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Prey selection of *Epixanthus dentatus* (Crustacea: Brachyura: Eriphiidae) as determined by its prey remains

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Epixanthus dentatus (Crustacea: Brachyura: Eriphiidae) is a predator crab, commonly inhabiting East African mangroves, whose nocturnal and elusive behaviour usually prevents analysis of its natural diet and prey selection. The present study was carried out on a population inhabiting a peculiar mangrove habitat in which *E. dentatus* produces heaps of non-ingested parts of its prey. Fifty-nine of these accumulations of prey remains were examined and 17 species were identified as part of the diet of *E. dentatus*. Relative prey consumption was then analysed with respect to the relative abundance of prey species within the local faunal community. This methodology provided important information about prey selection by *E. dentatus*; in particular, gastropods were always strongly under-represented, while there was an active selection among the different crab species. *Uca* species were under-represented, while swimming crabs were also part of the *E. dentatus* diet, which shows that the latter is able to prey both at low and high tide.

INTRODUCTION

Epixanthus dentatus is among the most common predator crabs in the East African mangroves (Cannicci et al., 1998; Dahdouh-Guebas et al., 1999). Previous observations show that it preys mostly on other Brachyura, which it captures by remaining immobile (half buried in the mud or grasping the mangrove aerial roots) and waiting for the prey to walk into it. The sudden strike of both claws can nearly cut in two crabs such as *Thalamita crenata* or *Neosarmatium meinerti*, as big as the predator itself (Cannicci et al., 1998). Unfortunately, various attempts to ascertain its natural diet on the basis of the stomach contents have failed because the collected crabs almost always had empty stomachs.

The prey selection and natural diet of many raptorial birds are commonly studied by analysis of their prey remains (Hunter et al., 1988; Cresswell, 1995). This methodology is possible because although these birds usually hunt within a relatively large activity range, they consume their prey close to their permanent refuge or temporary perches (Newton, 1979). The resulting accumulation of prey remains can furnish interesting information about the predator's habits (Tornberg, 1997). When the temporal and spatial distribution of the prey species are known, it is usually possible to infer information such as when the predator is most active, how far it ventures to hunt for prey and whether the predation is selective or not.

The present study took advantage of a peculiar behaviour shown by a large population of *E. dentatus* colonizing a wide belt of old mature *Avicennia marina* trees within a mangrove swamp in Kenya. The crabs used the carved, inner part of the older *A. marina* trunks and discharged heaps of prey remains at the base of the trunk itself, where they are protected from the water flow and can accumulate. A sampling protocol was designed: (i) to record the proportions of prey items within the remains; and (ii) to assess the relative frequency of the various mollusc and decapod species present along the *A. marina* belt.

MATERIALS AND METHODS

The species

Epixanthus dentatus is a Xanthoidea Eriphiidae relying on predation for more than 90% of its food intake (Cannicci et al., 1998). It has a carapace 3.5-cm wide, with obvious claw dimorphism, especially in males, as well as morphological characteristics of the claws commonly found in specialized gastropod crushers (Vermeij, 1977; Ng & Tan, 1985). In Mida Creek, *E. dentatus* is mostly nocturnal and hunts outside the water or a few centimetres below the water surface. It is common throughout the whole forest from the more landward *Avicennia marina* belt to the seaward *Rhizophora mucronata* zone. Within the *A. marina* belt it commonly ambushes its prey while half sunk in the mud at low tide, while in the *R. mucronata* belt it can grasp the aerial roots of the trees at high tide.

Locality

The observations were performed in the mangrove swamp at Mida Creek (Kenya Coast), in March and November 1999. The belt where the sampling protocol was carried out was a monospecific *A. marina* area composed of scattered old trees about 5-m tall, with the muddy bottom covered by pneumatophores (tree density was about 6.4 ± 0.39 trees $10\,m^{-2}$).

Epixanthus dentatus inhabited about one-third of all the trees. These trees were the older ones (30–45 cm diameter, 50 cm above the soil) whose base was rotten and trunk was deeply carved, thus creating a large funnel-shaped crevice in which the crabs lived.

Sampling

The prey remains were carefully removed by hand and placed separately in plastic bags for species identification and analysis in the laboratory. Since only mutually exclusive prey remains, such as limbs and small carapace pieces, belonging to the same species and to the same heap were considered to represent different individuals, the number of specimens of each species represents the minimum present in the prey remains.

