A STUDY OF THE ECOLOGY AND BEHAVIOUR OF FIVE SPECIES OF UCA CRAB.

by

Helen R. S. Gordon, B.Sc.Hons.(Rand).

Dissertation presented for the degree of Master of Science in the University of the Witwatersrand, Johannesburg.

October, 1955.

Thesis

CONTENTS.

INTRODUCTION

Mangrove swamps occur extensively on different parts of the low-lying coast of Inhaca Island, near the south-eastern part of Delagoa Bay, and such swamps are also found along the coastline of the bay. On the mudflats of these swamps several species of Uca, the fiddler crab, live in large numbers, the populations in their various habitats apparently consisting of groups of mixed species.

Such species are sympatric and are of great interest to us in the study of evolution. Any such group of species must have arisen as a result of geographic isolation (Mayr, 1942) and specific differences could have originated in response to varying environmental conditions. The purpose of this study is an attempt to determine such differences in both the ecology and the behaviour of these Uca species and, secondarily, to link certain aspects of their behaviour with their different ecological requirements.

MATERIAL AND METHODS

Five species of Uca have been observed, and have been identified by Dr. K.H. Barnard of the South African Museum. These species are:-

<u>U. annulipes</u> (M.Edw.)

<u>U. inversa</u> (Hoffm.)

<u>U. chlorophthalmus</u> (M.Edw.)

<u>U. marionis</u> (Desm.)

<u>U. urvillei</u> (M.Edw.)

The specimens found on the island and on the coast of the bay agree in their characteristics with the descriptions of Barnard (1950), but certain differences will be discussed in dealing with the different species.

<u>U. annulipes</u>. This species has been found near Port St. Johns, at Durban, at Delagoa Bay and along the east coast of Africa. The average length of the male is 11 mm.

and the average breadth 19 mm., while the female is slightly smaller, with average length and breadth of 10 mm. and 16 mm. respectively. The ambulatories are reddish and the large chela of the male has a salmon-red colour, while the finger and thumb are often whitish towards their tips. The carapace colour is blackish, very often with a whitish, sometimes greenish mottling. In about one-third of the males there are no enlarged teeth on the finger and thumb. About 48% of the males have the large cheliped on the right.

U. inversa. This species has been found in Natal, Mocambique and along the east coast of Africa. The male may reach a length of 15 mm. and a breadth of 23 mm., the female being slightly smaller. The ambulatories are reddish in colour, while the carapace is blackish with a light speckling of white. The third maxillipedes of the female are white. The large chela of the male is pinkish in colour, but the finger and thumb are white. About 50% of the males have the large cheliped on the right.

U. chlorophthalmus. This species has been found at Isipingo, Durban and Delagoa Bay. The male and female are more or less similar in size, with an average length of 12 mm. and breadth of 20 mm.. The ambulatories are red, but in some individuals one or more of these legs are blackish in colour. The large chela of the male is red, with paler finger and thumb. The carapace is not bluish-grey with paler mottling, but in both sexes the colour is black with a dense mottling of green or turquoise blue on the anterior two-thirds. About 50% of the males have the large cheliped on the right.

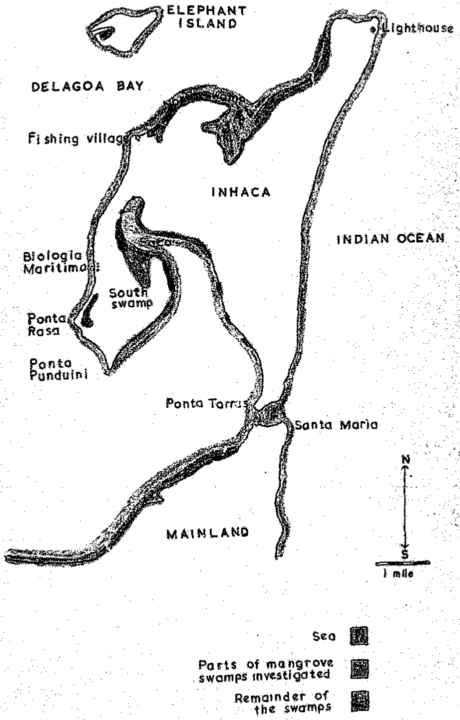
U. marionis. This species seems to be rare in South Africa but has been found near Port St. Johns, at Durban, and at Delagoa Bay. The males and females are, more or less, of similar size, having an average length and breadth of 15 mm. and 24 mm. respectively. The large cheliped of the male is orange in colour, while the carapace colour varies from brownish-orange to a light tan, sometimes with the posterior part blackish. In the female the carapace is blackish-brown and there are generally a number of white spots along the anterior margin. The ambulatories are brownish in colour. All males have the large cheliped on the right.

U. urvillei. This species has been found at Durban, at Delagoa Bay, and along the east coast of Africa. The female is slightly smaller than the male, which reaches a length of 18 mm. and a breadth of 30 mm.. The colour is not greyish-blue as described by Barnard, but generally the carapace and ambulatories are a dark purplish-blue with a sky-blue area around the front. Moreover, there are two centrally located sky-blue patches, one on either side of the midline, and the antero-lateral portions are royal blue. The female seems to differ somewhat from the male in coloration although the general body colour is also a dark purplish-blue. A number of sky-blue spots are situated towards the anterior margin of the carapace. Moreover, two sky-blue patches occur, one on either side of the thorax, and, on the merus of the first three ambulatories, there is a sky-blue spot on the anterior side. In addition, the large chela of the male is not bright red but orange, with the upper parts a purplish-blue. About 25% of males have the large cheliped on the right.

The five species were observed during several seasons, extending over a period of about a year; that is, from April 1954 to May 1955. The average difference between the maxima and the minima of spring tides at Inhaca is 3.26 m., the tides being semi-diurnal. The temperatures of tidal water, of standing water from previous tides and of burrows of the different species, were recorded. The salinities were determined for samples of water taken from

FIGURE 1.

INHACA ISLAND



various parts of the swamps, and from the sea near the laboratory of Biologia Maritima. Mud-scrapings were collected from the different habitats and their individual organic content determined through the loss of weight by ignition.

The behaviour study was aided by observations which were made on certain individuals of all five species, while in captivity. Tanks, 18" in length, 12" broad and 9" deep, were constructed of galvanized iron, and the representatives of individual species were accommodated, each in a separate container. For purposes of drainage, a tap was fitted to the base of each tank. A layer of mangrove swamp mud, 2" deep, was placed in each, and was kept constantly wet with fresh water, while being submerged weekly with water of 0.6% salinity. This saline water was allowed to remain for a few hours before being drained off. The captive crabs were fed on finely-ground rat cubes, sprinkled over the surface of the mud.

Preserved specimens, representative of all the species, were dissected with a view to comparing, firstly, their general gill structure and, secondly, the states of their gonads during the different seasons.

HABITAT

(1) THE MANGROVE SWAMPS

The Uca species studied live in habitats, differing in some respects from those described by Verwey (1930) in Batavia, by Crane (1941) in Panama, and by Peters (1955) in El Salvador. The main populations described by these three investigators were concentrated in deltas or at the mouths of small streams, while the populations on Inhaca Island and along the coast of Delagoa Bay are found in swamps which extend along the coastline. All these swamps, however, are located on the flatter parts of the coast which represent the remains of a dead delta. Five swamps have been investigated.

The North Swamp

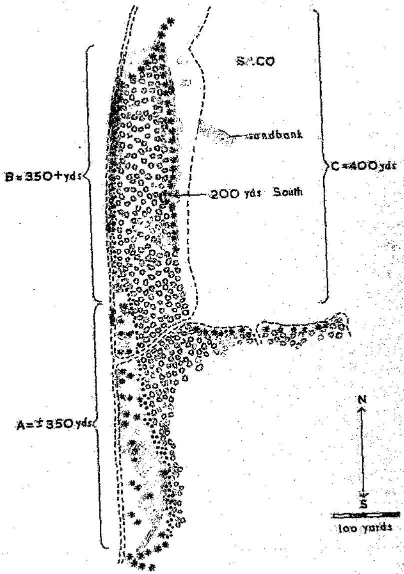
This swamp extends along most of the northern coast of Inhaca, but only about a mile of its length, from its beginning near the village, was studied. It starts as a narrow strip of Avicennia officinalis, widening to a stretch which is more or less constantly 20-30 yards wide. There is in the first half-mile a narrow inlet, surrounded by a mixed growth of Avicennia and Ceriops candolleana, and this is followed by a broad, more or less circular extension of the swamp inland, which has also a mixed growth of these two mangroves. Farther eastward, following on a strip with mainly Avicennia and Ceriops, Bruguieria gymnorrhiza occurs in fair numbers, mixed with Avicennia in the outer half of the swamp. This continues for several hundreds of yards and is followed by larger Avicennia trees only, for a similar distance, until a wide pathway or open space is reached, connecting the bush with the sea. Extending outwards from this open space, a large bare sandbank was found. In the whole stretch of swamp up to this point, the mud-flats are mainly of the greyish sandy type, but beyond it the swamp continues as a blacker, more soggy, mud, thickly overgrown with Avicennia. Along the whole length of the swamp the open water is bordered by large Avicennia trees.

The Saco Swamp

Mangrove swamp forms a nearly continuous belt on the western, northern and north-eastern shores of the Saco. The main area investigated on the north-western shore starts, following a break in the belt, with a few large Avicennia trees, but it soon widens into a stretch at least 50-100 yards wide. The inner core of this swamp is composed of black mud with a thick growth of Rhizophora mucronata, and this is fringed by other mangrove species, among which the various Uca populations are found.

THE MAIN REGIONS OF THE SACO SWAMP

FIGURE 2.



Key to Figures 2–5

- o Rhizophora
- ✱ Avicennia
- • Ceriops
- • Bruguiera

- U. annulipes
- U. chlorophthalmus
- U. urvillei
- U. marionis
- U. inversa

- ==== Footpath
- Sea

The habitats investigated have been divided into three regions, each of which is about 350 yards in length. Region C is the eastern stretch towards the northern end of this belt, and it lies alongside the open water. The growth consists mainly of large Avicennia trees on sandy mud, except towards the southern end where the central core of Rhizophora appears towards the outside. Region B runs parallel to Region C, but lies along the western or landward side of the swamp, and is bordered by a wide sandy pathway along its outer edge. This region includes the path and is narrow, the growth consisting mainly of Ceriops interspersed with Avicennia, although towards its southern end Rhizophora appears on the outer edge. Region A is an extension of B southwards and is also bordered on its outer or landward edge by the pathway. It differs from Region B in that it forms a wider area between the pathway and the black mud with Rhizophora, which has a skirting of Ceriops. For a distance of about 200 yards this area contains some Avicennia, and then follows a sandy flat, 150 yards long and 50 yards wide. This flat which is bordered on the east by Ceriops and on the south-east and south by Avicennia, presents a bare expanse except for a scattering of young Avicennia trees. Region D lies on the western shore of the Saco and extends southward for about 2 miles. Its average width is approximately 30 yards, and it consists almost exclusively of Avicennia on medium grey mud. The swamp is bordered on the landward side by bush and on the seaward side by a sandflat, about 100 yards wide. On this flat large numbers of a Dotilla sp. are intermingled with the U. annulipes individuals. Region E is situated on the eastern shore of the Saco, more or less opposite the middle of Region D. It is only about 200 yards long, and, at lowtide, it is separated from the sea by a sandflat about 200 yards wide. The swamp is very narrow,

7/ ...

consisting chiefly of large Avicennias interspersed with younger trees, on sandy mud which is whiter than that of Region D.

The South Swamp.

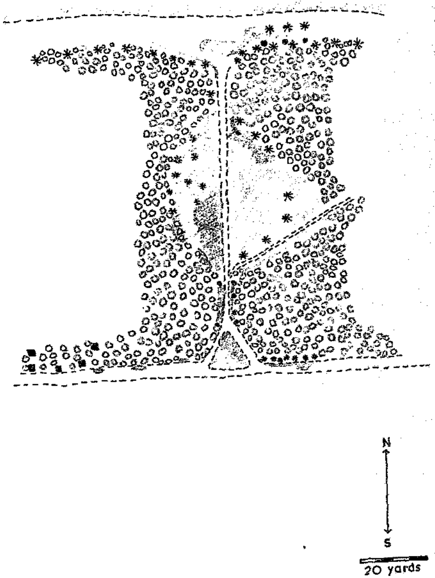
This swamp, which extends for about three-quarters of a mile, in a north-easterly direction, along the course of a narrow inlet entering the island from east of Ponta Rasa, is separated from the west coast by a narrow sand dune. Its central core and western parts consist of black mud, and are covered by Rhizophora and some Bruguieria, while on the eastern or more sandy side, there is a skirting of other mangroves. At the southern end this skirting or fringe consists of Ceriops, which also forms an extensive patch near the mouth of the inlet. Further north, an open space separates the Rhizophora from a fringe of Avicennia, and near the northern end is another open space extending across the swamp and bordered on its southern margin by Ceriops interspered with Rhizophora, the latter occuring on patches of soggy black mud, while the main open flat is more sandy. To the north of this open flat the swamp continues for a further 200 yards with some Avicennia, but mostly Rhizophora, which, however, seems to be dying out, since the tide rarely reaches this northern end.

The Mainland Swamp.

