PHUKET MARINE BIOLOGICAL CENTER

Phuket, Thailand

RESEARCH BULLETIN NO. 29

FIDDLER CRAB (OCYPODIDAE : GENUS *UCA*) SIZE, ALLOMETRY AND MALE MAJOR CHELA HANDEDNESS AND MORPHISM ON A THAILAND MANGROVE SHORE

by

Dawn W. Frith and Susan Brunenmeister

FIDDLER CRAB (OCYPODIDAE : GENUS *UCA*) SIZE, ALLOMETRY AND MALE MAJOR CHELA HANDEDNESS AND MORPHISM ON A THAILAND MANGROVE SHORE.

By Dawn W. Frith[1]

Phuket Marine Biological Center, Thailand.

AND

Susan Brunenmeister[2]

Department of Biological, University of Houston, Texas, U.S.A.

CONTENTS

ABSTRACT

Measurements of carapace length and breadth of males and females, and of the propodous (manus + pollex) and dactyl lengths of the major chela of the males of the four most abundant species of fiddler crabs, *Uca forcipata, U. urvillei, U. vocans and U. lactea*, inhabiting a mangrove shore on Phuket Island, western peninsular Thailand are given. Size comparisons of these morphological characters clearly illustrate allometry that is characteristic of all *Uca* species. Larger *U. vocans* and *U. lactea* males were mostly found in the upper limits of their intertidal range where they would have more time for display during low water.

Relative frequencies of left and right handedness differed among the species. No significant differences were found in the handedness of brachychelous, leptochelous or intermediate (*U. vocans* only) morphs. Brachychelous morphs were significantly more numerous than either of the other morphs.

Sex ratios varied with size class, males in general being more numerous in all shared classes, and in total two to three times more abundant than females. Differences may be related to differential migration, mortality and growth rates.

Present address : 1. 'Prionodura', Paluma via Townsville, N. Queensland 4810, Australia.
2. National Marine Fisheries Service, Miami Laboratory, 75 Virginia Beach Drive, Miami Fla 33133 U.S.A.

I. INTRODUCTION

Seven species of fiddler crabs have been recorded from Phuket Island, western peninsular Thailand : *Uca (Deltuca) dussumieri spinata* Crane 1975; *U. (D.) (coarctata) forcipata* (Adams & White 1848); *U.(D.) (coarctata) urvillei* (Milne-Edwards 1852); *U. (Thalassuca) tetragonon* (Herbst 1790): *U.(T.) vocans vocans* (Linnaeus 1758); *U.(Celuca) triangularis bengali* Crane 1975; and *U. (C.) lactea annulipes* (Milne-Edwards 1837), (Frith & Frith 1978). Frith and Frith (1977 a) record *U. (D.) d. dussumieri* (Milne-Edwards 1852) from Koh Surin, a group of islands in the Andaman Sea off the west coast of peninsular Thailand. Much qualitative and quantitative data are available on the ecology of these fiddler crab species (Frith, Tantanasiriwong & Bhatia 1976; Frith 1977; Frith & Frith 1977b; 1978; Frith & Brunenmeister, in 1980).

The present study was carried out at Ao Nam-Bor mangrove shore (98° 25′ E., 7° 51′ N.) on the east coast of Phuket Island. The shore consists of three quite different biotopes: the mangrove forest (further divided landward to seaward into four zones; see Description of Study Area), and seaward sand (further divided into three zones) and mud flats respectively. Details of shore profile, tidal range and physical factors (temperature, salinity, pH, and grain size, organic and moisture content of substrate) that operate thereon are described elsewhere (Frith *et al.* 1976; Frith & Brunenmeister 1980). All fiddler crab species listed by Frith and Frith (1978) for Phuket Island (see above) with the exception of *U. tetragonon* occur at Ao Nam-Bor. Frith and Brunenmeister (1980) discuss zonation, abundance and sympatry of the Ao Nam-Bor fiddler crabs in relation to environmental factors, provide a detailed analysis of the populations structure of the four most abundant species, *U. forcipata, U. urvillei, U. v.vocans* and *U. lactea annulipes,* and discuss the interspecific and intraspecific relationships between them.

Standard measurements (see Materials and Methods) and an analysis of handedness and morphism of the major chela of males of *U. forcipata, U. urvillei, U.v. vocans* and *U. lactea annulipes* collected during Frith and Brunenmeister's (1980) ecological study were made and it is this data that are presented here. Measurements were taken in order to examine size ranges, allometric relationships typical of the genus *Uca* (see Crane 1975 for detailed discussion and bibliography on the subject), and to investigate whether subpopulations of a species differed significantly in size measures at different shore levels and/or in different biotopes.

It should be noted that only one small population of *U.d.spinata* was found on the seaward mangrove edge just north of the present study site (Frith & Frith 1978), and only two specimens of *U.t.bengali* were found within the mangrove forest (zone 3). Thus, neither are discussed further here; for the discussion of their ecology see Frith and Frith (1978) and Frith and Brunenmeister (1980) respectively.

Male fiddler crabs have one cheliped larger than the other, whereas females have two smaller ones of similar size. Two major chela morphs, brachychelous and leptochelous (see Crane 1975 for detailed descriptions), occur in *U. forcipata, U. urvillei* and *U. lactea annulipes.* These two morphs, and a third intermediate one occur in *U. v.vocans.* The intermediate morph was refered to as '*cultifera*' by Green and Schochet (1972) may and as '*cultrimana*' by Serene (1972). A morph be right or left handed. Handedness and morphism of these four species were analysed in order to determine whether there were significant differences among species, or within species among subpopulations occupying different shore levels and/or biotopes. Frith and Frith (1977b) carried out a similar survey of *U. tetragonon* populations.

