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STUDY ON THE HABITAT PREFERENCE OF THE SNAPPING SHRIMP *ALPHEUS EDWARDSII* (AUDOUIN)[1]

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Ming-Shiou Jeng and Kun-Hsiung Chang (1988) Study on the habitat preference of snapping shrimp *Alpheus edwardsii* (Audouin). *Bull. Inst. Zool., Academia Sinica* 27(2): 91-103. *Alpheus edwardsii* (Audouin) is the dominant species of snapping shrimp in the intertidal area of Taiwan. The relation between its habitat and environment was studied by monthly sampling from September 1980 to December 1981 at Tam-Shui, northern Taiwan. Life specimens were brought back for the experiments of substrate preference.

It was found that the *A. edwardsii* distribute unevenly in the intertidal zone, but large assemblages were found under the low water mark of neap tide. The highest density of those assemblage observed in situ was 47 individuals per square meter. Nests of the snapping shrimps tended to distribute uniformly. The average distance between nearest neighbors was about 16.5 cm.

Around the habitat of *A. edwardsii*, other large decapods were also very abundant. Density of these decapods was around 580 individuals per square meter in an average. The Shannon-Weaver species diversity index (H′) was 1.32, and the average eveness component of diversity (J′) was 0.50. However, other decapods will not have competition with snapping shrimp since they inhabit on the upper substrate of the nest of *A. edwardsii.*

A. edwardsii behaved in a tendency of both positive thigmotaxis and negative phototaxis. When only one tropism was satisfied, the positive thigmotactic reaction would take priority of the negative phototic reaction.

More than eighty percent of shrimp individuals preferred pebble to coarse and fine sands. Furthermore, water depth also influenced habitat selection. However, the influence from particle size and water depth to the selection of habitate was not correlated.

Key words: Habitat preference, Snapping shrimp.

Habitat structure may have important effects on the structure of natural communities (McGuinness and Underwood, 1986). Workers on marine soft-bottom communities have paid attention to habitat composition since the majority of the organisms are buried in the substrate, rather than attached to it (Huling & Gary, 1976; Hockin, 1982). It has been suggested that the composition of these communities is the result of interactions between habitat structure and a variety of other environmental variables, including water content and drainage, particle size,

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oxygen content, food content, stability of the the temperature and substratum. These variables may be influenced by the organisms themselves (Ruello, 1973; Moore, 1972a, b; Hocking, 1982).

Snapping shrimp (genera *Alpheus* and *Synalpheus*) live in various marine habitats ranging from mud-flate to sumerged coral heads and sponge cavities (Banner, 1953; Hazlett, 1962; Williams, 1965; Schein, 1975; Abele, 1976). Although snapping shrimps are capable of swimming, they rarely do so in the adult stage. They are notably secretive and demand ready made or easily maintained burrows (Johdson *et al.*, 1974).

Several workers reported that snapping shrimps were found only where some sort of shelters were provided. Nolan and Salmon (1970) looked closely at the way that the snapping shrimps seek protection and manipulated various substrates to construct adequate shelters. Knowlton and Keller (1983; 1985) described the sibling species of alpheid shrimps associated with the Caribbean sea anemones. Harada (1969) described "burrow" construction by *Alpheus bellulus* in another report concerning the relationship between this Pacific snapping shrimp and a gobioid fish. Karplus *et al.* (1981a, b) investigated the distribution and partner specificity of six species of gobies and seven species of burrowing alpheid shrimp in the northern Red Sea. Bowers (1970) examined that the behavioral and ecological adaptions associated with construction and inhabitiance of algal tubes by *Alpheus clypeatus*. Johnson *et al.* (1947) and Knowlton & Moulton (1963) used hydrophones to record snapping noises over different bottom types and at various depths.

We (1985) examined snapping shrimps from the intertidal zone at Tam-Shui, Peng-Hu, and Nan-Wan in Taiwan and found that *Alpheus edwardsii* was the dominant species of snapping shrimp in Taiwan. It inhabited in burrows beneath the rubble or pebble on the rocky and/or coral filled sand-flat, either solitarily or as heterosexual pairs.

According to Banner and Banner's reports (1973; 1982; 1983), *A. edwardsii* distributes from Red Sea, Australia, Thailand, to the Philippines. It probably extends widely through the Indian Ocean, into Southeast Asia, but it is not known neither on the isiands of the Central Pacific nor from New Zealand. It has been reported by De Man (1888) that they inhabited in a part of the western Atlantic region from the coast North Carolina (United States) to Abrolhos (Brazil).