Mangrove swamps extend round a large part of the shore of Delagoa Bay, but only the first mile, near the south-eastern limit of the bay at Santa Maria, was investigated. The eastern end of this swamp is a narrow strip of Rhizophora on black mud covered with sand. The swamp soon widens into a stretch of black mud with a thick growth of Rhizophora and some Bruguieria. Along the seaward margin is a narrow skirting of large Avicennia trees, but on the outer or landward margin, this mangrove occurs at only a few spots. A pathway runs along this outer border,

FIGURE 3.

THE MAINLAND SWAMP



and, at about 500 yards from the start of the swamp, a cross-path leads down to the water for a distance of about 80 yards. On either side of the cross-path at its upper end, some Ceriops are found, and about mid-way this path is surrounded by an open stretch which is approximately 40 yards long and 25 yards wide. This space has a more sandy type of mudflat and, on the western side, it contains some young Avicennia, while, on the eastern side, it is bordered by large trees of the same species.

Elephant Island Swamp.

At the north-western tip of Elephant Island, a narrow, sinuous channel enters, bordered on its southern side by a swamp, several hundred yards long. The swamp consists of a thick growth of Avicennia and Ceriops on grey, sandy mud.

(2) FEEDING GROUNDS.

Uca lives on the organic sediment left behind by receding tides on the mudflats of the mangrove swamps. All five of the Inhaca species occupy feeding grounds, in which are located their burrows which are of a temporary nature. At first glance, it would appear that the different species exist as mixed populations, and therefore with no definite preference for any particular type of mudflat. On closer inspection, however, it becomes apparent that the distribution of certain of the species is limited by conditions, such as the type of mud, its degree of moisture, and the amount of shade. Uca is seldom found living in the black soggy mud of the inner core of the swamp, but the individuals range rather from the shady outer fringe, where the mud is of a more sandy, greyish type, to the exposed flats at the edges of the swamp.

The following are some of the general environmental factors affecting the living conditions of the Uca individuals at Inhaca :-

(1) Temperature. The mean air temperature throughout the

year ranges from about 20°C to about 28°C. At lowtide, the mudflats are warmed by the sun, and at hightide the water over this area is still very shallow. Therefore, it is soon warmed by the sun and by the heat which the mud itself retains. Generally speaking, the burrows appear to have a temperature as much as 3°C higher than the corresponding air temperature, during the day.

(ii) Salinity. The salinity of the water varies from one swamp to another; variation occurs also between different places within a swamp itself. The sea water near the laboratory of Biologia Maritima has a salinity which varies from 32.9 pts./1000 at hightide to 30.4 pts./1000 three hours later, after which the concentration again increases. Water from the channel of the Saco was found to have a salinity of 35.5 pts./1000, but water from the Saco mangrove near the feeding-grounds of U. annulipes had a concentration of 19.2 pts./1000 about three hours after hightide, and of 24.1 pts./1000 about eleven hours after hightide (these samples were taken on a rainy day); five hours after hightide, on a clear day, the salinity was 30.0 pts./1000. During January 1953 a sample was taken from the same area just after hightide, and this was found to have a concentration of 32.2 pts./1000. The water of the South Swamp channel varied, with a salinity of 21.7 pts./1000 at the northern end where U. annulipes is found, and 35.9 pts./1000 at the southern end near the mouth of the inlet, where no Uca is found. At the South Swamp also, samples were collected during February and May 1955 of standing water at the northern end of the open flat, in which many U. annulipes individuals had been seen feeding. The February sample with a salinity of 8.10 pts./1000 was collected on the last day of a neap tide period, with the result that the water had been standing for about eight days.

The water collected during May had been standing for about six days and was found to have a salinity of 6.35 pts./1000. These facts indicate that Uca can tolerate salinities ranging from about 6 pts./1000 to about 32 pts./1000.

(iii) Organic Content. The ignition loss was calculated for several samples of surface mud, collected from different parts of the South and Saco Swamps. This loss of weight following ignition, while for the most part representing the amount of organic matter originally present in the sample, also included the original $CaCO_3$ content, which is present in the form of broken-up shells. The results are shown in Table 1, with the loss by ignition expressed as a percentage in each case.

The Uca species in all the swamps were found to be occupying specific habitats, which are discussed below.

U. annulipes. This, the most common species of Uca, is found in all five swamps, and in varying habitats. In July 1954, it was the only species found at the western end of the North Swamp, and it occurs throughout the length of this Swamp, concentrated mainly at the following localities : -

(i) Along the margins of the inlet on greyish mud amongst Avicennia and Ceriops ($\pm$ 15/sq. yards).

(ii) On wetter mud, in the broad extension of Avicennia and Ceriops ($\pm$ 20/ sq. yards).

(iii) Throughout the 50 yards wide stretch of mixed Avicennia and Bruguieria, from the wet seaward margin through the drier, sandy, but shaded, part to the fairly dry inland margin (10-20/ sq. yard).

(iv) On the very wet mud on either side of the wide cross-path (10-20/sq. yards).

(v) On the bare, nearly white sand of the sandbank, extending outward from this cross-path area ($\pm$ 10/sq. yard).

11 /...

TABLE I.

Percentage Loss by Ignition in Scrapings of Surface Mud.

Samples 1955.	Inhabitated by:-	Location.	% Loss.
Feb.	Sesarma sp.	South Swamp:- black mud below Ceriops tree, adjoining the open flat.	18.75
Feb.	U. annulipes	South Swamp:- next to Avicennia to north of open flat.	5.79
May	U. annulipes	South Swamp:- black mud of open flat.	13.76
May	U. inversa	South Swamp:- grey mud, next to above.	3.61
Feb.	U. inversa	Saco A:- beneath tree on open flat.	10.84
May	U. inversa	Saco A:-open flat.	1.75
May	U. annulipes	Saco B:- top end of path.	1.98
Feb.	U. annulipes	Saco B-C:- connecting strip.	1.70
Feb.	U. marionis	Saco C:- 200 yards south, between holes of standing water.	3.16
May	U. marionis	Saco C:- 200 yards south, between holes of standing water.	2.09
Feb.	U. chloroph-thalmus.	Saco C:- 200 yards south.	2.53
Feb.	U. marionis and U. urvillei.	Saco C:- path at south end of the above.	1.61
Feb.	U. annulipes	Saco C:- in middle of the area 200 yards south.	1.88
Feb.	U. annulipes	Saco D:- open beach	1.78
Feb.	U. annulipes	Saco E:- in a hollow.	2.85.

This species occurs also in all five investigated regions of the Saco Swamp, along the lengths of Regions A, B, D and E, but in rather irregular groups in Region C. In Region C, the highest concentration is at the northern end (± 10/ sq. yard), and here their feeding-grounds extend seaward for a distance of about 20 yards from where they begin in the drier mud beneath the Avicennia trees, to where they end in the very watery mud amongst the Avicennia roots. Another high concentration of individuals is located 200 yards southwards in Region C, adjacent to the main habitat of U. marionis and U. urvillei (± 20/ sq. yard). U. annulipes is, however, more or less separated from these two species, occupying as it does the drier mud nearer the fringe of Avicennia. In Region B, this species occurs mostly on the pathway at the western border of the region, and at the northern end, where a very high population density of ± 50/sq. yard was observed. This feeding-ground has fairly dry sand, light in colour, in which the Avicennia roots are confined below the surface of the path. Further south along this pathway the density of population is variable, at some places there being only about 10/ sq. yard, while at about 250 yards southwards there is another population of about 40/ sq. yard. In Region A, the northern part of the pathway contains populations of up to 30/ sq. yard, but in the open flat this species appears to be limited to the eastern three-quarters, that is, towards the fringe of Ceriops. This area is bare, fairly dry, and with rather grey sand, and the Avicennia roots are present only in the south-eastern part, where the density of population is at its highest, i.e. ± 30/ sq. yard, as compared with ± 10/ sq. yard in the northern part. At Region D, U. annulipes occurs throughout the entire width of the swamp, and it is also found feeding on the open sandflat of the beach. The density of population

12/ ...

varies from 10-40/ sq. yard. At Region E, particularly in the hollow places between the trees, where leaves accumulate, U. annulipes is found with a population density of about 10/ sq. yard. This particular population appears to have a lighter grey carapace as compared with the darker grey of other populations.

In the South Swamp, the populations are concentrated along the eastern or inland margin. In the fairly shady Ceriops patch near the inlet, extensive feeding-grounds occur, with a population density of 10-20/sq. yard. Northwards, this greyish sand continues along the eastern margin as a fairly open strip with Avicennia roots, and here large numbers of individuals occur (± 30/ sq. yard in some places). On the southern part of the open flat, at the northern end of this swamp, large numbers (± 30/ sq. yard) are found on the more blackish type of mud, and these feeding-grounds extend into the area of mixed Ceriops and Rhizophora. Here, the mud is very wet, and the only ground not occupied by U. annulipes is the black, soggy mud surrounding each Rhizophora tree.

In the Mainland Swamp, small populations of U. annulipes are found at the eastern end, on white sand covering the black mud in which Rhizaphora grows. On the inner margin of this swamp, only small numbers of this species occur in a narrow fringe of blackish mud, especially where there are small patches of Avicennia on the outer margin of the main Rhizophora growth. On the seaward margin more extensive populations live in watery, sandy mud amongst the roots of the outer fringe of large Avicennia trees. Along the borders of the cross-path leading to the sea, fairly large numbers of U. annulipes are found, in blackish mud next to the Ceriops and Rhizophora, while the whole of the open space on either side of this path-way is covered with a large population of ± 30/ sq. yard. In the latter area, the mud is of a more greyish type, but this feeding-ground extends some distance into the black mud with Rhizophora.

U. inversa. Individuals of this species occur in only two localities, that is, on the open sandy flat of Region A of the Saco Swamp and on the open flat at the northern end of the South Swamp. In the former locality, the species is confined to the southern 100 yards, and the feeding-grounds extend from close to the fringe of Ceriops on the eastern margin to near the pathway on the western margin, with an average population density of 0.5-1/sq. yard. This flat is totally unshaded, consists of fairly dry sand, light in colour, and contains no Avicennia roots. In this habitat a mixture of U. annulipes and U. inversa is found, but only U. inversa occurs nearer the pathway. The intermingling of the two species was observed only on the northern, eastern and southern borders of this U. inversa feeding-ground. During neap tide periods, the burrows of this species are concentrated in small circular areas of a small succulent, Salicornia perrieri, round the bases of young Avicennia trees. On the open flat at the northern end of the South Swamp, two small colonies of U. inversa were found, near to one another, the one being north in position, the other south-west. These colonies live on the grey mud just to the west of the standing water, with a population density of about 1/sq. yard. Near this habitat, a small succulent, Anthrocnemum perennis, grows in abundance.

U. chlorophthalmus. During May 1954 (and July 1952), two isolated populations of this species were found in Region C of the Saco Swamp, one about 100 yards south, and the other about 200 yards south. In both cases, their feeding-grounds were close to the trunks of the outer fringe of large Avicennia trees. The population, 200 yards south, was found in the drier, blacker mud at the inner margin of the main habitat of U. marionis and U. urvillei. No individuals of this species were, however, observed in this locality during July 1954, but they were noticed once again during February and May 1955. The main population of U. chlorophthalmus in the Saco Swamp was found to be along the eastern edge of Region B, for a distance of about 200 yards from a starting point at about 50 yards from the northern end, with the highest population density located about midway along this stretch (± 10/sq. yards). Their habitat is very narrow, consisting of a strip of blackish mud at the edge of the inner core of black mud with Rhizophora. They feed amongst the Avicennia roots and are partly shaded by a mixture of Avicennia and Ceriops. Along the outer margin of their feeding-grounds, some intermingling with individuals of U. annulipes was observed. In the Mainland Swamp, small populations of this species were found skirting the open patch on either side of the cross-path, but chiefly to the east of it. Here they are located amongst Avicennia roots on the fairly wet and blackish mud adjacent to the black mud of the inner core of the swamp. The highest density of population (± 10/sq. yards) was found at the north-eastern part of this open patch, at a spot well-shaded by Avicennia trees and where there is some intermingling between U. annulipes, U. chlorophthalmus and U. urvillei. The latter two species, however, were found to be nearest the trunks of Avicennia and Rhizophora, the small isolated population of U. urvillei being the closer of the two. At the upper or northern end of the South Swamp, along the southern edge of the open flat, a small population of U. chlorophthalmus was discovered during May 1955, in black mud amongst Ceriops and Rhizophora.

U. marionis. This species was found during May and July 1954, and in February and May 1955 (also in July 1952) in Region C of the Saco Swamp. It is limited to two areas; a small population at the northern end connecting Regions B and C, and the main population at about 200 yards south of Region C and extending for a distance of about 50 yards, with a population density of ± ½/sq. yard. During July 1954, a few individuals were found in a similar habitat at the end of the cross-path in the Mainland Swamp. In Region C of the Saco Swamp, the feeding-grounds of this species are located in very wet mud with a thick growth of Avicennia roots, and they contain a number of pools of standing water left behind by the receding tide. Large numbers of a snail, <u>Te ralia palustris</u>, were found in this region. This mud extends seawards from a few yards outside the outer fringe of Avicennia for an average distance of about ten yards towards the lowtide mark.