Fiddler crabs collected during the present study are registered in the reference collection of the Phuket Marine Biological Center, Phuket Province, Thailand. Furthermore, representative specimens of each species have been donated to the Smithsonian Institution, Washington, U.S.A.

2

The nomenclature of Crane (1975) is followed throughout. All statistical tests used are described in Snedecor and Cochran (1967) or Sokal and Rohlf (1969).

II. DESCRIPTION OF STUDY AREA

Mangrove biotope

Zone 1. (Landward fringe)

An area approximately one hundred metres wide, bordered by rice paddi fields on the west and the landward edge of the mangrove forest on the east (Fig. 1). This area had been disturbed by burning and cutting a few years earlier and consequently only a few sparse populations of mangrove trees *Nypa fruticans* Wurmb, and *Phoenix paludosa* remain. Substrate was of muddy sand. The first landward fifty metres were covered

by less than 20.0% of tides and the remainder by 20.0% to 30.5%.

Zone 2 (Landward edge of mangrove forest)

A narrow strip of land, approximately nineteen metres wide, bordered by zone 1 to the west and the magrove forest proper (zone 3) to the east (Fig. 1). A channel about half a metre wide and six centimetres deep passed through this zone and continued into the mangrove forest. This zone lacked vegetation, apart from a few clumps of *N. fruticans*. Substrate was of sandy mud. The zone was covered by 30.5% to 40.4% of the tides.

Zone 3 (Mangrove forest)

The mangrove forest in the study area was approximately two hundred metres from landward to seaward edges (Fig. 1). The majority of forest
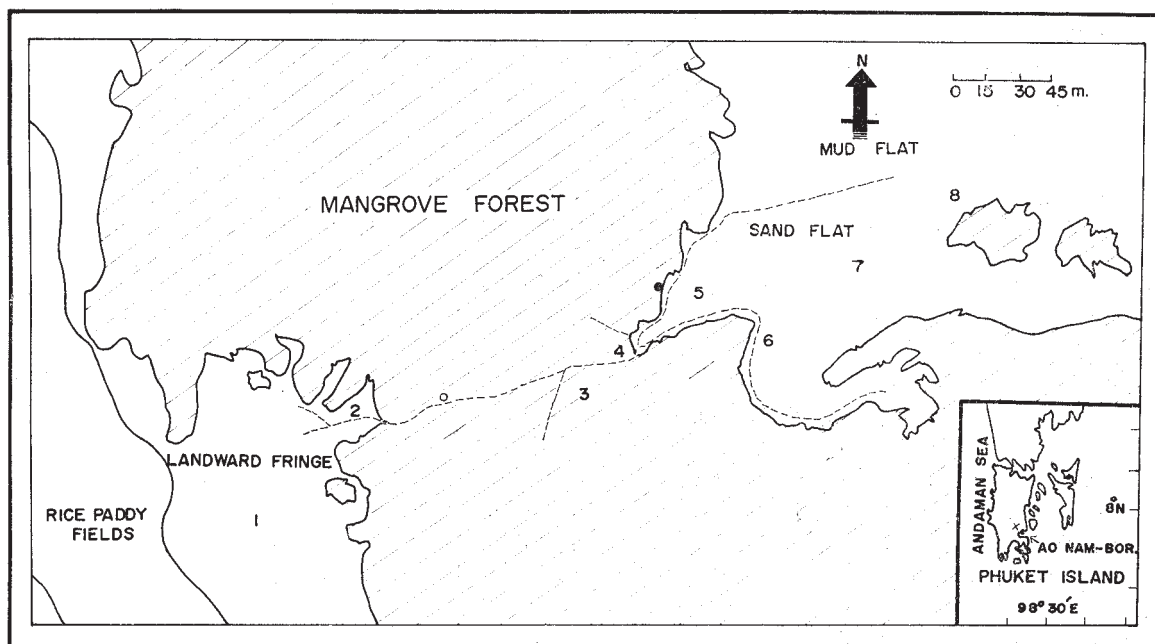

Figure 1. Map of the Ao-Nam-Bor mangrove shore, Phuket Island, showing relative positions of zones landward (zone 1) to seaward (zone 8).

Legend : x = Phuk Town
• = isolated population of *Uca dussumieri spinata*
o = isolated population of *U. triangularis bengali*
---------- = tidal channels remaining at low water

consisted of mangrove *Rhizophora apiculata* Blume, with fewer trees of *R. mucronata* Lmk., *Ceriops tagal* C.B. Rob., *Lumnitzera racemosa* Willd, *L. littorea* Voight and *Scyphiphora hydrophyllacea* Gaertn, mostly along the landward and/or seaward edges. A continuation of the channel through zone 2 provided a natural path through the forest at low water, and due to this accessibility zone 3 was established along its banks. For the first seventy metres the channel was about half a metre wide with approximately six centimetres remaining at low water. This channel then flowed into a much wider one which continued seaward through the mangrove forest for about another ninety metres. This latter channel was about three metres wide and approximately half a metre of water remained at low tide. Substrate was of firm mud. The more landward areas were wetted by 40.4% to 70.6% of tides whereas the more seaward areas were covered by all tides.

Zone 4 (Seaward edge of mangrove forest)

A narrow strip of land approximately eleven metres wide, bordered on the west by mangrove forest and separated from the adjacent mud flat on its eastern side by a channel. This zone lacked vegetation and its substrate was muddy sand.

Sand flat biotope

Zone 5 (Landward area of sand flat)

Bay-shaped, about seventy metres wide, relatively exposed and separated from Zone 4 by the above mentioned channel. Substrate contained much gravel and shell debris.

Zone 6 (Mud sand flat area)

About thirty metres wide, south of zone 6 (see Fig.1). Substrate contained less gravel than zone 5.

