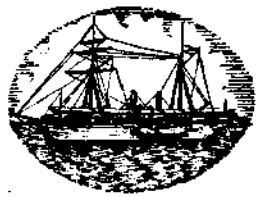
SYMPOSIUM ON CRUSTACEA

PART III



MARINE BIOLOGICAL ASSOCIATION OF INDIA

MARINE FISHERIES P.O., MANDAPAM CAMP

INDIA

PROCEEDINGS

OF THE

SYMPOSIUM ON CRUSTACEA

HELD AT

ERNAKULAM

FROM JANUARY 12 TO 15..1965

PART III

SYMPOSIUM SERIES 2

MARINE BIOLOGICAL ASSOCIATION OF INDIA

MARINE FISHERIES P.O., MANDAPAM CAMP

INDIA

FIELD INVESTIGATIONS ON THE SHORE CRABS OF THE GULF OF MANNAR AND PALK BAY, WITH SPECIAL REFERENCE TO THE ECOLOGY AND BEHAVIOUR OF THE PELLET CRAB *SCOPIMERA PROXIMA* KEMP[1]

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ABSTRACT

In the course of carrying out observations on the ecology and behaviour of shore crabs of Palk Bay and Gulf of Mannar in 1959–60, special attention was given by us for studying the burrowing habits, sexual dimorphism, mating behaviour, etc., of the pellet crab *Scopimera proxima* Kemp details of which are embodied in this paper.

INTRODUCTION

THERE is a paucity of information on the habits and behaviour of shore crabs from the Indian Region. Some observations in earlier literature may be found in the works of Henderson (1893), Anderson (1894), Alcock (1900, 1902), Kemp (1915, 1919) and Sewell (1922). Recently in a series of papers, Altevogt (1955 *a* & *b*, 1956, 1957 *a*, 1957*b*, 1957 *c* and 1959) has given accounts on the ecology, biology and ethology of shore crabs, especially of fiddler crabs of the genus *Uca* Leach [*U. annulipes* (H. Mlne-Edwards), *U. marionis marionis* (Desmarest), *U. m. nitidus* (Dana), and *U. triangularis* (A. M. Edwards) and the closely related genus *Dotilla* Stimpson [*D. blandfordi* Alcock and *D. myctiroides* (H. Milne-Edwards)] from India. On account of this want of information, we were prompted to make some observations during our spare time. In view of the short period during which the observations could be made, the study is incomplete in several aspects.

Our observations were restricted to the period from early September to the end of December 1959 in the areas close to Mandapam Camp and Rameswaram Island when field investigations were conducted both during daytime as well as at night. Special observations were made on the ecology and behaviour of the pellet crab *Scopimera proxima* Kemp in relation to other shore crabs in the eco-system.

Frequent field trips were made to the following three selected areas (as indicated in Fig. 1):

Area I. Beach west of C.M.F.R.I. Jetty, Mandapam Camp (Gulf of Mannar).

Area II. Between Pamban and Kundugal Point, Rameswaram Island (Gulf of Mannar).

Area III. Beach adjacent to C.M.F.R.I. Field Laboratory (Palk Bay).

It was observed that *S. proxima* is restricted to certain types of sandy beaches and in such areas they show a definite zonation in the intertidal region. Collection of an allied species, *S. pilula* Kemp indicated that both these species do not co-exist in the same area as they show preference to certain types of soil and also differ in habits.

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Distribution of Shore Crabs in Relation to the Tide

A list of the shore crabs encountered in the areas of study is given below:

Species	Area-I	Area-II	Area-III
Family Ocypodidae			
Ocypode ceratophthalma (Pallas)	X	X	X
Ocypode cordimana Desmarest	X	..	X
Ocypode macrocera H. Milne-Edwards	X	..	X
Ocypode platytarsis H. Milne-Edwards	X	..	..
Scopimera proxima Kemp	X	..	X
Scopimera pilula Kemp	..	X	..
Uca annulipes (H. Milne-Edwards)[1]	..	X	..
Dotilla myctiroides (H. Milne-Edwards)	X	X	X
Macrophthalmus depressus Ruppell[2]	..	X	..
Family Grapsidae[3]			
Metapograpsus thukuar (Owen)[4]	..	X	..

[1] An allied species *U. marionis* as well as the variety *U. m. nitidus* have been recorded by Gravely (1927) from Area-II.

[2] *M. telescopicus* and *M. convexus kempi* have also been reported from Area-II by Gravely (1927).

[3] *Grapsus albolineatus* and *Plagusia depressa* var. *tuberculata* found habitually on the granite blocks of the pier close to Area-I are not included in the present study.

[4] *Metapograpsus frontalis* found among dead coral blocks in the intertidal zone in the vicinity of Area-III is also not included in this account.

The species mentioned as occurring under the three areas in the above list are primarily specific to the particular areas. However, a species such as *O. platytarsis* could occur in Area-III though we have not collected it from there. On the other hand a species such as *Macrophthalmus depressus* will not normally occur in areas I and III.

Areas I and III are sandy beaches, while area II is typically marshy, a considerable part of which is exposed during low tide and the soil shows gradations from clayey to sandy condition.

The general distribution of the shore crabs in the three areas in relation to low and high water marks is shown in Figs. 2, 3 and 4. In area-I, the beach has a gentle slope between low and high water-marks, but rises more sharply above the latter, and about 4–6 meters of beach is exposed during low tide. Ocypodids were found inhabiting the area above the high water-mark but the burrows of these crabs found closer to the HWM are smaller in size inhabited by smaller crabs. *S. proxima* shows a distinct zonation immediately below the HWM. *D. myctiroides* was rare, but invariably was found to occur very close to LWM.

Area-II is located between Kundugal Point and Pamban covering a shallow bay which is mainly a mudflat with hardly any sandy beach. This area is submerged under water during high tide and during low tide a considerable part is left exposed. Our observations were restricted to

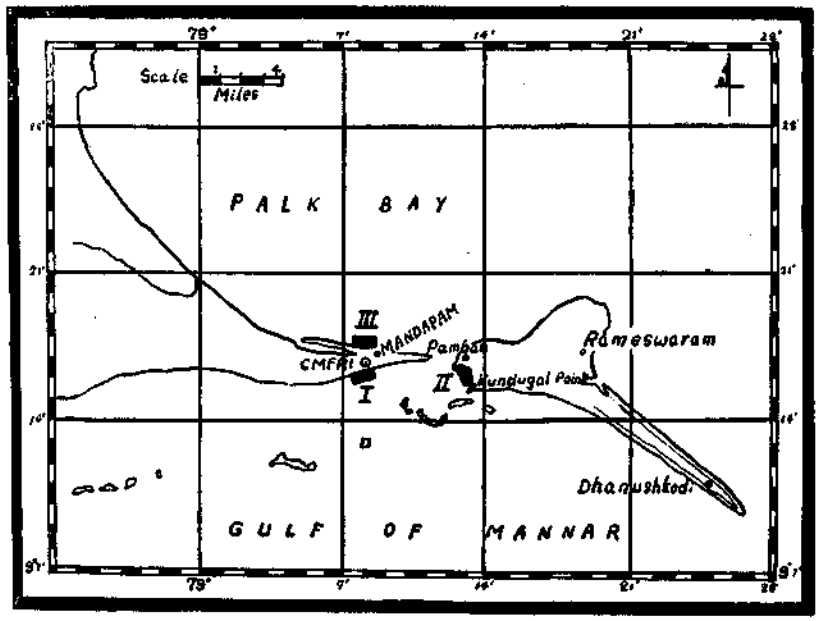


FIG. 1. Map showing Areas-I, II and III from where observations were conducted and collections made.