<u>U. Urvillei.</u> The feeding-grounds of this species were found to be slightly more varied than those of U. marionis. During May and July 1954, and February and May 1955 (also July 1952), this crab was found along the first 200 yards of Region C of the Saco Swamp, starting from its northern end. In this region three different kinds of habitat were observed. Firstly, a few individuals were found along the drier edge, outside the fringe of Avicennia; secondly, some individuals were observed amongst Rhizophora and pools of standing water in the black mud just inside this outer Avicennia fringe; thirdly, a larger number of individuals (± ¼/sq. yard) were found in pools of standing water, amongst the Avicennia roots at the southern end of its habitat, i.e. in the same area as that in which the highest population density of U. marionis was recorded. Three different types of feeding-ground were also observed in the Mainland Swamp during July 1954; firstly, an unshaded muddy area with pools of standing water where the cross-path and the path skirting the swamp join one another (population density (± 0.5/sq yard); secondly, a few

individuals were observed near the bases of Rhizophora and Ceriops in fairly blackish mud on either side of the upper end of the cross-path; thirdly, some individuals were found in a small area near the trunks of the large Avicennia trees on the eastern side of the path, near its seaward end (± 0.5/sq. yard). In the South Swamp, a different kind of U. urvillei feeding-ground exists. About 100 yards from the ocean edge of the swamp, this species was found in black mud along the fairly narrow banks of the main channel and among roots of Rhizophora and Bruguieria. The area is narrow, and consists mainly of the more or less open spaces on the banks of the channel. The range of the species extends for a couple of hundred yards to where the channel finally peters out.

In the laboratory, the mud used for the tanks was collected from the northern open flat of the South Swamp. This mud was fairly sandy, and all five species seemed to thrive comparatively well on it, although each species showed its own particular preference for wetter or drier mud. U. marionis and U. urvillei, for example, preferred the mud to be very wet, U. chlorophthalmus preferred it to be somewhat drier while the U. annulipes individuals survived best under fairly dry conditions. U. inversa preferred periodic submersions, lasting only a short while and then a drying mud. Normally, all the crabs did well at temperatures above 20°C but, when the temperature dropped below 18°C, it had a marked lethal effect on the crabs.

(3) SYMPATRY.

In a summary of the types of feeding-ground of the five species it may be noted that U. marionis, U. chlorophthalmus and U. inversa are the most specialized in their requirements,

U. urvillei is slightly more variable in this respect, while U. annulipes seems to be adapted to a much wider range of conditions.

U. marionis occurs as small populations, and is limited to the very wet mud on the seaward side of swamps, and this mud is covered by a thick growth of Avicennia roots. This habitat is submerged semi-diurnally and pools of standing water are usually left behind by the receding tide.

U. chlorophthalmus occurs as fairly dense populations, and is limited to a narrow fringe of swamp, usually on the landward side. This crab lives amongst the Avicennia roots in blackish mud, in habitats fairly well shaded by Ceriops and/or Avicennia, but which may extend somewhat into the more soggy black mud with Rhizophora.

U. inversa appears to be limited in its distribution to extensive, open, sandy or grey mudflats. Few, if any, roots of Avicennia grow in this habitat which is totally unshaded, and the population density is low.

U. urvillei apparently requires a very moist condition of the mud which may, however, be found in different parts of the swamp; i.e. amongst Rhizophora on the banks of channels or on the fringes of the inner core of the swamp; in shade amongst Avicennia roots; and in more exposed areas without Avicennia roots. Generally these localities have pools of standing water and the population density is low.

U. annulipes occurs as dense populations in the following habitats: on exposed beaches amongst Avicennia roots, where often there are pools of standing water; on the landward side of swamps alongside Avicennia, Ceriops or Rhizophora; on exposed flats or pathways with or without Avicennia roots; on fairly black, watery mud beneath trees of Avicennia, Ceriops or Rhizophora; or on bare sandbanks exposed during lowtide after storms. In many of these habitats, individuals of this species are found intermingled, to a certain extent, with individuals of another of the Uca species.

Some remarks may be made on the distribution and feeding-grounds of the species of Uca in the deltas or around the mouths of small streams, as studied in Batavia by Verwey (1930), in Panama by Crane (1941), and in El Salvador by Peters (1955). Verwey studied the Uca species in a delta in the western part of the Bay of Batavia. He defined five zones on the mud-banks on the seaward side of the mangrove swamp. The first or highest zone extends from the level of the spring tides to some distance below the level of the ordinary hightide, while the fifth zone is continuously under water. Demarcation of zones is apparently not due to the duration of the flooding, but is based mainly on the degree of moistness of the mud. In zone 2, which is more or less regularly covered by hightides, Verwey found U. consobrinus amongst the air roots of mangroves. This species resembles U. annulipes, but Verwey found the latter species in the wetter parts somewhat lower down. In zone 3 he found large numbers of U. signatus, and this zone extends from a short distance below the level of hightide to where the mud begins to get very wet and soggy. Zone 4 extends to near the lowwater mark and, while in northern Java it carries no Uca species, in eastern Java it is inhabited by large numbers of U. marionis, together with some individuals of both U. urvillei and U. annulipes. In southern Java also U. urvillei occurs in this zone, but there is a much smaller number of individuals of U. marionis. Verwey ascribes the difference in the populations of these areas to the differences in texture of the mud and to both the quantity and quality of the organic matter contained therein. Pearse (1912) has also described the zones along certain estuaries in the Philippine Islands. Here U. annulipes inhabits a zone (the third zone of Verwey) which is higher than the zone (the fourth of Verwey) with the softer mud of deeper parts of the estuary. In the latter zone, Pearse found U. marionis.

The striking fact to emerge from a comparison of the distribution of these species of Uca is that in northern Java, with a diurnal tide, no U. marionis and U. urvillei occur, while in the eastern and southern parts of Java, and at Inhaca, with semi-diurnal tides, both species occur in similar habitats. Especially striking is the fact that U. urvillei occurs higher upshore than U. marionis, although the two species do intermingle to some extent.

Crane (1941) studied the Uca species in a cove on the left bank of the Pacific mouth of the Panama canal, and found fifteen species in 600 square feet of mud. The mud of this area is extremely rich, and consists of a mudflat at lowtide, with a narrow muddy beach. At the inner end, Crane found a somewhat muddy sand, mixed with gravel, lying alongside a small cluster of mangroves. In all three main areas, Crane found an intermingling of species, but in any given area one species generally was dominant, with a second species plentiful or rare, and sometimes a third species in small numbers. Crane asserts that in less rich areas Uca species tend to keep separate from one another, with definite boundaries to their colonies. The fifteen species were found in four different habitats; one was limited to mud amongst mangroves, and it was at least partly shaded; two others were also found in this habitat, but of these one lived also on mud amongst unshaded mangrove shoots, and the other on unshaded tidal mudflats; two species lived only on these flats; one species was found on these flats but also on mud amongst unshaded mangrove shoots; four species lived on the mudflats but also on protected but unshaded muddy-sand flats or beaches; four species lived only in the latter habitat, while one species was found in all the main habitats.

None of the species found in Inhaca occurs among those described by Crane, but some comparisons may be drawn. The following were given by Crane as some of the criteria for structural specialization in Uca; increase in thickness through greater arching of the carapace and underparts; straightening of the orbits; divergence of the carapace sides posteriorly. In the Pacific species, the trend for the more highly specialized forms seems to be more and more towards living in protected, muddy-sand flats and beaches, instead of in the mud amongst unshaded mangrove shoots or on tidal mudflats. If such be the case for all Uca species, then at Inhaca, U. inversa should be the most highly specialized form, since it occurs exclusively on protected muddy-sand flats. This species, however, does not satisfy any of the above-mentioned criteria.

The species of Uca found in an estuary on the Pacific coast of El Salvador have been studied by Peters (1955). Here, the mudflats are apparently separated from one another by a large number of small channels. On these mudflats, mainly Rhizophora species is found, with Avicennia species growing only on the landward parts, where the ground is both finer and drier. In this mangrove swamp, Peters found several of the species, already described by Crane, inhabiting specific zones on the mudflats. In some areas, it would seem that a species is limited to a zone, either in the drier part at the landward edge of the swamp, or in the

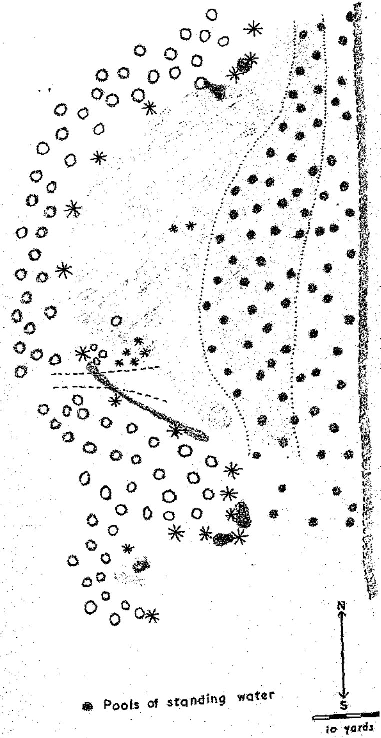
21/ ...

wetter mud. Peters does not specify the factors responsible for limiting a species to a particular part of the mudflats. He found too, that in certain areas there are many species intermingling with one another in one particular habitat.

Sympatric species are those with their geographical ranges either coincident or overlapping. Apparently geographic isolation is a condition for speciation, so that sympatric speciation never occurs (Mayr, 1947). Thus, it would seem, that sympatric species must have originated as allopatric species, in different geographical regions and under different conditions of both environment and habitat. If any such species should ultimately become sympatric, various points of difference could occur in their ecological niches (Mayr, 1947). A close study was made of some of the special localities in the various swamps at Inhaca, in order to determine whether or not this concept holds for the five Uca species found there. (i) In its main habitat on the open flat of Region A of the Saco Swamp, U. inversa shows a certain amount of intermingling with individuals of U. annulipes. This fact is rather more evident during neap tide periods although, at such times, the U. inversa individuals are concentrated mainly around the bases of young Avicennia trees. During spring tide periods, when the U. inversa individuals leave the tree-bases and advance over the open flat, U. annulipes is found occupying only the north, east and south-east fringes of the flat. (ii) In that part of the Mainland Swamp studied (Pl. VIII, Fig. 1), the three species, U. urvillei, U. chlorophthalmus and U. marionis are well separated from one another, as shown in Text - fig. 3. Nevertheless, their main concentrations are linked together by U. annulipes

FIGURE 4.

200 YDS. SOUTH IN REGION C, SACO SWAMP

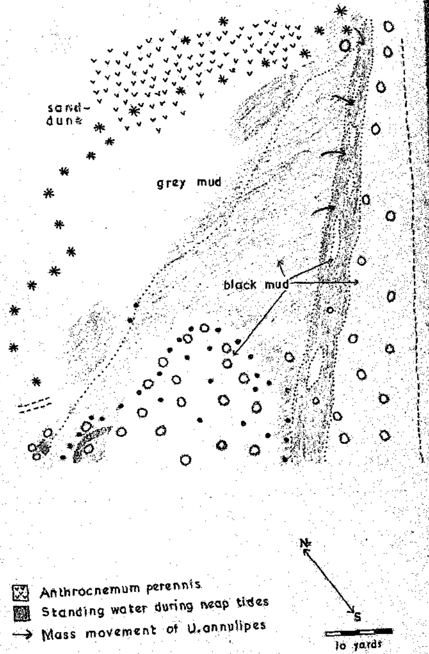


because of the ability of this species to occupy so varied an assortment of habitats. This intermingling of the U. annulipes individuals with the populations of the other three species takes place, however, only at the edges of their territories. (iii) A different state of affairs was discovered in the South Swamp, where three species occur together in a small, exposed triangle of mud on one bank of the channel. (Pl. VIII, Fig. 2). Here, the larger individuals of U. urvillei were found in the shade beneath t Rhizophora trees on the right of the photograph, while younger individuals, intermingled with both U. annulipes and young U. marionis individuals, were observed in the more exposed area, away from the trees. (iv) At about 200 yards south in Region C of the Saco Swamp, a particularly interesting example of the sympatric relationship between species is illustrated (Text - Fig. 4; Pl. VIII, Fig. 3; Pl. IX, Figs. 1-3, and Pl. X, Figs. 1-3). U. chlorophthalmus occurs in two places, widely separated from one another. The northern population is small and fringes not only on the U. annulipes population, but also on a small population of U. urvillei; the southern population is much larger, and is isolated from all other species. U. urvillei occurs as three populations, the first of which is the small, northern population already mentioned. The second population is a larger one, running along the southern margin of the open space, and isolated except where it fringes on the U. annulipes territory, near the path. The third population occurs further south, intermingled with U. marionis individuals. One population of U. marionis was found isolated on the exposed, wet, seaward part of the beach which is normally associated with this particular species. During the breeding season, however, the mating individuals were observed higher up on the beach, in drier mud towards the trees,

23/ ...

THE NORTHERN OPEN FLAT OF THE SOUTH SWAMP

FIGURE 5.



and intermingled with the main population of U. annulipes. A second breeding population was found further south, fringing on the population of U. urvillei near the path, while a third, non-breeding population was found, intermingled with U. urvillei at the southern end of the locality.

