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The Gaiting Behaviour of the Grass Crab, *Hemigrapsus penicillatus* on the Nettings

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The quantitative mechanics on the sideways walking of the crabs may provide a basic solution for entanglements of the walking legs in gillnets. The gaiting behaviour of the crabs on the flat board and the nettings 10, 16 and 23 *mm* in mesh size were experimented concerning about stepping positions and times in the laboratory using video set on July, 1984.

It was found that the irregular movements of walking crabs in stepping positions and patterns were appeared on the nettings due to the absence of mechanical contact in spite of neural control of compensating, while on the flat surface evolved systematic leg movements. The mean stride length and walking velocity, which were increased with the carapace width on the flat board, as well as the step period and forward by backward stroke time were greater than those values on the netting, not associated with the carapace or the mesh size. Also, the step period and the phase difference on the nettings revealed larger fluctuation than on the flat board.

The joint angles of the walking legs, on the nettings in meropodite-carpopodite and thorax-meropodite, which joint was varied especially up to below horizon because of the falling legs through the netting twine, were virtually wider than those on the flat substrate.

Introduction

Locomotion of the crabs, Brachyura, which were caught mainly by traps and gillnets, was appeared mostly as walking rather than swimming. For the walking movements, although the crabs can move in any directions easily in a short time, they usually move laterally using eight walking legs divided into leading and trailing.

Investigations for the gaiting behaviour of a few kinds of crabs were carried out on a normal surface in various experimental conditions (Sleinis and Silvey, 1980; Herreid and Full, 1986).

Approaching behaviour of the rock crabs toward plane nets was studied in relation to the size of carapace and mesh (Watanabe and Sasakawa, 1984).

However, walking and fishing mechanism of the crabs on an uneven substrate were hardly mentioned about stepping positions and times. It was necessary to find out difference between the gaiting patterns of the crabs on the flat board and the netting, and to clarify the entangling phenomenon of the walking legs through the mesh.

As conducted previously experiments for the shrimp (Kim and Ko, 1985), the walking movements of the grass crabs on the nettings were observed and analyzed on dorsal and lateral positions, and time variation of the steps by using video set.

Materials and Methods

The grass crabs, *Hemigrapsus penicillatus*, were collected from intertidal zone of the Dongback island, Pusan.

They were kept in an oval aquarium, L 100×B 50×D 30 cm, with a sloping sand floor and filtering sea water in the laboratory at the temperatures 23—27°C on July, 1984.

About twenty crabs ranged from 22 to 34 *mm* in carapace width were released and walked sideways in air on the flat board and three netting frameworks with the mesh size 10, 16 and 23 *mm*. The walking legs of a crab were represented by L for lateral leading and T for lateral trailing, designated 2—5 from anterior to posterior.

The most of step factors were compared with only four legs, L3, L4, T3, T4, which play major role in lateral walking and mean step periods of four legs were used for evaluating the phase difference between legs.

The joint angles of leading legs L3 and L4 were measured by setting the video camera laterally and measured directly from the monitor scene only for the thorax (horizontal)-meropodite (H-M) joint, meropodite-carpopodite (M-C) joint and propodite-dactylopodite (P-D) joint.

The other methods were same as described in the previous paper (Kim and Ko, 1985).

Results and Discussion

The relationship between carapace width (C. W, *mm*) and length of 3rd and 4th walking legs (L. L, *mm*) in the crabs was shown in Fig. 1, and the regression line can be calculated as follows:

$$L.L = 1.4\ C.W - 1.0 \quad (n = 100,\ r = 0.87).$$

However, the walking legs of the grass crabs were relatively weaker and shorter than those of *H. sanguineus* (Kim, 1973).