Our aims in this paper were (1) to investigate the habitate characteristics of *A. edwardsii* in the intertidal zone at Tam-Shui; (2) to understand which sedimentary factors were correlated with its distribution in the area; and (3) to determine whether identifiable snapping assemblages were present.

MATERIAL AND METEHODS

Study site

Study area was located at the intertidal zone of northwest coast at Tam-Shui town (121°25′E; 25°11′N) where the estuary of Tam-Shui river was closely neighbored. One side of the area faced the river and other approach to the sea so that a triangular area was formed (Fig. 1). For the sands aggregation of Tam-Shui river, the right bank of the river protruded in the sea to form a tableland and volcanic terrains where the coastline was more even and smooth, and the erosion effect was mainly influenced by northeast monsoon.

Near the main study area there was a small creek, called Lintzu creek where the substrates at estuary were varied. There were three kinds of substrates: sands, muds, and pebbles dispersed in the area, The area was a typical brackish water area but the change of salinity of the sea water was also clear. The *Alpheus lobidens* De Haan was the most abundant species of snapping shrimp in this area.

The intertidal zone, to the northwest of Lintzu creek, was the main field study area

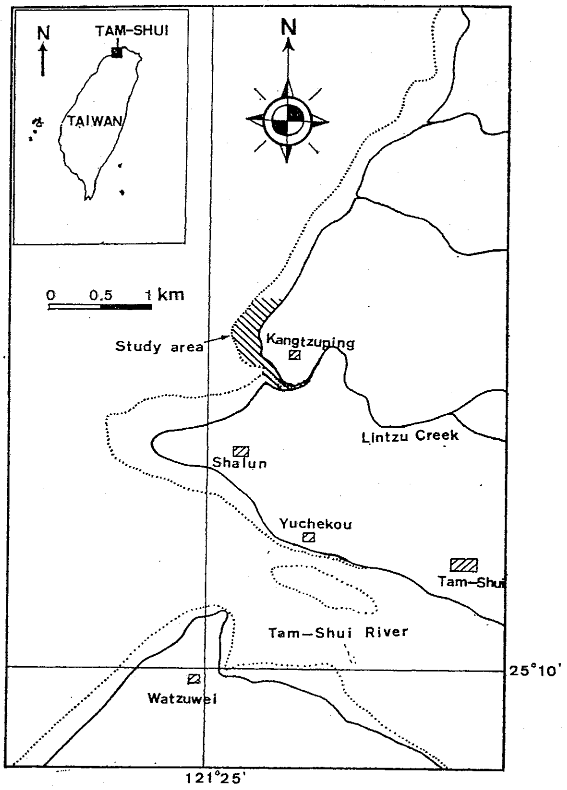

Fig. 1. Map of study area.

about 500 meters long. Besides, the coast was mainly composed of gravels and boulders, Though many huge rocks scattered, only a few tidal pools scattering in this area. There was a stone-made fish trap with length about 100 meters. Eight species of snapping shrimps were found under the substrates of pebble of the fish trap. They were *A. edwardsii* (Audouin), *A. pacificus* Dana, *A. leviusculus* Dana, *A. splendidus* Coutière, *A. sulcatus* Kingsley, *A. gracilus* Heller, *Betaeus granulimanus* Yokoya, and *Automate dolichognatha* De Man. Among them, *A. edwardsii* and *A. pacificus* were the two dominant species.

Tidal change at Tam-Shui was apparent. The maximum of tide range could reach 3.36 m (Hsu, 1962) and according to the results of authors' monthly survey from Dec. 1980 to Ded. 1982, the tempearture of sea water in the tidal pool fluctuated between 14°C and 31.4°C and the salinity was between 25.95‰–35.73‰.

Particle size analysis

In the area between fish trap and coast we took seven sampling stations. The distances from firsh trap to each test station were 10, 30, 50, 70, 90, 110, and 130 m seperately. At each station we brought back samples of substrates with $15 \times 15 \times 15$ cm^3 of each. The analytical method of particle size in the present study was from Folk (1974) and Stoddart (1978).

Spatial distribution

Accrding to the method of Underood's 1981). we set six straight line, 30 m apart between lines from the fish trap, to one fixed spot at inland area. The individual number of shrimp was collected and counted from substrate of 1 m^2 quadrat every 10 m on each line.

To understand the effect of other biological factors on shrimp distribution, we collected all large decapods from three arbitrary 1 m^2 quadrats seperately. Each quadrat was about 10 m from firsh trap. The specimens were identified and counted for each species and the index of diversity and eveness (Poole, 1974; Pielou, 1966, 1975) were calculated.