(v) The northern part of the South Swamp (Text - fig. 5; Pl. XI, Figs. 1-3; and Pl. XII, Figs. 1-3) shows some sympatric relationships between three species. U. chlorophthalmus occurs as a small population scattered amongst the Rhizophora trees at the southern margin of the open flat and interspersed with individuals of U. annulipes. U. inversa occurs as a small population towards the north of the open flat, intermingled with individuals of U. annulipes at the margins of its territory. A larger population, also of U. inversa, was found at the south-west of the open flat, concentrated in an area surrounded by U. annulipes individuals, some of which were again intermingling at the edges of the U. inversa territory.

The relationships existing between the species indicate that each species, with the exception of U. annulipes, has its own particular ecological niche. The selecting of a particular habitat is controlled by such factors as the degree of moisture and shade, the nature of the mud, and the periodicity of the tides. One locality may contain several niches, so that the feeding-grounds of various species may overlap slightly. Therefore, a certain degree of intermingling between individuals of different species may be found within a particular locality.

(4) NEW COLONIES.

The distance travelled by the larval forms of Uca in their spread from one place to another are not known. The recent discovery of a number of new Uca colonies yields, however, some facts which are relevant to this problem.

24/ ...

(i) In 1952, it was found that the channel in the Elephant Island Swamp had been silted up. The swamp was dry and contained only a few stunted Avicennia and Ceriops trees, and there were absolutely no Uca individuals present. By April 1955, the channel had reopened, and there was a thick growth of Avicennia and Ceriops bordering on the channel. Scattered amongst the Avicennia roots, fair numbers of U. annulipes were found. The only possible method by which such a colony could have been established was by way of a migration of larval forms, across the sea from Inhaca Island.

(ii) The small population of U. chlorophthalmus, found during May 1955 at the southern end of the open flat of the South Swamp, may have originated from a few individuals, the relics of a previous population. The only other way in which such a colony could have arisen, was as the result of an influx of larval forms from another swamp, probably the Saco Swamp, due to the transporting action of the tides.

FEEDING.

(1) METHODS OF FEEDING.

Uca crabs feed on the organic debris which is left in the wake of the receding tide. With the aid of binoculars, the feeding-habits of many Uca individuals of the various species were closely examined.

U. annulipes. Observations of this species were carried out chiefly at the Saco Swamp. During feeding, the males use only their rather "spooned" minor cheliped, the major cheliped being held at rest. A mixture of sand or mud with organic particles is scooped in a thin layer from the ground by the minor cheliped, and conveyed to the mouth. Mud may even be picked off the Avicennia roots. The mouthparts, which are extremely well-developed, separate out the organic particles until, after the mastication of several such mouthfuls, enough sand and other rejected material has collected to form a roundish pellet which hangs from the lower edge of the mouth. The pellet may either be so moist that it drops to the ground automatically, or, if it is of a more solid type, the claw of the minor cheliped is used to remove it forcibly and place it on the ground, usually just in front of the crab. The female crabs differ from the males for, possessing two small chelipeds rather than a large and a small, they are able to use their chelipeds more or less alternately, in order to scoop up mud from the ground. As Peters (1955) has pointed out, there is no correlation between the left and right chelipeds of the female during the feeding-process, but the two claws usually alternate rapidly, and the resulting pellets, if they do not fall to the ground of their own accord, are removed by one or other, or by both of the claws. The actual process of mastication by the mouthparts and the method whereby the sand is sifted out are very difficult to observe, especially since the whole procedure occupies a very short period of time.

U. annulipes individuals spend much time out of their burrows, feeding busily and almost continuously. The pellets formed are usually of a homogeneous texture, and their degree of wetness or dryness depends on the state of the particular feeding-ground on which they occur. It was noted that each crab usually remains in one spot whilst feeding, although he may walk sideways, leaving in his wake a more or less straight row of pellets, leading from his burrow. In order to feed, U. annulipes individuals may move very far from their burrows. In certain rather dry, hard areas, where the large number of pellets present indicates that much feeding has previously taken place, several furrows were seen to be radiating from each burrow. These furrows, which cut through the irregular mass of pellets surrounding the entrance to each burrow, represent the paths by which the individual either left or returned to his burrow. These paths are reminiscent of the longitudinal rows of pellets which Verwey (1930) describes as radiating from the burrows of the Uca species of Batavia.

At the South Swamp certain U. annulipes individuals were seen feeding near the channel. They appeared to have difficulty in remaining anchored on one spot whilst feeding, for the mud was very wet and slippery. Again and again, they would stretch their ambulatories to the fullest extent, and then suddenly bend them again, so that their bodies nearly rested on the ground. This movement was fast and rhythmic, giving the impression that the crabs were "bouncing" up and down, while continuing to feed.

On the open patch of the South Swamp, several U. annulipes individuals were observed, partly immersed in the standing water left from the previous spring hightide. The crabs appeared to be drinking, for the small chelipeds were being used to scoop water rather than mud into the mouth. This drinking-process, the movements of which are essentially similar to those normally associated with feeding, was also observed in a few individuals at the Mainland Swamp. U. annulipes was the only species ever observed drinking.

U. inversa males and females have a method of feeding essentially similar to that observed in U. annulipes. In U. inversa, however, the minor cheliped of the male, and the two small chelipeds of the female, appear to be far more efficient organs generally than those of any other of the Inhaca species except, perhaps, U. marionis. Therefore, the movements involved in the feeding of U. inversa are very much better co-ordinated and far more definite than usual. The small chelipeds are very flexible, well-developed organs, which are more than usually large in relation to the rest of the body. During feeding, individuals of this species were frequently seen opening the claws of their small chelipeds to the very fullest extent before pressing them into the mud and finally drawing the two parts of the claw together again. In this way, the crab scoops up quantities of mud which are conveyed to the mouth as usual. As a result of this method of obtaining mud, deep, sharp, short scrape-marks, characteristic of this species, may be found covering the ground areas where feeding has taken place. By means of their small chelipeds, U. inversa individuals can be seen to pick and choose the food-particles from the mud to a far greater extent than was seen in any other species. Unwanted particles are simply deposited on the ground by the small cheliped, before they can get as far as the mouth. During feeding, female crabs generally alternate their right and left chelipeds, in order to scrape up mud from the ground and convey it to the mouth. Now and then, however, a female crab was seen to use only one of her chelipeds for scraping up the mud while, with the other, she removed the pellets from her mouth, so that a small heap of pellets was formed on the side of the latter cheliped. U. inversa individuals are definitely rather lethargic and tend to move about very little, although they may walk a distance of more than two yards from their burrows - a greater distance than that usually associated with U. annulipes. Individuals of both sexes move slowly to a spot suitable for feeding; then settle down in a low, "crouching" position, with their ambulatories bent. They remain in the one spot for some time keeping fairly still but feeding busily, before moving on to another suitable place to feed. The pellets of U. inversa are not only larger than those usually associated with U. annulipes, but they are also more oval in shape.

On closer examination of pellets of U. inversa, collected on the sandy, open flat of Region A of the Saco Swamp, it was observed that they consisted of a core of sticky, black mud, surrounded by a ring of dry sand. It is of interest to note that the U. annulipes pellets found in the same area as those of U. inversa, were also rather oval in shape and of the same composition as the U. inversa pellets, although they were smaller, and far more plentiful.

U. chloropthalmus. The feeding-habits of both sexes of this species were examined at the Saco and Mainland Swamps. In no detail did their habits differ significantly from those of U. annulipes. U. chloropthalmus, however, does not roam very far from its burrow to feed. The pellets formed are homogeneous in texture.

U. marionis. Once again, the method of feeding of both sexes of this species appeared to be much the same as that described for U. annulipes. Like U. inversa, the two small chelipeds of the female and the minor cheliped of the male are rather well-developed and very flexible. No food-pellets were seen in the feeding-grounds of U. marionis, due to the watery state of the mud in which they live.

U. urvillei. The feeding-habits of both sexes of this species were observed, and again their method of feeding did not appear to vary in its essentials from that described for the other species. The individuals have quite well-developed smaller chelipeds, which are nevertheless not as efficient as those of either U. inversa or U. marionis, but which are certainly better-developed than those of U. annulipes and U. chloropthalmus. The U. urvillei individuals are fairly lethargic and do not appear to wander very far from their burrows in order to feed.

The feeding-habits of the five Inhaca species of Uca crab do not appear to vary to any great extent from those described by Crane (1941) for the species at Panama, or by Pearse (1912) for other American species and for the Uca crabs of Manila Bay in the Philippines. It is important to note that none of the Inhaca species appears to scavenge, although, on one occasion, a U. annulipes individual was seen dragging a fairly large, dead shrimp towards his burrow; whether or not it was intended for eating was never established. Verwey (1930) discusses the feeding process of the Batavian Uca species in elaborate detail, even to the extent of describing the individual rôle played by certain of the mouthparts. Crane (1941), on the other hand, finds the actions of the mouthparts difficult to understand, and she is by no means sure of the actual method by which the sifting out of the sand is achieved. Peters (1955) claims that very often the intestinal canal of a Uca individual is filled with sediment, and he asserts, therefore, that the sifting out of the sand is performed by the stomach mill. The resulting sand-pellets, which the small chelipeds remove, are not given out through the mouth but rather through the anus, opening on the ventral surface of the telson. Observations made on the five Inhaca species of Uca would seem to indicate that the sifting-out process is performed by the mouthparts, because the sand accumulating anteriorly to form pellets definitely appears to emerge from between the mouthparts, the individual rôles of each of which are nevertheless rather difficult to follow. Young individuals of U. annulipes, U. chlorophthalmus and U. inversa were observed feeding, and it is of interest to note that they were apparently able to feed not only as fast but also as efficiently as the corresponding adult forms.

(2) PERIODS OF FEEDING.

Peters (1955) claims that the rate of feeding of the Uca individuals diminishes with the drying out of the mud, a fact borne out by all five Inhaca species. Moreover, it was observed that, under laboratory conditions, individuals representative of all the five species remained underground in their burrows when the mud had dried out. Many crabs of all the species emerged after the mud had been saturated, and, at such times, they appeared to be very active indeed. They fed busily, and some were even wading in pools of water. As was to be expected from their normal habitats in the field, U. marionis and U. urvillei preferred their mud to be kept very moist and, under such conditions, their feeding was maximal. Because of the rather dry state of the feeding-grounds of U. inversa and certain of the U. annulipes habitats, there is a scarcity of organic sediment suitable for feeding, and hence the individuals living in these areas are made to wander farther from their burrows than is usually associated with Uca individuals.

Since Uca is a day-feeder, very few individuals of any of the species are to be seen at dusk. From a little after sunrise until the early afternoon, most of the feeding takes place. An analysis has been made of the times of feeding of the five species, a discussion of which follows.

(a) Duration and Periodicity of Feeding.

The tides at Delagoa Bay are semi-diurnal, with each hightide being 30-60 minutes later than the previous one. Consequently, even those areas which are flooded daily have a lowtide period, and are exposed at least once during the daytime. As an illustration of tidal variation, the two periods in 1954 during which observations were made on Uca had average lowtides of 0.56 m. in May and 0.79 m. in July, while the average hightides were 3.43 m. and 3.01 m. respectively, for the two months. The average amplitude of tides for the year was about 2.50 m.. Verwey (1930) investigated certain swamps in Batavia and found them to have an average diurnal amplitude of about 1.20 m.. In this region, apparently, the tide was earlier every day, so that for only about half the year did lowtide occur during the daytime, in this way exposing the mud for feeding.

Although Uca individuals can feed daily in the Inhaca swamps, the actual period of feeding varies from day to day, sometimes extending from the early morning to the afternoon, at other times limited to the morning, or to the afternoon. On the average two spring tides occur per month, and only during these periods are the high-lying parts of swamps flooded, in some areas for three days only during each spring tide, in others for seven to eight days. Some parts are reached by the highest tides only once in a month.

The conditions of flooding and the depositing of food, however, vary for the different species as a result of their occupying such diverse habitats.

U. annulipes. In the different swamps, this species was found inhabiting certain localities, some of which are flooded daily, while others are flooded, at the most, only during three days in a month. Some of the most important habitats are the following, the conditions described being those for the years 1954 and 1955.

(1) In the North and the Mainland Swamps, the inland margins are occupied by U. annulipes, these habitats being reached by floodwater probably only during the semi-monthly spring tides, i.e. during two periods, totalling from eight to fourteen days per month. At that part of the North Swamp investigated, U. annulipes was found inhabiting the whole of the swamp because, should the outer fringe of the swamp become too dry during the periods between flooding, the populations are able to move to the inner, wetter parts

of the swamp. In the Mainland Swamp, the outer fringe has a wetter black mud, and the sparse U. annulipes populations found here seem to feed in the same areas during the period between flooding. In any case, the individuals are never found in the black mud of the inner parts of the swamp where Rhizophora grows, and thus they do not seem to migrate in this locality.

