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OBSERVATIONS ON FIDDLER CRABS (OCYPODIDAE : GENUS *UCA*) ON SURIN ISLAND, WESTERN PENINSULAR THAILAND, WITH PARTICULAR REFERENCE TO *UCA TETRAGONON* (HERBST)

by

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OBSERVATIONS ON FIDDLER CRABS (OCYPODIDAE : GENUS *UCA*) ON SURIN ISLAND, WESTERN PENINSULAR THAILAND, WITH PARTICULAR REFERENCE TO *UCA TETRAGONON* (HERBST)

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CONTENTS

ABSTRACT

The fiddler crab populations of a mangrove forest and adjacent sand and mud flats were investigated at Koh Surin, a group of islands in the Andaman Sea off the west coast of Peninsular Thailand and just south of the Burmese border. The distribution, density and sympatry of the four species of fiddler crabs, *Uca dussumieri dussumieri*, *U. lactea annulipes*, *U. tetragonon* and *U. vocans vocans*, found within the study area are discussed and these factors are examined in relation to the nature of the substrate in the mangrove, sand and mud flat biotopes.

A detailed study was made of a dense sand flat dwelling colony of *U. tetragonon* in order to (1) examine the distribution of the species relative to the nature of the substrate, (2) population structure, and (3) relative growth rates.

The presence of *U.d. dussumieri* at Koh Surin, discovered during the present study, represents a major extension to the distributional range of the subspecies. It is also the first recorded instance of this subspecies occurring in Thailand.

I. INTRODUCTION

The fiddler crab populations of a mangrove forest and adjacent sand and mud flats were investigated at Koh Surin[2], a group of islands in the Andaman Sea off the west coast of Peninsular Thailand (9° 25′N., 98°50′E.), close to the southern Burmese border. The study area was located in a sheltered bay on the south of Koh Surin Nua (see Fig. 1). The inner part of the bay was fringed with the mangrove trees *Bruguiera gymnorhiza* Lmk., *Rhizophora apiculata* Blume, *R. mucronata* Lmk. and *Sonneratia alba* Smith. Adjacent to the mangrove forest in the inner bay was a sand flat and in the outer part of the bay a mud flat, the area between the sand and mud flats consisting of a mixture of the two substrates (see Fig. 2).

Fiddler crabs were collected at low water from the mangrove, sand and mud flat biotopes during approximately twenty hours of field work in April 1976. Four species of fiddler crabs, namely *Uca*

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[2] Koh = island or islands in Thai language.