Distribution of nests with paired shrimps

Study area is situated at the low water line. A total number of six quadrats, 1 m^2 each, were taken in this area. Only the nests with paired shrimps were adopted to to select those nests which had the nearest neighbor within the quadrate and then the distance of their nearest neighbors were measured according to Clark and Evans (1954).

Test of thigmotaxis and phototaxis

The following three treatments were carried out in laboratory:

1. Put snapping shrimps into a plastic contatiner, and half of which was covered by black plastic sheet to make a dark zone.

2. Put snapping shrimps into the container as above and then put 5 dark and 5

transparent tubes in the light zone. The diameter of tubes is 15 mm.

3. Put snapping shrimps into the container as above and only 10 transparent tubes were put in the light zone.

Ten individuals of shrimps with total length more than 20 mm were used to do the above three treatments. Each treatment was replicated four times.

The reaction of the snapping shrimps during the first five minutes in the container was recorded. The exact positions of of these snapping shrimp were then recorded after 24 hours. During the observation period, no food was supplied and indoor light was about 200 lux.

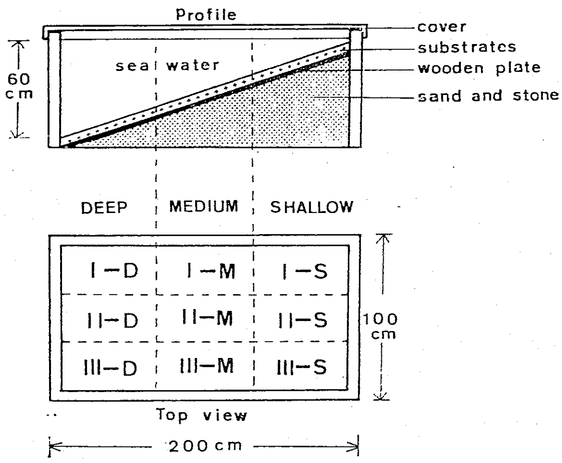

Fig. 2. Design of experimental tank for substrate-depth test.

Substrate preference

We divided the experiment into two groups, the first group was to study the substrate preference of snapping shrimp alone, and the second was to study the interaction of water depth with different substrates to substrate preference. For the first group of experiment, three kinds of experimental substrates were collected near the study area. The first one was pebbles with -4.43ϕ in average and more than 80% of particles with the diameters larger than 4 mm. The second kind was coarse sand with size mainly between 0.5 mm and 4 mm, and the average particle size was -0.73ϕ. The last one was fine sand which sizes of main particles were mostly between 0.125 mm and 0.5 mm with average of particle size was 1.83ϕ.

The above three substrates were laid and equally divided longitudinally into an large concrete tank of 2 m long, 1 m wide, and 0.8 m high. The depth of substrate was about 15 cm and water depth is 30 cm. Two hundred healthy indiduals of *A. edwardsii* were put together into the tank each time. The experiments were completed within 2 day after the specimens were collected. The tank was covered to avoid any interference of sunlight. After 48 hours, the tank was drained to count the individual number of shrimp on each kind of substrate.

For the second group of experiment, three kinds of substrates were laid as three parallel longitudinal zones in the tank. The layer of these substrates was about 10 cm in thickness which were arranged as a slope of 30° as shown in Fig. 2. The whole bottom were divided into 9 sectoins representing different depths and substrates. A total of 120 individuals were put into the tank. After 48 hours, the tank cover was removed and the numbers of shrimp on different sections were counted. The above experiments were repeated three times by switching the order of substrates arrangement. The above data were analyzed by Chi-square test to study the interaction of substrate and water depth to the habitat preference of snapping shrimps.

RESULTS

Particle size analysis

Fig. 3. shows that the coarse particles occupied the largest portion in all seven quadrats. The average degrees of pariticles $Mz\phi$ in these quadrats was between -3.07ϕ and -4.77ϕ, which means that the substrate was mostly made by gravels at every test quadrat. The sorting degrees in each test station were all more than 1.5ϕ which indicated that the