Zone 7 (Seaward edge of sand flat)

About sixty metres wide, relatively exposed and continuous with seaward mud flat. Substrate as zone 6.

4

Mud flat biotope

Zone 8

The first fifty metres of mud flat which at low spring tides is uncovered up to about three hundred metres seaward. To the south of this zone (about five metres) was a small stand of mangrove forest (Fig. 1), predominantly of *R. apiculata* with a few trees of *R. mucronata* and *Sonneratia alba* Smith. Substrate of soft mud.

III. MATERIALS AND METHODS

Sampling was distributed over all months of fieldwork from August 1974 to March 1975 (130hours). Each shore visit (on average once a week) involved about four hours in the field over a neap or spring low water period. Samples were always taken in dry weather conditions at the time when no rain had fallen during ebb tide prior to sampling.

Transects were made landward to seaward across each zone and the length of each varied according to the width of the zone. Along each transect at equidistant points a half metre square quadrat frame was placed. All visible crabs were firstly removed from the surface. The substrate within the frame was then excavated down to a depth of twenty five centimetres and additional crabs removed from it. The burrows of the notably large fiddler crabs, in particular those of *U. forcipata*, *U. urvillei* and *U. vocans*, occasionally extended down below this depth and in these instances were traced further down individually and their occupants, if any, removed. The number of quadrats sampled and the total number of crabs collected by this method are given in Appendix 1.

To supplement data collected by the above transect/quadrat methods additional crab material was sampled from selected 3 × 1 metre areas in each zone (Appendix). Furthermore nineteen additional males and females of *U. forcipata* were collected at random from the surface of zone 3.

Standard measurements (as defined by Crane 1975), that is carapace length and breadth of males and females, and of the propodous (manus + pollex) and dactyl lengths of male major chela, were recorded for each fiddler crab specimen of *U. forcipata*, *U. urvillei*, *U. vocans* and *U. lactea* to 0.1 millimetres of accuracy using vernier calipers. Most crabs with a carapace length less than 3.5 millimetres were difficult to identify and/or sex satisfactorily. Thus, these very small crabs are referred to collectively as juveniles in the present paper. It should be noted that this size distinction is not used as a criterion for distinguishing juveniles from adults as the size at which fiddler crabs become sexually distinguishable was not investigated in the present study.

Crab sizes and allometry

Comparisons of the sizes of males and females of *U. lactea* among zones using analysis of variance on $\log_{10}$ transformed carapace length indicated significant heterogeneity in the average sizes of males ($F_s = 6.871$, $p < 0.001$) and females ($F_s = 4.192$, $p < 0.005$). The Student-Newman-Keuls test indicated that males in zone 4 were significantly larger than those in all other zones except zone 1 ($p < 0.05$), and on the lower end of the scale, that males in zones 5 and 7 were also significantly smaller than those in zone 1 ($p < 0.05$). The average sizes of females in all zones except 2 were significantly larger than that in zone 5 ($p < 0.05$).

Comparison of the sizes of *U. urvillei* among zones, 2, 3 and 6 using the same kind of test indicated significant heterogeneity in the average sizes of males ($F_s = 7.464$, $p < 0.005$) and homogeneity in the average sizes of the females ($F_s \triangle 2.494$, $0.10 > p > 0.05$). The Student-Newman-Keuls test indicated that the average size of males in each zone differed significantly ($p < 0.05$), increasing seaward. The average sizes of males *U. vocans* in zones 4 and 7 were similar ($t_s = 0.910$, $p > 0.20$); the average sizes of the females, however, were significantly greater in zone 4 than in zone 7 ($t_s = 2.99$, $p < 0.01$).

Back-transformed means and their 95% confidence limits for males and females of each species occurring in their respective zones are indicated in Table 1. The average sizes of *U. lactea* males and females are smaller than both *U. urvillei* and *U. vocans* in their respective zones of overlap ($p < 0.05$). Within the mangrove forest (zone 3), *U. urvillei* males and females were larger than the sympatric *U. forcipata* ($p < 0.05$).

Size frequency distributions based on the carapace length of males and females of *U. forcipata*, *U. urvillei*, *U. vocans* and *U. lactea* are given in Table 2. In *U. lactea*, males clearly attain larger sizes than females. In other species, although data are few, the size frequency distributions of males and females suggest that in *U. urvillei* and *U. vocans*, females attain similar sizes to those of males, whereas in *U. forcipata*, females may not attain such large sizes as males. Comparisons among species indicate that the maximum size attained by males or females of *U. lactea* is much smaller than that attained by its congeners. Moreover, as shown in Table 2, sex ratios varied with size notably in *U. lactea* and *U. forcipata*; in general, at small sizes, there was a larger percentage of females than males.

To compare the carapace dimensions of conspecific males and females, carapace breadth was regressed on carapace length. Both variables were transformed to $\log_{10}$. Each regression was highly significant. Residuals were examined and found visually satisfactory. The regression equations, sample sizes, significance values and percent explained variability of each regression are indicated in Table 3a. Analysis of covariance indicated that the regression lines of males and females of *U. lactea*, respectively, did not differ significantly in slope ($F_s = 3.21$, $0.10 > p > 0.05$) but did differ in elevation ($F_s = 5.79$, $p < 0.025$). Similarly, the regression lines of males and females of *U. urvillei*, respectively, were similar in slope ($F_s = 0.25$, $p > 0.50$) and different in elevation ($F_s = 11.25$, $p < 0.005$).

Table 1. Average sizes of males and females (based on carapace length in mm.) of each fiddler crab species within zones. Means ($\overline{Y}$) and their 95% confidence limits (L_1, L_2) are back-transformed (see Results); n = number of crabs.