The species structure of the invertebrate population colonizing the study area was assessed randomly. Eight 4×4 m plots were defined within a 40×100 m uniform area at spring tide, i.e. during the 5 d surrounding the second day from the full/new moon, and the densities of the different species of crabs and gastropods were calculated. For fiddler crabs, genus *Uca*, a preliminary binocular count of the whole plot was carried out to assess the species present and their relative numbers. Then within four randomly selected 1×1 m quadrats, a visual count of the holes was made. Finally, when more than one species was identified within the plot by the binocular count, the frequencies recorded with binoculars were used to attribute to the different species the relative number of holes. All the binocular and hole counts were made during the first part of the low tide to avoid missing crabs and holes (Nobbs & McGuinnes, 1999; Skov & Hartnoll, in press). For the medium/small sesarmids, *Sesarma ortmanni* Crosnier and *Sesarma guttatum* A. Milne Edwards, binocular counts along the whole transect were performed and, in a further analysis, the recorded numbers were increased by one-third, because of the intrinsic errors involved in this technique (Skov & Hartnoll, in press).

With JMP® (SAS Institute Inc.), a stepwise multiple regression model was used to search for relationships between the frequency of each food item and all the other items within the prey heaps, in order to assess if the occurrence of one prey in the heap excluded other items.

The Ivlev Electivity Index was used to examine *E. dentatus* feeding preferences, as suggested by Krebs (1989). For each food item, the values of the Ivlev Index are based on its relative frequencies in the diet and in the environment and vary from +1.0 to −1.0, with positive values indicating preference and negative ones avoidance.

RESULTS

In total, 59 prey accumulations were collected, containing the remains of 205 animals. Most of them could be identified at the species level. The average number of prey per accumulation was 3.49 (±SD 2.96; 95% confidence limits, ±0.64) with an expected nearly Poisson distribution, except that class 0 was missing (i.e. the number of predators without any prey remains could not be assessed, since *Epixanthus dentatus* was never visible).

The stepwise multiple regression test proved that the probability of a species being present among the prey remains was not negatively affected by the number of any other species, i.e. single *E. dentatus* did not show any individual preying specialization. Because of this result and the relatively constant size of the prey remains, all data were pooled (Table 1) for a more general frequency analysis.

Table 1. *List and frequency of Decapoda and Gastropoda taxa found in the 59 accumulations of prey remains.*

Family	Species	Frequency	Frequency %
Decapoda			
Sesarmidae	*Neosarmatium meinerti* (De Man)	60	31.9
	Sesarma guttatum A. Milne Edwards	48	25.5
	S. ortmanni Crosnier	2	1.1
	S. villosum A. Milne Edwards	1	0.5
	Helice leachii Hess	1	0.5
Ocypodidae	*Uca annulipes* (H. Milne Edwards)	12	6.4
	U. inversa (Hoffman)	12	6.4
	U. chlorophthalmus (H. Milne Edwards)	10	5.3
	unidentified *Uca*	1	0.5
Portunidae	*Scylla serrata* (Forskål)	3	1.6
	Thalamita crenata H. Milne Edwards	8	4.3
	Portunus pelagicus (L.)	1	0.5
Pilumnidae	*Eurycarcinus natalensis* (Krauss)	14	7.4
Eriphiidae	*Epixanthus dentatus*	6	3.2
	White unidentified brachyurans	7	3.7
Diogenidae	*Clibanarius longitarsis* (De Haan)	2	1.1
	Total Decapoda	188	100.0
Gastropoda			
Littorinidae	*Nodolittorina natalensis* (Philippi)	11	78.6
Cerithiidae	*Cerithidea decollata* (L.)	3	21.4
	Total Gastropoda	14	100.0

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The great majority of prey were Decapoda (see Table 1) belonging to six families and 13 species.

Gastropoda were only represented by two species (Table 1) while sessile species, such as oysters or barnacles (both very common), were not present. If the latter are captured, they are probably eaten *in situ* and not carried 'home' for later consumption.

The results of the direct binocular counts did not include many of the above species and showed that the *Uca* density was extremely high with respect to the other decapod species (Table 2).