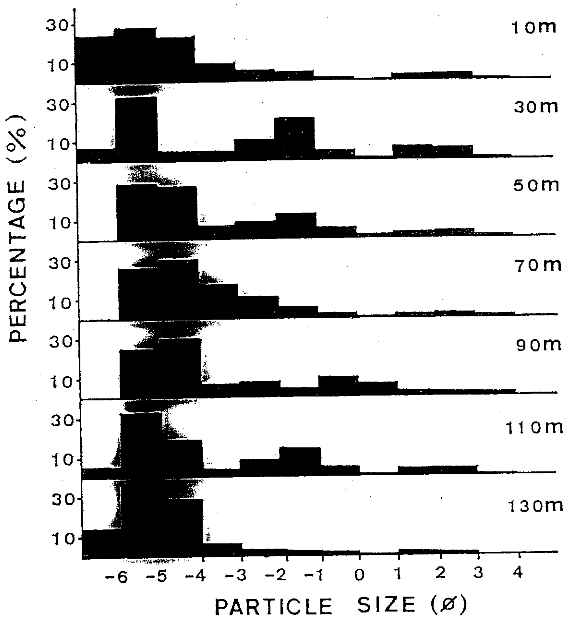

Fig. 3. Percentage composition (by weight) of substrate samples with different particle size collected at a series of intertidal levels.

degrees of particles were much irregular. As to the degrees of aslant of substrate samples only the guadrat at 30 meters was fine-skewed, all other quadrats were strongly fine—skewed.

Based on the results of cumulative frequency of percentage compositioon by weight, it is known that more than 80% particle in all quadrats were larger than 2 mm in diameter except the quadrat of 90 meters (73.6%). According to Wentworth's particle size classification (Folk, 1974) the 90 meters quadrat belong to the catalog of "sandy pebble gravel" and the other guadrats "gravel".

Spatial distribution

Fig. 4 shows the abundance of shrimps in the study area. The highest density can reach 47 individuals per square meter which mostly distributed in the zone 30 meter away from the low water line. The individual

TABLE 1

Abundance (ind./m^2) of decapod collected at three sampling stations

Species	Stations I	II	III	Mean
Alpheus edwardsii (Audouin)	29	43	40	37.3
Alpheus lobidens De Haan	0	2	2	1.3
Alpheus pacificus Dana	0	0	1	0.3
Automate dolichognatha De Man	1	0	0	0.3
Petrolisthes japonicus De Haan	236	218	182	212.0
Petrolisthes coccineus (Owen)	4	3	1	2.7
Petrolisthes sp. 1	1	3	2	2.0
Petrolisthes sp. 2	0	1	0	0.3
Thalamita danae Stimpson	2	3	1	2.0
Eriphia smithii MacLeay	1	2	0	1.0
Gaetice depressus (De Haan)	49	26	31	35.3
Leptodius exaratus (H. Milne Edwards)	19	25	23	22.3
Leptodius sanguineus (H. Milne Edwards)	2	1	1	1.3
Metopograpsus messor (Forskål)	0	1	2	1.0
Metopograpsus sp.	0	0	1	0.3
Hemigrapsus sanguineus (De Haan)	0	0	1	0.3
Hemigrapsus sp.	239	286	251	258.6
Pagurus sp. 1	2	0	1	1.0
Pagurus sp. 2	0	1	1	0.7
Number of species	12	14	16	14
Number of individuals	585	615	541	580.3
Species diversity (H′)	1.31	1.30	1.34	1.32
Evenness (J′)	0.53	0.49	0.48	0.50