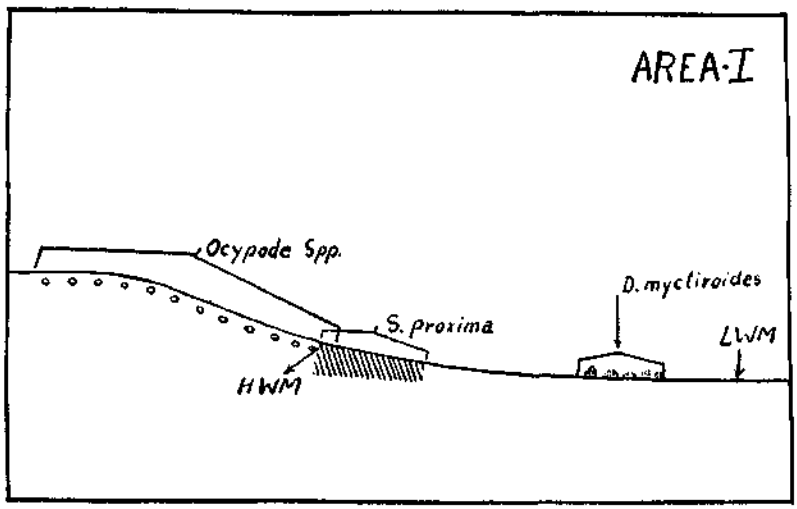


FIG. 2. Schematic section of Area-I showing zonation of shore crabs.

the area between HWM and LWM, in which was also present a dense congregation of gastropods (*Potamidis, Cerethium,* etc.) in a distinct zone just above LWM. The mudflat below LWM during low tide may have large puddles of water and only *Macrophthalmus depressus* was seen occurring. Inclusive of the gastropod zone above the LWM, about 9–10 meters of beach is generally exposed in this area. The areas above the gastropod zone to the HWM is ploughed up in large patches

here, as a result of the burrowing and feeding of the crabs. *U. annulipes*, *S. pilula* and *D. myctiroides* occur in this zone of which the last-mentioned species was always present close to the gastropod zone which is nearest the LWM. At the time of our observation quantities of sea-weeds were washed up in patches along the intertidal zone which areas were not generally found to be occupied by the crabs. Fig. 3 shows the details of occurrence.

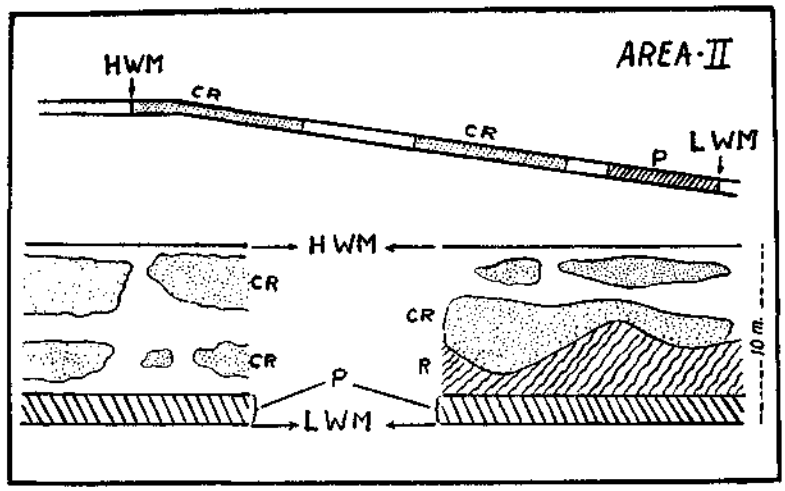


FIG. 3. Schematic section of Area-II showing zonation of shore crabs. (CR—areas 'ploughed' by crabs; P—'gastropod zone' of chiefly *Cerethium* and *Potamidis*; R—washed up sea weeds; HWM—high water mark; LWM—low water mark).

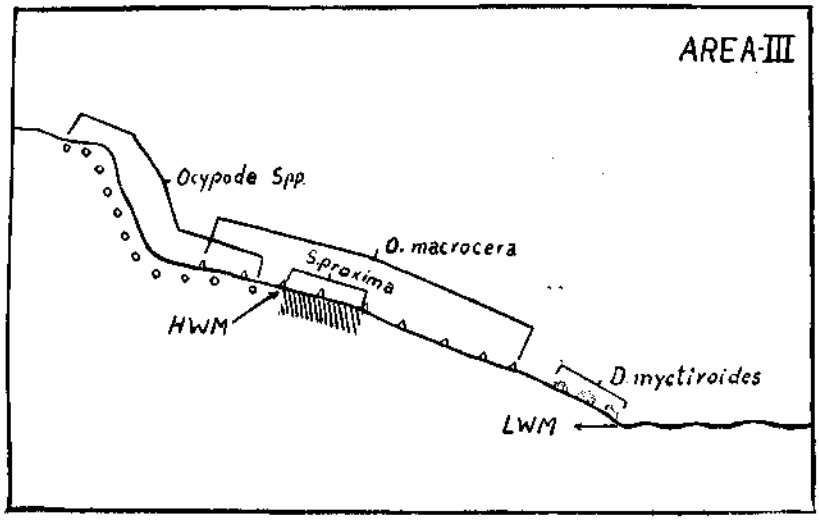


FIG. 4. Schematic section of Area-III showing zonation of shore crabs.

Area-III (Fig. 4) resembles Area-I except that the beach slopes steeply as a result of which the intertidal zone is narrower. Another notable difference is the occurrence of *O. macrocera* in larger numbers even extending to well below the HWM where they are generally found making mudballs, etc.

Occurrence of Species of *Scopimera* in Relation to Tide

It was observed that generally *Scopimera proxima* has its burrows closer to the HWM than to the LWM. Sample counts were made as the one given below to find out the frequency of occurrence of burrows at different levels in the inter-tidal zone. For instance in Area-I two test plots 4 meters square were chosen at random as soon as the tide had receded. The exposed intertidal zone at the time was 4 meters wide in this area. Each plot was further subdivided into two as shown in Fig. 5 and observations were made at intervals between 10·30 and 14·00 hours on

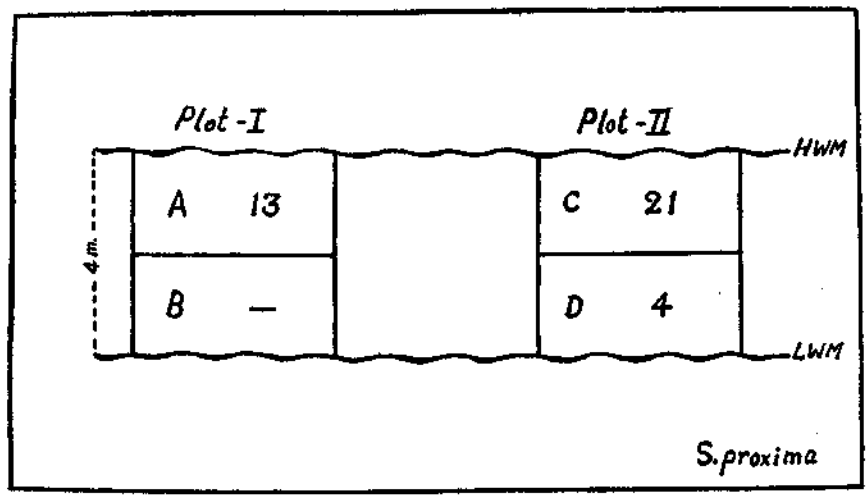


Fig. 5. Test plots in Area-I indicating occurrence of burrows of *Scopimera proxima* more towards HWM than LWM.

11–9–1959. The total number of burrows in the different squares are given in the figure and the frequency of the appearance of the burrows were as follows:

Plot numbers				Time (hr.)
I			II	
A	...	C	..	10·30
B	—	D	...	10·30
A	1	C	14	11·45
B	—	D	1	11·45
A	4	C	17	12·25
B	...	D	4	12·25
A	13	C	21	14·00
B	...	D	Burrows plugged	14·00

By about 14·00 hours the rising tide had caused the crabs in square C of plot II to plug their burrow entrances and a similar action by the crabs of squares A and C of plots I and II was noticed as the water approached the HWM by about 14·00 hours. These observations lead us to deduce that:

1. *S. proxima* has its burrows in a definite zone having a width of about 1·5 meters from HWM. This may also depend on the slope of the beach as the zone occupied by the crabs will be relatively narrow when the slope is greater (as in Area-III) or extended when the slope is very gentle.

