence of *U. tangeri* is given by Universidade do Algarve (1986), Belchior (1988) and Wolfrath (1992).

Feeding experiments were performed from March 1989 to November 1990. Weekly samples from the mudflat and from the salt marsh area were taken to determine quality and quantity of the food source. Sediment of the upper 2 to 3 mm was scraped off with a small spade and sampled in 2 ml Eppendorf test tubes. This is the sediment layer that is taken up by *Uca tangeri* with the minor chela. With a pair of forceps the 'feeding pellets' and faeces were sampled and also collected in 2 ml Eppendorf test tubes. Ten tubes (20 ml) from each source were collected in each area. In the laboratory 5 tubes were frozen at -80 °C for later experiments the other 5 tubes were processed immediately. Because previous studies had shown the content of one tube to be too small for a reasonable interpretation, 5 samples were pooled each time.

The size of sediment particles was determined with light microscopy by direct measurements with a grid (5 µm intervals). To determine the content of organic matter samples were dried on preweighed aluminium trays (60 °C, 36 h). After determination of dry weight (DW) samples were burned in a muffle furnace at 450 °C for 6 h, ashfree dry weight (AFDW) was determined and the organic matter content of sediment, feeding pellets and faeces was calculated.

The frozen samples of surface sediment, feeding pellets and faeces were thawed and their volume measured by water displacement in a 10 ml cylinder. Afterwards samples were put into 50 ml beakers filled with a particle-free 35‰ NaCl solution and placed in an ultrasonic bath (Bransonic 1200) for 5 min. Previous studies had shown this period to be sufficient to detach intact microalgae and bacteria from sediment particles. The solution was carefully poured off and examined with 2 different methods, regarding shape and size, but not species of algae.

Light microscopy was used for determination of microphytobenthos. Lugol solution was added to the sample and 2 subsamples were left standing over night in 10 ml Utermöhl chambers for sedimentation. Afterwards samples were counted under an inverted microscope.

Fluorescence microscopy was used to determine the smallest forms of microphytobenthos. Two subsamples with a volume of 200 µl were filtered through a Nuclepore filter with a pore diameter of 0.2 µm. Prior to filtration, the filters were dyed with Irgalan black to avoid autofluorescence. Samples were then stained with a 10 % solution of acridine orange for 2 min. Filters were washed twice with 5 ml sterile seawater to remove surplus solution. Maximum excitation wavelength was 458 nm and maximum emission 540 nm. Particles were counted and measured with a grid.

To determine the particle size fraction which *Uca tangeri* ingests and which is sorted out beforehand, inert particles with a defined diameter were used, so-called luminophores. These are sand grains stained under sterile conditions with different fluorescent colours (staining by the Bundesanstalt für Wasserbau, protected patent). The colour is deposited in cracks and unevennesses, does not change the physical properties of the sand grain, and lasts several years. Fluorescence is initialised by UV-light (Ruck 1972, 1977, Mahaut & Graf 1987). Luminophores are not influenced by digestion of *U. tangeri* and are hence easy to recover.

In the experiments luminophores with a diameter of <63 µm (golden-yellow), 63-125 µm (green), 125-250 µm (yellow), 250-500 µm (red-orange) and 500-1000 µm (blue) were used. Studies took place on the mudflat only. With the beginning of low tide and before activity of *Uca tangeri* started, luminophores of all sizes were equally distributed on the sediment surface of the study area with a salt dispenser. About 6 h later, when crab activity had stopped, ten 2 ml Eppendorf test tubes were filled with feeding pellets and faeces. In the laboratory the volume of 5 pooled samples was determined by water displacement in a 10 ml cylinder and the number of luminophores in feeding pellets and faeces was directly counted under UV-light.

RESULTS

Sediment

The sediment of the mudflat and the *Arthrocnemum* salt marsh area consisted of clay silt and very fine sand with grain sizes between 2 and 92 µm, with average diameter 12 µm. The organic substance of the mudflat and the *Arthrocnemum* area consisted of bacteria, microphytobenthos (diatoms) and detritus and, in winter, of a layer of green algae (*Enteromorpha* spp., *Ulva* spp., *Cladophora* spp.) that covered the mudflats.