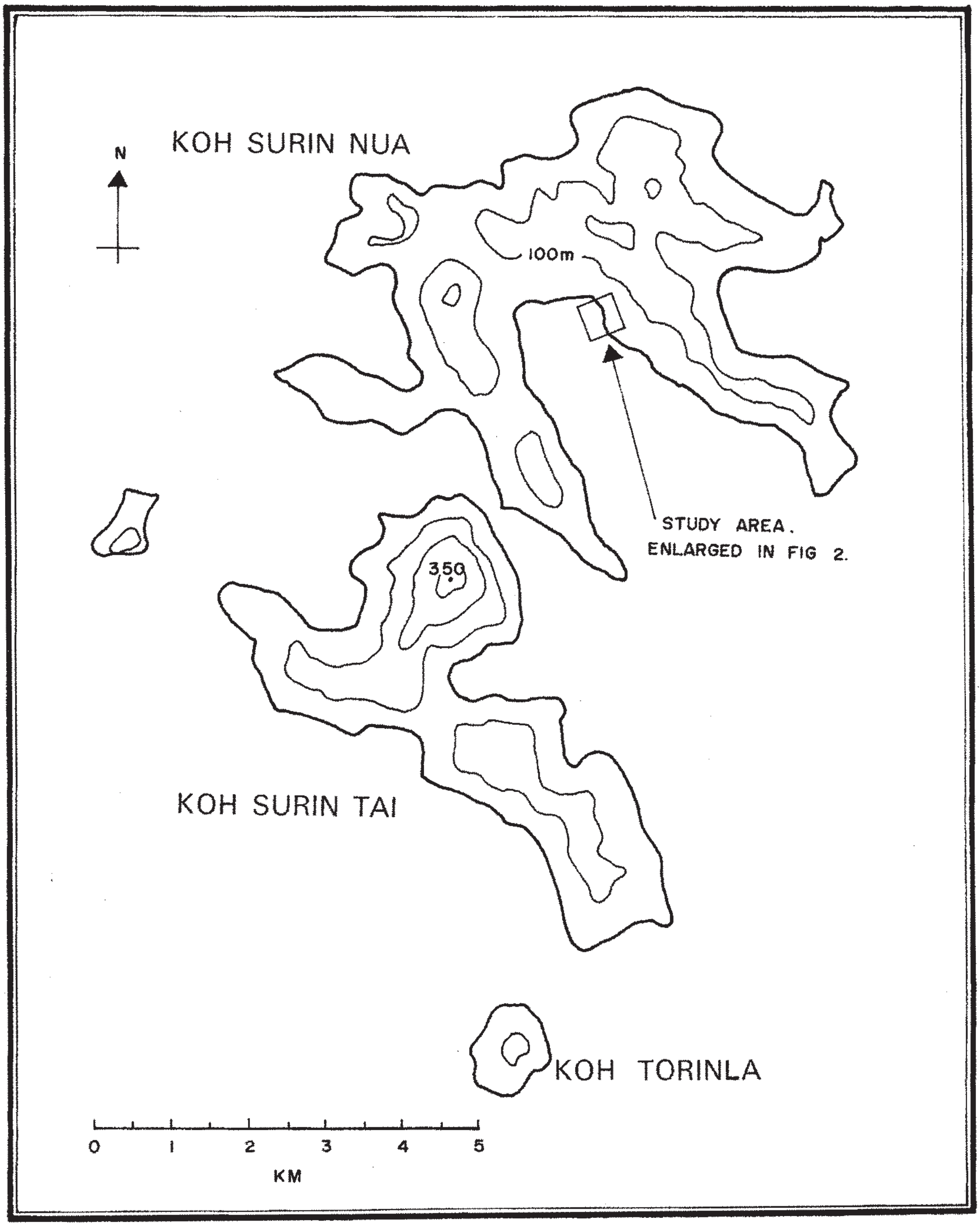

Fig. 1—Map of the Surin Island Group indicating the position of the study area, in the southward facing bay of Koh Surin Nua.
See Fig. 2 for enlarged map of study area.

dussumieri dussumieri (H. Milne-Edwards), *U. lactea annulipes* (H. Milne-Edwards), *U. tetragonon* (Herbst) and *U. vocans vocans* (L.), were found within the study area. *U. d. dussumieri* and *U. lactea annulipes* were found sympatrically in the mangrove biotope, *U. lactea annulipes*, *U. tetragonon* and *U. v. vocans* sympatrically in the sand flat biotope, and *U. v. vocans* was allopatric in the mud flat biotope. It is noteworthy that the presence of *U. d. dussumieri* on Koh Surin Nua represents a considerable extension of the previously known distributional range (Crane 1975) of this subspecies (Frith & Frith 1977).

During the present investigation, a study was made of the distribution and density of fiddler crab species within the mangrove, sand and mud flat biotopes. Many workers have shown that the distribution of ocypodid crabs is closely related to the particle size of the substrate from which they feed, and that the mouth parts of them are highly specialised to extract organic material and micro-organisms from the substrate of certain particle size (Crane 1941, 1975, Altevogt 1955, Teal 1958, Miller 1961, Ono 1965, Macnae 1968, von Hagen 1970). In view of the findings of these workers, and due to the limited time available for the present study, the nature of the substratum, that is grain size and organic content, was the only environmental parameter to be investigated during the present study.

A detailed examination was made of a dense colony of *U. tetragonon* found in the sand flat biotope, in order to examine the distribution of this species relative to particle size of the substratum, population structure and growth rates. This was considered particularly desirable in view of the apparently atypical situation of this particular colony (see below).

The identifications of all species were made by direct comparison with material at the Smithsonian Institution, Washington D.C., which had previously been identified by Jocelyn Crane. In addition Koh Surin specimens were subsequently identified to both the present authors complete satisfaction by using Crane's (1975) diagnosis and figures, with particular attention being paid to the major cheliped and gonopod structures of the male crab.

II. DESCRIPTION OF THE STUDY AREA

The study area consisted of mangrove, sand and mud flat biotopes, details of which follow:

MANGROVE BIOTOPE

The mangrove forest, in the area where collections were made, was approximately 105 metres from landward (west) to the seaward edge (east) and was clearly divisible into three zones.

Zone 1

Fifteen metres wide from the landwardmost edge of the mangrove to seaward (see Fig. 2); a relatively open area with a few *Bruguiera gymnorhiza* mangrove trees. This zone backed onto a steep hill which was covered in forest (see Fig. 2).

Zone 2

Fifty metres wide seaward of zone 1 (see Fig. 2); a dense forest of *B. gymnorhiza* with a few *Rhizophora mucronata* mangrove trees.

Zone 3

Forty metres wide seaward of zone 2 (see Fig. 2); a dense forest of *R. mucronata* with a few *R. apiculata* trees.

SAND FLAT BIOTOPE

The particular area of sand flat investigated was situated in the inner bay, and was approximately 40 metres wide extending towards the center of the bay. A small freshwater stream ran from a nearby hill, through a thin line of mangrove into the bay at the edge of the sand flat (see Fig. 2).

MUD FLAT BIOTOPE

The particular area of mud flat investigated was situated in the more seaward outer part of the bay, south of the sand flat (see Fig. 2), and was approximately 40 metres wide extending from the edge of the mangrove forest westwards towards the centre of the bay.