2. The surface activity of the crab is restricted to a period of about 3 to 4 hours from the time of setting in of low tide to high tide.

3. The feeding habits appear to influence the zonation in this species.

In the case of *S. pilula* occurring in Area-II a difference was noticed in the zonation as well as the frequency of occurrence in relation to HWM and LWM. Briefly stated this is as follows: The species occupies a fairly wide zone between HWM and LWM separated from the latter only by the gastropod zone. Within this area of occurrence, it was found to be more abundant closer to the LWM as shown in Fig. 6.

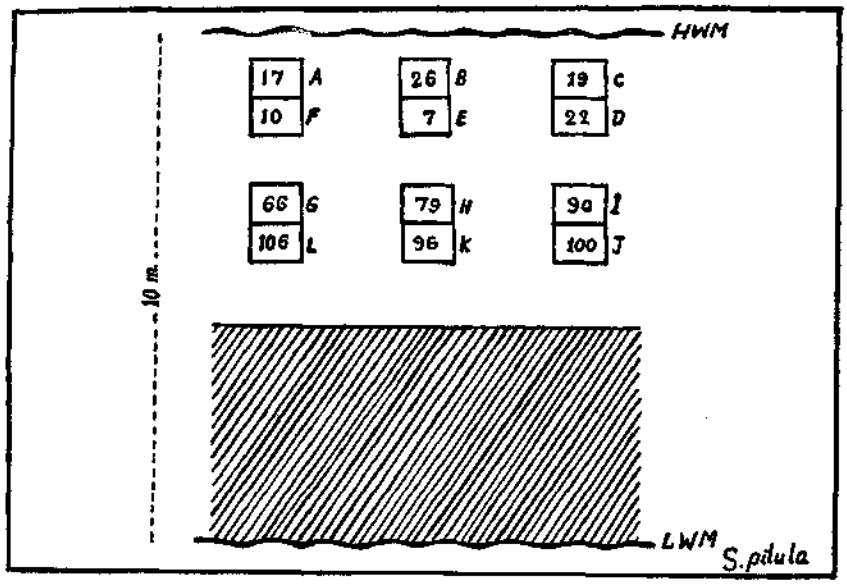


FIG. 6. Test plots in Area-II indicating occurrence of burrows of *Scopimera pilula* in relation to HWM and LWM. Area shown in hatching indicates 'Gastropod zone'.

BURROWING HABITS OF SHORE CRABS

Scopimera proxima.—Adult crabs were not generally found to wander about at the surface seeking new locations for burrowing, the exception being males seeking females. Within a short time after the water recedes, openings of burrows were seen with one or two pellets outside the entrance. Vertical sectioning of such burrows indicated their extension to even 100 mm. suggesting that the burrows were not freshly made. Normally the burrows have a 'neck' about one-fourth their length followed by a slightly wider 'chamber' where the crab rests. This is followed by a narrow tube going vertically downwards. The burrows do not have secondary escape routes (Fig. 7).

When settling on the beach, very small crabs occupied areas in the *S. proxima* 'zone' nearer to LWM. This would mean that there may be a certain amount of shifting of burrow sites with growth, the larger crabs occurring closer to HWM.

Scopimera pilula.—The burrow in this species is slightly different from that of *S. proxima*, being deeper, having a longer chamber and not generally vertically descending downwards below the level of the chamber. A typical burrow of 180 mm. shows the following dimensions: Length of 'neck' 55 mm.; diameter of surface opening 7·0 mm.; diameter at base of 'neck' 10 mm.; length of 'chamber' 50 mm.; diameter at widest part of chamber 18 mm.; diameter at base of 'chamber' 12 mm.; length of tube below 'chamber' 75 mm. No lining was noticed in any part of the burrow (Fig. 7).

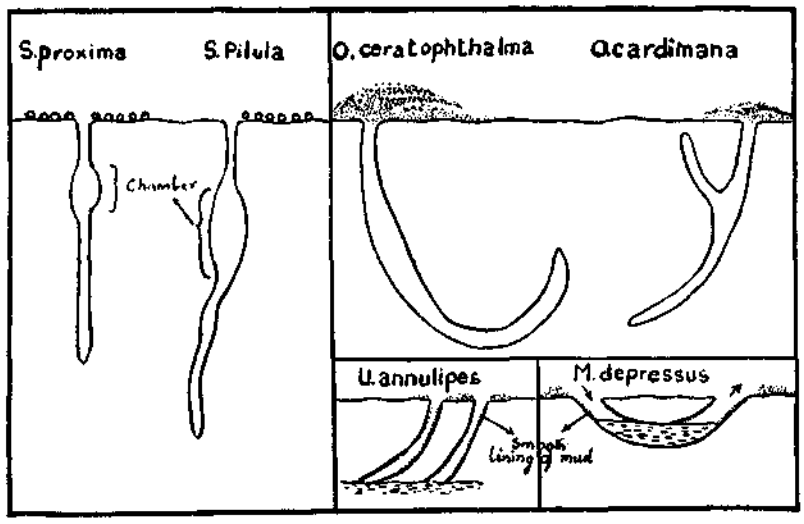


FIG. 7. Typical burrows of shore crabs in the areas investigated.

Uca annulipes.—The burrow typically descends almost vertically for about one-third its length and then slants and goes obliquely downwards to the level of the water. The burrow wall is lined by a thin layer of clay (Fig. 7).

Macrophthalmus depressus.—In the mudflats in Area-II large burrows, each with also an exit opening of the same size as the inward opening were seen, and this species was found to inhabit such burrows. The shallow loop of the burrow is always found to have water in it and the walls of the burrow above this (inward and outward routes) are lined with mud (Fig. 7).

Ocypode ceratophthalma.—The burrow is deep often exceeding a depth of even a meter from the surface, as the burrows of the larger crabs are situated further away from HWM. The burrow usually descends vertically for some distance and then runs obliquely downwards. In one case a slight U-shaped bend was noticed at the lower end but there are no indications of secondary escape routes. The burrow opens out at an angle, and will have heaps of sand at the entrance dug up and brought from below in addition to the wet sand brought up as mud balls and discarded away from the entrance in one direction.

Ocypode cordimana(?).—The burrow of this species (?) has a striking resemblance to that of *O. arenaria* described by Cowles (1908), as shown in Fig. 7. The notable feature is that the burrow has a secondary escape route reaching to below the surface giving the burrow a Y-shaped appearance.

Closing of burrows.—As the tide comes up towards the HWM many of the burrows were found to have large wet pellets or mudballs covering the entrances. This was specially noticeable in the burrows of larger crabs and occurring progressively from LWM to HWM in relation to the

incoming water. A typical instance of plugging of the entrance of the burrow by *Scopimera proxima* was observed as follows: In a burrow about 0·75 m. away from water, we noticed a crab come out and move about the entrance and cover a distance of about 5 cm. from the entrance and on the way making about four or five pellets. Just as it was making a fresh pellet, a wave brought the water to about 10 cm. from the entrance of the burrow, and immediately the crab scampered to the burrow drawing behind it a few pellets which were close to the entrance with its right walking legs, the pellets rolling into the entrance of the burrow at the same time, and thus effectively plugging the opening. The action of drawng in the pellets by the crab was intentional, and not accidental, and the movement was such that the pellets did not roll in one after the other which would have only resulted in their falling straight into the burrow.

Temperature inside the burrows.—In Area-II temperature inside the burrows of *S. pilula* at 5 cm. below surface at 10·40 hours (on 9–9–1959) was found to be 28·5° C. while the sea-water temperature (Surface) opposite the burrows had risen to 33·0° C. [The shallowness of the water beyond the LWM (about 0·5 m.) is responsible for the higher water temperature].

The temperature recorded at 09·00 hours in Area-I from a burrow 5 m. away from LWM (of *Ocypode* sp.) was 28° C. at a depth of 220 mm. from the surface and 30·5° C. at a depth of 50 mm. below surface. At this time the surface sea-water temperature was 28·5° C.