The organic content varied during the year and differed markedly between mudflat and salt marsh ($p = 0.05$, ANOVA): smallest amounts were found from September to the end of March with 10 to 15 mg g^{-1} DW on the mudflat and about 40 mg g^{-1} DW in the salt marsh. Towards summer (July/August) the organic content increased to between 30 and 40 mg g^{-1} DW on the mudflat and about 150 mg g^{-1} DW in the salt marsh (Fig. 1a, b). Mudflat as well as salt marsh showed strong patchiness of organic substance; plant debris was found in the upper sediment layer of the *Arthrocnemum* area.

Microphytobenthos consisted of pennate diatoms only. Conspicuous all year round were the genera *Navicula*, *Diploneis*, *Amphora*, *Gyrosigma* and *Pleurosigma*. Size classes varied with the season: in spring and autumn larger forms (50 to 130 µm) were dominant on the mudflat, while from June to August many very

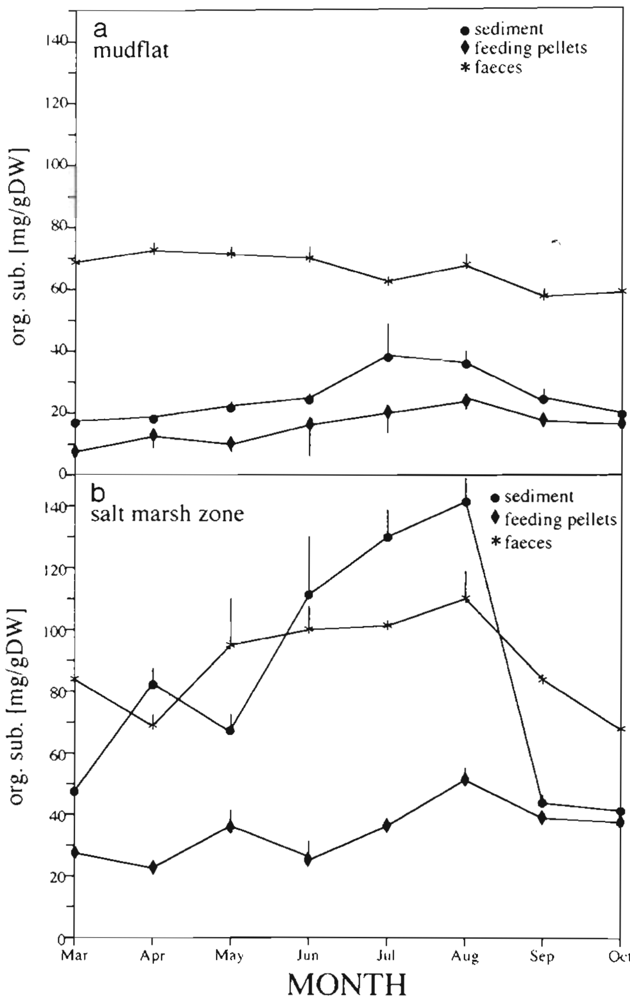

Fig. 1. Organic content of sediment, *Uca tangeri* feeding pellets and faeces (a) on the mudflat and (b) in the salt marsh area from March to November 1989. Values are averages of weekly measurements. Vertical bars show SE (only given in one direction to avoid confusion)

small forms (length 2 to 20 µm) were observed. In the salt marsh area large forms were dominant during all the year, while small forms were only observed from the middle of August to the middle of September. From the beginning of November to the middle of February no microphytobenthos was found.