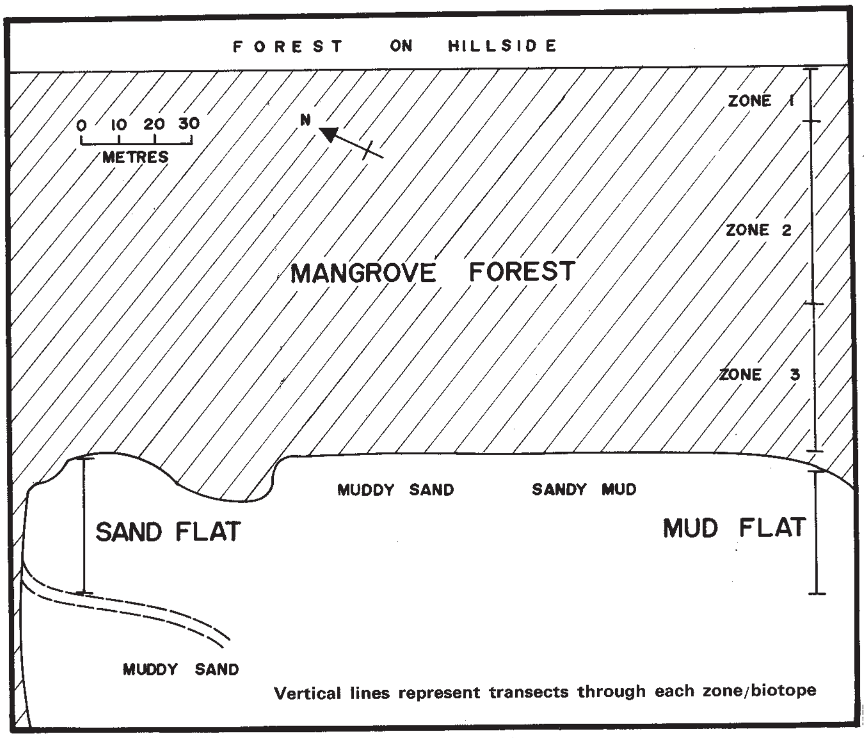

Fig. 2—Schematic map, drawn to scale, of the Koh Surin Nua study area. See Fig. 1 for relative position of this area in the Surin Island Group.

III. MATERIALS AND METHODS

a) COLLECTION OF FIDDLER CRABS

Transects were made through the mangrove and across the sand and mud flat biotopes (see Fig. 2) in order to examine and compare the distribution and density of fiddler crabs found in each of the three areas. Along each transect equidistant points were fixed at five metre intervals for the mangrove and mud flat transects, and one metre intervals for the sand flat transect. The larger number of sampling points in the latter biotope was made in order to examine the population structure of the *Uca tetragonon* colony found there. A half metre square quadrat frame was placed at each sampling point, and all fiddler crabs were collected from within the frame area by digging them up from their burrows. It should be noted here that for more convenient comparisons, with most previous published work, the figures for crabs resulting from the half metre square have been multiplied by four to give a value for a metre square in all subsequent reference to population density herein. The crabs were immediately washed and preserved in 70% alcohol on the island, and then returned to the laboratory for identification, analysis and measuring.

b) ANALYSIS OF SUBSTRATE

Substrate surface samples were collected from the majority of quadrats along each of the three transects (see Table 1 for sample number). On return to the laboratory the samples were treated in the following way:-

One hundred grams of each sample were dried for 24 hrs. at 105°C. Fifty grams of this dried sample were then sieved for 20 minutes through graded sieves in an automatic sieving machine.

Table 1. Density of fiddler crab species and nature of substrates in which they occurred at the Koh Surin study area.

	MANGROVE Zone 1	Zone 2	Zone 3	SAND FLAT	MUD FLAT
FIDDLER CRAB DENSITY (expressed as the number of crabs per metre square)					
Number of samples (N)	*N*=3	*N*=10	*N*=7	*N*=36	*N*=7
Uca dussumieri dussumieri	-	-	8.0	-	-
U. lactea annulipes	-	2.5	14.5	9.0	-
U. tetragonon	-	-	-	27.9	-
U. vocans vocans	-	-	-	1.1	20.0
PARTICLE SIZE (expressed as a % of the total weight)					
Number of samples (N)	*N*=3	*N*=10	*N*=7	*N*=17	*N*=7
Gravel (> 2.0 mm.)	33.1	29.5	24.0	32.6	15.7
Very coarse sand (1.0 – 2.0 mm.)	31.3	26.0	22.5	25.7	16.7
Coarse sand (0.5 – 0.1 mm.)	16.1	25.2	11.3	14.8	8.8
Medium sand (0.25 – 0.5 mm.)	10.5	13.0	10.6	9.0	9.4
Fine sand (0.125 – 0.25 mm.)	5.4	8.4	8.7	5.2	7.2
Very fine sand (0.063 – 0.125 mm.)	2.1	4.4	8.3	2.7	3.3
Mud (< 0.063 mm.)	1.5	3.5	14.6	10.0	39.0
ORGANIC CONTENT (expressed as a % of dry weight)	0.7	1.9	1.9	2.1	1.4

Sieve hole diameters were 2.0, 1.0, 0.5, 0.25, 0.125 and 0.063 mm. respectively. Each resultant grain size sample was weighed to within 0.1g. of accuracy. The mean values of each grain size for each of the three mangrove zones, sand and mud flats were calculated and expressed as percentages of the total weights, and these data are given in Table 1.

Fifteen grams of each of the original dried samples were ashed for two hours at 550°C. and then reweighed to determine the organic content. The mean values of the organic content were determined for each of the three mangrove zones, sand and mud flats and expressed as percentages of the dry weights, and these data are also given in Table 1.

c) MEASUREMENTS OF FIDDLER CRABS (*Uca tetragonon* only)

Measurements of carapace breadth and length in males and females, and the propodous (manus + pollex) and dactyl of the major cheliped in males, were taken in order to illustrate the size range within the population and to show the growth of these structures relative to each other. The method used for measuring these characters were those used and descibed by Crane (1975).

IV. RESULTS

a) DISTRIBUTION AND DENSITY OF FIDDLER CRABS IN THE STUDY AREA

The distribution and density of four fiddler crab species, *Uca dussumieri dussumieri, U. lactea* *annulipes.*, *U. tetragonon* and *U. vocans vocans* within each of the three biotopes is shown in Table 1; in which the density of each crab species in each biotope is expressed as the number of fiddler crabs per metre square. In addition the composition (i.e. the particle size) and organic content of the substrate is presented in Table 1, so that direct comparisons can be made between substrate type and density of fiddler crabs found living therein.

