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NATURAL DIET AND FEEDING HABITS OF *THALAMITA CRENATA* (DECAPODA: PORTUNIDAE)

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ABSTRACT

Thalamita crenata is one of the most common swimming crabs of the mangrove creeks of the East African coast. In Mida Creek, Kenya, this species inhabits the extreme seaward fringe of the mangrove swamp and the intertidal platform in front of the mangal, sheltering in small pools during low tide.

Gut content analysis reveals that *T. crenata* is a generalistic predator, its diet being mainly composed of bivalves and slow-moving crustaceans. Both the stomach fullness and the relative presence of animal prey in the contents were significantly higher in crabs collected at sunset than in those caught at dawn. Stomach fullness seems to depend also on the tidal rhythm; in fact, it is higher during spring tide periods. Females had stomachs slightly fuller than those of males, while there was no difference in diet between juveniles and older specimens.

Thalamita crenata forages more actively during daytime, thus differing from the majority of swimming crabs.

Both the great abundance of this species and its diet, based on a wide range of slow-moving or sessile species, testify to the importance of the role played by this predator in the mangrove ecosystem of Mida Creek.

Thalamita crenata H. Milne Edwards is a common and widespread swimming crab that inhabits the shallow waters of all the Indo-Pacific region. Along the Kenyan coast, large populations of this crab are very often associated with mangrove swamps. Although they do not live deep in the mangal, they inhabit the rocky and muddy intertidal platforms in front of the *Sonneratia*-fringe and swim in the swamps during their activity periods (Vezzosi *et al.*, 1995), a behavior also observed for *Scylla serrata* (Forskål) (see Hill, 1978, 1979), another swimming crab of the Indo-Pacific region.

Nothing is known about the feeding habits of East African populations of this species. In Australia, Williams (1981) found that the most common food in the gastric mills of intertidal populations of *Thalamita crenata* and *T. danae* was algae. Preliminary observations in Kenya revealed that this swimming crab preys on fiddler crabs (genus *Uca*) and digs for bivalves, and suggested that *T. crenata* has a predatory habit more similar to the majority of the portunid crabs. In fact, detailed studies on the diet of other shallow-water portunid crabs, *Scylla serrata* (see Hill, 1976), *Portunus pelagicus* (L.) (see Williams, 1982), *Carcinus maenas* (L.) (see Elner, 1981), *Callinectes sapidus* Rathbun (see Blundon and Kennedy, 1982; Hsueh *et al.*, 1992), *C. ornatus* Ordway (see Haefner, 1990), *C. arcuatus* Ordway and *C. toxotes* Ordway (see Paul, 1981), *Ovalipes stephensoni* Williams (see Haefner, 1985), and *O. catharus* (White) (see Wear and Haddon, 1987) have shown that they are scavengers and predators, mostly on slow-moving and sessile invertebrates, and that algae form a small percentage of their diet.

Preliminary observations in the same locality on the predatory behavior of *T. crenata,* linked with the large number of crabs in populations associated with mangrove swamps, suggested that this crab could play an important role, as a predator, in the food web of Kenyan mangrove ecosystems.

The aims of this study were to analyze the natural diet of a large population of *T. crenata* inhabiting a Kenyan mangrove creek, to determine the relationships between food ingestion and both diurnal and tidal rhythms, and to attempt an assessment of the ecological importance of this crab in the mangrove ecosystem.