A comparison can be made between the ranks of importance of the species in the remains and those in the observational data (Table 3). Indeed, the relative hierarchy of importance of the various species is quite different (correlation rank is obviously far from being significant, Spearman correlation test, $r=0.071$, $P=$ns); *Uca inversa* (Hoffman) and *Uca* crabs in general were the most commonly observed species, while *Neosarmatium meinerti* and *Sesarma guttatum* were the most common prey, their Ivlev Index being high and positive.

The estimated *E. dentatus* density was 0.4 crabs 10 m^{-2} ($\pm$0.03); thus they occupied about 1/5 of the trees that in our opinion were suitable, i.e. old trees with crevices similar to those where the accumulations of prey remains were actually recorded. This would give each animal a hunting territory of 2.7 m radius, with little or no overlapping with conspecifics. Our crab density measure is surely an underestimate since some of the heaps of remains were probably too inconspicuous to be seen; thus the radius of each crab territory was probably closer to 2 m than to 3 m.

Table 2. *List of Decapoda and Gastropoda species directly observed within the* Epixanthus dentatus *habitat, with their average density, indicated as individuals per square metre.*

Species	Density (ind m^{-2})
Decapoda	
Neosarmatium meinerti	0.5
Sesarma guttatum	2.5
S. ortmanni	0.1
Uca annulipes	7.9
U. inversa	10.1
U. chlorophthalmus	6.9
Clibanarius laevimanus	1.3
Gastropoda	
Cerithidea decollata	0.2
Terebralia palustris	4.8

Among the 35 specimens of *Uca* (Table 1), there was a higher proportion of *Uca chlorophthalmus* (H. Milne Edwards) than *U. inversa* and *Uca annulipes* (H. Milne Edwards), both much more common in the direct counts (Table 3). This seems to confirm the short range of the *E. dentatus* foraging area since *U. chlorophthalmus* is typically concentrated in the mud among the roots and pneumatophores, with a 50–80% canopy cover, while *U. annulipes* prefers more sandy areas and *U. inversa* more open areas, conditions which are not common near *Avicennia marina* trunks.

DISCUSSION

Is the analysis of prey remains a reliable and factual technique to study the feeding habits of *Epixanthus dentatus*? To answer this question it first must be stressed that recent attempts to study its natural diet by analysing the stomach contents of collected specimens were unsuccessful (Cannicci et al., 1998; Dahdouh-Guebas et al., 1999), despite the success obtained with this technique for other predator species (Hill, 1976; Williams, 1982; Wear & Haddon, 1987; Hsueh et al., 1992; Cannicci et al., 1996). In fact, the great majority of the specimens had empty stomachs and no real information could be gathered on *E. dentatus* feeding preferences. On the other hand, the list of decapods found within the *E. dentatus* prey remains (Table 1) is even longer than the one compiled from direct observations (Cannicci et al., 1998), confirming some known trends and providing new information on the feeding habits of this species. In fact, Cannicci and co-workers (1998) found that *E. dentatus* in another mangrove swamp in Kenya was mainly active during the night, hunting at both low and high tide, climbing the aerial roots and always maintaining itself a few centimetres above the water level. The nocturnal activity of *E. dentatus* seems to be confirmed by the relatively low frequency of *Uca* crabs (all East African species are active only at diurnal low tide) within the prey remains analysed in the present study, while the high frequency of *Neosarmatium meinerti* can be linked to its crepuscular and nocturnal

Table 3. *Comparison of the rank of importance of Decapoda. The relative frequency of each species within the* Epixanthus dentatus *habitat is shown as the average number of individuals per square metre together with the confidence limits (cl). The frequency of each species in the diet is shown as the number of prey accumulations containing the species and is ranked. All species are ranked twice, according to their density within the habitat and in the diet.*