MANGROVE BIOTOPE

In zone 1 of the mangrove forest, the landward-most part of the forest, the substrate was extremely coarse, consisting predominantly of gravel and very coarse sand (64.4%), and to a lesser extent coarse and medium sand (26.6%) mixed with a relatively small amount of finer sand and mud (9.0%), (Table 1). No fiddler crabs occurred in this area (see Discussion).

In zone 2 of the mangrove forest, the substrate was also very coarse, but there was slightly less gravel and very coarse sand (55.5%) with a greater proportion of coarse and medium sand (38.2%) mixed with finer sand and mud (16.3%) than in zone 1, (Table 1). One species of fiddler crab, *U. lactea annulipes*, occurred in this zone but it was not abundant (see Table 1).

In zone 3 of the mangrove forest, the seaward-most zone, the substrate was notably finer with a much higher percentage of fine sand and mud (31.6%) than was found in zones 1 and 2, (Table 1). Two fiddler crab species, *U. d. dussumieri* and *U. lactea annulipes*, were abundant in this zone, the latter more so than the former, (Table 1). It is noteworthy that during the present investigation populations of *U. d. dussumieri* were observed to be more abundant in soft muddy banks near narrow (less than 0.5 m.) run-off channels within this zone than in the sandier substrates where the actual transect was made. In these former areas, *U. d. dussumieri* was in fact found to be allopatric. Unfortunately the significance of this preference for a muddier substrate by *U. d. dussumieri* was not fully appreciated at the time the field work was carried out and, consequently, a sample of the substrate was not collected for analysis.

SAND FLAT BIOTOPE

The sand flat substrate was generally similar in particle size and organic content to that of mangrove zone 3 (see Table 1), but contained slightly less finer deposits. Three sympatric species of fiddler crabs, *U. lactea annulipes*, *U. tetragonon* and *U. v. vocans*, were found in this biotope, details of which are described more fully below.

MUD FLAT BIOTOPE

The mud flat substrate, although extremely muddy, contained a relatively large amount of gravel and coarse sand, (Table 1). One species of fiddler crab, *U. v. vocans*, occurred in this biotope where it was notably more abundant than in others (see Table 1).

It should be particularly noted that the organic content of the substrates in all three biotopes was significantly low (Table 1), irrespective of particle size (see Discussion).

b) DISTRIBUTION AND DENSITY OF FIDDLER CRAB SPECIES ACROSS THE SAND FLAT BIOTOPE

Of the three species of fiddler crabs found to occur sympatrically in the sand flat biotope, *Uca tetragonon* was conspicuously more abundant than *U. lactea annulipes* or *U. vocans vocans* (Table 1). *Uca lactea annulipes* was less numerous in this area than it was in zone 3 of the mangrove forest, and *U. v. vocans* was extremely sparse compared with its notable high densities in the mud flat biotope (see Table 1).

The distribution and density of these three fiddler crab species across the sand flat from the seaward mangrove edge westwards towards the centre of the bay is given in Table 2, the sand flat being divided into six subdivisions each of six metres in length for this purpose. No attempt has been made to specifically identify juveniles of these populations (i.e. fiddler crabs with a carapace breadth of less than 5 mm. across), and the data

Table 2. Density of fiddler crab species and nature of substrates across the sand flat biotope of the Koh Surin study area.

Subdivisions (see text)	1	2	3	4	5	6
	SAND FLAT BIOTOPE (Mangrove edge westwards → towards centre of bay)					
FIDDLER CRAB DENSITY (expressed as the number of crabs per metre square)						
Number of samples (N)	*N*=6	*N*=6	*N*=6	*N*=6	*N*=6	*N*=6
Uca lactea annulipes	21.2	5.2	9.0	13.2	4.8	1.2
Uca tetragonon	13.3	37.3	41.2	44.8	24.0	6.6
Males only	8.8	18.0	20.6	20.0	10.0	3.3
Females only	4.7	19.3	20.6	24.8	14.0	3.3
U. vocans vocans	-	0.7	0.7	1.3	1.3	1.3
Uca juveniles	0.7	0.7	2.0	6.7	2.0	-
PARTICLE SIZE (expressed as a % of the total weight)						
Number of samples (N)	*N*=3	*N*=3	*N*=3	*N*=3	*N*=3	*N*=2
Gravel (> 2.0 mm.)	32.4	39.0	32.3	36.6	25.6	28.5
Very coarse sand (1.0 – 2.0 mm.)	26.8	25.5	26.3	24.7	24.4	26.9
Coarse sand (0.5 – 1.0 mm.)	14.8	13.5	14.1	14.2	17.6	14.3
Medium sand (0.25 – 0.5 mm.)	8.5	8.2	8.8	8.6	10.9	8.4
Fine sand (0.125 – 0.25 mm.)	5.0	4.1	5.3	5.0	7.1	5.1
Very fine sand (0.063 – 0.125 mm.)	2.9	1.5	2.3	2.7	3.7	3.3
Mud (< 0.063 mm.)	9.6	8.2	10.9	8.2	10.7	13.5
ORGANIC CONTENT (expressed as a % of dry weight)	0.4	0.3	0.4	0.3	0.2	0.3

given for juveniles in Table 2 thus deals with all three species collectively. Particle size and organic content data for each subdivision are also given in Table 2 in order that correlations between zonation of crab populations and these environmental factors can be clearly noted.