		ZONES						
		1	2	3	4	5	6	7
Uca forcipata								
Males	n	—	—	15*	—	—	—	—
	$\overline{Y}$	—	—	7.0	—	—	—	—
	L_1	—	—	5.6	—	—	—	—
	L_2	—	—	8.7	—	—	—	—
Females	n	—	—	11*	—	—	—	—
	$\overline{Y}$	—	—	6.6	—	—	—	—
	L_1	—	—	4.8	—	—	—	—
	L_2	—	—	9.0	—	—	—	—
U. urvillei								
Males	n	—	31	46	—	—	14	—
	$\overline{Y}$	—	7.9	9.3	—	—	11.4	—
	L_1	—	7.2	8.5	—	—	9.4	—
	L_2	—	8.7	10.2	—	—	13.9	—
Females	n	—	16	15	—	—	8	—
	$\overline{Y}$	—	8.8	9.3	—	—	11.6	—
	L_1	—	7.3	8.1	—	—	9.8	—
	L_2	—	10.6	10.7	—	—	13.6	—
U. vocans								
Males	n	—	—	—	4	—	—	32
	$\overline{Y}$	—	—	—	12.4	—	—	10.3
	L_1	—	—	—	7.9	—	—	9.0
	L_2	—	—	—	19.3	—	—	11.8
Females	n	—	—	—	3	—	—	16
	$\overline{Y}$	—	—	—	12.8	—	—	7.4
	L_1	—	—	—	8.8	—	—	6.3
	L_2	—	—	—	18.6	—	—	8.9
U. lactea								
Males	n	47	70	—	39	58	31	128
	$\overline{Y}$	5.9	5.3	—	6.6	5.0	5.7	4.8
	L_1	5.4	5.0	—	5.8	4.4	5.2	4.6
	L_2	6.5	5.7	—	7.5	5.6	6.2	5.1
Females	n	23	58	—	15	24	15	54
	$\overline{Y}$	5.4	4.9	—	5.8	4.5	5.8	5.3
	L_1	4.9	4.6	—	5.1	4.1	5.4	5.1
	L_2	6.0	5.3	—	6.6	5.0	6.3	5.6

Note: * = excludes 19 crabs captured individually at random within zone 3 (see *Materials and Methods*)

Table 2. Size frequency distributions based on carapace length of males and females, and the percentage number of females per size class, of fiddler crabs.

	U. forcipata			U. urvillei			U. vocans			U. lactea		
	M	F	%F	M	F	%F	M	F	%F	M	F	%F
Carapace length (mm.)												
2.0 – 2.9*	–	1	100.0	–	–	–	–	–	–	19	2	10.0
3.0 – 3.9*	2	–	0.0	–	–	–	1	–	0.0	53	14	20.9
4.0 – 4.9	2	1	33.0	1	–	0.0	–	2	100.0	77	57	42.5
5.0 – 5.9	3	5	62.5	8	3	27.2	2	2	50.0	74	62	45.6
6.0 – 6.9	3	5	62.5	12	2	14.3	2	3	60.0	49	34	41.0
7.0 – 7.9	3	7	70.0	11	6	35.3	3	2	40.0	53	17	24.3
8.0 – 8.9	4	4	50.0	11	6	35.3	2	2	50.0	30	3	9.1
9.0 – 9.9	9	5	35.7	11	3	21.4	1	1	50.0	11	–	0.0
10.0 – 10.9	3	1	25.0	7	4	36.4	4	1	20.0	5	–	0.0
11.0 – 11.9	2	1	33.0	7	2	22.2	4	5	55.5	–	–	–
12.0 – 12.9	–	–	–	8	7	46.7	3	–	0.0	1	–	0.0
13.0 – 13.9	1	–	0.0	6	4	40.0	6	–	0.0	–	–	–
14.0 – 14.9	1	–	0.0	5	–	0.0	5	–	0.0	1	–	0.0
15.0 – 15.9	1	–	0.0	3	2	40.0	2	1	33.3	–	–	–
16.0 – 16.9	–	–	–	–	–	–	–	–	–	–	–	–
17.0 – 17.9	–	–	–	1	–	0.0	1	–	0.0	–	–	–
Total number	34	30		91	39		36	19		373	189	

Note: * = crabs species in these size classes undoubtedly biased as the majority were no sorted to species or sexed (see *Materials and Methods.*)

Thus, in both these species, males are greater in carapace breadth than females at the same carapace length. The regression lines of males and females of *U. forcipata*, respectively, did not, however, differ in slope ($F_s = 1.87$, $p > 0.10$) or in elevation ($F_s = 1.50$, $p > 0.10$), nor did those of *U. vocans* (slope : $F_s = 1.87$, $p > 0.10$; elevation : $F_s = 1.50$, $p > 0.10$). Thus, in *U. forcipata* and *U. vocans*, the carapace dimensions of males and females, respectively, are similar.

As both carapace breadth and carapace length have been used to describe sizes of fiddler crabs, the length of the male major chela (=propodous) was regressed on each variable for each species. All variables were transformed to $\log_{10}$. Each regression was highly significant. Residuals were examined and found visually satisfactory.