(ii) In the South Swamp, the northern open flat of dark muddy sand, bordered on the south by Rhizophora and Ceriops on patches of black mud, is flooded twice monthly for periods varying from three to seven days, the latter period being the more common. In this area, during a period in which the hightide level was falling at the rate of about 0.16 m. per day, many individuals of U. annulipes seemed to be following the receding hightide line southwards (Pl. IV, Fig. 4; Pl. XII, Fig. 3), although fair numbers were still found at the northernmost end of this open flat, which had received no floodwater. One particular morning, however, these individuals were found in their burrows about two hours after hightide, while the crabs further south, on the recently flooded mud, were busy feeding. North of this open flat, the last 200 yards of swamp are found, with some Avicennia but mainly Rhizophora trees; this area can be flooded, at most, only once monthly for periods averaging from three to five days. Old feeding-grounds were observed in this area and, consequently, when the tide-line had receded southwards, the crabs must have evacuated this area, a migration of several hundred yards. Whether or not this upper end of swamp had received any floodwater for a period of two months was doubtful. The type of evacuation movement just described was actually witnessed on the 19th February 1955, the last day of a neap tide period. U. annulipes individuals were seen moving from the northernmost area, which had received a spring hightide twelve days previously, into the area of standing water (Pl. XI, Fig. 2).

(iii) Region C of the Saco Swamp is flooded daily throughout the year, because even the lowest hightides cover the fringe of Avicennia roots. The large populations of U. annulipes living in this region must consequently have a regular daily feeding-period, the optimum hours of which vary with the shifting of the tide. In this area, individuals were observed feeding under very wet conditions. Region B of the Saco Swamp has its main population on the pathway bordering the western margin. This path is regularly flooded by spring tides and is therefore covered by water for at least two periods per month, each period often extending over eight days. During periods of neap tide, the very dense population at the northern end of the path could migrate round the Avicennia trees to the upper end of Region C, so as to extend their feeding-grounds to flooded areas. The population living more towards the south, however, would not be able to migrate into the black mud alongside their habitat and would, therefore, have to remain in their old habitat during periods of neap tide. In this area, a smaller number of individuals were observed feeding during such a period than during periods of spring tide. For example, on the 25th February 1955, large numbers of these crabs were feeding even at 3 p.m. during a period of spring tide, while on the 30th April, the fourth day of a neap tide period, very few individuals were observed feeding even at 10 a.m.. On this day, fair numbers were seen feeding at the water-edge, at the upper end of Region C. The open flat at the southern end of Region A of the Saco

Swamp is also flooded semi-monthly for periods varying from three to eight days. During some of these periods, or parts thereof, the hightide mark does not reach the pathway, which borders the western margin of the swamp, but stops halfway across the flat. The crabs which remain in this drier, landward area throughout such periods, must come out to feed during the early morning, and there are large numbers of pellets covering the surface of the ground, although by 11 a.m. most individuals were found to have re-entered their burrows. At such times, however, larger numbers of crabs were found feeding on the moister part of the open flat, nearer the fringe of Ceriops. During periods of neap tide, when no floodwater reaches the open flat, very few crabs were seen feeding in the hotter part of the day. There were some feeding in the shade, however, especially under the few smaller Avicennia trees. A similar curtailing of the feeding-period was observed in the extensive Ceriops patch at the southern part of the South Swamp. For example, on the 28th of June 1954, at 9.30 a.m., after five days of neap tides, no crabs were found feeding in this area, but, instead, large numbers of young crabs were found, each individual in its own burrow. On the 1st of July, the second day of spring tide period, large numbers of crabs were feeding at this spot at 9.30 a.m..

(iv) On two occasions when lowtide was at 12 noon and 1.40 p.m. respectively, very large numbers of U. annulipes were observed feeding at about midday on fairly bare sand-banks exposed at lowtide. One such population was observed on a white sandbank off the path which traverses the North Swamp, and the other on a more muddy sandbank extending seawards for about 40 yards from the Avicennia root area at the northern part of Region C of the Saco Swamp. These two habitats must have been of a temporary nature since, both before and after this period, the two sandbanks could not have been exposed during lowtide. It must be concluded that these individuals moved into the new habitat after the first exposure of the sand. On the Saco sandbank the crabs were found up to a distance of 50 yards from the farthest limit of their usual habitat on the beach. From these facts, it is evident that populations of U. annulipes may migrate over long distances if and when new habitats, adjacent to their usual feeding-grounds, are exposed at lowtide.

In general, it may be said for U. annulipes individuals, that their feeding-period extends throughout most of the day when the tides are favourable, but that during periods of neap tide, when the mud-flats are drying out, the feeding-period is shortened to the early morning and, perhaps, to the late afternoon, so preventing the feeding individuals from drying out excessively, during the hottest part of the day. Towards the end of a neap tide period, there seems to be no feeding taking place on the landward side of swamps.

The effect of the advancing tide on the behaviour of Uca crabs has been studied. In the case of U. annulipes, the following are some of the observations which were made. On the 4th of May 1954, there was a hightide of 3.54 m. at 5 p.m., and this tide was high enough to flood the northern open flat of the South Swamp. Throughout the afternoon, many crabs were seen feeding on this flat but, by 4 p.m., they had gone into their burrows. On the 28th of June, this area was not flooded by the hightide of 2.96 m. at 3 p.m., and the crabs were found to be feeding at 4 p.m. and later. On the 29th of June with a hightide at 3.45 p.m., many crabs were feeding on the cross-path and open space of the Mainland Swamp at about 11 a.m. On the 4th July, however, with a hightide at 6.30 p.m., very few crabs were feeding in this locality at 12 noon, and an even smaller number at 3 p.m., although at 1 p.m. large numbers were feeding in the wet mud at the seaward end of the path. It might be noted that, on the 29th of June, the sky was overcast in the morning and only cleared towards noon. During the course of several days, with hightides between 1 and 2 p.m., many crabs were observed feeding in Region C of the Saco Swamp, just in front of the advancing tide. On the 1st of July, with a spring hightide at 5 p.m., no crabs were observed at the northern end of the swamp, and a few only towards the middle of Region B at 4 p.m., while at the southern end of Region B and the adjoining part of Region A, many crabs were still feeding at 4.30 p.m., not 10 yards from the advancing tide. On the 6th of July, which was at the start of a neap tide period, the hightide was 7.15 p.m., and more crabs were out feeding at a late hour, towards the middle of Region B, than were observed on the 1st of July. It should be noted that the upper end of Region B is in shadow earlier in the afternoon than the middle part, while the latter, in its turn, is in shadow earlier than both the southern end of Region B and the adjacent Region A.

On the evidence of these observations it seems that U. annulipes continues feeding right up to the edge of the advancing tide, except on those days when this water arrives too late in the afternoon. Exceptions to this particular reaction to the combined effects of tide and shadow, as for example on the 6th of July, may be due to a later start in feeding in the early morning, as the result of rain or an overcast sky, or to the fact that the tide is too low to reach the feeding-ground concerned.

U. inversa. The facts which have been noted in regard to the feeding-period of U. annulipes during periods of neap tide, are also valid for U. inversa. This species was found only on open sandy flats, one at the southern end of Region A of the Saco Swamp, and the other at the northern end of the South Swamp, and it thus inhabits territories which are not flooded during the whole of the three to eight day periods of semi-monthly spring tide. On the 1st of May 1954, with a spring hightide of 3.45 m., many of these crabs were observed feeding on the open sands of the Saco A flat from 12 noon to 1 p.m., while on the 27th of June, with a hightide of 2.74 m., none of these crabs were observed at an earlier hour. The 27th of June followed on a period of three weeks, during which the very low tides could not have reached the western part of the U. inversa habitat, and it was at least eight days since the last floodwater reached the eastern border of this habitat. From the 30th of June to the 2nd of July, a period of spring tides, U. inversa was again observed feeding from early morning to late afternoon, but mainly on the wetter portion of the open flat. On the 6th of July, when the period of spring tides was ending, very few of these crabs were observed from 11.30 a.m. to 12 noon, although individuals were found in their burrows even in the drier, landward part of their range, near the pathway. In this area large numbers of dried-out pellets were observed, surrounding the burrows. On the 19th of February 1955, U. inversa individuals were seen feeding at 10 a.m., under the small Avicennias on the open flat of Region A of the Saco Swamp, on a day which was about seven days after the last flooding of the area by a spring tide. On the 22nd and 23rd of February, at the beginning of a spring tide period, a population of 0.5/sq. yard density was found feeding on the flat of Region A, from the Ceriops fringe to about three-quarters of the way across the flat, but not on the pathway. Here, from 10.30 a.m. to 2 p.m., individuals were observed feeding on mud with a very wet surface. On the 26th of April, the last day of a spring tide period, feeding individuals were observed on the open flat, and very few crabs were feeding under the small Avicennias. On the 27th of April, at the start of a neap tide period, many crabs were observed, still feeding on the open flat at 4.20 p.m., but on the 30th of April, the few individuals feeding at 9.30 - 10 a.m., were found to be under the small Avicennia trees. At the South Swamp, U. inversa individuals were seen feeding at 6 p.m. on the 20th of February 1955, on grey mud which had been moistened slightly, a few hours previously, by the first spring hightide. Individuals were observed to be feeding in this area at 1.30 p.m. on the 29th of April, the third day of a neap tide period, but the day was rather overcast. On the 1st of May, a sunny day, no feeding was observed from early morning to late afternoon.

The main feeding-period of U. inversa seems to be at times when the mud on the flats has been well moistened during spring tides, but it is limited to early morning feeding during periods of neap tide, in order to conserve the moisture needed for respiration.

__U. chlorophthalmus.__ During May 1954, small populations of this species were found alongside the fringe of Avicennia in the middle part of Region C of [illegible] Taco Swamp; that is, in the area which is flooded semi[illegible]ally. In July 1952, these populations had also been noticed, but in June-July 1954 no trace of them remained. In both February and May 1955, however, small populations were found here once again. These populations may have arisen as small infiltrations through the narrow strip of black mud, separating this area from the adjacent main habitat of the species in Region B. The habitat of U. chlorophthalmus is better protected than those of other species, for it contains large numbers of Avicennia roots and shoots with some small Ceriops trees, scattered here and there. In Region B, this species is confined to a narrow strip, a few hundred yards long. This habitat is flooded regularly during semi-monthly spring tides, as has been described for its neighbour, U. annulipes. A comparison of the frequencies of individuals, feeding over a period of three days, gives an indication of the type of periodicity observed in the feeding-periods of *U. chlorophthalmus*. These observations were made at the main feeding-ground, that is, between eighty and a hundred yards southwards in Region B. On the 27th of June 1954, after eight days of neap tides, with a hightide of 2.74 m. at 1.50 p.m., very few individuals were noticed at 1 p.m., and most had already re-entered their burrows by 12 noon. On the 1st of July, at the beginning of a spring tide period, with a hightide of 3.39 m. at 5 p.m., many crabs were feeding at 1 p.m., but they had totally disappeared by 3.30 p.m. On the 19th of February 1955, after seven days of neap tides, the U. chlorophthalmus population in the main area had moved into the tree-fringe and inner black mud of the swamp, and had been replaced by individuals of U. annulipes. On the 22nd of February, the third day of a spring tide period, U. chlorophthalmus individuals were back in their old territory. Feeding took place throughout most of the day, and many new burrows were observed. On the 25th of April, the second-last day of a spring tide period, many individuals were seen feeding in their main area. There were even some individuals west of the path, opposite the main area, and this group was not separated from the group occupying the main area by a dense U. annulipes population on the path. The U. chlorophthalmus individuals were feeding as late as 4.30 p.m., in spite of the fact that the afternoon was rather overcast. As is the case for other species, it would seem that, when the feeding-grounds of U. chlorophthalmus dry out, especially towards the end of a period of neap tides, their feeding-period is curtailed, and they remain in their burrows during that time of the day when, during spring tide periods, they would be most actively feeding.

U. marionis. In the three main habitats in which this species has been found, that is, outside the fringe of Avicennia in Region C of the Saco Swamp, on the seaward side of the Mainland Swamp, and on the banks of the South Swamp channel, the feeding-grounds are flooded semi-diurnally throughout the year. Individuals of this species are sparsely distributed in their habitat but have been seen during the warmest part of the day; their feeding-period would be curtailed only on days in which the hightide falls during this time of the day.

U. urvillei. The details which have been noted for the [illegible]er species are valid also for U. urvillei, except for the fact that this species has a somewhat more varied habitat. The U. urvillei feeding-ground at the top end of the cross-path in the Mainland Swamp is not reached by the lower neap tides, but on the other hand, this area contains pools of standing water and would thus not dry out to such a great extent. In other localities, too, this species is found in the more shaded fringes of black mud which retain their water longer than the more open types of sandy flat. It is not known whether U. urvillei migrates from the more open part of its habitat to these protected areas during periods of neap tide. As is the case with the other species, individuals of U. urvillei are found feeding during the warmest part of the day.

(b) Mass Movement.

Large-scale movements of whole populations were noted on several occasions, and only in U. annulipes. On the first occasion, such a mass movement was observed at 11 a.m. at the northern end of the Saco Swamp. Large numbers of crabs were seen moving landwards in the direction of the fringe of Avicennia from the watery mud at the outer margin of the Avicennia root area. Lowtide on this particular day was at 9.30 a.m., and it was the first day of a period of spring tides. Apparently, the crabs had left the territory of their burrows, and followed the receding tide-line seawards during their morning period of feeding, in order to reach newly-exposed feeding-grounds. On the second occasion, a similar mass migration was observed at 1 p.m. at the seaward end of the cross-path in the Mainland Swamp. The crabs concerned were also moving towards the Avicennia trees, from the watery mud at the seaward margin of the Avicennia roots. Lowtide on this day was at 12.30 p.m., and it was the last day of a period of spring tides. On this day, the movement of crabs returning en masse to the territory of their burrows, took place at a later hour, apparently because the tide receded about three hours later than in the previous case described. Many crabs were observed still feeding in the area to which the main body of crabs was returning. If the above interpretations of the mass movements are correct, it seems that populations of U. annulipes may sometimes travel rather long distances from their burrows for daily feeding on newly exposed mud, during periods of very low tide.