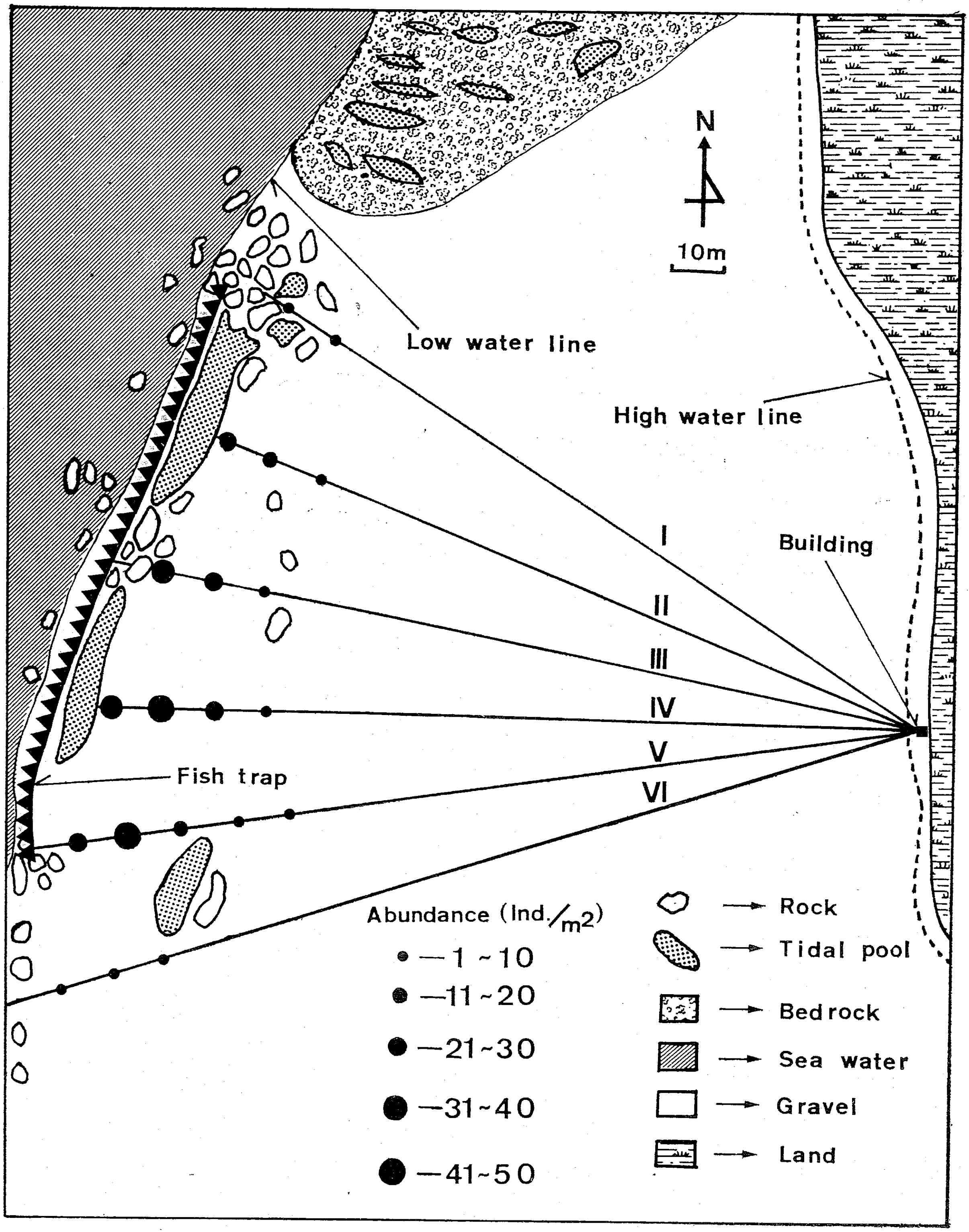

Fig. 4. Distribution of *Alpheus edwardsii* (Audouin) in Kangtzuping, the study area.

number gradually decreased toward the land. It is almost absent in the zone 50 meter away from the low water line.

Table 1 lists the abundance of all decapods distribution at three sampling quadrats. Among these decapods, the porcelain crabs and hermit crabs were the two most abundant species. These were 212 individuals of porcelain crabs and 258 individuals of hermit crabs on an average per square meter.

A. edwardsii could always be found under every stone were removed in the study area and the average density was 37 indiviuals per quadrat. The second dominant decapods in this area was *Gaetice depressus* and *Leptodius exaratus*. The abundance of the rest of 14 species of decapods were much less; no more than 4 individuals could be colleted in each quadrat. The average total number of individual in the 3 quadrats was 580. The average Shannon-Weaver diversity index (H′) was 1.32 and average eveness component of diversity (J′) was 0.50.

Distribution nests with paired shrimps

A total number of 88 nests which had paired shrimps were observed from six 1 m^2 quadrats. Among these nests, 35 nests had the nearest neighbor. The average distance of nearest neighbor was 16.5 cm. The shortest distance was 10 cm and the longest was 35 cm.

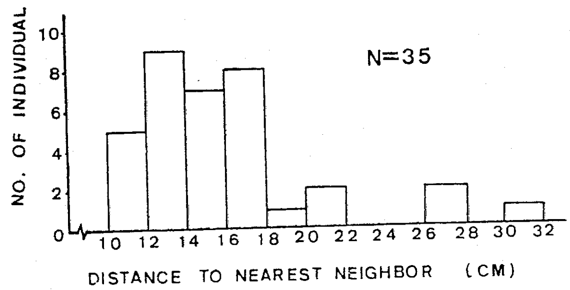

Fig. 5. Frequency distribution of distance to nearest neighbor among pairing nests.