Feeding pellets and faeces

The first feeding pellets were found on the sediment surface about 10 min after the beginning of the feeding activities of *Uca tangeri*. The pellets were relatively loosely packed, drop-shaped aggregates with a diameter of about 5 mm and an average grain size of 12 µm. Calculation of confidence range and ANOVA test ($p = 0.05$) showed that organic content was significantly less than in the sediment but showed the same variations. A sample of 1 g (DW) of feeding pellets from the mudflat contained about 10 mg (± 0.6) less organic substance than 1 g (DW) of the sediment. In the salt marsh area 1 g (DW) of feeding pellets had 10 to 20 mg (± 0.7) less organic substance in spring and autumn and about 100 mg (± 5.1) less in summer than 1 g (DW) of the sediment (Fig. 1a, b). Feeding pellets from the mudflat and the salt marsh contained no remains of macroalgae, *Arthrocnemum* spp. or microphytobenthos.

The first faeces were found about 30 min after the beginning of feeding activities. Faeces of *Uca tangeri* were compact cylinders of about 3 mm length and a diameter of about 1 mm. Average grain size was very small (4.5 µm). Organic content was nearly constant throughout the year. Only at the beginning (late March) and the end (October) of the crabs' annual active season did the organic content decrease. In the mudflat area faeces contained 60 to 75 mg g^{-1} DW organic substance in summer and about 50 mg g^{-1} DW in spring and autumn (Fig. 1a, b), which is significantly higher (ANOVA, $p = 0.05$) than the organic content of the sediment. In contrast, faeces in the salt marsh zone contained less organic substance (about 100 mg g^{-1} DW) than the sediment from June to September, while during the rest of the crabs' annual active season faeces contained about 80 mg g^{-1} DW organic substance which is significantly more (ANOVA, $p = 0.05$) than in the sediment (Fig. 1a, b). In contrast to the feeding pellets, the faeces contained debris of macroalgae and *Arthrocnemum* and most of all empty frustules and frustule fragments of a variety of benthic diatom species. Very few intact, mostly needle shaped, diatoms were found.

The results presented above show that *Uca tangeri* completely extracted the microphytobenthos from the sediment. Furthermore, it preferentially fed on the young shoots of *Arthrocnemum* spp. and on macroalgae, such as the filamentous green algae that cover the mudflats in winter and early spring, as regular food. With the beginning of the crabs' annual active season in spring, the layer of algae decreased and finally disappeared. Crabs were also seen to feed on carcasses, e.g. dead fish, when available.

Using the data on the organic content of sediments, feeding pellets and faeces, the uptake (U) by *Uca tangeri* and the ratio of organic substance in faeces to uptake (F/U) were calculated (Table 1). Calculations showed that *U. tangeri* did not exclusively use microphytobenthos in the sediment as its food source to fulfil feeding requirement because F/U was always >1. Only from June to August in the salt marsh, when F/U was nearly 1, did the sediment there seem to contain enough organic substance.

Table 1. *Uca tangeri*. Uptake of organic substance from the sediment and the ratio of organic substance in faeces to that in uptake (F/U). Values are averages of weekly measurements from March to November 1989

Month	Mudflat		Salt marsh	
	Uptake	F/U	Uptake	F/U
Mar	8.0	8.5	16.0	5.2
Apr	3.2	23.5	49.2	1.6
May	13.0	5.5	49.0	1.9
Jun	12.5	56.2	93.0	1.1
Jul	22.0	2.8	97.4	1.0
Aug	9.0	6.4	91.3	1.0
Sep	1.3	38.4	4.7	17.4
Oct	1.0	51.0	5.8	12.5