As illustrated in Table 2, however, the substrate varied little from one subdivision to the next, except in the most seaward subdivision where there was a notable increase in fine sand and mud content. It should be pointed out that beyond the sand flat study area (seawards) the substrate became increasingly finer in composition until at lower tide levels a mud flat occurred (see Fig. 2). It is noteworthy that both *U. lactea annulipes* and *U. tetragonon* were less numerous in the most seaward subdivision than elsewhere in the sand flat biotope, and beyond this study area(seawards) were altogether absent (see Table 2 and Discussion). However, *U. v. vocans* was extremely sparse in the sand flat biotope but increased in density in the more seaward areas as the substrate became increasingly finer, and the species reached its maximum density in the mud flat biotope, (Table 1).

It is of particular interest that *U. lactea annulipes* was more numerous in the more landward areas of the sand flat, that is in areas directly adjacent to the mangrove forest, where *U. tetragonon* was least dense (see Discussion). *Uca tetragonon* was

Table 3. Burrow occupancy by the fiddler crabs *Uca lactea annulipes*, *U. tetragonon* and *U. vocans vocans* in the sand flat biotope of the Koh Surin study area.

	NUMBER OF BURROWS	% OF TOTAL NUMBER	
TOTAL NUMBER OF BURROWS (Quadrats 1 – 36)	679	-	
NUMBER OF BURROWS OCCUPIED BY:			
Uca lactea annulipes	83	12.2	
U. tetragonon	253	37.3	53.0%
U. vocans vocans	7	1.0	
Uca juveniles	17	2.5	
Macrophthalmus parvimanus	4	0.6	1.6%
Sipunculid worms	7	1.0	
NUMBER OF BURROWS UNOCCUPIED	308	46.4	

notably more abundant in the more open oentral area of the sand flat study area (see Table 2).

Within the 36 quadrats laid across the sand flat study area, 679 burrows were ccunted, of which 53.0% were found to be occupied by fiddler crabs (predominantly *U. tetragonon*), and 1.6 % by other burrowing animals (sipunculid worms and the ocypodid crab *Macrophthalmus parvimanus* Guerin). The remaining 46.4% of the burrows were apparently unoccupied (see Table 3 and Discussion).

c) THE SAND FLAT DWELLING POPULATION OF *UCA TETRAGONON*

In total 251 *Uca tetragonon* fiddler crabs were collected from 36 quadrats laid across the sand flat (on average 28.0 crabs per metre square, see Table 1), of which 48.2% were males and 51.8% females. Thus the sex ratios of the species, within the sand flat as a whole, were equal; with a notable imbalance between the two sexes occurring only in the landwardmost sand flat subdivision, adjacent to the mangrove forest, where males were more abundant (see Table 2). Of the females, 12.3% were carrying eggs, whilst the appearance of the pleopods of other mature females suggested that the majority had recently released their eggs.

The size distributions of males and females of *U. tetragonon* within the sand flat colony are presented in Table 4. Both male and female populations have been divided into 6 size classes, each of 3 mm. in range, based on the carapace breadth. The mean values ($\bar{x}$) and standard deviations (s) for carapace breadth and length in males and females, and propodous (manus + pollex) and dactyl lengths of the major cheliped of males are given in Table 4 for each size class and for the population as a whole.

As can be seen from the figures (Table 4) the relative number and the mean values of carapace breadth and carapace length in each size class, and for the population as a whole, were similar for both sexes. Results indicate that the carapace breadth of crabs increased approximately an additional 1 mm. more during its growth than the carapace length in each size class; that is, for every 2 mm. growth of carapace length the carapace breadth increased by 3 mm. Young crabs are, therefore, somewhat square in shape whereas in the adults the carapace breadth is notably wider than is the length. It should be noted that the relative growth rate of the two characters (i.e. carapace breadth and length) are similar in both males and females (Table 4).

In young crabs the length of the propodous of the major cheliped was slightly smaller than the carapace breadth and slightly larger than the

Table 4. Size distribution of the *Uca tetragonon* population in the sand flat biotope of the Koh Surin study area.

SIZE DISTRIBUTION CLASSES OF CARAPACE BREADTH (mm.)		5.0–7.9	8.0–10.9	11.0–13.9	14.0–16.9	17.0–19.9	20.0–22.9	Total
Uca tetragonon Males								
Number of individuals	(n)	n=13	n=19	n=21	n=29	n=27	n=12	n=121
% of total sample		10.7	15.6	17.2	23.8	22.1	9.8	-
Carapace breadth	$\bar{x}$	6.50	8.88	12.50	15.18	18.56	21.80	14.14
	s	0.72	0.85	0.85	0.78	0.81	0.74	4.61
Carapace length	$\bar{x}$	4.63	5.97	8.74	10.62	12.76	14.36	9.77
	s	0.50	0.60	0.35	0.73	0.65	0.82	3.14
Propodous length	$\bar{x}$	5.48	7.76	12.60	17.29	25.30	32.26	17.41
	s	0.53	1.13	2.03	2.23	2.81	3.38	8.40
Dactyl length	$\bar{x}$	3.00	4.05	7.22	9.61	15.26	21.01	10.26
	s	0.30	0.60	1.79	1.42	2.01	2.73	5.63
Uca tetragonon Females								
Number of individuals	(n)	n=9	n=27	n=27	n=30	n=29	n=8	n=130
% of total sample		6.9	20.8	20.8	23.1	22.3	6.1	-
% of females with eggs		-	-	0.8	2.3	6.9	2.3	12.3
Carapace breadth	$\bar{x}$	7.10	9.21	12.50	15.52	18.26	21.01	13.95
	s	0.44	0.61	0.76	0.76	0.75	0.59	4.08
Carapace length	$\bar{x}$	5.12	6.17	8.71	11.22	13.11	15.04	9.88
	s	0.57	0.64	0.80	0.95	0.76	0.54	3.08