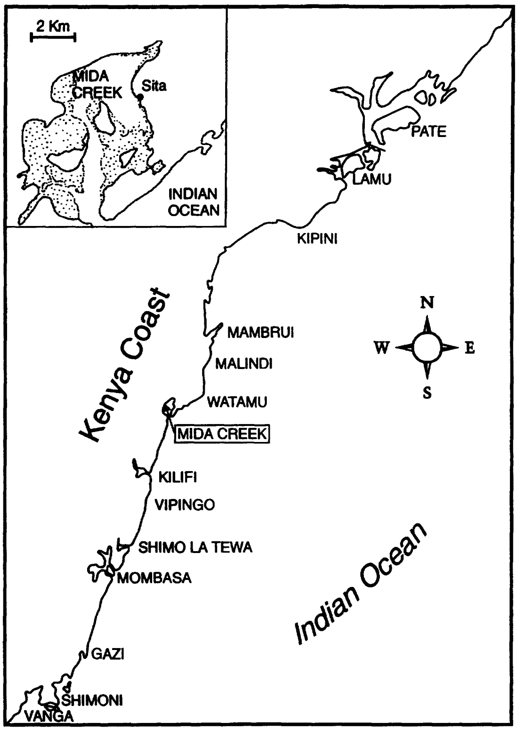

Fig. 1. Map of the Kenyan coast, with details of the Mida Creek area, where the sampling took place.

Materials and Methods

Sampling Methods.—The sampling took place in November 1992 near Sita, in Mida Creek (20 km south of Malindi, Kenya) (Fig. 1). It was carried out on a madreporic intertidal platform, covered with mud and sand, lying just in front of the mangrove swamp, which was flooded twice a day by 100 (Neap Tide) or 160 (Spring Tide) cm of water. In total, 260 crabs (about 10–15 crabs per day) were collected, both by dip nets and by hand, during their periods of maximum activity, i.e., during ebb and flood tides, since the crabs swim only when the water is between 5 and 40 cm high (Vezzosi *et al.*, 1995).

Only adult specimens were used. All the captured specimens were killed in 70% alcohol immediately after collection.

Analysis of Foregut Contents.—The gastric-mill analysis took place within 3 weeks after sampling. A visual estimate of the fullness of the stomach was made immediately after its removal; the scoring was from 1–5, according to the degree of fullness, i.e., about 100%, 75%, 50%, 25%, and 0%. All stomachs were subsequently opened and their contents were washed with alcohol into a Petri dish and examined under a binocular microscope.

Analysis of the contents was performed by dividing the complete records into 13 major categories (Table 1). Where possible, animal remains were identified to the lowest taxonomic level. Organic material included animal tissues which were too strongly digested to be identified at any taxonomic level. Sand was considered a stomach content category, but was not included in the further qualitative analysis of the diet.

The qualitative analysis of the diet of *T. crenata* was carried out using Percentage Point and Frequency of Occurrence methods. As described in detail by Wear and Haddon (1987), in the Percentage Points method each of the more common food categories (9 in this study) is given a value, ranging from 0 to 100, according to the percentage of content it represents within each stomach. Then the number of points each category received are weighted according to the real fullness of the stomach in which it was found. For instance, in a stomach half full, containing 25% bivalves and 75% algae, the bivalves were scored 12.5 and algae 37.5 points, respectively.

Frequency of occurrence (Williams, 1981) is calculated by dividing the number of stomachs which contained a food category by the total number of stomachs observed.

Table 1. Frequency of occurrence (Freq.) and Percentage Points (Pts) (see Materials and Methods) of the 13 food categories found in 211 nonempty stomachs of *Thalamita crenata.*

Food category	Freq.	Pts	Types of records
Mollusca:			
Bivalvia	44	3,581	Pieces of shell and tissues
Gastropoda	5	488	Whole specimen, except shells
Crustacea:			
Brachyura	29	3,369	Pieces of carapace and tissues
Anomura	2	125	Pieces of carapace and tissues
Other Crustacea	4	475	Pieces of carapace and tissues
Polychaeta	6	713	Jaws, more rarely body wall
Fish	2	190	Vertebrae
Polyplachophora	6	21	Whole specimen (young)
Foraminifera	4	14	Whole specimen
Organic material	5	381	
Algae	28	1,925	
Mangrove leaf litter	19	1,369	
Sand	19	713	

Table 2. Differences in the quantity of food ingested between crabs of different sexes, between small (carapace length >2.5 and <3.6 cm) and large specimens (carapace length ≥3.6 and <5 cm), and between crabs captured under different environmental conditions. Quantity of food is expressed as percentage of stomach fullness (see Materials and Methods). ANOVA five-factor analysis. None of the interactions among the five factors was significant.