Species	Frequency within the habitat				Frequency in the diet			Ivlev Index
	ind m^{-2}	cl (95%)	frequency %	rank	N	frequency %	rank	
Uca inversa	10.11	4.95	36.1	1	12	8.2	3.5	−0.63
U. annulipes	7.93	5.27	28.3	2	12	8.2	3.5	−0.55
U. chlorophthalmus	6.86	3.78	24.5	3	10	6.8	4	−0.57
Sesarma guttatum	2.46	1.29	8.8	4	48	32.7	2	0.57
Neosarmatium meinerti	0.55	0.37	2	5	60	40.8	1	0.91
S. ortmanni	0.07	0.07	0.3	6	2	1.4	5	0.69

activity (Micheli et al., 1991). However, the presence of Portunidae (swimming crabs) in the prey remains, even though they made up only about 6% of crustaceans in the *E. dentatus* diet, shows that the latter is able to prey under water at high tide, when the Portunidae forage, and not only above the water level, as shown by the previous observations (Cannicci et al., 1998). Regarding other Decapoda, *Sesarma ortmanni* and *Helice leachii* are rare because the former concentrates on the upper shore level while the latter is more common at lower levels. *Eurycarcinus natalensis*, very common among the prey remains but never observed with binoculars, is probably also active at night and/or underwater, but nothing is know as yet about the habits of this crab.

The study of prey remains is probably more informative than the analysis of gut contents also for another reason. The rate of gut clearance in carnivorous crabs is thought to be very rapid (Hill, 1976) and the ingested food is often retained in the gut for only a few hours. On the other hand, although it is not possible to tell the age of the collected prey remains, the average number of prey contained in the heaps, together with the advanced decomposition of the remains, strongly support the hypothesis that the remains could have resisted many tidal cycles, providing information on more than one feeding act.

Moreover, the habit of *Epixanthus dentatus* of consuming its prey inside its natural shelter accounts for the above-mentioned unsuccessful attempts to study its natural diet by means of analysis of stomach contents of collected specimens (Cannicci et al., 1998; Dahdouh-Guebas et al., 1999). Most probably, this crab stays within its shelter until after it has consumed its prey and then exits the refuge only when it again needs to hunt. Given the rapid rate of stomach clearance in other predatory crabs, the *E. dentatus* individuals actively hunting outside their refuges would almost always have empty stomachs (Cannicci et al., 1998; Dahdouh-Guebas et al., 1999).

Gastropods were poorly represented among *E. dentatus* prey remains (Table 1), and the pieces of their shells were largely outnumbered by crab remains. The small number of gastropods in the *E. dentatus* prey remains confirms its preference for crab hunting (Cannicci et al., 1998), but contrasts with the morphological studies performed by Ng & Tan (1985). These authors pointed out that the crabs belonging to the genus *Epixanthus* have a specialized cutting tooth on the larger claw, often associated with a diet based on gastropod hunting and cutting (Vermeij, 1977). In our opinion, two interrelated hypotheses can be advanced to explain this difference between the conclusions of the comparative morphological study and our data from prey remains. First, it must be stressed that the actual percentage of gastropods in the *E. dentatus* diet was probably underestimated by our analysis. In fact, these crabs could have completely eaten the shell of smaller gastropods, as in other carnivorous crabs (Hill, 1976), leaving no remains in the heaps. Moreover, if they peel and cut the shells with the specialized claw, they could tear them into such small fragments that they would be washed away by the tide more easily than the thick pieces of carapace and claws of the crab prey. The second hypothesis is that, in the habitat colonized by our study population, crabs were easier to hunt than gastropods. In fact, *Terebralia palustris* (L.), which was missing from the *E. dentatus* diet, was by far the most commonly observed gastropod in the study area. However, it was only represented by very heavy and robust individuals, 7–11 cm long, which are resistant to predation by crabs (and, as far as we know, by any other predator, at least in Kenya). Regarding the other two gastropod species present, *Cerithidea decollata* (L.) (a mud grazer) was found both among the prey remains and on the mud, but it was not common (Table 2), while *Nodilittorina natalensis* was more prevalent, but it colonized the small mangrove branches and leaves, where *E. dentatus* never ventures. Between *T. palustris* and *N. natalensis*, the latter is rarer in the foraging area of *E. dentatus* but is the weaker of the two. This likely explains its higher frequency among the *E. dentatus* prey remains.

In conclusion, it must be pointed out that the whole data analysis suffers from a major weakness, i.e. the lack of spatial replications for our observations. This is mostly due to the fact that it was not possible to find another area within the study site where old *A. marina* trees were inhabited by this predator, i.e. an area where environmental conditions prevented the heaps of remains from being washed away by the tides. Although aware of this fact, we still think that the prey remains analysis, entirely new for studies of decapod diets, is the only suitable method to investigate the natural diet of *E. dentatus* and, more in general, provides valuable information about the diet and feeding habits.

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