carapace length (Table 4). As can be seen from the figures (Table 4), the propodous growth rate relative to that of the carapace length was not the same in each frequency class (unlike the relationship between the growth in carapace breadth and length), but a greater increase in length of the propodous relative to carapace length (and carapace breadth) is indicated in the larger size classes of the adult males. It is noteworthy that there is also a greater increase in the length of the dactyl relative to propodous length in the larger size classes of male crabs (see Table 4) so that in young crabs the dactyl is about half the length of the propodous and in adults almost two thirds of the propodous length.

The majority of females with eggs had a carapace breadth within the size class of 17.0 – 19.9 mm.; very few females with a carapace breadth less than 14.0 mm. were found with eggs (Table 4).

A survey of the male major cheliped revealed that of the 121 crabs examined, 73 (59.8 %) had a brachychelous claw, 20 (16.4 %) had a leptochelous claw and 28 (23.8 %) were crabs too small to permit determination of cheliped structure or had chelipeds missing. Of the brachychelous forms, 71 (97.3%) had the major cheliped on the right and were thus 'right handed' and only 2 (2.7 %) left handed. Of the leptochelous forms, 19 (95.0 %) were right handed and only 1 (5.0 %) left handed. Thus the vast majority of male *U. tetragonon* in the Koh Surin sand flat population were right handed crabs with brachychelous chelipeds (see Discussion).

V. DISCUSSION AND CONCLUSIONS

As a result of the present investigations, the four species of fiddler crabs *Uca dussumieri dussumieri*, *U. lactea annulipes*, *U. tetragonon* and *U. vocans vocans* were found in the Koh Surin study area, western Peninsular Thailand. The presence of the latter three species on Koh Surin is not unexpected in view of the fact that the Surin group of islands lies well within the generalised distributional range illustrated by Crane (1975) for these species/subspecies. The presence of *U. d. dussumieri* on Koh Surin, however, represents a considerable extension of its known range eastwards by approximately 500 km. This would appear to extend the range of this subspecies well into the range of *U. dussumieri spinata* Crane in view of the known range of the latter population (Crane 1975, Frith & Frith 1977). In view of this, the possibility of these two subspecies of *U. dussumieri* occurring sympatrically in this general area must be considered.

Results from the present investigation show that the distribution and relative density of the four fiddler crab species studied were apparently correlated to the grain size of the substrate in which they occurred. It has previously been shown that crabs belonging to the family Ocypodidae have highly specialised mouth parts adapted to enabling them to efficiently extract food, in the form of organic material and micro-organisms, from certain particle sizes in a favoured substrate (Crane 1941, 1975, Altevogt 1955, Teal 1958, Miller 1961, Ono 1965, Macnae 1968, von Hagen 1970). Thus, some ocypodid crabs have mouth parts which are particularly adapted to feeding from sand grains, or from mud, whilst some species inhabiting a mixture of sand and mud substrates have intermediate feeding adaptations.

It is noteworthy that the organic content of the substrates in the Koh Surin study area was extremely low, possibly for the reasons given elsewhere (see Frith 1977), irrespective of the particle size of the substrate; and it is possible that this apparent lack of a locally abundant food source for certain fiddler crab species may have restricted their diversity, distribution and density at Koh Surin (see below).

On Koh Surin, *U. lactea annulipes* occurred predominantly in the mangrove (zone 3) and sand flat biotopes where the substrate consisted very predominantly of coarse sand mixed with a relatively small amount of fine sand and mud. Ono (1965) and Macnae (1968) have shown that the setae on the maxillipeds of *U. lactea* are well adapted for feeding from a sandy substrate. In view of their findings the restriction of this species to the sandier substrates in the Koh Surin study area is to be expected, as this is the type of substrate to which the mouth parts of this species are particularly adapted.

It is of particular interest, however, that the sparsity of *U. lactea annulipes* in zone 1 and its absence from zone 2 of the mangrove forest correlated directly with the increasing gravel and coarse sand content of the substrates in these zones and the associated decrease of fine sand and mud content (see Table 1). The extremely low organic content of the substrate in zone 1, representing a lack of an abundant food, may have also contributed to its absence from this area. Moreover, it is possible that the lack of a regular tidal coverage in these more landward areas may have also contributed to this sparsity and/or absence, but this seems unlikely in view of the fact that studies on Phuket (Frith *et al.*, 1976) show this species colonizes intertidal areas which receive as little as 7.0% tidal coverage. It was unfortunately not possible within the scope of the present investigation to examine the percentage tidal coverage of the biotopes within the Koh Surin study area.