The walking movements of the crabs in sideways straight walking and turns on the four substrates

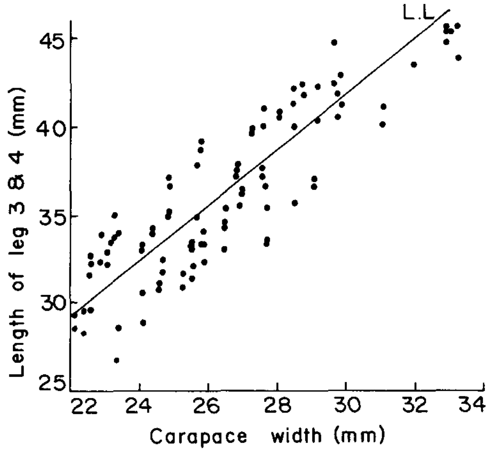

Fig. 1. Relationship between the carapace width and the length of walking legs in the grass crabs.

were observed and analyzed for the stepping positions and time variations as follows.

1. General features

Analysis of the gaiting behaviour in the grass crabs showed that general patterns of walking motion on the nettings were similar to those of the shrimp (Kim and Ko, 1985). Leg positions and stepping times were disturbed and made an excursion on the nettings while remained constant octapedal walking typically on the flat board. A false step during swing of leg produced a lurching gait due to an absence of mechanical contact with the netting twine and then passed through its segments in accordance with relationship between the size of crab and the mesh. Unusual walking movements of crabs were generated by the organ ablation(Fourtner and Evoy, 1973) as well as by abnormal substates (Varju and Sandeman, 1982).

The lateral view of walking crabs on the nettings was seen in Fig. 2. An abdomen of the crabs was in contact with the netting twine since the most of the walking legs passed through the mesh. As the falling legs swung fore and back or pushed forward stroke, the gaiting patterns became very irregular and were adjusted in order to compensate the unbalance of walking movement by control of resistance

Fig. 2. Lateral view of walking motion in the grass crabs on the nettings of (A) 16*mm* and (B) 23*mm* in mesh size.

reflexes in the walking (Evoy and Ayers, 1982; Dunham and Schöne, 1984). The entangled segments of falling legs were commonly seen in dactylopodite, propodite and meropodite associated with the mesh size 10, 16, and 23 *mm* respectively.

The examples of the step positions dorsally at the tips of walking legs on the flat board and the nettings were shown in Fig. 3. An arrow in the step positions indicates that false stepping leg during stroke moved to a new position and a prime index of the number means falling leg between netting twine. The principal difference of the stepping position was exposed that the relative leg positions between walking legs on the nettings were interrupted largely with increasing the mesh size, while on the flat substrate kept a constant interval of inter-leg position.

The sideways walking crabs change their walking directions to right or to left readily in a while even though turning is a complex manoeuvre involving all eight legs. When turning of the crabs achieved on the flat surface centering around one point of axis, there was a different .stepping movement depend on inner or outer legs from the center of turning axis. It was observed that the stride length of the outer legs were longer than those of inner legs like as the cases of the turning insects (Franklin, Bell and Jander, 1981). However, when the crabs turned on the netting, stepping positions and strides were very irregular in a leg as well as inter-legs regardless inner or outer legs because of the differences in substrate.

The representative examples of the step patterns for leading and trailing legs of the crabs were depicted with the function of time as shown in Fig. 4. When coupling of the steps was absent