Source of variation	Average stomach fullness		F	$d.f.$	P
Males versus females	50.18	62.50	3.974	1	<0.05
Small versus large sp.	57.93	50.18	0.092	1	n.s.
Day versus night	63.11	43.88	19.797	1	<0.001
High versus low tide	46.87	61.04	2.325	1	n.s.
Spring versus neap tide	60.46	54.75	4.973	2	<0.01

Data Analysis.—Data were grouped by (1) comparison of stomachs collected at the end of low or high tide, independent of the time of day, (2) comparison of stomachs collected at the end of the day or night, independent of ebb or flood phase, and (3) comparison of stomachs collected on 6 days around Neap Tide and 6 days around Spring Tide, independent of both the time of day and the tidal phase.

ANOVA was then used to analyze the above data as well as the relative influence of the sex and size of the crabs (thus making a total of 5 factors under study), with regard to both the quantity and quality of the food ingested, i.e., the amount of animal matter (points of animal prey categories) versus vegetable matter (points scored for the plant tissues).

The basic data were thus represented by score values following an unknown distribution and should have been analyzed by nonparametric tests. However, there are no tests of this kind able to treat a 5-factor data matrix, with an unbalanced number of data for each of the matrix cells. With a parametric ANOVA test, the probability of β-type error increases. Nevertheless, the power of a 5-factor ANOVA test, in rejecting A-type error (in our case, in "discovering" differences when they exist) is such that parametric ANOVA is still to be preferred to weaker nonparametric approaches.

RESULTS

Natural Diet

Only a minority of stomachs proved to be empty or nearly so (49 out of 260).

The diet of *Thalamita crenata* is composed of a wide range of items, principally sessile and slow-moving invertebrates, algae, and plant detritus (Table 1).

Foraminifera were recorded in stomachs containing sand; it seems that there is no direct feeding on these small specimens. Polychaeta were also common, but they were strongly digested, and, with the exception of two records of *Arenicola* sp., it was not possible to identify them in detail.

Bivalves were recorded very often (in 93 out of 211 nonempty stomachs). When they were present, their shells were crushed into pieces. All specimens belonged to two species only, *Loripes clausus* Philippi and a species of the genus *Dosinia,* both of them commonly living within the first 15 cm of the mud that covers the platform. Gastropods were not common ($N = 11$); all the specimens belonged to the genera *Littorina* and *Cerithidea* (Prosobranchia) and to an unidentified species of the order Nudibranchia ($N = 2$). The Prosobranchia were found ingested without their shells, while the opercula were always present. All chitons were very similar and small (0.5 mm long), probably young specimens of a single species of the genus *Acanthopleura.*

The hermit crabs were represented by *Clibanarius laevimanus* Buitendijk and *C. longitarsus* (de Haan) (Diogeneidae) very common both in the mangrove swamp and on the intertidal platform. Shrimps were also present in the stomach of *T. crenata,* but it was not possible to determine the species to which they belonged.

Crabs were found (all in different stomachs) as follows: 7 *Metopograpsus thukuhar* (Owen) (Grapsidae); 4 *Pilumnus vespertilio* (Fabricius) (Pilumnidae), 3 *Uca* spp. (Ocypodidae), 10 crabs of the genus *Sesarma* (Grapsidae), 2 *T. crenata* (i.e., cannibalism), and, finally, 8 carapaces too digested to be identified at any taxonomic level. All the species recorded are abundant on the Sita plateau and in the mangrove swamp of the area where *T. crenata* is active. Two very small Tanaidacea and Leptostraca were also recorded.

The only three soft-shelled crabs collected had the gastric mill full of small pieces of gastropod and bivalve shells, which may have been selectively ingested.

Factors Affecting the Quantity and Quality of Food Intake

Sex.—Stomachs of females of *T. crenata* were significantly (ANOVA) fuller than those of males (Table 2). However, they ate the same items and there was no difference in the frequency of occurrence of the different types of food (Table 3) nor in the amount of animal and vegetable matter ingested (Tables 4, 5).

Size.—There were no differences in stomach fullness (Table 2) nor in diet composition (Table 3) between small specimens (carapace length < 3.6 cm) and large specimens (carapace length > 3.6 cm); in both cases ANOVA did not reveal any significant difference between the two groups (Tables 4, 5).