In the same area on 11–9–1959 temperature readings were taken between 08·00 and 10·45 hours in burrows of ocypodids at 10 cm. below surface, and these are given below:

Diameter of burrow (mm.)	Temperature at 10 cm. depth °C.	Time hr.
15	30·5	09·45
20	29·5	09·50
20	29·5	10·00
10	29·25	10·00
15	30·0	10·05
9	30·0	10·05

The surface water temperature beyond LWM at 10·45 hours was 29° C.

On the same day, in one burrow 15 mm. in diameter, the temperature at 09·50 and 10·55 hours were 30·5° C. and 31·0° C. respectively when the surface water temperatures were 29·0° C. and 29·5° C. In view of the fact that burrows of ocypodids were very deep and not vertical it was not possible to take the temperatures at greater depths.

Observations made at night.—Observations were made at various times during the night to note the habits of the shore crabs, especially *Scopimera proxima*. Species of *Ocypode* were found invariably to be active foraging on the beach, especially during the earlier part of the night. The burrows of *S. proxima* were found with the entrances plugged with pellets and the crabs not seen at the surface. This inactivity of the crab at the surface was noticed at night when the level of water was far away from the HWM. However, the species was seen to be active as early as 05·00 hours in the morning. It was not possible to see the conditions in Area-II during night time.

Reactions of *Scopimera proxima* Towards External Disturbances

1. In Area-I large quantities of sea grass (*Cymodocea* sp.) are generally washed ashore and in the afternoon and evening when there is a steady sea to land breeze, bits of grass are blown over the sand. We found that when this happened for the first few times *S. proxima* scuttled into the burrow when the weeds were blown close to it or over the burrow. However, watching individuals for some time, we noticed that the crabs once they were used to the weeds being carried by the wind did not run into their burrows when disturbed thus. However, if they were working in one of the paths, they showed momentary alertness when a bit of the grass or weed was blown closeby. When there were very strong breeze, especially in the evenings, very few crabs were seen to come out of the burrows to make pellets. So also when there were heavy downpours of rain, the crabs were not seen outside and the pellets disintegrate and after the rains the crabs are active.

2. The crab was not seen to evince any reaction when sunlight was reflected with a mirror when it was normally working in a path.

3. We tried to see whether the crab would show any reaction to its image reflected from a mirror placed close to its burrow. The animal working on a path parallel to the mirror was not seen to show any reactions to the image as well as to its own movements reflected by the mirror.

4. In order to see whether the crab reacted to sound or vibrations, an alarm clock was set repeatedly at various distances from 15 cm. from the burrow to 200 cm. from the burrow, and also placed in a pit below the surface about 20 cm. away from the burrow when the crab was normally working in a path. Prior to this the crab's activities of visiting the burrow was watched for some time and the alarm was adjusted when the crab visited the burrow and set to go off when it was on a path. No reactions were noticed.

These experiments carried out in the field are of a very preliminary nature and could not be repeated several times to arrive at conclusive results.

Natural Enemies of *Scopimera proxima* and Other Shore Crabs

Altevogt (1959) records three birds as the natural enemies of the fiddler crabs at Bombay, namely the Indian house crow *Corvus splendens*, the paddybird *Ardeola grayii* and the whimbrel *Numenius phaeopus*. The following birds were found to be common on the mudflats and shores in Area-II: the curlew *Numenius arquata orientalis*, the spotted sandpiper *Tringa glareola*, the redshank *Tringa totanus*, the common sandpiper *Actitis hypoleucos*, the little ringed plover *Charadrius dubius*, the paddybird *Ardiola grayii* and the little egret *Egretta garzetta*. All these birds except the first mentioned have been seen to chase and peck at objects in the ploughed up areas in the intertidal zone where more than one species of crab occurs. It is likely that some were at least feeding on crabs. The spotted sandpiper and the common sandpiper were most commonly seen in Areas-I and II. Solitary individuals of both these species are found moving about in the intertidal zone and the beach above HWM and they were found to be active even at night. Only once did we find chelipeds of male fiddler crabs in a spot where a little egret was seen chasing and pecking at objects in the 'ploughed' intertidal zone in Area-II which indicated that the bird had been preying on these crabs.

On Pellet making by *Scopimera proxima*

Observation was made from the time the crabs started coming to the surface for feeding to find out the quantity of sand worked into pellets. The crab scrapes the sand at the surface with its chelae and brings it to the mouth where the specialized setae of the second maxilliped may help it to sort out the interstitial fauna and reject the sand which appears as a wet ball (covered copi-

TABLE I

Table showing details of size of crabs, pellets, etc., of Scopimera proxima*

No. of crabs in burrow	..	1	1	1	1	1	1	1	1
Sex	..	..	M	M	..	..	M	F	F
Length of carapace	..	3·8	2·9	3·2	..	..	2·8	4·0	3·7
Width of carapace	..	5·9	4·5	5·0	..	..	4·6	5·5	5·8
Diameter of burrow at surface	..	5·3	5·0	5·0	5·8	4·7	..	5·0	5·0
Depth of burrow	..	60	..	..	..	..	100	160	124
Number of paths	..	3	5	6	8	4	4	2	1
Combined length of paths	..	180	320	410	730	510	228	90	100
Wet weight of 10 pellets (gm.)	..	..	0·170	0·220	0·200	0·191	0·095	0·320	0·270
Wet weight of 20 pellets (gm.)	..	..	0·353	0·408	0·390	0·365	0·195	0·658	0·490
Total wet weight of all pellets	..	..	8·688	17·030	14·425	22·645	9·107	25·150	5·190
Dry weight of all pellets	..	..	8·390	16·450	14·215	22·495	8·975	..	4·980
Diameter of largest pellet	..	3·0	3·0	3·2	2·9	2·7	2·4	4·0	3·0
Diameter of smallest pellet	..	2·4	2·7	3·00	2·7	2·5	1·9	3·5	2·7
Duration taken for making total No. of pellets (minutes)	..	..	250	255	265	255	270	200	65

* All measurements in millimeters and weights in grams.

ously with water). On completion of the pellet the water is 'sucked' in and the pellet is knocked off by a sharp movement of the right chela. The information given in Table I would give some idea of the activity of the crab. To this may also be added the following data on the number of pellets made by adults during specified time intervals (Table II). This was found to vary from

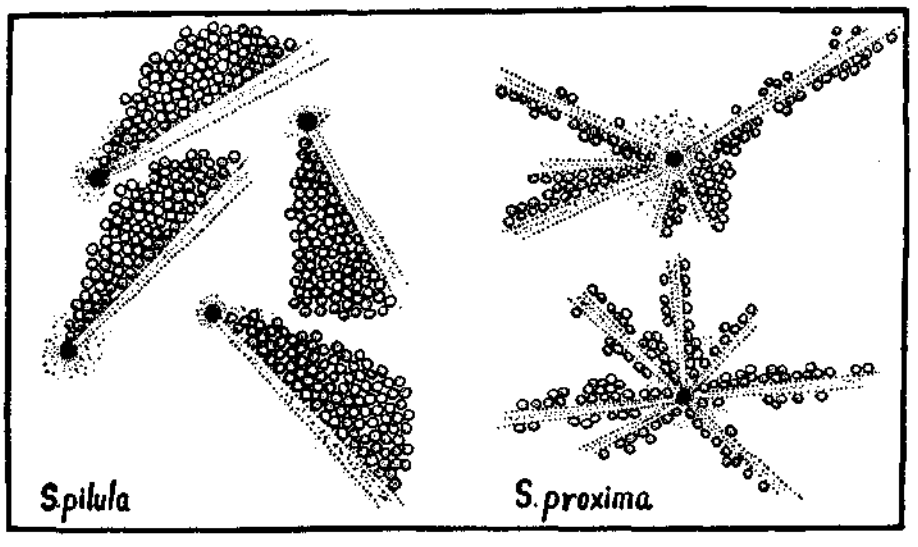


FIG. 8, Pattern of paths and arrangement of pellets in two species of *Scopimera*, *S. proxima*, and *S. pilula*.

specimen to specimen depending also on the size of the crab, the visits it made to the burrow, the periods it remained quite at the burrow entrance, etc. It was not possible to record and time all these activities for correlation with the number of pellets made.