Apart from such mass migrations for purposes of daily feeding, a periodic mass movement, taking place during periods of neap tide, was noticed amongst a population of U. annulipes on the open flat, at the northern end of the South Swamp. On the 19th of February 1955, the last day of a neap tide period, some U. annulipes individuals were observed feeding in the standing water remaining from the previous spring hightide, twelve days before. These individuals were almost completely submerged, and were moving "downstream" at a fairly steady rate. A similar mass migration was observed again over a period of a few days, from the 28th of April to the 1st of May 1955, that is, from the second to the fifth day of a neap tide period. During this time, the migrating individuals moved gradually from the grey mud of the open flat, beside the Avicennias, through the stretch of black mud to the edge of the standing water and, finally, right into the standing water itself, (Pl. XI, Fig. 2; Text - fig. 5). The main migration took place on the 1st of May, when a dense mass of U. annulipes individuals was seen moving slowly and steadily "downstream", through the standing water. Most of the large number of individuals were half-immersed in the water and were feeding and drinking busily, or were standing feeding on the small "islands" of black mud, between the lanes of standing water. Some of the individuals were feeding as they walked, while others would run ahead for a distance of a few inches, pause to feed, and then run on again. The migrating crabs were so closely packed together, that they kept jostling one another. Besides the main stream of individuals, there were other smaller streams of crabs moving in other directions to that of the main stream; but these smaller streams were also always moving in the direction of, or actually through, the standing water. Towards evening, it was found that most of the migrating individuals had gone into burrows for the night. There were large numbers of new burrows in the black mud, very near to the standing water, as well as in the "islands" of mud. There were also large numbers of U. annulipes individuals in burrows in the drier mud away from the standing water, an area in which no feeding had taken place that day.

B U R R O W S.

Uca crabs occupy burrows in the mudflats on which they live, a habit which is of great advantage to the crab in several ways. Firstly, the burrow is the means of escaping enemies when the mudflats are exposed at lowtide; secondly, it is a means of escaping those enemies present in the floodwater; thirdly, it serves as a protection against desiccation during periods when the mudflats are not flooded.

(I) Structure of the Burrows.

The shape and depth of the burrows made by the various species of Uca crab at Inhaca were examined, chiefly at the Saco Swamp. Each species appears to have a fairly characteristic type of burrow, with a more or less constant shape and depth. It was noted, however, that the burrows of various individuals of the same species tend to vary considerably, the variation depending on the location of the burrow and on the size of the individual concerned. This variability was also noticed by Crane (1941) in the species she investigated at Panama. As the size of the burrow varies according to the individual occupying it, so naturally does the diameter of the hole or entrance to the burrow vary in size. Each crab of the Inhaca species possesses its own burrow, and in no species were interconnections between the burrows found. Because of the presence of the major cheliped, the male crabs are more bulky than the females, and so they have the larger burrows.

In her paper, Crane refers to very young crabs which do not dig, but run freely in and out of the burrows of adults, both of their own and of other species. This habit did not, however, prevail amongst the young of the Inhaca species. At the South Swamp, in the extensive patch of Ceriops, where no adults or their burrows were visible on the 28th of June 1954, many small burrows were found, in each of which a young male or female individual was residing. The average size of these individuals of U. annulipes was 11 mm. by 6 mm.. Unlike the species described by Crane, the young crabs at Inhaca dig their own burrows. During February and April 1955, towards the middle of Region B of the Saco Swamp, many young individuals of U. annulipes and U. chlorophthalmus were noticed, their carapaces varying in width from three to ten millimetres. Each individual had its own burrow, the size of which was proportionate to the size of the individual. Young forms of U. inversa were also found during April 1955, on the open flat of Region A of the Saco Swamp. The young varied from about four to ten millimetres across the width of the carapace, and their burrows were about two inches deep, and were once again scattered amongst those of the adults. The burrows of the young forms were more vertical and, naturally, of smaller diameter than those of the adults. In none of the Inhaca species, were there any signs of parental care, and even the smallest young forms appeared to be very independent.

It was noticed that under laboratory

conditions, all the species apparently preferred to have their burrows as near as possible to the sides and, especially, to the corners of their particular tank, although quite a number of individuals made their burrows more towards the middle of the tank. Not only were the burrows of all the species rather indefinite in shape, but they were also very shallow, since the layer of mud at the base of each tank was only about two inches deep. Moreover, the burrows tended to slant to a greater extent than those in the field. Due to the fact that the tanks were over-populated, the captive crabs representing each of the five species did not appear to own individual burrows.

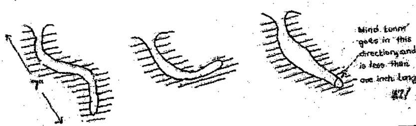
U. annulipes. Burrows typical of this species were examined at various parts of the Saco Swamp. Firstly, in the mudflats at the northern end of Region C, a few burrows were investigated and were found to slant slightly as they travel downwards into the ground. This almost vertical channel is of more or less uniform diameter and leads into a blind pocket about two inches long which slants less steeply. In this blind sac, the crab occupies most of its hours spent "indoors". The many U. annulipes burrows in this very wet, muddy locality, are scattered amongst the partly aerial Avicennia roots which tend to dominate the area. On the path at the northern end of Region B, more U. annulipes burrows were investigated. This area is somewhat drier than that previously described, and the Avicennia roots form a dense mat below the surface of the ground. Here the burrows are very plentiful, and, since they are situated actually on the main pathway of the swamp, the ground in which they are built is very hard indeed. Nevertheless, they are more or less similar to those previously described, except that the more vertical channel is often about five inches deep, and may be rather unevenly widened. In captivity, individuals of U. annulipes made a far better attempt to dig as natural a burrow as possible, than did individuals of any other species. Their burrows often sloped quite markedly, and were up to about one and a half inches deep.

U. annulipes burrows.

In wet mud. In dry sand.

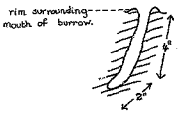
U. inversa. In the open flat of Region A of the Baco Swamp, where this species is so common, the individuals dig burrows which slant slightly and continue downwards for a distance of about seven inches, without flattening out to any marked degree. The shapes of these burrows vary to a certain extent, and three typical shapes are shown in the diagram. An interesting feature of certain of these burrows is the fact that the blind tunnel, which is generally less than one inch in length, may go off in a direction almost at right angles to the most vertical part of the burrow. The entrance to the burrow of a U. inversa individual is somewhat wider than that of a U. annulipes crab, and the sand at the bottom of the U. inversa burrow is almost saturated with water. In captivity, the U. inversa individuals make burrows about one inch deep, which have no definite shape but which slope quite considerably.

U. inversa burrows.



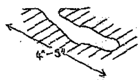
U. chlorophthalmus. Burrows of this species were examined in an area just to the side of the main pathway, and towards the northern end of Region B of the Sado Swamp. In this area, where the species is so very plentiful, there are some burrows of U. annulipes scattered amongst those of U. chlorophthalmus, on the fringes of its territory. The burrows of U. chlorophthalmus are, however, easily distinguished from those of U. annulipes because they have a distinct rim of mud built around the entrance to the burrow. Each burrow slopes for about four inches as it goes downwards in the soft muddy ground, and then it slopes down more obliquely for a further two inches. The rims surrounding the mouths of the burrows of both sexes of this species should not be confused with the walls built by U. stenodactyla females, or with the shelters constructed by the males of U. terpsichores, U. latimanus and U. beebei. The above four species are found at Panama and have been fully discussed by Crane (1941). As in the case of the walls and shelters just mentioned, the rims surrounding the mouths of the burrows of U. chlorophthalmus seem to play a minor rôle in the courtship behaviour of this species. In captivity, the U. chlorophthalmus individuals made burrows rather similar to those of U. annulipes, but they were not as deep nor as well-made as those of the latter species. The best of their burrows were dug in soil which was moist, but not too wet.

U. chlorophthalmus burrow.



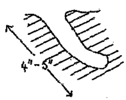
U. marionis. Burrows belonging to this species were examined in an area towards the middle of Region C of the Saco Swamp. They were found to be usually about four to five inches deep and to slope very obliquely. They are situated in very wet mud and are always full of water. Very often, the opening of the burrow is below the water-surface of pools, which abound in this area. Individuals in captivity made burrows fairly similar to those found in the field, although their shape was rather more vague, being merely irregular hollows, generally filled with water.

U. marionis burrow.



U. urvillei. Burrows of this species were investigated chiefly at the Saco Swamp, and were found to resemble those of U. marionis, except that they slant more steeply. It is of importance to note that such burrows are found in very soft ground and are often filled with water. In captivity, U. urvillei preferred fairly wet mud, and the larger individuals lived in rather indefinite hollows, which did not really resemble burrows. The smaller crabs made definite burrows, which were nevertheless rather irregular in shape.

U. urvillei burrow.



On comparing the above descriptions with those of Verwey (1930), Pearse (1912), and Crane(1941), it is evident that the general shape of Uca burrows does not appear to vary much from place to place. All Uca burrows, it would seem, consist of a long and rather sloping vertical channel which terminates in a shorter, blind tunnel where the crab resides. Crane's general statement that Uca individuals, living on yielding mud, build shallower burrows than those which live on harder ground, appears to hold good for the Inhaca species. It is of interest to note that Verwey found that all the Batavian species which he investigated, have their burrows going down as far as lowtide level, irrespective of the zone in which they occur. These burrows vary in depth from 0.5m. to 1m..

Uca crabs usually remain comparatively close to their burrows while feeding. Among the U. annulipes crabs at Inhaca, however, an odd individual here and there appeared to have difficulty in finding, or possibly, in recognising its own hole. This was especially noticeable in densely populated areas (such as the northern end of Region C of the Saco Swamp), and when the tide was coming in rapidly. At such times, these crabs scurry about in search of their holes, often disappearing down one already occupied, and emerging rapidly again. On several occasions the northern end of Region C was observed carefully, just as the tide was coming in. The U. annulipes crabs dominate this area and were observed to continue feeding busily and near to their holes until the advancing water had reached within a foot of their individual burrows. Each crab then rapidly sought the entrance to his burrow and soon disappeared from view, having usually plugged his hole behind him with one deft movement. To plug the hole, the male crab of U. annulipes generally uses the ambulatories on the side of the minor cheliped, ain [illegible] side with the major cheliped usually enters the burrow first. The female uses the ambulatories on either side for this purpose. The ambulatories on the side opposite to that entering the burrow collect together a heap of food-pellets and shovel them into the hole in the wake of the crab. This loose mass of pellets forms the plug, which is usually very light and is situated some distance down from the top of the burrow.

As the incoming tide steadily covers the Uca burrows, some air-bubbles appear on the water-surface, the bubbles rising from the burrows a few seconds after the water has covered them. This is because it takes some time for the water to reach the bottom of the burrows, whether these possess plugs or not. As the plugs are soft, they offer little or no resistance to the advancing water. They may be merely to show that the burrow concerned is already occupied, or as Verwey (1930) suggests, they may be a means of protection from enemies coming in from the sea.

As the emerging crab leaves his burrow, he pushes the plug before him. During his feeding-period he runs in and out of his burrow for any of several reasons, and on such occasions, he does not insert a plug.

Crabs were frequently observed in the act of digging new burrows, and in several of the habitats it was noted that, situated near some of the burrows, were mounds of relatively large sandballs, which were obviously the result of earlier digging. At the southern end of the South Swamp, many of these burrows were small ones, occupied by young individuals of U. annulipes, and interspersed with these burrows were those of another crab.

A male Uca individual which is seeking a burrow often probes down the entrance of a burrow with his straightened major cheliped. If he finds the burrow already occupied by another crab, he emerges hastily or a fight may ensue. If, however, the burrow is unoccupied, the crab may be seen to tidy it up before occupying it. He climbs down into the burrow and removes the surplus sand with the ambulatories on the side opposite to that emerging first from the hole and, possibly, with the minor cheliped. He makes several journeys to remove all the excess sand which he deposits generally in one spot, in the form of large sandballs, a short distance away from the mouth of the burrow. If the burrow is too narrow for a male crab, he may widen it by entering on the side of his major claw, re-emerging almost immediately, a performance which he repeats several times until he is able to enter or leave the burrow without being in any way hindered. Individuals of both sexes and of all the species may be seen, from time to time, "tidying up" their burrows, widening them or even re-aligning them.

(2) Submersion of the Burrows.