Fig. 5 indicated the frequency distribution of average distance when nearest neighbor occurred. Expected average distance of nearest neighbor calaulated from the nest number in a known unit area was 13.1 cm. The ratio R of the experimented and expected average was 1.26 which was falling into the range of 1 and 2.15. It meant that the spatial distribution of shrimps was uniform.

Test of thigmotaxis and phototaxis

The results of first the experiment show that all the snapping shrimps escaped to the dark zone and never stayed in the light zone during experimental period. Thus, the *A. edwardsii* was negative phototaxis.

In the second of experiment, 77% of the snapping shrimps stayed in dark tubes, 15% in transparent tubes and 8% around the sides of tubes (Table 2). It was apparent more snapping shrimps stayed in dark tubes

TABLE 2
Results of thigmotactic and phototactic test of *Alpheus edwardsii* (Audouin).
Three groups (1, 2, 3) of conditions were tested separately.
Further explanation please see text

Expt. conditions / Repeat	1		2			3		
	Light	Dark	Dark tube	Glass tube	Side	Dark	Glass tube	Side
I	0	10	8	1	1	0	9	1
II	0	10	7	2	1	1	8	1
III	0	10	7	2	1	0	8	2
IV	0	10	9	1	0	1	8	1
Total	0	40	31	6	3	2	33	5
Total (%)	0	100	77	15	8	5	82	13

TABLE 3
Results of *Alpheus edwardsii* (Audouin) preference test on three kinds of substrate

Experiments	I		II		Mean (%)
	Count	%	Count	%	
Sand type	29	14.5	24	12.0	13.3
Pebble type	156	78.0	166	83.0	80.5
Coarse sand type	7	3.5	4	2.0	2.7
Death	8	4.0	6	3.0	3.5
Total	200	100.0	200	100.0	100.0

than in transparent tubes (t=11.8>t (n=6. p=0.01) =3.71). Thus, they were inclined to select a condition which could provide both positive thigmotaxis and negative phototaxis.

In the third expriment, the snapping shrimps would escape to the dark zones immediatly after put them into the container. Then. they would move gradually into the transparent tubes in light zones about 5 minutes later. Through the whole experimental period, there were large amount of snapping shrimps in light zones, of which, 82.5% stayed in transparent tubes on an average.

Moreover, the snapping shrimps which stayed in transparent tubes were apparently larger than those in dark tubes (t=24.02>t (n=6, p=0.01) =3.71), which indicated that the positive thigmotaxis was more important than negative phototaxis when only one taxis was satisfied.

Substrate preference

In Table 3, the results indicated that 80% of the tested snapping shrimps preferred pebble the most. The fine sand was next comprising of 13.3% and the the coarse sand was the least according to only 3.5%. It was noticed that many snapping shimps which selected the coarse sand and fine sand as habitat were situated along the edge of the tank. Because the substrate of fine sand could produce concave surface more easily than that of coarse sand, the amounts of snapping shrimps in the substrate of fine sand were more than those of coarse sand.

Snapping shrimps were significantly different in their preference toward the three substrates. Difference between pebbles to coarse sand and fine sand was t=29.78 and t=24.06> (n=2, p=0.05)=4.30 respectively. And the differences between coarse sand and fine sand was t=7.20>t (n=2, p=0.05)=4.30. It was noticed that snapping shrimps would excavate many nests in the substrate of pebbles after 48 hours in the tank. Some times, more than two individuals were found living in the same nest.

As to the interaction of both substrates and depths to substrate preference, Fig. 6 shows that most snapping shrimps prefer pebble in different water depth. However,

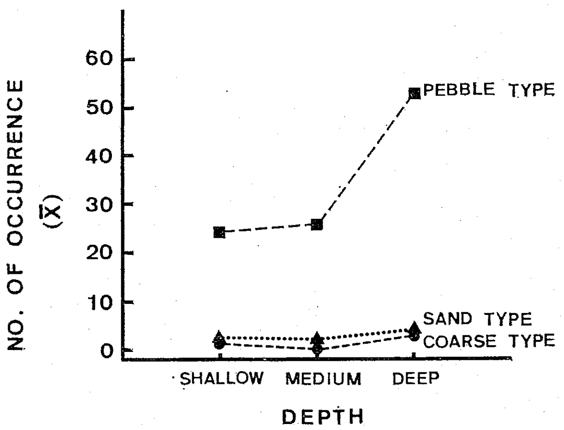

Fig. 6. Preference test of the effects of three kinds of substrates and three kinds of water depths on *Alpheus edwardsii* (Audouin).

with the pebble substrate, the individual number was much greater (44.2% in average) in deep water than the shallow and medium depths based on the pebble type. The sand type and coarse type had the same tendency but not so significant. Thus, water depth would affect habitat preference of snapping shrimps.