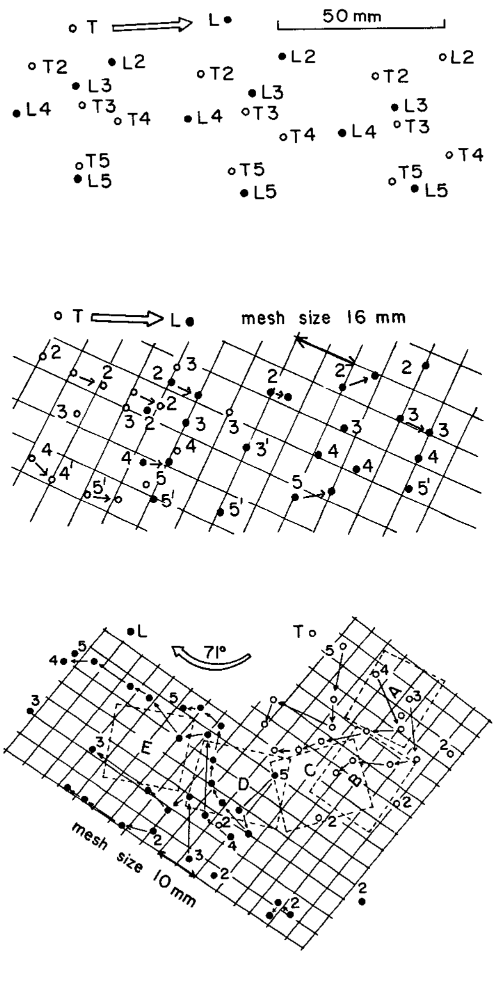

Fig. 3. Examples of the stepping positions in the walking crabs on the flat board and the nettings.

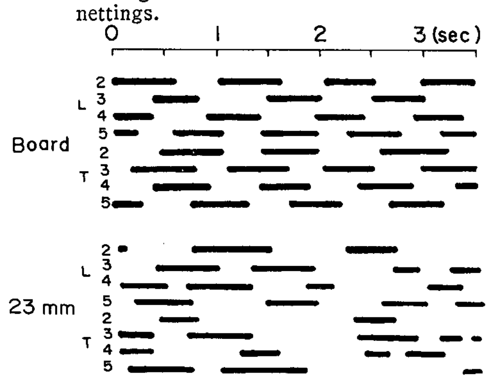

Fig. 4. Stepping patterns of the walking legs on the flat board and the nettings.

on the nettings, as shown in the stepping positions, a number of unusual step patterns appeared remarkably. Although, there were many conditions bring about abnormal step patterns, the variation of the stepping times in the grass crabs on the netting was resembled to those in insects on the slippery surface under a point of uneven substrate (Epstein and Graham, 1983).

The irregularity of step patterns in accordance with the mesh size also caused to the irregular change of periods, phase difference and walking velocity, on the contrary to the movements of the restraint legs (Miyamoto and Yamaguchi, 1977; Cruse and Müller, 1986).

According to the results of general features in walking movements of the grass crabs, the stepping positions and times were influenced briefly by the contact conditions of substrates so that the patterns of the walking movements on the nettings were significantly different from those on the flat board.

2. Stepping positions and times

The quantitative descriptions of the walking movements for the grass crabs concerning stride, period, phase difference, and joint angle were performed in detail to compare with the substrates.

The mean stride length of the crabs which was measured from the gaiting distance moved per step of legs L3, L4, T3, T4, under the four substrates was given in Fig. 5. There was apparent relationship on the flat board between the stride length (S. L, *mm*) and the carapace width as follows;

$S.L = 1.7\ C.W + 1.6$ ($n = 59$, $r = 0.50$, $p < 0.001$)

While there was no correlation on the nettings where the mean stride length was about 20 *mm* regardless the mesh size. The walking on a flat surface was raised a longer stride length, about 1.2 times of leg length, than on the nettings by a paired difference T test ($p < 0.001$) and large crab traveled longer distance per step than small one (Burrows and Hoyle, 1973; Herreid and Full, 1986).