Comparison of the error of mean of squares of the regression obtained for each species, however, indicated that chela length was less variable per carapace breadth than carapace length in each species but only significantly less so in *U. urvillei* ($F_s = 2.000$, $p < 0.001$) and in *U. vocans* $F_s = 3.50$, $p < 0.01$). Thus, in view of the fact that Crane (1975) uses carapace length as the standard measure of size, interspecific variation in chela size was examined using the regression of chela length on carapace length. The regression equations, sample sizes, significance values and percent explained variability of each regression are given in Table 3b. Analysis of covariance indicated homogeneity among slopes ($F_s = 1.68$, $p > 0.10$) and heterogeneity among elevations ($F_s = 100.9$, $p < 0.001$) among the species. Subsequent testing

7

Table 3a   Carapace breadth on carapace length regression statistics.

	number of crabs	Regression equation	F_s value	% explained variability
Uca forcipata				
Males	25	$Y = 0.27237 + 0.93359X$	472.701**	95.36%
Females	30	$Y = 0.30549 + 0.89432X$	462.733**	94.37%
U. urvillei				
Males	73	$Y = 0.30203 + 0.91672X$	1585.141**	95.71%
Females	37	$Y = 0.25210 + 0.95020X$	457.615**	92.90%
U. vocans				
Males	31	$Y = 0.27512 + 0.90869X$	776.324**	96.39%
Females	18	$Y = 0.33092 + 0.83837X$	327.833**	95.36%
U. lactea				
Males	70	$Y = 0.26388 + 0.97514X$	676.562**	90.95%
Females	46	$Y = 0.32548 + 0.86660X$	432.291**	90.78%

Notes: $Y = \log_{10}$ carapace breadth; $X = \log_{10}$ carapace length.
      ** $= p < 0.001$

Table 3b   Male major chela length on carapace length regression statistics.

	number of crabs	Regression equation	F_s value	% explained variability
Uca forcipata	25	$Y = -0.37603 + 1.59309X$	261.155**	91.91%
U. urvillei	73	$Y = -0.46296 + 1.72103X$	849.531**	92.29%
U. vocans	28	$Y = -0.42300 + 1.70499X$	515.986**	95.20%
U. lactea	70	$Y = -0.34767 + 1.88211X$	403.638**	85.57%

Notes: $Y = \log_{10}$ chela length; $X = \log_{10}$ carapace length.
      ** $= p < 0.001$

Table 3c   Male dactyl length on chela length regression statistics.

	number of crabs	Regression equations	F_s value	% explained variability
Uca forcipata	25	$Y = 0.20835 + 0.98348X$	414.315**	94.74%
U. urvillei	73	$Y = 0.26410 + 1.06080X$	2766.083**	97.50%
U. vocans	31	$Y = 0.31161 + 1.09540X$	1517.387**	98.12%
U. lactea	71	$Y = 0.27949 + 1.08376X$	4304.046**	98.12%

Notes: $Y = \log_{10}$ dactyl length; $X = \log_{10}$ chela length.
      ** $= p < 0.001$.

8

Table 4. Handedness of male fiddler crabs.

	Left handed	Right handed	Total number
Uca forcipata	17	11	28
U. urvillei	33	52	85
U. vocans	2	32	34
U. lactea	179	179	358

indicated that the elevations of the lines obtained for *U. lactea* and *U. forcipata* differed from one another ($F_s = 129.92$, $p < 0.001$) and from those of *U. urvillei* and *U. vocans* ($F_s = 100.92$, $p < 0.001$) which were similar ($F_s = 2.54$, $p > 0.10$). Thus, at the same carapace length, *U. lactea* males carry a larger chela and *U. forcipata* a smaller chela than *U. urvillei* and *U. vocans*.

To determine if the general dimensions of the male major chela of the species were similar, dactyl length was regressed on chela length. Both variables were transformed to $\log_{10}$. Each regression was highly significant. Residuals were examined and found visually satisfactory. The regression equations, sample sizes, significance values and percent explained variability for each species are indicated in Table 3c. Analysis of covariance indicated no significant difference among slopes ($F_s = 2.267$, $p > 0.05$). The elevations of *U. forcipata* line, however, significantly differed from those of other species ($F_s = 6.312$, $p < 0.001$) whose elevations were homogeneous ($F_s = 2.000$, $p > 0.10$). Thus, dactyl of the major chela of male *U. forcipata* is longer than those of *U. urvillei, U. vocans* and *U. lactea* at the same chela length, although the rate at which dactyl length changes with chela length is similar among species.

Handedness and morphism of male major chela

The numbers of left and right handed males of each morph for each species is given in Table 4.

The frequencies of left and right handed males of *U. lactea* were compared among respective zones using R × C Tests of Independence. No significant heterogeneity in the handedness of brachychelous ($G = 6.22$, $p > 0.10$) or leptochelous ($G = 0.770$, $p > 0.975$) morphs was found among zones. In *U. urvillei*, the frequencies of left and right handed brachychelous males were found to be homogeneous among respective zones ($G = 1.078$, $p > 0.50$). Too few leptochelous males of this species were collected for similar analysis. Insufficient numbers of any of the *U. vocans* morphs from zones 4 and 7 were collected for similar comparisons to be made. Thus, results indicated that, at least for *U. lactea* and *U. urvillei*, no significant heterogeneity in handedness within morphs occurred among zones.

The frequencies of left and right handed morphs of *U. urvillei, U. vocans* and *U. lactea* pooled from respective zones and *U. forcipata* from zone 3 were compared using 2×2 Tests of Independence. No significant heterogeneity was found in handedness of the morphs of *U. forcipata* ($G_{adj} = 0.480$, $p > 0.10$), *U. urvillei* ($G_{adj} = 0.480$, $p > 0.10$) *U. vocans* ($G = 0.894$, $p > 0.50$) or *U. lactea* ($G = 0.034$, $p > 0.50$). Thus, left and right handed individuals were represented in similar frequencies in each species' morphs.

To determine if the frequencies of left and right handed males differed from an expected 1 : 1 ratio a Goodness of Fit Test was applied to each species. All crabs, including those without a major chela or an undeveloped one (either immature or regenerating), were included in this analysis. No significant deviation from the expected frequency was found in *U. forcipata*

9

Table 5 Morph frequency and average sizes of males (based on carapace breadth in mm.) within each zone. Means ($\overline{Y}$) and their 95% confidence limits (L_1, L_2) are back-transformed (see Results); n = number of species.