TABLE II

No.	Time (hr.)	No. of pellets	L/W of carapace of crab (mm.)	Weight of crab (gm.)	No. of paths	Length of each path *plus* total length of paths
1	10·50	38	2·9/4·5	0·021	1	70 mm.
	12·45	230			4	45, 40, 90, 40 = 215
	14·30	494			5	50, 50, 90, 50, 80 = 320
2	10·52	81	3·2/5·0	0·023	2	25, 40 = 65
	12·45	(Disturbed			2	90, 40 = 130
	14·35	783			6	90, 70, 60, 110, 40, 40 = 410
3	10·55	37	Crab not collected	..	1	65
	12·50	350			3	111, 120, 30 = 261
	14·45	759			8	120, 120, 100, 80, 40, 100, 110, 60 = 730
4	11·22	47	..	..	1	22
	14·50	*ab*1,500			4	80, 110, 100, 120 = 410
5	11·30	208	2·8/4·6	0·020	1	60
	14·45	997			4	70, 50, 50, 58 = 228
6	11·34	13	..	..	..	..
	12·40	322	..	..	4	40, 40, 70, 80=230
7	11·35	14	4·0/5·5	0·025	..	..
	12·30	206			2	40, 50 = 90
	14·20	785				(Paths not distinct)

The above observations were taken on 11–9–1959 from Area-I. The average time taken for making a pellet was found to be 4 seconds. The longest single path measured at any time was 410 mm. and at this burrow there was only one additional short path of 40 mm. However, the average lengths of path was found to be about 75 mm. The width of the path depended on the size of the crab, being as wide as the carapace *cum* the space covered by the walking legs.

The pellets made by the same individual were found to vary slightly in diameter even in the fresh condition. Desiccation of pellets exposed for longer periods may also result in very slight changes in the diameter. During the period when mating was noticed, it was found that the males (generally smaller) working in the same paths as the female (generally larger) made smaller pellets.

In the case of *S. pilula* which is a larger species being about double the size of a normal adult *S. proxima*, the pellet size was also consequently larger. The average diameter of the pellets for a crab with carapace length and width of 5·7 and 7·0 mm. respectively was 6·5 mm. This species also differs from *S. proxima* in the habit of working the path as well as the disposition of the pellets which are cast off. Typically it has only a short broad path and the pellets are cast off on one side, so much so the pellets appear to be arranged in a triangular area with the path bordering one side. In addition to the path, which on account of the size of the species is broader and slightly deeper, often the space covered by the discarded pellets was also seen to be scraped. This species has a

tendency to wander even beyond the path, but when disturbed scuttles back along the path to the burrow. Figure 8 shows schematic drawings of the types of paths made by these two species and the arrangement of pellets. The second maxillipeds and the spatulate setae help in pellet making. The spatulate setae (Fig. 9) are relatively longer and well developed in *S. pilula*, apparently as the surface sand grains in areas inhabited by this species are much finer than that seen in areas where *S. proxima* abounds. Typical sizes of the surface sand grains seen from pellets made by the two species are shown in Fig. 10.

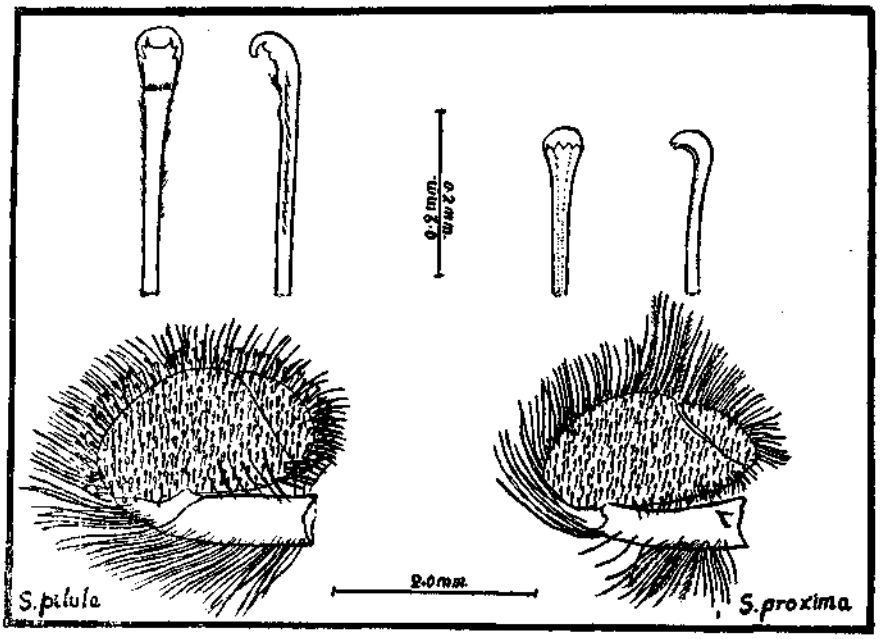


FIG. 9. Second maxilliped and spatulate setae (spoon-shaped) in *S. pilula* and *S. proxima*, of carapace size L/W 4·7/6·0 mm. and 4·3/5·8 mm. respectively.

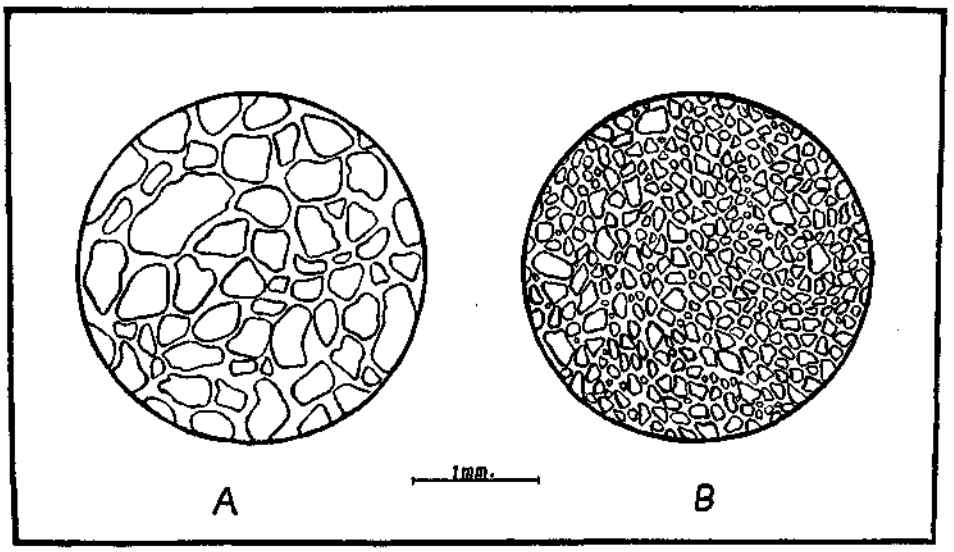


FIG. 10. Surface sand grains in Areas-I and II inhabited by (*A*) *S. proxima* and (*B*) *S. pilula* from pellets made by the two species.

MATING BEHAVIOUR OF *Scopimera proxima*

Information pertaining to direct observation on mating of shore crabs from the Indian Region is very meagre, practically nothing has been known but for the observations of Altevogt (1955, 1959) on the fiddler crabs of the genus *Uca* (*U. annulipes, U. marionis* and *U. triangularis*). Altevogt (1959) remarks that "···nobody has so far seen any copulation in the Indian species, the total number of fiddler copulation seen in the field amounting to a meagre five witnessed in the Americas by Miss J. Crane (1941–44)." We have been able to make some observations on the mating behaviour and copulation in *Scopimera proxima* on a few occasions between 19–9–1959 and 4–10–1959. These have helped in elucidating some problems relating to: the mating duration including approaching and leaving; number of times copulation is effected by the male during each active phase in relation to the tide; actual duration of copulation; successful and unsuccessful copulations; intervals between copulations; wandering habits of male in seeking female; burrowing habits of male during this period, etc. The instances and the conditions observed are given below datewise. The various activities noted were recorded with a stopwatch, and notes taken in the field. These are given below.