In the discussion of the periodicity of feeding of the various species of Uca, the periods of submersion of the burrow were also indicated. It is evident that, because of the differences in their habitat, the species differ considerably in the length of the period during which the crabs have to remain in their burrows. On the average, the two species, U. marionis and U. urvillei, appear to be the least resistant to desiccation. It is seldom that U. marionis burrows are not flooded semi-diurnally, and, in any case, their burrows never appear to be empty of water. Also, the burrows of U. urvillei are frequently filled with water, even at the outlying borders of their habitat, in the black mud inside the tree-fringe. U. chlorophthalmus must be more resistant to desiccation, because, in certain of their habitats, the burrows may not be submerged for periods of up to a week at a stretch, during periods of very low neap tides. On the other hand, the habitat of this species is more shaded and consists of a darker, wetter mud which retains water for longer periods, although, between tides, no water is found collected at the bottom of their burrows. In spite of the fact that U. inversa lives on open flats which are periodically dried out during periods of neap tide, the burrows of this species are fairly deep and the sand at the bottom nearly saturated with water. At the end of a period of neap tides, however, when there has been no arrival of fresh hightide water for over a week, these crabs must reach the limit of their ability to resist drying out. U. annulipes seems to be the species which is best adapted to a variety of conditions of moistness. Some U. annulipes populations have their burrows regularly submerged semi-diurnally, others only during periods of spring tide which occur twice monthly, while yet other populations seem to survive in localities which would seem to be flooded, at the most, only during one short period per month. Like U. chlorophthalmus, no water is found at the foot of their burrows, between tides.

Uca crabs have gills, and are true water-breathing animals. They have been described by Verwey (1930) as non-pumpers, which circulate air through the water in the branchial chamber. Each crab has special respiratory organs on either side of the body, between the third and fourth pair of ambulatories and, through these organs, water is absorbed into the branchial chamber. A comparative study was made of the general gill-structure of all the Inhaca species, and it was found that in U. chlorophthalmus, U. marionis and U. urvillei, the gills are all of the same width. In U. annulipes and U. inversa, on the other hand, the second gill from the anterior end on either side of the body, is much wider than the rest, in this way providing a greater surface-area for respiration, so that more efficient use can be made of the oxygen dissolved in the water in the branchial chamber.

The individuals of all the species held in captivity appeared to be very active generally, following a submersion of the mud in their tanks with water of 0.6% salinity. So a submersion took place once a week and, after it, individuals of all the species could be seen busily repairing or "tidying up" their burrows. The most active was definitely U. inversa, and the individuals of this species especially were seen to be digging new burrows.

BEHAVIOUR.

The general habits and patterns of behaviour of the Uca crabs of Inhaca Island were observed, and are discussed below.

(1) CLEANING.

Uca crabs, on emerging from their burrows, usually clean themselves before starting to feed, especially if their burrows happen to be situated in wet mud. The crabs may alternate feeding with cleaning - a task which they seem to perform very thoroughly. The male generally makes use of the minor cheliped to scrape mud off his major cheliped, his ambulatories, and his eye-stalks, etc., a process which he repeats several times in order to remove every trace of dirt from these organs. The female uses both her chelipeds for cleaning. The small cheliped of U. inversa, in male or female, is again a far more efficient cleaning-organ than that of any other species except, perhaps, U. marionis. In order to scrape the major cheliped clean, the U. inversa male opens the nipper of his minor cheliped to the very fullest extent, as he does when he scrapes sand-particles from the ground during feeding. In this species, too, the small cheliped is frequently used to pick particles of sand off the major cheliped especially, and these particles are often simply transferred to the mouth. In all the species, the small cheliped in particular is used to scrape mud off the eye-stalks, which are either held upright or are made to lie horizontally in their orbital grooves. However, especially in U. inversa, a crab may use his third pair of maxillipeds for cleaning the

54/...

eye-stalks, in which case the latter are always made to lie in their orbital grooves. The third maxillipeds are bent outwards and then inwards again over the eye-stalks several times in succession, so scraping off all the sand-particles, and passing them into the mouth. After this procedure, or between two such bouts of cleaning, the eye-stalks resume their normal, upright position. The set of ambulatories on either side of the body may sometimes be rubbed together to remove any mud collected between them, a process which is frequently aided by drops of water secreted from the branchial chamber through the respiratory openings on either side of the body. In order to clean the mouthparts, water oozes out through the mouth, so giving the impression that the crab is blowing bubbles. In captivity, the crabs were particularly active following their weekly submersion in saline water. They would stand half-immersed in the water, sometimes with only their eye-stalks visible above the surface, cleaning and blowing bubbles busily.

(2) RECOGNITION.

(a) Visual. Uca crabs are able to detect movements of any kind provided that such a movement takes place within their own particular range of vision. Such an individual appears to respond very quickly should an aggressive member of its own species or of another Uca species approach it suddenly. Moreover, the individuals scurry rapidly into their burrows at the sudden approach of an intruder on their territory, with the result that a human observer must be prepared to remain quite motionless, if he wishes to see a Uca crab at close range. Thus these crabs can usually see the approach of a preying bird or any other enemy in time to jump to one side or even to hurry into their burrows, out of harm's way. Frequently, such a response would seem to be due to the fact that the individuals detect the moving shadows cast by a preying bird, for example, rather than the bird itself, for, at certain times of the day, when such a bird is not throwing a direct shadow on the ground occupied by the crabs, less response was noticed.

The effect of moving shadows on Uca crabs was particularly well illustrated towards the middle of one rather windy day spent at the Mainland Swamp. Very few Uca crabs were visible on the open patch to one side of the pathway where, a few days previously, there had been quite a number of U. annulipes and U. chlorophthalmus individuals and a few U. urvillei individuals in evidence. A strong wind was blowing steadily, and the trees skirting the area were restless. The shadows of the leaves kept moving on the ground, and the crabs appeared to be "terrified" at these sudden movements, scampering rapidly back into their burrows each time they emerged. As a result of this repeated disturbance, very few crabs were venturing forth on that particular morning.

Uca males appear to have no difficulty at all in recognising fellow-members, and females in particular, of their own species. It is of interest to note, however, that the females of most of the Uca species at Inhaca have no distinguishing colours. The different species, however, generally possess their own specific habitats, and so there is little chance of the males becoming confused as to which females belong to their own species. Towards the northern end of Region B, where U. annulipes and U. chlorophthalmus occur together in the same habitat, the females of the two species are often very similar in appearance and yet the males never appeared to show any interest in the females of the other species.

(b) Auditory. There is no evidence that the Inhaca species of Uca crab are able to hear. Certainly, these crabs never appear to be in any way disturbed by human voices. When the incoming tide reaches within a foot of U. annulipes individuals, they rapidly enter their burrows, and repeated observations point to the conclusion that the crabs probably see rather than hear the approaching water. They seem thus to respond to a visual stimulus rather than to an auditory one.

(3) TIMIDITY.

The five species of Uca appear to differ in their degree of timidity. Although Barnard (1950) refers to U. marionis as the most timid species, these crabs do not scuttle away to disappear down the nearest burrow when disturbed, as individuals of the other species do. This fact may be due to their very wet muddy habitat which does not permit of easy movement. When the observer approaches such an individual, it simply sinks down, digging itself into the watery mud where it is not easily detected because of its tarnish colour. It was noticed, however, that during the breeding-season, when the breeding population had moved to an area of drier mud higher upshore, the individuals moved about far more quickly than usual and, when disturbed either by a human observer or by a threatening crab, they rushed down their burrows or, at least, ran out of harm's way. When individuals of U. urvillei are disturbed they do not scurry about much either, probably because their habitat is similar to that of U. marionis. Thus both U. marionis and U. urvillei illustrate how the habitat of a species may affect its behaviour. It was observed that, in certain areas where the U. urvillei males were apparently able to sight one another amongst the Avicennia roots, from as much as three to four yards away, they appeared to make every effort to dodge away and so avoid coming into contact and possibly having to fight with one another. The individuals of U. inversa are very shy and timid. This may be due to the fact that the species occupies such very open flats. Crabs of this species do not allow an observer to get within 15 yards of them, before disappearing down their burrows. It may be noted that, on the open flat of Region A of the Saco Swamp, even U. annulipes individuals seem more timid than in their adjacent habitat on the pathway; naturally, on the flat, the distant approach of an intruder is more easily detected. If a male U. inversa is forcibly removed from its burrow, or if the observer comes between him and his burrow, some interesting features of his defence-behaviour may be observed. In order to defend himself from a human intruder only, the crab stretches his major cheliped upwards, holding it straight, stiff and high above his head in a very characteristic manner. The claw is held slightly open, and the crab backs away steadily as the observer approaches. This defence-posture is rather similar to that discussed by Pearse (1912) for U. pugnax. If one should manage to grab hold of the crab by his major cheliped, one finds that he immediately sheds it and scampers off. In no other species do the male crabs hold their major cheliped as straight, when called upon to defend themselves from human observers, and in no other species do the males shed their major cheliped as readily. In captivity U. inversa individuals never brandish their major cheliped, when threatened by an observer. Instead, such an individual generally runs into a corner of the tank where he holds his cheliped bent and with the claw unopened, in a rather cowering manner, as if he were warding off an attack. On the whole, however, U. inversa, which is probably the most shy species in the field, is certainly the boldest in captivity as far as its attitude towards human observers is concerned. The other species take cover in their holes much sooner than do the U. inversa individuals.

The degree of timidity of Uca seems to vary according to the locality and the time of day. (a) Locality:- The best example of this is furnished by U. annulipes which, in any case, is the boldest of the Inhaca species in the field. The tamest members of this species live actually on the main pathway running through the Saco Swamp, especially towards the northern end of Region B. On this path there is a continuous stream of traffic to which apparently the crabs have become accustomed. Even those individuals which are found in Region A, just north of the open flat and alongside the pathway, are much less timid than those living on the flat itself. The individuals of U. chlorophthalmus living near the main pathway of the Saco are the least timid.

(b) The time of day:- Individuals of all the species are the least timid towards the middle of the day when it is hottest, a habit which was especially noticeable in U. chlorophthalmus.

Generally speaking, when one comes across a mass of Uca individuals at any moment during the feeding-period, one notices more males than females. The excess of males may be due to the fact that the females, using both chelipeds for the purpose, probably feed at a faster rate than do the males, who use only one cheliped. The females are thus able to return to their burrows all the sooner. An alternative is that female Uca crabs are possibly more timid than the males, thus spending more time hiding down their burrows. The exception to the general rule is U. chlorophthalmus, in which species the number of males seen feeding at any time does not appear to exceed the number of females. It should also be noted that, on one occasion, in their main habitat at about mid-day, more U. marionis females than males were in evidence.

(4) FIGHTING.

Fighting between Uca individuals was noticed amongst all five of the Inhaca species, particularly during their individual courtship and breeding-periods. Since the different Uca species generally have their own specific habitats, intraspecific fighting was naturally seen more frequently than fighting between individuals of different species. Fighting in these crabs generally centres around the ownership of burrows, but a certain amount of aggressive rivalry over females exists amongst male crabs. Generally speaking, the male individual uses almost the same movement of the huge claw of his major cheliped, whether he is warding off some other male from his territory or courting a female crab, and, as a rule, the greater the size of the major cheliped of the individual in relation to the rest of the body, the greater is the degree of authority which the crab has in his immediate surroundings. Moreover, male crabs which are large in all respects, command a great deal of respect from their smaller fellows.

The territory or feeding-area of each individual is limited, and the crabs do not appear to move very far from their burrows while feeding. Each crab seems to make his burrow the centre from which all his activities are conducted, and he may retreat into his burrow from time to time. The individual often keeps those ambulatories on the side of his body, opposite to that of the major cheliped, firmly anchored in the entrance to the burrow, whilst feeding. Male crabs, in particular, defend their burrows staunchly against intruders, treating the approach of any strange crab as an unfriendly act. Every time an intruder threatens to encroach on his territory, the defending male will warn off the stranger by brandishing his claw aloft, just as in courtship-display. Verwey (1930) maintains that the claw-beckoning action of the male crab is possibly to warn other individuals that he is the owner of a particular burrow. Should the threat-display fail, the crab may use his claw as a weapon, and actual fighting will ensue. On the other hand, should the threat be effective, the threatened male scurries off the territory of the agressive crab. Tinbergen (1951) feels that fighting in animals usually consists of threatening or bluff, but Crane (1941) found that, in the Uca species of Panama, threat-display only very rarely preceded a duel. In the Inhaca species certainly, however, such threatening movements were far more noticeable than actual combat.

U. annulipes. During threat-display, a male U. annulipes individual "beckons" with his major cheliped in a highly characteristic manner, a movement which is regular and continuous, and which is repeated several times in quick succession. The movement starts with the claw of the major cheliped pointing slightly forward, and the ambulatories slightly bent as usual. The cheliped is straightened and moved outwards, then raised upwards until the claw is held high above the individual. At the same time, the crab stretches his ambulatories until he is standing on their very tips, and, occasionally, should the state of tension between two threatening males be sufficiently great, the crab may raise his small cheliped simultaneously with the major cheliped, and possibly one or two ambulatories may be raised momentarily from the ground. As the major cheliped drops once again into its normal position, the ambulatories are bent, and the small cheliped is lowered.