		ZONES						
		1	2	3	4	5	6	7
Uca forcipata								
Brachychelous	n	–	–	18	–	–	–	–
	$\overline{Y}$	–	–	14.2	–	–	–	–
	L_1	–	–	12.7	–	–	–	–
	L_2	–	–	15.9	–	–	–	–
Leptochelous	n	–	–	5	–	–	–	–
	$\overline{Y}$	–	–	15.9	–	–	–	–
	L_1	–	–	8.9	–	–	–	–
	L_2	–	–	28.3	–	–	–	–
Total no.		–	–	23	–	–	–	–
% Brachychelous		–	–	78%	–	–	–	–
U. urvillei								
Brachychelous	n	–	24	34	–	–	10	–
	$\overline{Y}$	–	13.8	15.1	–	–	20.5	–
	L_1	–	12.5	13.7	–	–	17.9	–
	L_2	–	15.1	16.7	–	–	23.5	–
Leptochelous	n	–	2	7	–	–	–	–
	$\overline{Y}$	–	19.0	17.0	–	–	–	–
	L_1	–	12.2	14.3	–	–	–	–
	L_2	–	29.5	20.2	–	–	–	–
Total no.		–	26	41	–	–	10	–
% Brachychelous		–	92%	83%	–	–	100%	–
U. lactea								
Brachychelous	n	26	38	–	26	28	17	70
	$\overline{Y}$	13.2	11.1	–	13.0	10.9	11.4	9.6
	L_1	11.6	10.4	–	11.9	9.8	10.4	9.0
	L_2	15.1	11.9	–	14.2	12.1	12.6	10.3
Leptochelous	n	12	19	–	4	7	5	9
	$\overline{Y}$	11.1	10.9	–	13.4	9.3	8.9	8.8
	L_1	9.6	9.8	–	8.3	7.6	6.2	7.6
	L_2	13.1	11.4	–	21.6	11.4	12.7	10.3
Total no.		38	57	–	30	35	22	79
% Brachychelous		68%	67%	–	87%	80%	77%	87%

10

Table 5 (cont'd)

								Total no.
U. vocans								
Brachychelous	n	—	—	—	3	—	—	17	20
	$\overline{Y}$	—	—	—	—	—	—	—	17.4
	L_1	—	—	—	—	—	—	—	15.4
	L_2	—	—	—	—	—	—	—	19.6
Leptochelous	n	—	—	—	1	—	—	7	8
	$\overline{Y}$	—	—	—	—	—	—	—	18.7
	L_1	—	—	—	—	—	—	—	16.6
	L_2	—	—	—	—	—	—	—	21.1
Intermediate	n	—	—	—	0	—	—	3	3
	$\overline{Y}$	—	—	—	—	—	—	—	16.1
	L_1	—	—	—	—	—	—	—	7.1
	L_2	—	—	—	—	—	—	—	36.3
Total no.		—	—	—	4	—	—	27	31

% Brachychelous 64%
% Leptochelous 26%
% Intermediate 10%

($\chi^2 = 1.825$, p > 0.10) or *U. lactea* ($\chi^2 = 0.0$, p > 0.975). Thus, in these species the frequency of left and right handedness were similar (Table 4). In *U. urvillei* and *U. vocans*, however, right handed males were predominant ($\chi^2 = 4.247$, p < 0.05; $\chi^2 = 26.470$, p < 0.005, respectively).

In all the species, *U. forcipata, U. urvillei, U. vocans* and *U. lactea*, there was a notably higher proportion of brachychelous morphs than leptochelous or intermediate (in the case of *U. vocans*) morphs (see Table 5). The frequencies of brachychelous and leptochelous morphs of male *U. lactea* were compared among zones using an R × C Test of Independence and found to be heterogeneous (G = 11.070, p < 0.025). A posteriori testing indicated that the percentage of leptochelous morphs were significantly greater in zone 2 than in zone 7 although each of these zones did not differ significantly from zones 1, 4, 5 and 6. However, the trends in variation of these percentages suggest that the frequency of leptochelous morphs is greater in the landward zones (1 and 2) than in the seaward zones (4, 5, 6 and 7). The

frequencies or brachychelous and leptochelous males of *U. urvillei* were found to be homogeneous among zone 2, 3 and 6 (G = 0.0, p > 0.90). Insufficient numbers of *U. vocans* were collected from zones 4 and 7 for similar comparisons to be made for this species.

As significant heterogeneity in the sizes of males of *U. lactea* and *U. urvillei* was found among zones (see above), mean sizes of brachychelous and leptochelous males of these species were compared following transformation of the data to $\log_{10}$. Carapace breadth was used as this was the measure more highly correlated with chela length than was carapace length (see above). The back-transformed means and their 95% confidence limits are shown in Table 5. In *U. lactea* there was no significant difference in the sizes of morphs within each zone, except in 6 where the brachychelous males were significantly larger than the leptochelous ($t_s = 2.372$, p < 0.05). In *U. urvillei* no significant difference was indicated between the average sizes of the morphs in zone 2 ($t_s = 1.934$, p > 0.05), or 3 ($t_s = 0.271$, p > 0.50). No leptochelous males

of *U. urvillei* were collected from zone 6 to allow similar comparisons. Thus, morph frequency does not appear to be related to crab size in *U. lactea* and *U. urvillei*. Furthermore, the average sizes of brachychelous and leptochelous males of *U. forcipata* which occurred in zone 3 did not differ significantly (t_s = 0.806, p > 0.40) and those brachychelous, leptochelous and intermediate males of *U. vocans* were found to be homogeneous using analysis of variance (F = 0.390, p > 0.50).