It was noteworthy that Watanabe and Sasakawa (1984) reported the relation beween carapace length and mesh size that allows rock crab to pass through

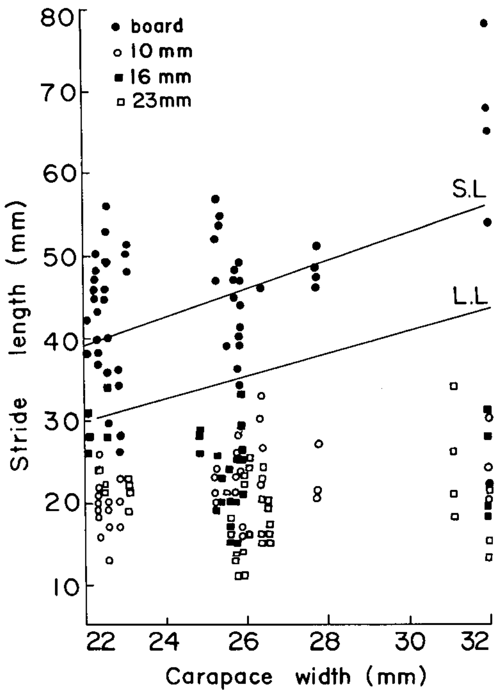

Fig. 5. Relationship between the carapace width and the stride length of the glass crabs.

and to climb up. However, its results hardly explained gaiting behaviour on the nettings, and the gap deriving between passing and climbing mesh size for the crabs. Fishing mechanism of gillnets being entangled crabs must be reconsidered in relationship between mesh size and swing motion of legs on walking movements (Sasakawa, 1982).

As calculated from the step patterns, the mean step period and forward by backward stroke time (F.S/P.S) on the four legs were shown in Table 1, and have a large fluctuation either in a leg or a crab regardless the carapace width. There were considerable differences between any of two periods among the four substrates ($p < 0.05 - 0.01$) except for between the flat board and mesh size 10 *mm*. Furthermore, the mean period and its standard deviation (S.D) on the nettings were gradually increased with increasing the mesh size (Foth and

Table 1. The period and the F. S/B. S of the walking crabs on the flat board and the nettings

Gaiting parameter		Flat board	Netting 10 *mm*	16 *mm*	23 *mm*
Period	mean(*sec*)	0.83	0.87	1.04	1.35
	S.D	0.26	0.29	0.35	0.60
	n	40	20	20	20
F. S/B. S	mean	0.98	0.67	0.76	0.75
	S.D	0.17	0.09	0.17	0.09
	n	10	10	10	10

Bässler, 1985).

Estimated walking velocity was determined from mean distance of the walking crabs moved per one sec. on the flat board and the nettings as shown in Fig. 6. The mean walking velocity of the crabs was higher on the flat board than on each mesh size of the nettings ($p<0.001$) and was slightly reduced from 30 *mm*/sec to 10 *mm*/sec with increasing the mesh size ($p<0.05$), The relationship between the mean speed (V, *mm*/sec) and the carapace width was achieved only on the flat surface by least squares regression line as follows:

$$V=2.1\ C.W+1.3 \quad (n=30,\ r=0.4,\ p<0.05)$$

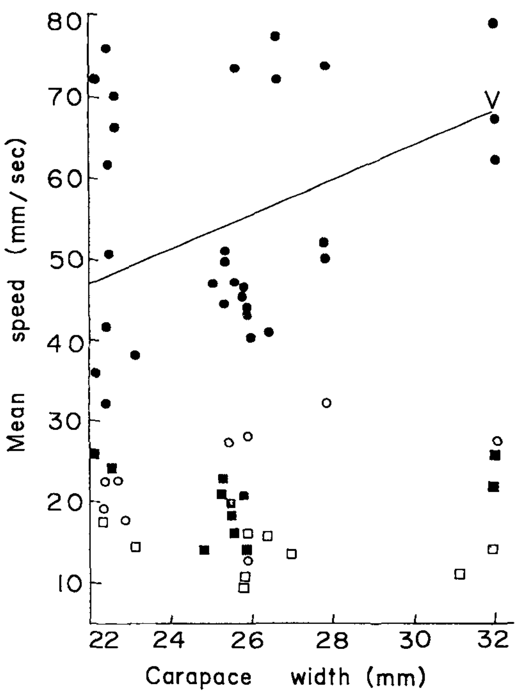

Fig. 6. Relationship between the carapace width and the walking velocity of the crabs.