The result of Chi-square test, $\chi^2=4.63<\chi^2(n=4, p=0.05)=9.49$; $(n=4, p=0.01)=13.28$, indicated that the relationship between water depths and substrate types was not significant, i. e. the two factors independently influence habitat preference of snapping shrimps.

DISCUSSION

Banner and Banner (1982) mentioned that most species of the edwardsii group of the genera *Alpheus* live in burrows of sandy to silty bottom, often constructed under rocks. From our field observation, we found that *A. edwardsii* stayed in the nests at gravel bottom about 5–15 cm in depth. These nests were tightly packed by upper layer of gravels. We also found that there were one to several entrances among those gravels above the nests. Some gravel substrates could still keep small amount of water where a pair of *A. edwardsii* was usually observed.

Our results of the nests distribution showed that there were 12 to 18 nests in each quadrat per square meter within the area between 10 and 20 meters away from the low water line. According to the results of distances of nearest neighboring, it was apparently that the nests of *A. edwardsii* were inclined to distribed uniformly. Besides, with the data of actual measurement of nearest neighboring distances, it was found the nearest distance between two nests was more than 10 cm which also so indicated that each pair of snapping shrimps had fixed territory. *A. edwardsii* had territory behavior around the nest since the territory behavior of paired snapping shrimps also existed in coral head. For example, a pair of *Alpheus lottini* which lived branching corals mostly in the colonies of *Seriatopora* and *Pocillopora* has strong terriorical behaviour (Patton, 1966; 1974).

Although Hazlett (1962) performed an experiment to determine thigmotactic and phototactic reactions of snapping shrimp which probably would influence shelter seeking, he did not provide his raw data and the results were still ambiguous. In the present study, we found that the positive thigmotaxis of snapping shrimps was more important than negative phototaxis in this experiment. Because snapping shrimps would rather choose the transparent tube in the light area instead of staying in th dark area without tube.

Certain kinds of benthic decapods stayed in intertidal zone could use substrates as their shelters, feeding sites and sources of nutrition (Abele, 1974). Thus, substrates was an important factor in nonbiological environment for the benthic decapods. The mean diameter (Mzϕ) of particle degree of the substrates in the study area were all between -3.07ϕ and -4.77ϕ. And the diameter of almost 80% particles were more than 2 mm in every test station so that the sorting degrees in the study area was relatively poor. This indicates that the substrates in all intertidal zone were mainly composed of gravels with irregular particle size. This kind of substrate may provide a good shelters for snapping shrimps.

William (1958) mentioned that the amount of water in substrates and the substrate composition would also influence the extent of being excavated. The throats of gravel is larger than that fine and coarse sand since the latter two substrate have better sorting degree, so that the substrate of gravel is easier to be excavated by snapping shrimps.

A. edwardisii could live for several hours under the condition of no water existed. Especially when air temperature was below 20°C. the *A. edwardsii* would live more than

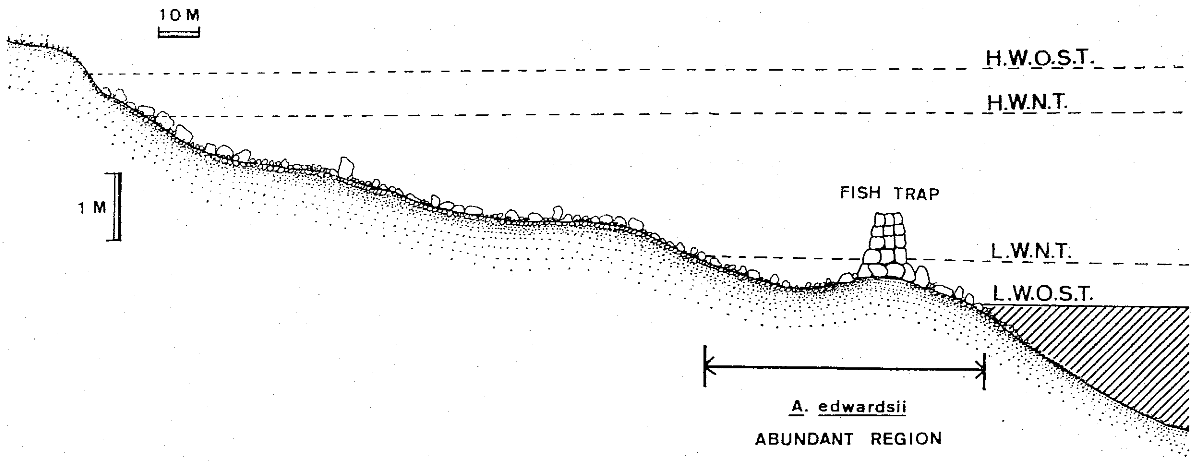

Fig. 7. Profile of study area.
H. W. O. S. T. : High water mark of ordinary spring tide.
H. W. N. T. : High water mark of neap tide.
L. W. N. T. : Low water mark of neap tide.
L. W. O. S. T. : Low water mark of ordinary spring tide.