1. *On* 11–9–1959 *at* 10·00 *hours in Area-I.*—For the first time we found two crabs entering into the same burrow. At the time it was not known that each burrow was occupied only by a single animal. Collections made between 11–9–1959 and 19–9–1959 confirmed this and indicated the possibility that the two crabs at one burrow may indicate that they were male and female.

2. *On* 19–9–1959 *at* 10·05 hours in *Area-I.*—Two crabs were found disappearing into one burrow. There were no burrows atleast for a distance of about 30 cm. from this. The smaller of the two crabs collected and identified as male and indicated here as A came out and remained outside the burrow in a path which had just been begun, while the larger crab identified as female and indicated here as B often came upto the burrow entrance, but at the slightest disturbance of our movement darted back into the burrow. On the path close to the entrance A remained unconcerned. After sometime B came just out of the burrow entrance with its right side foremost and its legs almost extending up to the legs of the right side of A. They were found to keep still in this position for 14 seconds after which A approached B which slightly withdrew to the entrance of the burrow until A moved directly opposite it and pressed against the flexed abdomen of the female and started copulation. B was found to take a stance slightly inclined over A. They remained in this position for exactly 1 m. 40 sec. after which with a quick backward movement they separated and both were active in a path, B making a few pellets. After 3 minutes B which was about 5 cm. away from A approached the latter. A became alert and immediately moved to the side of B and tried effecting copulation which lasted for only 4 seconds, the partners then separating. After an interval of about 3 minutes A was found trying to excavate a burrow itself 3 cm. away from burrow of B at the end of a short path made by the latter. For some reason or other it gave up its efforts after a few digging movements for a few seconds and moved to a spot 5 cm. from the burrow of B and started again to excavate its own burrow. In the meantime B was found to be normally active, entering its burrow and coming up at intervals to make pellets. At 10·12 hours B was seen to start a new path leading directly towards the new burrow of A where the latter was busy bringing up excavated sand, to the mouth of the burrow and had not started making its own path or pellets. At 10·15 hours B approached the entrance of A and when the latter went in followed it into the burrow, but immediately reappeared at the entrance. A also came out of the burrow and after a few moments made a quick sidewise movement with chelipeds extended towards B and tried effecting copulation which lasted for 4 seconds when a piece of wind blown sea grass disturbed them, separating the two, each darting back to its own burrow. After this B resumed pellet making and frequently entering its burrow, while A was busy excavating its own burrow. The pair was watched during the next 30 minutes, but did not come together.

A few points of interest are that before the first mating (unsuccessful) took place, A was not disturbed by slight external movements, but only two or three times when there was some marked movement in the surroundings by our shadow falling across the burrow entrance did it follow

B into the latters burrow. The surroundings of the entrance of the burrow of B did not have any loose sand in heaps as was seen in the case of the new burrows started by A. From this and other such observations it is deduced that the presence of such loose sand at the entrance of burrows may indicate that such burrows have been freshly dug from the surface and does not represent plugged old burrows from which the crabs have come out. It may also be stated that a few of the latter type of burrows had the pellets around the burrow entrance loosened by amphipods, giving the false appearance of fresh burrows made from the surface. But by experience these could be easily identified.

During mating, A was slightly supine and exhibited slight movement of both chelipeds, at the same time trying to right itself by its walking legs pressed against the sides of B. The latter remained passive except for some slight movement of the dactyli of the first walking leg of one side.

Some of the questions that come up are, whether the pair had copulated prior to 10·05 hours when they were first spotted by us; whether closely adjacent burrows of one larger than the other usually placed about 5 cm. apart are those of male and female; whether two sizes of pellets seen in the path of a burrow could have been made by the female as well as a visiting male, one of which may be a smaller animal and consequently make smaller pellets; and whether the occurrence of such mixed pellets could indicate easily the mating period of the crabs.

3. *On* 19-9-1959 *at* 11·22 hours *at Area-I.*—At 11·22 hours in a burrow with eight paths, the longest being 12 cm. a crab later found to be a female[5] and hence indicated here as B was found to be normally active. Approaching the burrow from about half a metre away was found a second crab caught and identified later as a male and indicated here as A. When A approached B along one of the paths, the latter darted into its burrow. Still on one of the paths about 10 cm. from the burrow entrance of B, the former showed markedly excited behaviour and rapidly approached the burrow resulting in the pushing in of a few pellets, which were in turn brought up to the surface by it. In the present case A was larger than B and this helped to keep track of the movements of both the specimens; the length and width of carapace of A and B being 4·7 and 6·0 and 4·3 and 5·8 mm. respectively.

Between 11·20 and 11·27 hours A came upto the surface of the burrow three times bringing up excavated sand, while B was never seen to come up. At 11·30 hours A once again came upto the burrow entrance bringing up some excavated sand and remained at the entrance for 12 seconds. Between 11·30 and 11·40 hours A made three more visits to the burrow entrance each time remaining for a few seconds shoveing a little bit of sand away from the entrance of the burrow. Between 11·35 and 11·40 hours A made frequent visits at almost regular intervals to the surface of the burrow each time again bringing up a little bit of sand and also smoothening the sides of the burrow entrance. The time it remained at the burrow entrance each time it came up during the last five minutes was noted to be roughly 5 seconds each, and equal time was spent by it inside the burrow. During all this time, B never came up to the surface. It is unlikely that copulation could have taken place inside the burrow in the 'chamber', as A was coming up and going down at such regular intervals. It is also not known whether this action on the part of the male was a type of sexual display in order to excite the female. Between 11·40 and 11·45 hours A made four quick visits to the burrow opening returning immediately (not staying each time for even 2 seconds at the entrance) as though beckoning B to come up to the surface. At 11·45 hours A came out of the burrow followed by B and for 14 seconds both animals were found exhibiting an offensive defensive display which made us wonder whether B was trying to drive away A or *vice versa* or whether they were of the same sex. After this display, which appeared to be more in the nature of a struggle, each holding the chela of the other the animals without loosing their holds moved a few millimeters to one side. In this position they remained without showing any movements for 40 seconds after which quickly closing up copulation was effected. This lasted for exactly 1 minute

[5] Secondary female.

and 42 seconds after which with a jerky movement both the animals separated, A working on the path and B remaining near the entrance of the burrow. After an interval of 45 seconds the animals once again effected copulation without any preliminaries and were together for exactly 3 minutes and 10 seconds. During the copulatory phase, twice the animals were observed to show slight side to side swaying movement and more often an attempt by A to press down on B. But for this movement, appendages (chelipeds and legs) showed no movements. Soon after this second copulation A moved to the end of the path about 10 cm. from the entrance of the burrow and after making three pellets was seen moving off and was captured ¾ meter away from the burrow of B. The latter was found to resume normal activity of making pellets and excavating the sand from the burrow. This specimen was also later caught and preserved, and it turned out to be a secondary female showing the narrow abdomen.