Day-Night.—Stomachs of specimens collected at sunset were significantly fuller than those of crabs captured at dawn (Table 2). This strong difference in food intake affected both the amounts of animal and vegetable matter ingested, which are higher during the day (Tables 4, 5).

Low-High Water.—The tidal level seems not to affect the quantity of food ingestion of *T. crenata* (Table 2). There are still no differences between animal/vegetable amounts of ingested matter (Tables 4, 5).

Spring-Neap Tide.—During spring tides, the crabs are able to feed better than in neap tides (Table 2), but the quality of food intake seems not to change between these two periods (Tables 4, 5).

Discussion

Thalamita crenata, like other swimming crabs, is a generalistic predator and scavenger that feeds largely on invertebrates. Both for the large size of its populations and the wide variety of invertebrates that were recorded in its stomachs, *T. crenata* can be considered, together with *Scylla serrata* (see Hill, 1979), as one of the major predators of small invertebrates colonizing the mangrove swamps of Kenya.

In Mida Creek, Kenya, the diet of *T. crenata* is largely dependent on molluscs and crustaceans of the mangroves and of the adjacent intertidal platform. Predation of slow-moving invertebrates seems to be a common feature in the shallow-water swimming crabs, such as *Carcinus maenas* (see Elner, 1981), *Scylla serrata* (see Hill, 1976, 1979), *Portunus pelagicus* (see Williams, 1982), and species of the genus *Callinectes*

Table 3. Frequency of occurrence (Freq.) and Percentage Points (Pts) of the eight major categories of food from stomachs of *Thalamita crenata.* For the Percentage Points computation see Materials and Methods.

Food category	Females		Males		Small sp.		Large sp.		Day		Night		High tide		Low tide		Neap tide		Spring tide	
	Freq.	Pts	Freq.	Pts	Freq.	Pts	Freq.	Pts	Freq.	Pts	Freq.	Pts	Freq.	Pts	Freq.	Pts	Freq.	Pts	Freq.	Pts
Organic material	4	87.5	5	293.8	2	50.0	8	306.3	3	181.3	8	200.0	3	87.5	6	293.8	7	262.5	3	93.8
Bivalves	46	1316.9	43	2163.8	51	1735.0	43	1638.1	44	2460.6	45	1020.0	46	1126.9	43	2353.8	43	1696.3	45	1298.8
Gastropods	1	37.5	8	450.0	2	62.5	10	375.0	5	275.0	6	212.5	5	162.5	6	325.0	4	162.5	8	281.3
Crabs	24	1143.8	30	2025.0	33	1631.3	17	1018.8	30	2112.5	25	1056.3	29	1037.5	27	2131.3	31	1750.0	20	831.3
Other Crustacea	5	218.8	4	337.5	4	293.8	6	262.5	4	356.3	5	200.0	6	318.8	3	237.5	6	393.8	3	137.5
Polychaeta	11	456.3	4	256.3	8	400.0	6	312.5	7	475.0	5	237.5	10	362.5	4	350.0	6	331.3	6	237.5
Algae	33	812.5	26	1112.5	24	556.3	29	1056.3	33	1318.8	21	606.3	26	568.8	30	1356.3	35	1268.8	20	487.5
Leaf litter	22	600.0	18	768.8	20	625.0	18	550.0	20	1000.0	19	368.8	22	518.8	18	850.0	15	456.3	28	637.5
Total	147	4748	141	7523	146	5429	137	5594	148	8367	135	3904	147	4183	140	8088	147	6359	138	4155

Table 4. Differences in the average Percentage Points (Pts) of animal matter ingested between crabs of different sexes, between small and large specimens, and between crabs captured under different environmental conditions. ANOVA five-factor analysis. None of the interactions among the five factors was significant.

Source of variation	*N*		Average Pts		*F*	*d.f.*	*P*
Males versus females	111	72	43.66	40.65	0.670	1	n.s.
Small versus large sp.	77	106	42.29	41.51	0.109	1	n.s.
Day versus night	108	75	47.40	33.83	14.683	1	<0.001
High versus low tide	79	104	37.34	45.25	2.216	1	n.s.
Spring versus neap tide	63	100	42.16	41.44	0.312	2	n.s.