one day in a small bottle without sea water. If there was enough humidity in the bottle *A. edwardsii* would live even longer than two days.

Under large stones in gravel intertidal zone or the rocks on gravel beaches as well as under the cover of mud sediments, the anaerobic condition should occur frequently. It was apparent that those animals which stayed in these environments should have the ability to adapt or imporve the environments (Cobb, 1971; Meadow and Campbell, 1972).

Many animals in intertidal zone had the ability of aerial respiration (Nicol, 1960). *A. edwardsii* seems to be one of them. Because they would expose themselves to air after ebb, they should keep their gills wet for aerial respiration. However, we found that snapping shrimps still preferred the low tide area (Fig. 7) which meant that they would avoid being exposed themselves in the air too long.

When studied the habitat of *A. edwardsii* with the two factors of substrates and water depths, we found that there were more than 80% snapping shrimps inhabit in gravel area. The number of individuals increased with the water depth. Because tidal cycle could not be simulated in experimental tank, we could not test the effect of ebb or flow on habitat preference of *A. edwardsii.* As to the condition of habitat preference between substrate and water depth in this experiment, the results indicated that these two factors were independent to each other.

Around the habitat of *A. edwardsii,* other large decapods were very abundant. Among them, the porcelain crab *Petrolisthes japonicus* and hermit crab *Pagurus* sp. 1 were the two dominant species. If they inhabited in the nest, they might affect the habitat selection and distribution pattern of *A. edwardsii,* but their habitat are on the upper substrate of the nest. So, it is believed that their existence will not affect the distribution of the species of present studies.

Many marine invertebrates which are sessile or sedentary as adults have motile larvae which may account for much or all of the movement that occurs during the life cycle. So, it is difficult to study the behavior of those larvae. Recently, Knowlton and Keller (1986) reported that the larvae of three sibling species of alpheid shrimp, which live symbiotically with the Caribbean sea anemone *Bartholomea annulata*, had highly localized recruitment with extended larval development. They also suggested that a detectable proportion of the successful recruits settled extraordinary close to it parents. The larvae of *A. edwardsii* may use the same way in our study area since large assemblages were found under the low water mark of neap tide.

In addition to the biotic and abiotic factors discussed above, there are many other factors which will influence the habitat preference of the snapping shrimps. Factors such as individual size, individual density, height of tide, and food resources will also influence the procedure of habitat preference of snapping shrimps. These factors remain to be studied.

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艾氏槍蝦 *Alpheus edwardsii* (Audouin) 對其棲所選擇之研究

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艾氏槍蝦 *Alpheus edwardsii* (Audouin) 是臺灣淡水地區潮間帶數量最豐富的一種槍蝦，1980 自年 9 月至 1981 年 12 月之間，每月採集調查研究其棲所與環境之間的關係，並將活的個體帶回實驗室從事其對棲所選擇的試驗。

艾氏槍蝦在潮間帶的分布並不均勻，但發現較多的個體聚集在低潮線之處，其每平方公尺數量可達47尾。巢穴趨向於均勻分布，各巢穴最近隔鄰距離的平均為 16.5 公分。

在艾氏槍蝦棲所周圍之大型十脚類的數量非常豐富，平均每平方公尺內十脚類的個體數為 580 尾，羣集的平均歧異指數（H′）為 1.32，平均均勻度（J′）為 0.50。然而因其它十脚類棲息於艾氏槍蝦巢穴的上層底質，因此與槍蝦並無競爭情形。

在行為反應上，艾氏槍蝦具有背光性和向觸性，當環境只能滿足其中一種趨性時，其向觸性反應會大於背光性。以三種不同顆粒組成的底質環境提供給艾氏槍蝦自由選擇棲所，結果顯示棲息於礫石底質的數量最多，平均佔總尾數的80％以上。此外，海水的深度亦影響其對棲所的選擇，但是底質和水深兩種因子的影響是獨立的。