4. *On* 20–9–1959 *at* 11·09 *hours in Area*-I.—At 11·09 hours at one burrow with none others in the immediate vicinity a medium sized crab was seen outside the burrow entrance (later identified as male and indicated here as A) while a larger crab (female indicated here as B) was seen entering the burrow and coming out. Both crabs were moving the chelipeds and maxillipeds as during pellet making for seven seconds when A approached B which in turn darted into the burrow and emerged after 25 seconds. Soon A left the burrow of B and wandered to about 50 cm. away to another burrow and rolled a few pellets into this burrow from near the opening and waited a few moments. At 11·17 hours it moved on to another burrow nearby after taking a circuitous route. No crab was seen at the entrance of this third burrow to be visited by A. Entering a path, A went into the burrow and after a few seconds emerged followed by another crab which had been inside the burrow (female and designated here as C). A and C entered the burrow once again and immediately came out. A was completely out, while the left side of C was out, the legs almost touching A. For exactly 1 minute and 20 seconds they remained still in this position and then A made a slight movement with its first walking leg touching C which immediately darted into the burrow. Soon A and C changed positions, A going to the opposite side of the burrow and C coming up from the burrow to the position occupied previously by A. In this position they were for 20 seconds when both the animals come together and copulation was effected. When this lasted for 50 seconds, the animals got disturbed by outside movements. C was seen entering the burrow and coming out at regular intervals and each time it came up it was moving its chelipeds as though trying to clean them, probably rubbing off adhering sand. All this while A was seen to show no marked movements, but everytime part of the body of C showed outside the burrow entrance it became alert. At 11·20 hours soon after C disappeared into the burrow, A followed suit, but emerged 16 seconds later followed by C which seemed extremely agitated as it was darting in and out of the burrow at very short intervals. A again tried to approach C following it into the burrow but again came out after 15 seconds followed immediately by C. A was then seen touching the legs of C with the hind two dactyli and both animals remained still for 14 seconds, soon after which C again darted into the burrow. Every time C came up to the burrow entrance A made a slight movement towards it and at 11·27 hours copulation was effected without any further display or preliminaries. For the first 40 seconds both crabs were jogging for position holding on to each others chelae, C eventually occupying a slightly inclined position over A. After coming to this attitude both animals were completely still. After 4 minutes 45 seconds slight movements were noticed and then the animals were still and 6 minutes from the commencement of the copulation again slight movements were noticed the animals separating after 6 minutes and 35 seconds of being together. Soon after separating, C was poised threateningly over A and all of a sudden it resumed normal poise and activity of cleaning the chelipeds and making pellets. After a few moments A darted towards C which became alert and moved towards A which in turn ran 6 cm. away from C. Latter entered the burrow and A once again approached the burrow entrance, but when C appeared at the burrow entrance A left along one path and started digging about 10 cm. away from burrow of C. The characteristic sand mount appeared as the burrow was dug from the surface. The distance travelled by A from burrow of B–C was 630 cm. and enroute it passed close to three burrows which it did not visit, except at the first of these burrows it stopped at a path and moved two or three pellets with the chelipeds as though 'tasting' them. Enroute it also stopped at the side of small stones, shells and weeds for short periods. By 11·42 hours A had started making pellets having completed its burrow.

5. *On* 21-9-1959 *at* 10·00 *hours in Area-I.*—Photographs of male and female at burrrow prior to copulation and male digging burrow from surface were taken.

6. *On* 4-10-1959 *at* 10·00 *hours onwards in Area-*I.—A small crab (male indicated here as A) was seen clearing a path near burrow entrance littered with pellets. A left the burrow and travelled one metre reaching the burrow of another bigger crab (female indicated here as B) which was staying outside the burrow entrance. Without any preliminaries both the crabs were seen to copulate and the duration of the copulation was 5 minutes and 50 seconds. During this period, for the first 20 seconds both crabs were making adjusting movements, the walking legs of A pressing against the sides of B and during the next 20 seconds the crabs showed slight rocking movements from side to side. After 3 minutes and 15 seconds further side to side rocking movements were noticed for 15 seconds after which the crabs were still, and at 5 minutes 20 seconds both crabs showed slight movement of the legs, for 30 seconds when they separated. After this B entered the burrow twice and came up. A tried to dig its burrow about 3 cm. from burrow of B in the midst of pellets made by the latter. A was seen thrusting sand towards the burrow of B. Both assumed an aggressive stance with extended chelipeds for 3 seconds, the female as though guarding its burrow entrance. A made a detour to opposite side of burrow of B and approached the latter. No attempt was made to copulate and B was in a defensive attitude. A returned to the new burrow it had started and was found digging for 20 seconds and started making a path towards burrow of B. At least once A was seen to push some sand into the brurow of B. When B came out, A was alert at the burrow entrance while the former was trying to clear the entrance. B made a quick movement towards A, touching the latter's legs with its own on which A moved away from the burrow entrance and B returned to its own burrow. After a few seconds B was seen approaching the burrow of A while A was 2 cm. away from its burrow entrance. Both were making pellets and B was seen to raise and lower itself on its legs a few times. After a few moments B started making pellets close to the burrow of A and the latter moved away when B was seen deliberately to push some sand and roll one pellet into the burrow of A. Just then A made a quick movement towards B and the latter raised itself on its limbs with extended chelipeds in an offensive attitude; A also assuming a similar pose, both animals were seen trying to cling on to each other's chelipeds parting with a quick jerky movement after a few seconds. Thence B was seen to deliberately shove sand and pellets into the burrow of A completely covering up the burrow and was seen to walk and turn around the covered burrow. All this time A which was 5 cm. away, started moving away from the area while B was trying to readjust pellets in a new path.

At 10·52 hours A started digging a second burrow about 5 cm. from the burrow of B in another direction. B was seen coming as close as 3 cm. away from this and making pellets while A was actively digging the burrow. B approached A, but when disturbed darted into its own burrow, all the while A undisturbed was digging its burrow. B again approached A's burrow within 2 cm. This was at 10·54 hours. A had started to make its own path, with pellets. It is not known whether the deliberate closing of the partly made burrow of A by B represents territorial behaviour. At 10·59 hours A was busy with the digging of its burrow, while B was resting at the entrance of its burrow. No unusual behaviour was seen on the part of the animals.

At 11·00 hours B walked to about 2 cm. from burrow of A at the same time rolling a few pellets. A was seen going in and out of its new burrow removing sand. A also started making a path with pellets, leading towards B, meeting the path on which B was at one extreme. The movement of A resulted in the rolling of a few pellets on to the path made by B which made the latter to move with lightning speed to this point of intrusion, seeing which A returned (fled) to its burrow. This was noticed happening 5 times in five minutes. After this B started making another path from this point towards the burrow of A, which when reached, it again deliberately shoved some sand into the burrow. When disturbed by our shadow, B ran back to its burrow. At 11·08 hours A tried to roll pellets from the new path made. At 11·10 hours B again approached the burrow of A showing some sand in front at which A left its burrow and moved in an opposite direction for 5 cm. and made 4 pellets before moving on to path of B and approaching the latter tried effecting copulation lasting hardly 5 seconds when the animals separated with a jerkey movement. This was

caused by external disturbance. Both animals returned to their respective burrows, and again at 11·12 hours B was seen approaching the burrow of A and showing sand into it. A coming outside the burrow entrance assumed an offensive pose as B, but after a few seconds both animals returned to their respective burrows.

In summing up it may be stated that in *S. proxima*:

1. The courting males wander seeking the females, but were not seen to enter the burrows of other males.

2. The female, if outside the burrow, evinces little excitement on the approach of the male.

3. When the female is within the burrow, the male enters the burrow without any pause at the opening of the burrow. However, immediately it enters an active phase of ascending to the burrow opening and disappearing within, in quick succession, suggesting courting. The female follows the male to the burrow opening usually after several such 'passes'. While outside the burrow, during the phase of courtship, the male was not seen to nip, nibble or jab at the female with its chelae.

4. Mating took place outside the burrow, at the burrow entrance or in one of the 'paths'.

5. More than one successful mating by the same pair has been observed. At the same time, unsuccessful mating attempts have also been noted when the pairs came in close contact of each other, but one of the pair (male) left.

6. The duration of successful mating (copulation) varies, the maximum duration noted being 6 minutes and 35 seconds.

7. During one tidal phase, it was found that a single male in addition to successfully mating one or more times with a single female, also wandered entering the burrows of other females.

8. Aggressive behaviour of the female towards the male after successful mating was also observed. This was seen when the female deliberately plugged the freshly excavated burrow of the male with which it had mated.