Now and again, actual combat follows unsuccessful threatening behaviour. The fighting males jostle one another, knocking their bent major chelipeds together with a clicking sound. The major cheliped may be held at almost right-angles to the body, acting as both shield and weapon, and, unless the fight stops in the incipient stages, the crabs eventually grip one another firmly by the claws, in a manner reminiscent of a human handshake. The pair then lunge backward and forward, the weaker crab sometimes being lifted right off the ground, until the stronger individual has asserted himself. Only then is the strong grip finally released, and the two combatants separate, the victor taking possession of the burrow, while the beaten male scampers off. Fighting may be resumed after a brief pause, but, generally, one bout is sufficient to settle the matter once and for all, and both crabs eventually resume their feeding normally, some distance from one another. A claw was never seen to be broken off during fighting, and it did not appear to make much difference whether the major cheliped was on the right or on the left side of the body --- a fight between a "left-handed" and a "right-handed" crab could take place as easily as one between two "right-handed" crabs. When a "left-handed" male fought with a "right-handed" male, however, the usual "handshake" - method could not be adopted, but the combatants were nevertheless able to grasp one another's claws quite strongly.

The females of U. annulipes show very little aggressive behaviour, but appear to be rather timid creatures, scampering off down their holes whenever a male crab approaches them and only occasionally struggling with members of their own sex, in minor skirmishes, over the ownership of burrows.

In U. annulipes, fights involving three individuals occur very occasionally. Usually such fights involve three males, but three females have, on rare occasions, been seen engaged in such a combat. It is of interest to note that the three fight one another as individuals, for they never seem to team up at all. Such fights are invariably over the ownership of burrows.

<u>U. inversa</u>. The burrows of this species are rather widely - spaced, with the result that fighting over the ownership of territories is unnecessary and, therefore, relatively rare. The individuals themselves are rather lethargic in their general behaviour, but a certain amount of aggressiveness was noticed, especially amongst the male individuals. Their aggressiveness was seen to consist largely of threat-gestures and to be chiefly concerned with the protection of their burrows. Any individual, whether male or female, venturing too near the burrow of a male crab is chased away immediately.

Generally speaking, an individual chases off his opponent in a rather jerky fashion - that is, both crabs run a short distance, pausing momentarily, from time to time, quite simultaneously, before resuming the chase. In U. inversa, more than in any other Uca species, there is a marked difference in the behaviour of an attacking male as compared with that of a defending crab. The former runs on the very tips of his straightened ambulatories and has a rather stiff, tense appearance, while the latter scurries off with his ambulatories bent as usual. The greater the tension between the two crabs, the stiffer the appearance of the attacking individual. The weaker crab usually fends off his attacker by holding his major cheliped defensively before him. In such a case, the major claw is held bent and in the normal plane, but pointing slightly forward or even at right-angles to the body, depending on the position of the weaker crab in relation to the attacker. This defence-posture is rather different from that shown by a U. inversa male defending himself from a human observer, as has been described under "Timidity". Since there is no question of over-population on the feeding-grounds of U. inversa, however, attempts actively to steal burrows from their owners take place comparatively rarely. Here and there, a pair of males were noticed, standing a few inches away from one another, very tense and, perhaps, with the claws of their major chelipeds held open. One or other or both crabs would suddenly break the tension by moving off, whereupon both combatants would scurry away from one another hurriedly, often entering their burrows. Because of the low population density, a pair of rival males would occasionally appear to sight one another over a distance of more than a yard and they would rush at one another, with the claws of their major chelipeds held open. Such a male would even try to nip the ambulatories of his opponent, making use of the claw of his

63/...

major cheliped for this purpose.

Very occasionally, a definite threat-display movement was detected amongst certain U. inversa males, particularly amongst the individuals defending burrows. Such a male may move slightly sideways or remain in one spot while displaying, but he does not jump about as much as U. annulipes males do, and his movements are less jerky, with long pauses in between. Such an individual holds the claw of his major cheliped slightly raised but bent and in the normal plane, and he moves it outwards and in again. This movement, which is repeated several times with pauses in between, is fairly fast, but, generally speaking, it gives the impression of being rather lethargic. Sometimes, the small cheliped may also be lifted slightly when the major cheliped is raised.

Female U. inversa individuals are fairly aggressive towards each other and may be seen to rush at one another with both their small claws slightly raised. Very rarely, females defending burrows were seen to show a very definite threatening-gesture which was directed only at other females. Such a threat-gesture was seen only at moments when a female appeared to be very tense, due to the fact that a neighbouring female was approaching too near her burrow. The threatening female would raise both her claws and then move them outwards and in again, usually simultaneously. The movement was fairly fast and was repeated a few times before pausing.

In U. inversa, the individuals seldom come to grips with one another, but generally such fights as were witnessed appeared to be of low intensity and of short duration, usually lasting for only moments at a time. As was the case for U. annulipes, a major cheliped or claw was never seen to be broken off during such a fight, in spite of the fact that U. inversa tends to shed its somewhat muscular major cheliped far more readily than any other species when caught by a human observer. Fighting males, however, grip claws in a special way, different from the usual "handshake" - method as already described for U. annulipes. Instead of this, the fighting U. inversa individuals generally have their claws loosely interlocked, with the tips poking into the ground. This weakened grip possibly accounts for the fact that the crabs do not lose their claws during fighting.

U. chlorophthalmus. Threat-display in this species, while essentially similar to that of U. annulipes, nevertheless consists of faster, more jerky movements which tend to be less clearly defined than those of the latter species. The major cheliped is held slightly slantwise across the body so that the claw points over the opposite "shoulder", and it is moved away from and then in towards the crab again. This movement is highly characteristic and is repeated several times before pausing. The method of fighting in U. chlorophthalmus is also very like that of U. annulipes, with the combatants again gripping claws as in a human handshake. Like U. annulipes, too, fights involving three individuals take place from time to time.

The females of U. chlorophthalmus, like those of U. inversa, tend to be remarkably aggressive, devoting their pugnacity to keeping other individuals away from their burrows. Such a female lunges sideways at any trespasser, so chasing the latter off her territory, and she is just as aggressive whether the intruder happens to be another female or even a male, while being particularly aggressive towards individuals smaller than herself.

U. marionis. During periods in both February and April-May 1955, when the breeding-season of this species was at its height, individuals in nuptial dress were observed in their special breeding-ground about 200 yards south in Region C of the Saco Swamp. Only breeding individuals occupied this breeding-ground in the drier mud nearer the trees, and they had moved up-shore from the usual wet and exposed seaward part of the beach, which represents the feeding-ground of U. marionis in this particular locality. In the breeding-ground, each male and female individual appeared to have its own particular burrow, and most of the crabs were out of their holes and running about busily, often very far from their burrows. Very little feeding was noticed, since the crabs were devoting most of their time to mating. The individuals were courting busily, and a great deal of fighting was taking place, sometimes for no apparent reason. There was, however, terrific rivalry over females amongst the male individuals, who gave the impression of being particularly tense and pugnacious, and who were repeatedly seen to be actively chasing trespassers, of both sexes, off their territories. One such male, for example, was seen to rush at a female which had inadvertently come too close to his burrow. She was unable to escape fast enough, and he ran up behind her, passing his bent major cheliped forward suddenly and so banging her across the back of her carapace with his claw.

During February threat-display was more noticeable than during April-May. Since the claw of this species is rather cumbersome, the movement involved in threat is rather slow, and it is also used when a male is attempting to attract a female's attention. A threatening male crab moves his major cheliped away from him, then raises it fairly high above his head, while keeping the claw itself closed. At the same time, he lifts himself on to the very tips of his straightened ambulatories and raises his minor cheliped slightly. Occasionally, at this point, he runs a few paces either to his left or to his right, still with the ambulatories straightened, although this moving about is generally confined only to those occasions when the male concerned is displaying before a female individual. The male crab stands in one spot while bringing his major cheliped down quickly into its natural position. At the same time, he lowers his minor cheliped and bends his ambulatories, so that his normal stance is once more adopted. After a brief pause, the movement is repeated. In May, the crabs appeared to spend less time threatening one another and more time in actual combat. Should a male be unable to chase his opponent away, the two come to grips almost immediately, and with the claws of their respective major chelipeds held wide open, they grip each other in the usual "handshake" - method. Their claws click together, as was noticed especially for U. annulipes. When the grip is particularly strong, however, a characteristic grinding noise can be heard, due to the two claws being harshly rubbed together. A pair of combatants with locked claws often shake each other violently, and each appears to be actually "trying" to throw his opponent off. Such a hold generally lasts for a few seconds, after which the two crabs scamper away from one another hurriedly. Threatened males and females were seen to hold up their small chelipeds fairly high, particularly while being chased away. In this species, especially, male crabs with undamaged chelipeds were seen to bully crippled crabs considerably, a habit already discussed by Crane (1941) for her species at Panama. For example, a certain male had lost the claw of his major cheliped. He was continually being pestered by fellow-males who interrupted their threat-display or courting behaviour to chase him back into his burrow whenever he ventured forth. None of the crabs tried to follow him down his burrow or plug his hole behind him - a fact which was noticed also by Crane - but they continued to intimidate him throughout the period of observation. On the other hand, however, another male crab, with a badly damaged claw on his major cheliped, was seen to be more than holding his own amongst his fellows. This was probably due to the fact that he was an unnaturally large crab, but he certainly never entered his burrow for any length of time during the observation period. He spent his time displaying frantically and incessantly, and he kept chasing neighbouring males into their burrows. He spent very little time feeding, and he appeared to be the superior crab in his immediate vicinity. This male, however, was definitely an exception.

In the breeding-ground, females of this species also appeared to be very tense in their behaviour, and were fairly aggressive towards one another. They had no threat-display as described for U. inversa, but they were continuously chasing one another away from the vicinity of their burrows.

The normal, wet, exposed feeding-grounds of U. marionis are situated low down on the beach, and the population density is not as great as in their breeding-grounds. Fighting and claw-waving are therefore reduced to a minimum, for the crabs are sluggish in their behaviour and seldom come into any contact with one another. Instead, they are very lethargic and spend their time feeding or merely sitting in their burrows immersed in water.

U. urvillei. In particular, a small population of this species living in the shade of some Avicennia trees, 200 yards south in Region C of the Saco Swamp, was observed in both February and April-May of 1955. Both males and females were feeding quietly and were far less tense in their behaviour than the neighbouring U. marionis individuals, in spite of the fact that it was also the breeding-season of U. urvillei. The crabs appeared to be very lethargic and were slow to emerge from their burrows. The females were not particularly aggressive towards one another, and no males were ever seen engaged in actual combat. In spite of the fact that they never appeared to come to grips, however, the males seemed to be definitely very wary of one another and kept dodging behind the Avicennia roots in order to avoid meeting one another. A threat-display was occasionally noticed amongst the males, however, and the same movement was once again used also for courtship-display. Although the displaying individual does not raise himself on to the tips of his ambulatories, or jump about, or raise his minor cheliped as in other species, such a male does, however, make use of his major cheliped as usual, and he moves it in a straight line, forward slightly and then back towards himself again, in a slow and rather leisurely movement, which is repeated only a few times at one spell. As in U. marionis, threatened males and females hold up their small chelipeds, particularly when they are backing, or running away from an attacker.

In localities where the feeding-grounds of the Uca species overlap one another to a greater or lesser extent, a certain amount of interspecific hostility is noticed, although male individuals of different species seldom come to grips with one another. This interspecific aggressiveness serves one purpose only, to safeguard the territory and burrow of each individual, not only from individuals of the same species, but also from individuals belonging to neighbouring species. For example, the males and even the females of U. chlorophthalmus at the northern end of Region B of the Saco Swamp, are particularly aggressive in their attitude towards the U. annulipes individuals, which are definitely smaller and whose burrows lie scattered amongst those of their own. A U. chlorophthalmus individual is frequently seen lunging sideways at any U. annulipes individual venturing, generally inadvertently, too near his burrow, in this way chasing the trespasser off his territory. Even the U. annulipes males appear to be intimidated by the U. chlorophthalmus females and still more so by the males of this species, and they were frequently seen to rush into their burrows in order to escape these individuals. A further example is that of the U. inversa males and females, on the open flat of Region A of the Saco Swamp, which bully the smaller U. annulipes individuals in their midst whenever the latter come too close to them and their burrows. Male and female individuals of U. marionis and U. urvillei, to a lesser extent, also tend to bully the smaller U. annulipes individuals living amongst them, a fact which was especially noticeable 200 yards south in Region C of the Saco Swamp. In the breeding-ground of U. marionis, a male was actually seen to lock the claw of his major cheliped with that of a U. annulipes individual. After a very brief struggle, he threw the U. annulipes off, so that the latter was thrown a few inches away, landing on his back. For the most part, however, the U. marionis and certainly the U. urvillei male individuals did not attempt to come to grips with the relatively much smaller U. annulipes males. They simply chased both male and female U. annulipes crabs away from the vicinity of their burrows. Also at 200 yards south in Region C of the Saco Swamp, a limited amount of aggressiveness was noticed on the part of U. urvillei individuals towards individuals of U. chlorophthalmus. This particular case of interspecific rivalry was not nearly as noticeable as any of the other cases mentioned, for the U. urvillei individuals are not very pugnacious. Nevertheless, one U. urvillei female, especially, appeared to have a particular enemy in the form of a U. chlorophthalmus female, who was naturally slightly smaller than herself, and whose burrow lay alongside that of her own. In spite of the slight difference in size between the two, neither appeared to be superior to the other, and every time the two emerged from their burrows, they would lunge sideways at one another, each crab trying to chase the other back into its burrow. It is interesting to note that,