IV. RESULTS

Zonation

Uca lactea was the most widely distributed species, occuring in all other zones, except 3 (mangrove forest). *Uca urvillei* occurred at the landward edge of the mangrove forest (zone 2), within the forest (zone 3) and seaward of the forest along the edge of a channel (zone 6). Thus, *U. urvillei* was sympatric with *U. lactea* in zones 2 and 6. *Uca forcipata* was only found within the mangrove forest (zone 3) where it was sympatric with *U urvillei*. *Uca vocans* occurred in the more seaward zones on the shore : at the edge of the mangrove forest (zone 4) and on the sand flat (zone 7), and in both areas was sympatric with *U. lactea*. No fiddler crabs were recorded from the seaward mud flat (zone 8), (see Frith & Brunenmeister, 1980).

V. DISCUSSION

The sizes of the four fiddler crab species, *Uca forcipata*, *U. urvillei*, *U. vocans* and *U. lactea*, were comparible to those given for them by Crane (1975). Very large males were rarely found, the majority of males having a shorter carapace than the maximum size we recorded for a species (Table 2). This, however, is typical of *Uca* populations (Crane 1975). Female *Uca* are usually smaller in carapace dimensions than the largest sized conspecific males and generally always smaller than the average sized males (Crane 1975). We found that *U. forcipata* and *U. lactea* males

clearly attain carapace lengths larger than females, but *U. urvillei* and *U. vocans* females were of similar size to the average size males in the populations, although none were as large as the largest male.

The maximum sizes attained by male and female *U. lactea* are much smaller than those which their congeners *U. forcipata*, *U. urvillei* and *U. vocans* attain. Frith and Brunenmeister (1980) record this species as numerically dominant and its average population density higher than any of the other fiddler crab species occurring in the study area. Since display territory size is related to crab size (Crane 1975), Frith and Brunenmeister (1980) suggest that the smaller size of mature *U. lactea* permits greater individual packing within an area compared to its larger congeners.

Fiddler crabs, particularly large males, tend to move to upper levels of their intertidal habitat at the onset of display to allow more time during the low water period for these activities. Thus, it was noteworthy to find the largest males and females of *U. lactea* in the landwardmost zones (1 and 4 respectively) of the disjunct landward and seaward areas they occupied. Similarly the largest males and females of *U. vocans* occurred in the landwardmost zone (4) of its two zones Frith and Brunenmeister (1980) record the largest number of juveniles of these two species in the more seaward zones occupied by them. *Uca urvillei*, unlike its congeners, was largest and most abundant in its seawardmost zone (6), (Frith & Brunenmeister (1980). Frith and Brunenmeister (1980) relate this to the preference shown by this species to lower shore levels (Crane 1975) as zone 6, of the three zones it occupied (2, 3 and 6 respectively) was the only one covered by all tides.

Sex ratios were found to vary with size classes, our findings being similar to those recently described for *U. pugnax* (Wolf, Shanholtzer & Reimold 1975). Wenner (1972) examined sex ratio per size class in various marine crustanceans and

identified four patterns. Of these, one of which he termed an anomalous curve corresponds to our findings, particularly for *U. lactea* (Table 2). He suggested four reasons for this curve : differential migration, mortality and growth and sex reversal. Whilst the latter does not occur in fiddler crabs, the other factors could account for these differences. Differential migration occurs in fiddler crab populations both seasonally and during a tidal cycle (Crane 1975). With respect to differential mortality Wolf *et al* (1975) proposed that the male claw and the display use of it may function to deter predators, whereas the female lacks such a claw and as a result may suffer heavier predation. However, due to their prolonged display activities, males should be more vulnerable to predation and/or starvation than females (Crane 1975) and therefore be less abundant. A higher mortality rate would not explain our findings (males two to three times more numerous than females) nor those of Wolf *et al* (1975), unless as Elmen (1966) noted where survivorship of males and females is significantly different, proportionally more of the greater risk sex would need to be zygotically produced for optimum reproductive potential. Hence to understand such sex ratio imbalance it is necessary to know what it is at hatching. It is noteworthy that a deviation from a 1 : 1 sex ratio is not unusual in marine crustaceans (Wenner 1972). Finally, growth data on crustaceans are sparse, and with respect to fiddler crabs have dealt primarily with allometry. Energy budgets certainly differ between male and female *Uca* but their effects on growth remain to be investigated.

The growth of fiddler crabs is conspicuously allometric, that is, the rate of growth differs in different parts of the anatomy. Crane (1975) discusses and illustrates allometry in fiddler crabs and briefly reviews previous work on the subject. Comparisons made between different morphological characters clearly illustrate allometry which is typical of the genus *Uca* (Crane 1975). Crane (1975) noted that the measurements of the major cheliped and to a lesser extent the carapace breadth show the greatest relative change with growth. Our data clearly illustrate this, as did Frith and Frith's (1977b) study of *U. tetragonon*. The relative proportions of the morphological characters we examined differed between species and sexes. Differences observed in chela size at similar carapace lengths among the males of the four species may be important in interspecific encounters. Male *U. lactea*, although considerably smaller than males of its sympatrics, is perhaps less disadvantaged due to its relatively longer major chela.

The relative frequencies of left and right handedness of male major chela can vary from population to population (Vernberg & Costlow 1966), but in general right and left handed crabs occur about equally (Crane 1975). The ratio of left and right handedness was similar in the *U. forcipata* and *U. lactea* populations. Marshall and Medway (1976) report similar findings for a population of *U. lactea* they examined in New Hebrides, south west Pacific. In our *U. urvillei* and *U. vocans* populations, however, right handed males predominated; as was also found in an *U. tetragonon* population (Frith & Frith 1977b). There were, however, no significant differences in the handedness of brachychelous and leptochelous morphs of *U. urvillei* and *U. lactea* between zones, or overall for any of the species. Brachychelous morphs were significantly more numerous than leptochelous morphs in all the species, and than the intermediate morph of *U. vocans*. Frith and Frith (1977b) report a similar situation for *U. tetragonon*. These findings suggest that in South East Asian populations there is an apparent tendency toward brachychelous morphism, whereas in the American populations examined by Crane (1975) leptochelous morphs predominated.