Crane (1975) described the typical substrate for *U. lactea* as "ranging from sandy mud to muddy sand", but noted that populations were often found in "sand with very little silt, especially close to mangroves occurring in such a substrate". At Koh Surin it appeared to be the latter less typical substrate in which the *U. lactea* were found not only in areas adjacent to the mangrove, but also within the forest itself where the substrate was atypically sandy (see Frith 1977). It is noteworthy that similar studies on Phuket, an island almost connected to the west coast of Peninsular Thailand (see Frith *et al.*, 1976), showed this fiddler crab to be extremely abundant in substrates that, according to Crane (1975), were more typical for the species (i.e."sandy mud to muddy sand") and was only found within the mangrove forest itself where the substrate was of sandy mud (Frith & Frith—in prep.). Thus, the rather unusually high proportion of sand beneath mangrove forest at Koh Surin would appear to permit this crab to utilise areas on the shore less typical of it at other locations. The apparent intolerance of *U. lactea* to a muddy substrate was emphasised on Koh Surin, as it was notably absent from the muddier mangrove forest substrates (outside the transect area) and the mud flat and was less numerous in the more seaward areas of the sand flat where the deposit was increasingly finer.

Teal (1958) showed from his studies of fiddler crabs in a Georgia salt marsh that " the presence of one fiddler crab often interferes with the use of that area by another species", even though both species were adapted to living in that area. In view of Teal's statement, it seems possible that a certain amount of interspecific competition between *U. lactea annulipes* and *U. tetragonon* might have existed in the sand flat study area at Koh Surin, the former species limiting the distribution and density of the latter. It is extremely interesting to note, in this respect, that in the sand flat biotope the substrate was apparently favourable to *U. lactea annulipes*, but in areas where *U. tetragonon* was abundant, noticeably in the central sand flat area, the former species was certainly not abundant. This point is further emphasised by the fact that on Phuket studies of fiddler crab populations in a similar biotope showed that *U. lactea annulipes* was abundant throughout an area examined which lacked other fiddler crab species which might, otherwise, have excluded it (Frith & Brunenmeister —in prep.).

Crane (1975) recorded *U. lactea* as having been found sympatrically with *U. vocans*, and *U. vocans* sympatrically with *U. tetragonon*. Both of these combinations were found in the sand flat biotope of the Koh Surin study area. Crane had not, however, found *U. tetragonon* occurring sympatrically with *U. lactea*. That this latter situation was found at Koh Surin is most noteworthy in view of the shore location occupied by *U. tetragonon* at Koh Surin being apparently atypical for the species. Crane (1975: p. 77) described *U. tetragonon* as being common on islands "either offshore or mid-ocean, and always rich in living coral" (as is the case at Koh Surin), and as (p.79) being found at lowest tide levels "Often among conglomerates of mixed coral and shell, on mud or muddy sand, sometimes with underlying dead coral". At Koh Surin, however, this species was found in stony sand overlying mud; an apparently atypical substrate for this species. It should be pointed out, however, that Crane (1975 : p. 445) subsequently refers to this species as being found in her biotope category no. 4, "Stony sand with underlying mud, ranging sometimes to a hard substrate of coral or shelly conglomerate, with mud in interstices and overlying the surface in a thin layer". Taking into account only this latter biotope description of Crane's, *U. tetragonon* was in fact occupying a substrate typical for the species at Koh Surin, but it was nevertheless found there at much higher tide levels than it had previously been found according to Crane (1975).

The sympatry of *U. tetragonon* with *U. lactea annulipes* at Koh Surin would appear to be due to the fact that, faced with an apparent absence of a more favourable or typical situation on the island, *U. tetragonon* apparently displaces *U. lactea annulipes* from areas it occupies (on Koh Surin Nua), presumably being dominant at least its respect of its larger size. An additional possible explanation of the *U. tetragonon* colony in its higher tide level sand flat biotope, and the resultant sympatry with *U. lactea annulipes* should not, however, be overlooked. Crane (1975) has observed that some fiddler crab species tend to move "to the upper levels of their intertidal habitat" during courtship and display territoriality. Moreover, von Hagen (1962) found that a drier substrate was favoured by some crabs during the courtship period as it provided a better resonator for the acoustic drumming which many species of *Uca* perform during courtship. In view of these observations, and in consideration of the breeding activity found to be under way in the Koh Surin Nua study population (see Table 4), it must be accepted as possible that the presence of the *U. tetragonon* colony in the open sand flat biotope at a higher tide level was due to a 'local migration'. That is to say that, in accordance with observations of Crane (1975) and von Hagen (1962) concerning breeding season movements of crabs, the Koh Surin *U. tetragonon* colony may have been in temporary residence at the sand flat study area for courtship and/or breeding activities only. Unfortunately suitable time and tides were not available in order to permit the means of testing this possibility. The explanation would appear, however, to provide an applicable solution to the somewhat puzzling density of crabs in a location so atypical and poor in foods (organic content, see Table 2) compared with elsewhere (see Frith *et al.*, 1976). At least with regard to *U. tetragonon* the presence of dense populations of crabs in an area so poor in available food is certainly more easily explained if their presence is in fact only temporary, during breeding. It should be noted that *U. tetragonon* was not found in the adjacent mangrove forest edge (zone 3) and that the presence of the trees themselves and the resulting slightly finer substrate must presumably be contributing factors making this biotope less favourable. The possibility that the mangrove dwelling fiddler crabs *U. d. dussumieri* and other crab species might represent competitors should not be overlooked.