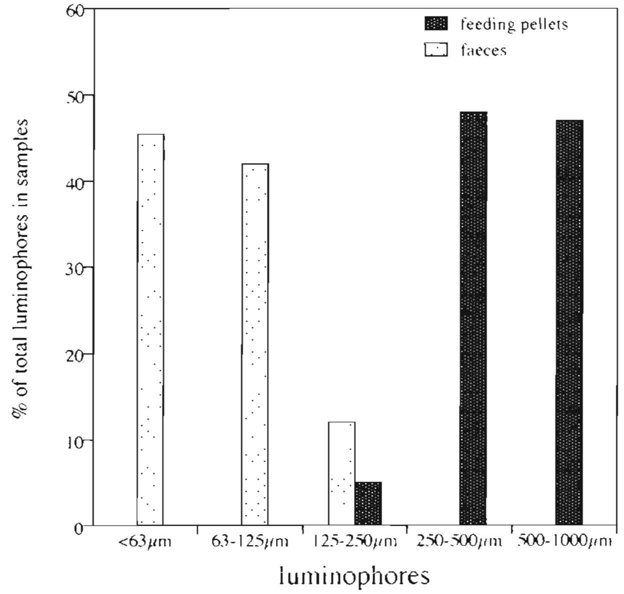

Fig. 2. *Uca tangeri*. Content of luminophores in feeding pellets and faeces. A value of 100% is the total number of all luminophores found in the samples

Size of food particles

In the experiments with luminophores the feeding pellets were found to contain mostly (95 %) luminophores with a diameter of 250 µm and more, but very few (5 %) with a size of 125–250 µm. No luminophores with a diameter of <63–125 µm were found in feeding pellets.

In contrast, the faeces predominantly contained luminophores with a diameter of <63–125 µm (88 %), and small amounts (12 %) of 125–250 µm luminophores (Fig. 2).

DISCUSSION

Like all fiddler crabs *Uca tangeri* feeds by scraping off the upper 2 to 3 mm of the sediment with its minor chela. In the mouth cavity particles are sorted and either ingested or dropped as feeding pellets (Altevogt 1957, Miller 1961, Valiela et al. 1974, Robertson et al. 1980, Robertson & Newell 1982). This selective feeding behaviour leads to restructuring of the sediment and changes the living conditions for other organisms.

Comparisons of sediment, feeding pellets and faeces show that *Uca tangeri* completely ingests the microphytobenthos of the upper 2 to 3 mm of the sediment, but only uses part of it as food. Very few large intact needle shaped diatoms were found in faeces, probably because *U. tangeri* is not able to crack their frustules. The smallest microphytobenthos found had a size of about 1.5 µm. It is not quite clear whether this is the smallest fraction attached to sediment particles. However, longer treatment in the ultrasonic bath did not give other results. It is also unclear whether *U. tangeri* is able to detach smaller diatoms from the sediment and use them as food. To answer this, it would be necessary to study the hairs which cover the mouth appendages and which play an important role in sorting particles in the buccal cavity of the crab (Miller 1961, Robertson & Newell 1982).

Comparisons of organic content of sediment and faeces show that *Uca tangeri* excretes more organic substance than it could obtain solely from the microphytobenthos. Hence other food sources must be used by the crabs. This is reflected in the F/U ratio. If all organic substance found in the faeces had its origin in the microphytobenthos, the ratio must be 1. The much higher values of F/U calculated indicate a high contribution of other food sources external to the sediment. This corresponds with the observations of voracious uptake of filamentous green algae and *Arthrocnemum* shoots (and fish carcasses, when available) by *U. tangeri* in the Ria Formosa.

It may be that *Uca tangeri* became a sediment eater only during phylogeny, as Altevogt (1957) presumed for Indian *Uca* species. Miller (1961) also observed in his studies that crabs preferred algae, plants and carcasses. *Uca* spp. have suitable mouth appendages to take up and chew these large particles.

As described above *Uca tangeri* feeds on the filamentous green macroalgae that cover the mudflats from the beginning of winter until spring. This is the period during which the crabs are not active at the sediment surface. With the beginning of the crabs' annual activity in spring, the layer of algae decreases and finally vanishes. Hence it is possible that feeding activities of *U. tangeri* are an important factor in the decrease of algae towards summer. The considerable uptake of *Arthrocnemum* and filamentous green algae by *U. tangeri* especially in spring leads to another hypothesis: during production of eggs and sperm in spring crabs need high amounts of energy which they may obtain from filamentous green algae and *Arthrocnemum* shoots.

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