9. Males of *S. proxima* are slightly smaller and lighter in colour than females (the width/length of carapace in the largest male and female seen being 6·1/4·6 mm. and 6·5/4·7 mm. respectively. However, such large specimens are rare). Apparently males predominate as out of 137 specimens collected from the burrows in Area-I, as many as 78 were males, 37 normal females and 12 'secondary' females. It is likely that the lighter body colour of males which merges with the colour of the sand and the higher male sex ratio may be adaptive features as during the breeding season the males wander about and may be subject to predation.

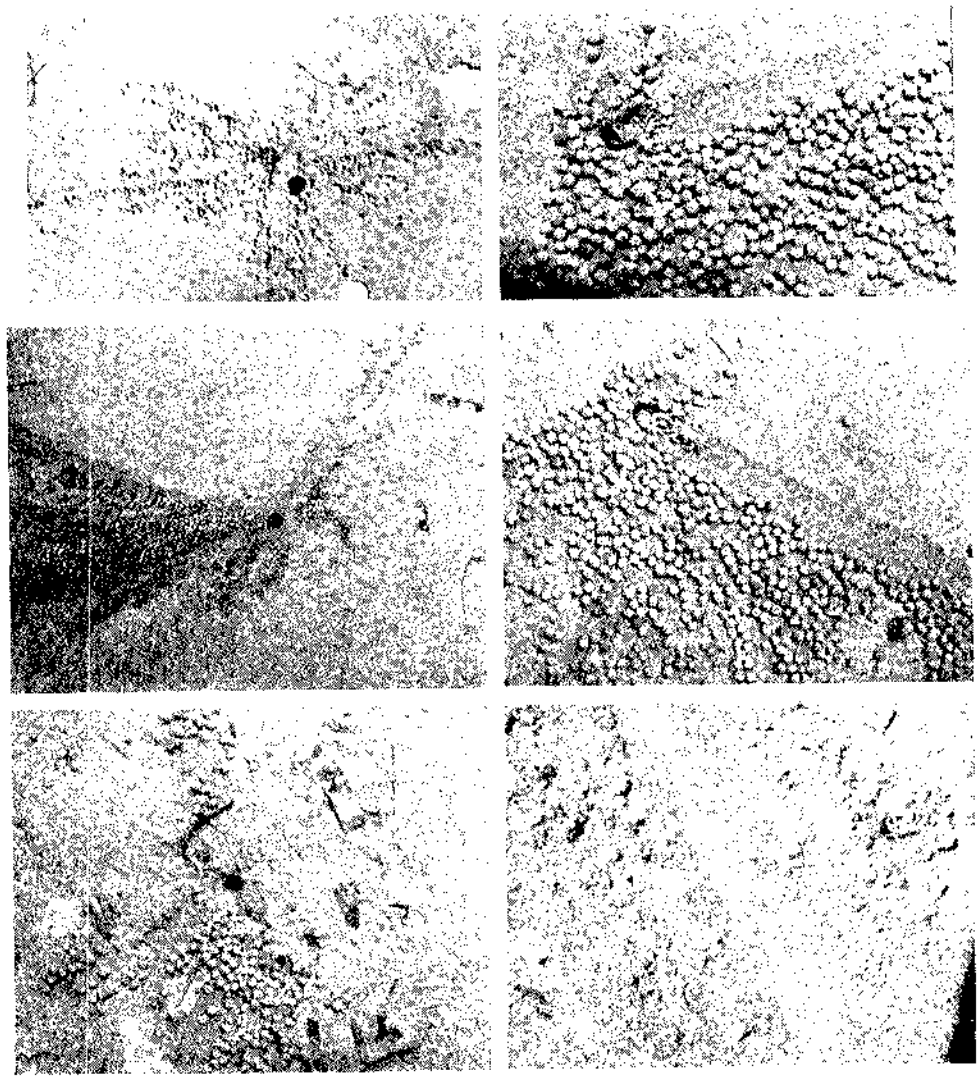
10. At least once a male was found to have a successful mating with a 'secondary' female. Egg bearing 'secondary' females with the characteristically narrow abdomen have also been collected. The presence of such females, first reported by Kemp (1919) in *S. proxima* has not been fully explained and calls for further investigation, as to: (*a*) the effect of parasites (not evident in our specimens); (*b*) whether they are abnormal and if so whether the abnormality is genetic; or (*c*) whether these females begin their development as males.

In conclusion we may say that the pellet crab *Scopimera proxima* is an extremely interesting animal for studies on behaviour.

References

Alcock, A. 1900. Material for a carcinological fauna of India. No. 6. The Brachyura, Catometopa, or Grapsoidea. *J. Asiatic Soc. Bengal*, **2**: *Nat. Sci.*, **69** (3): 272–456.

——— 1902. *A Naturalist in Indian Seas.* John Murray, London.



TOP LEFT AND MIDDLE LEFT: Patterns of paths and pellet arrangements in *Scopinera proxima*.
TOP RIGHT: Female *S. proxima* clearing burrow entrance.
MIDDLE RIGHT: Male and female of *S. proxima* at the same burrow.
BOTTOM LEFT: Male *S. proxima* just finishing making a pellet.
BOTTOM RIGHT: Male of *S. proxima* digging a burrow from surface, after mating with female in adjacent burrow.

ANDERSON, A. R. 1894. On the sound produced by Ocypoda ceratophthalmus. *J. Asiatic Soc. Bengal*, **63** (1): No. 2.

ALTEVOGT, R. 1955 *a*. Beobachtungen und Untersuchungen an indischen winkerkrabben. *Z. Morphol. u. Okol. Tiere*, **43**: 501–522.

———— 1955 *b*. Some studies on two species of Indian fiddler crabs, *Uca marionis nitidus* (Dana) and *Uca annulipes* (Latr.). *J. Bombay nat. Hist. Soc.*, **52**: 702–716.

———— 1956. Der Mechanismus der Nahrungsaufnahme bei winkerkrabben. *Naturw.*, **43**: 92–93.

———— 1957 *a*. Zur Biologie indidcher winkerkrabben. Hochschulfilm des Instituts fur den wissenschaftlichen Film, No. 756.

———— 1957 *b*. Untersuchungen zur Biologie, Okologie und Physiologie indischer Winkerkrabben. *Z. Morphol. u. Okol. Tiere*, **46**: 1–110.

———— 1957 *c*. Beitrage zur Biologie und Ethologie von *Dotilla blandfordi* Alcock und *Dotilla myctiroides* (Milne-Edwards) (Crustacea, Decapoda). *Ibid.*, **46**: 369–88.

————, 1959. The love and life of Fiddler crabs. *J. Bombay nat. Hist. Soc.*, **56**, (1): 1–7.

COWLES, R. P. 1908. Habits, Reaction and Associations of *Ocypode arenariu. Pap. Tortugas Lab. Carnegie Inst. Washington*, **2**, 1–41.

CRANE, J. 1941. Crabs of the genus *Uca* from the West coast of Central America. *Zoologica* (*N.Y.*), **26**: 145–207.

———— 1943. Display, Breeding and relationships of fiddler crabs (Brachyura, genus *Uca*) in the North Eastern United States. *Ibid.*, **28**: 217–223.

———— 1944. On the colour change of fiddler crabs (genus *Uca*) in the field. *Ibid.*, **29**: 161–68.

GRAVELY, F. H. 1927. Brachyura In *Fauna of Krusadi Island. Madras Govt. Mus. Bull.*, (*n.s.*), **1** (i): 135–155.

HENDERSON, J. R. 1893. A contribution to Indian Carcinology. *Trans. Linn. Soc. London, Zool.*, **5**: 325–458.

KEMP, S. 1915. Fauna of Chilka lake. Crustacea—Decapoda. *Mem. Indian Mus.*, **5**: 199–325.

————, 1919. Notes on Crustacea Decapoda in the Indian Museum-Scopimerinae. *Rec. Indian Mus.*, 17: 305–349.

SEWELL, R. B. S. 1922. A survey season in the Nicobar Islands in the R.I.M.S. '*Investigator*', October 1921 to March 1922. *J. Bombay nat. Hist. Soc.*, **28** (4): 971–989.