Crane (1975) described the biotope of *U. dussumieri* as being "Muddy stream banks and protected flats, near mouth, near mangroves". At Koh Surin, however, this species was found exclusively within the seawardmost part of the mangrove forest (zone 3), and although found sympatric with *U. lactea annulipes* (a sympatry not recorded by Crane, 1975) within the sandier substrates of this forest area, was noticeably more abundant in more open muddier bank areas similar to those described by Crane (1975),(see also under results). These findings are to be expected in view of the fact that Macnae (1968) showed the mouth parts of *U. dussumieri* to be well adapted for feeding from fine mud.

According to Crane (1975 : p. 85) *U. vocans* is one of the most abundant fiddler crabs in the world. She described its biotope as "Unshaded sandy mud along lower tide levels of protected bays". At Koh Surin this species occurred predominantly in the mud flat at lower tide levels in accordance with Crane's statement, and it also occurred sparsely at higher tide levels on the sand flat where it was sympatric with *U. lactea annulipes* and *U. tetragonon*. It is particularly interesting that *U. v. vocans* was very nearly exclusively restricted to the lower tide levels of the mud flat study area at Koh Surin where the organic content was relatively poor. Under normal conditions the finer substrate composition of mud (see Newell 1970) usually contains a higher percentage of organic material than coarser substrates (as was found to be the case on Phuket Island, see Frith *et al.*, 1976). Thus at Koh Surin, *U. v. vocans* is restricted to an area poor in foods due to its morphological adaptations to the substrate of the area involved. It does, however, lack competitors in these finer substrates, at least on Koh Surin.

The growth of fiddler crabs is conspicuously allometric, that is, the rate of growth differs in different parts of the anatomy and is subsequently of considerable interest. Crane (1975) discusses and illustrates allometry in fiddler crabs and briefly reviews previous work on the subject. She has pointed out that the size and proportions of the major cheliped and to a lesser extent the carapace breadth show the greatest relative change with growth. In the Koh Surin *U. tetragonon* population, the growth of the carapace breadth relative to that of the carapace length, in both sexes, was greater, but it is noteworthy that the growth rate ratio between these two characters was similar throughout the growth period. This was not the case, however, between the growth of the propodous of the major cheliped relative to the growth rate of the carapace length (and breadth), for the propodous becomes progressively longer relative to the carapace characters, noticeably more so in the larger size classes. Thus, in the largest males the propodous attained a length of over twice that of the carapace length and two thirds that of the carapace breadth, whereas in young crabs the propodous was of a similar length to both carapace characters. These findings are, according to Crane (1975), typical for all *Uca* species. The dactyl elongated allometrically relative to the growth of the propodous, notably more so in the larger males when it attained a length of approximately two thirds that of the propodous whereas in younger crabs it was just over half the length of this structure.

It is noteworthy that a survey of the claw dimorphism showed that the major cheliped of males in the *U. tetragonon* population at Koh Surin were predominantly'right handed' brachychelous forms. This is most interesting inasmuch as Crane (1975) pointed out that in American populations of fiddler crabs there is a tendency towards the leptochelous cheliped form, whilst the opposite is true of the *U. tetragonon* population at Koh Surin. It should be noted, however, that Crane (1975) does not apparently comment upon the relative proportions of the brachychelous or leptochelous forms in the non-American species. It is noteworthy that in populations of *U. lactea annulipes*, *U. urvillei* and *U. v. vocans* on Phuket (Frith & Brunenmeister—in prep.) the majority of fiddler crabs were found to have brachychelous cheliped forms. Thus, within the Southeast Asian populations of fiddler crabs there is an apparent tendency towards a brachychelous cheliped, an apparently opposite trend to what Crane (1975) found in American populations. This has been discussed in more detail elsewhere (Frith & Brunenmeister —in prep.).

Results from the burrow occupancy investigation in the sand flat biotope of the Koh Surin study area showed that there was a high percentage (46.4) of unoccupied burrows. Crane (1974) pointed out that " Biotopes normally have more burrows than crabs when the tide is out" and the findings at Koh Surin are not, therefore, peculiar. It is possible that some crabs escaped capture in our quadrats by digging down deeply into the substrate but this is not considered to have been frequently the case. A number of burrows in excess of the actual number of fiddler crabs within a colony must obviously have considerable survival value both to the individual crabs and, as a result, the colony as a whole. Unoccupied burrows, while apparently serving no purpose under normal circumstances, probably function as important refuges to crabs under attack by predators. Selective pressures (predation) for additional burrows to the number of crabs would be maintained by the survival of crabs with a local availability of more than one (i.e. its own defended) burrow. This is obvious when one considers that a crab foraging some distance from its defended burrow frequently situates itself nearer to an undefended burrow, as a result of the abundance of superfluous burrows. If, at that point, it is attacked it is far more likely to escape by using the closer undefended burrow than by travelling a further distance to its own burrow. In this respect, it should be noted, that other occupied crab burrows are often entered by crabs escaping from attack which have been caught away from their own burrow or an unoccupied one. Superfluous unoccupied burrows simply help to improve the chances of escape by making available a denser frequency of burrows relative to the number of resident crabs within the colony. Moreover, an unoccupied burrow undoubtedly proves more effective in enabling a fleeing crab to escape predation, as the crab can both enter the burrow more rapidly and go down it further to avoid being retrieved by probing predators such as long-billed birds (waders– Scolopacidae and kingfishers– Alcedinidae).

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