(see Seed, 1980; Paul, 1981; Hsueh *et al.*, 1992). *Thalamita crenata,* like all of these large powerful crabs, preys only occasionally on fishes and prawns; the few occurrences of such prey that we found are probably due to scavenging activity on dead animals more than to active predation.

The population that we studied showed a feeding habit different from the population of Moreton Bay, Australia, studied by Williams (1981), which was mainly an algal feeder. Detailed studies of prey availability in both environments are not available. In addition, even when prey availability may be comparable, behavioral plasticity might play an important role, for example, among *Eriphia smithi* MacLeay, which is said to be a predator of Neritidae in several localities (Vermeji, 1977), but which in comparable Somalian environments avoided Neritidae, in spite of their wide availability (Vannini *et al.,* 1989).

In connection with the relative frequency of food items ingested, one important consideration must be recalled: the resistance of different items to digestion. A good example is the relative importance of different molluscs in the stomach contents. Bivalves are recorded more frequently as food items, but *T. crenata* eats them with their shells which remain in the gastric mill for a longer time than gastropods which are always ingested without shells. Bivalve shells, in fact, remained as long as 9 days in the foregut of *S. serrata* (see Hill, 1976), while animal tissues were digested in less than one day.

Differences in stomach fullness between females and males can be related to the major energetic demand of females for ovogenesis. Although the breeding cycle of this species was never studied, 50% of the females that we collected were carrying eggs on their pleopods.

Our results show that feeding activity occurs throughout the day and night. It is not uncommon, in fact, to find crabs with a full stomach at any hour of the day. However, stomach fullness in *T. crenata* is significantly higher during daytime. This feeding pattern is rather dissimilar to that of the related species. Hill (1976), using infrared light, showed that *Scylla serrata* waits for the sunset inside its burrow and then spends the night feeding. *Callinectes arcuatus* (see Paul, 1981), in laboratory experiments, has shown a greater feeding activity at night, especially just after dusk, and the same author reported a similar feeding activity pattern in *C. sapidus* and *C. latimanus* Rathbun.

This difference in diurnal feeding rhythm between *T. crenata* and the majority of other portunid crabs can be related to the importance of the role that sight plays in the spatial activity of this species (Cannicci *et*

Table 5. Differences in the average Percentage Points (Pts) of vegetable matter ingested between crabs of different sexes, between small and large specimens, and between crabs captured under different environmental conditions. ANOVA five-factor analysis. None of the interactions among the five factors was significant.

Source of variation	*N*		Average Pts		*F*	*d.f.*	*P*
Males versus females	111	72	13.85	17.36	1.561	1	n.s.
Small versus large sp.	77	106	10.63	18.57	3.244	1	n.s.
Day versus night	108	75	17.02	12.67	8.426	1	<0.005
High versus low tide	79	104	13.77	16.35	0.228	1	n.s.
Spring versus neap tide	63	100	17.86	14.69	1.111	2	n.s.

al., 1995), and perhaps to the fact that among its major predators are two mainly nocturnal portunids (the above-mentioned *S. serrata* and *Portunus pelagicus*) and the nocturnal cuttlefish *Sepia* sp.

Sight is surely important in the predation technique of this portunid which concentrates its feeding activity during the diurnal ebb and flood tides (Vezzosi *et al.*, 1995) and behaves as an ambush predator, making sudden short rushes at slow-moving prey. This behavioral pattern is similar to that of *Ovalipes guadulpensis* (Saussure) (see Caine, 1974), a swimming crab adapted to digging in hard-packed sand, and to that of juvenile *Scylla serrata* (see Macnae, 1968), while larger crabs of this species are known to be more vagile (Hill, 1978).

Even though *T. crenata* is not the only predator of the mangrove swamps of Mida Creek, its impact on the ecosystem is certainly very strong on account of its density in this habitat (about 4 crabs/m^2; Vezzosi, personal communication).

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