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

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Marco Vannini

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 
escosystem 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 re-
vealed that this swimming crab preys on 
fiddler crabs (genus Uca) and digs for bi-
valves, and suggested that T. crenata has 
a predatory habit more similar to the ma-
jority of the portunid crabs. In fact, de-
tailed 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 Haef-
ner, 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 lo-
cality on the predatory behavior of T. cren-
ata, 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 be-
tween food ingestion and both diurnal and 
tidal rhythms, and to attempt an assessment 
of the ecological importance of this crab in 
the mangrove ecosystem.
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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.

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

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Average stomach fullness</th>
<th>F</th>
<th>d.f.</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males versus females</td>
<td>50.18</td>
<td>62.50</td>
<td>3.974</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Small versus large sp.</td>
<td>57.93</td>
<td>50.18</td>
<td>0.092</td>
<td>n.s.</td>
</tr>
<tr>
<td>Day versus night</td>
<td>63.11</td>
<td>43.88</td>
<td>19.797</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>High versus low tide</td>
<td>46.87</td>
<td>61.04</td>
<td>2.325</td>
<td>n.s.</td>
</tr>
<tr>
<td>Spring versus neap tide</td>
<td>60.46</td>
<td>54.75</td>
<td>4.973</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>

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 thukhar (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 Lepstostraca 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 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.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>N</th>
<th>Average Pts</th>
<th>F</th>
<th>d.f.</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males versus females</td>
<td>111</td>
<td>72</td>
<td>43.66</td>
<td>40.65</td>
<td>0.670</td>
</tr>
<tr>
<td>Small versus large sp.</td>
<td>77</td>
<td>106</td>
<td>42.29</td>
<td>41.51</td>
<td>0.109</td>
</tr>
<tr>
<td>Day versus night</td>
<td>108</td>
<td>75</td>
<td>47.40</td>
<td>33.83</td>
<td>14.683</td>
</tr>
<tr>
<td>High versus low tide</td>
<td>79</td>
<td>104</td>
<td>37.34</td>
<td>45.25</td>
<td>2.216</td>
</tr>
<tr>
<td>Spring versus neap tide</td>
<td>63</td>
<td>100</td>
<td>42.16</td>
<td>41.44</td>
<td>0.312</td>
</tr>
</tbody>
</table>

(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 oogenesis. 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.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>N</th>
<th>Average Pts</th>
<th>F</th>
<th>d.f.</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males versus females</td>
<td>111</td>
<td>72</td>
<td>13.85</td>
<td>17.36</td>
<td>1.561</td>
</tr>
<tr>
<td>Small versus large sp.</td>
<td>77</td>
<td>106</td>
<td>10.63</td>
<td>18.57</td>
<td>3.244</td>
</tr>
<tr>
<td>Day versus night</td>
<td>108</td>
<td>75</td>
<td>17.02</td>
<td>12.67</td>
<td>8.426</td>
</tr>
<tr>
<td>High versus low tide</td>
<td>79</td>
<td>104</td>
<td>13.77</td>
<td>16.35</td>
<td>0.228</td>
</tr>
<tr>
<td>Spring versus neap tide</td>
<td>63</td>
<td>100</td>
<td>17.86</td>
<td>14.69</td>
<td>1.111</td>
</tr>
</tbody>
</table>

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 guadalupensis* (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/m²; Vezzosi, personal communication).

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