The significance of chela polymorphism of male *Uca* is poorly understood. Crane (1975) suggests that since young leptochelous and brachychelous males are found in the same biotope the difference in chela cannot result from nutritional differences. Our observations that the average size of morphs within zones did not differ,

and that in *U. lactea* difference in morph frequency among zones was not correlated with average crab size, support her contention. However, she does note that 'well grown' males generally regenerate claws with leptochelous charateristics. This suggests that growth rate or energy allocation may be a factor. Hence if it costs less to produce leptochelous claws (which weigh less than brachychelous claws at the same length (Crane 1975) then those males near an energy minimum may grow in carapace size at the same rate as males producing a less formidable weapon. Crane (1975) states that the majority of morphological specializations are used only in agnostic behaviour, primarily between males, rather than in courtship.

ACKNOWLEDGEMENTS

REFERENCES

CRANE, J., 1975, *Fiddler crabs of the world. Ocypodidae: Genus Uca.* New Jersey: Princeton University Press. 736 pp.

EMLEN, J.M., 1968, A note on natural selection and sex ratio. *Amer. Nat., 102* : 94-95.

FRITH, D.W., 1977, A preliminary list of macrofauna from a mangrove forest and adjacent biotopes at Koh Surin, western peninsular Thailand. *Phuket Mar. Biol. Center Res. Bull., 17* : 1-14.

FRITH, D.W. & BRUNENMEISTER, S., (1980). Ecological and population studies of fiddler crabs (Ocypodidae : Genus *Uca*) on a mangrove shore at Phuket Island, western peninsular Thailand. *Crustaceana, 39(2)* : 157-184.

FRITH, D.W. & FRITH, C.B., 1977a, Range extensions of fiddler crabs (Ocypodidae: Genus *Uca*) in the north-western Malay Peninsula area. *Crustaceana, 32* (1) : 100-102.

FRITH, D.W. & FRITH, C.B., 1977b, Observations on fiddler crabs (Ocypodidae : Genus *Uca*) on Surin Island, western peninsular Thailand, with particular reference to *Uca tetragonon* (Herbst) *Phuket Mar. Biol. Center Res. Bull., 18* : 1-14.

FRITH, D.W. & FRITH, C.B., 1978, Notes on the ecology of fiddler crabs (Ocypodidae: Genus *Uca*) on Phuket, Surin Nua and Yao Yai islands, western peninsular Thailand. *Phuket Mar. Biol. Center Res. Bull., 25* : 1-13.

FRITH, D.W. TANTANASIRIWONG, R. & BHATIA, O., 1976. Zonation and abundance of macrofauna on a mangrove shore, Phuket Island. *Phuket Mar. Biol. Center Res. Bull,. 10* : 1-37.

14

GREEN, J. & SCHOCHET, J., 1972, Chela type in *U. vocans. Amer. Zool., 12* : 714-715.

MARSHALL, A.G. & MEDWAY, Lord, 1976. A mangrove community in the New Hebrides, southwest Pacific. *Biol. J. Linn. Soc., 8* : 319-336.

SERENE, R., 1972, Notes on the Indo-Pacific species of *Uca. Phuket Marine Biol. Center,* unpublished report.

SNEDECOR, G.W. & COCHRAN, W.G., 1967, *Statistical Methods.* 6th ed. Iowa : State University Press. 593 pp.

SOKAL, R.R. & ROHLF, F.J., 1960, *Biometry* San Francisco : W.H. Freeman & Co. 776 pp.

VERNBERG, F.J. & COSTLOW, J.D., JR., 1966, Handedness in fiddler crabs (Genus : *Uca*). *Crustaceana, 11* : 61-64.

WENNER, A.M., 1972, Sex ratio as a function of size in marine crustaceans. *Amer. Nat., 106* : 321-350.

WOLF, P.L., SHANHOLTZER, S.F., & REIMOLD, R.J. 1975. Population estimates for *Uca pugnax* (Smith 1870) on the Duplin Estuary Marsh, Georgia, U.S.A. (Decapoda, Brachyura, Ocypodidae). *Crustaceana, 29* (1) : 80-91.

APPENDIX

The number of quadrats and random samples taken in each zone, and the number of males, females and juveniles of the species collected from each zone overall.

	Quadrats				3 × 1 metre areas				Total no. of crabs		
	S	M	F	J	S	M	F	J	M	F	J
Zone 1											
Uca lactea	23	31	15	14	1	17	8	0	48	23	14
Zone 2											
U. urvillei	23	17	10	38	1	14	6	11	31	16	49
U. lactea		63	48			7	10		70	58	
Zone 3											
U. forcipata	52	16	11	57	2	1	0	18	36*	30*	75
U. urvillei		35	12			13	4		48	16	
Zone 4											
U. lactea	7	28	10	6	1	16	5	6	42	15	12
U. vocans		3	2			1	1		4	3	
Zone 5											
U. lactea	20	36	15	15	1	24	9	37	60	24	52
Zone 6											
U. urvillei	5	6	4	5	2	9	4	14**	15	8	20**
U. lactea		6	4			25	11		31	15	
Zone 7											
U. lactea	15	61	18	36	5	68	36	143	129	54	179
U. vocans		7	6			26	10		33	16	

Notes : S = no. of samples; M = male; F = female; J = juvenile.
* = totals include an additional 19 individually captured crabs of each sex.
(see *Meterials and Methods.)*
** = juveniles sampled from only one of the two sample areas.