The results above were inferred from the variations of the stride length and the period which were different from the case of the shrimp in water (Kim and Ko, 1985) and the ghost crab in air (Burrows and Hoyle, 1973).

Since the walking on the netting involved an absence of mechanical contact with the substrate, it tends to impede orderly movements of the walking leg and to become an irregular step pattern. Therefore, an evaluation of the phase difference referring to mean period was restricted at least to the four legs with bilateral and ipsilateral under the four conditions. The phase difference histograms were composed of two types of positive and negative phase values on the nettings, but the mean phase difference was treated by all samples as shown in Fig. 7.

The mean phase difference about 0.4 and its standard deviation about 0.2 on the flat board were definitely dissimilar to those values on the nettings which were decreased from 0.4 to 0.2 in the mean phase while increased from 0.3 to 0.6 in standard deviation with increasing the mesh size. The negative phase value, which was commonly seen when interruption occurred by changing of period in a leg or in all legs, also appeared more increasing with the mesh size.

There are many expermients to produce a different step period between legs on crabs fixing legs (Evoy and Ayers, 1982) and on stick insects (Foth and Bässler, 1985). However, the description of the negative phase has been employed already by others (Land, 1972; Miyamoto and Yamaguchi, 1977) somewhat like this result. The more detailed statement was described on the stepping time variation from lagging to leading or vice versa when the legs appeared different periods each other by Cruse and Müller (1986).

The schematic diagrams of the three joint angles during protraction i.e extension and retraction i.e flexion of the leading legs L3 and L4 were illus-

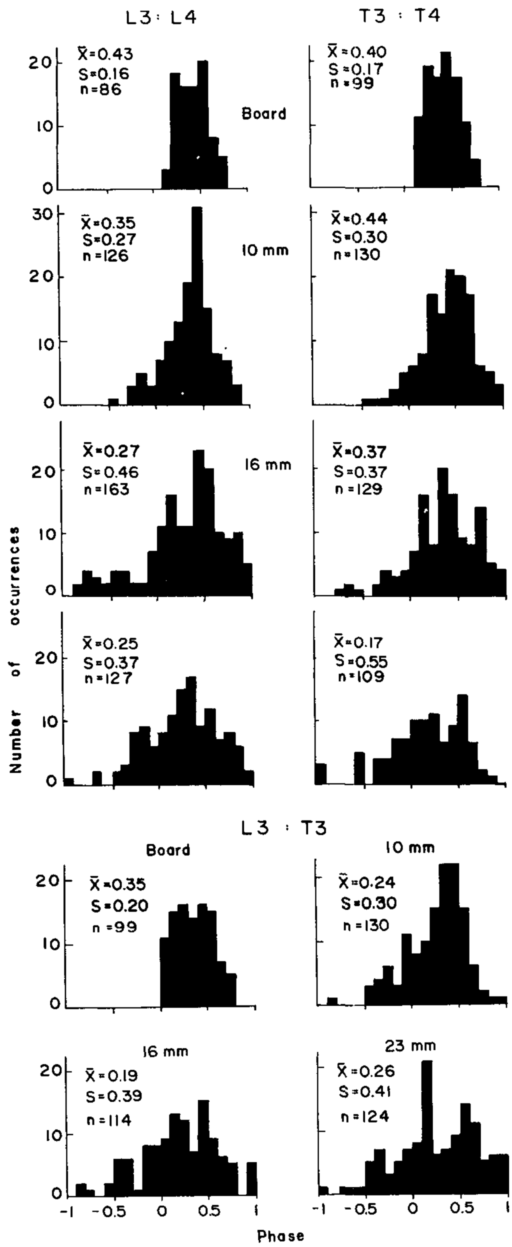

Fig. 7. Relative phase histograms of the walking crabs for ipsilateral and bilateral legs. X: mean phase, S: standard deviation, n:number of sample.

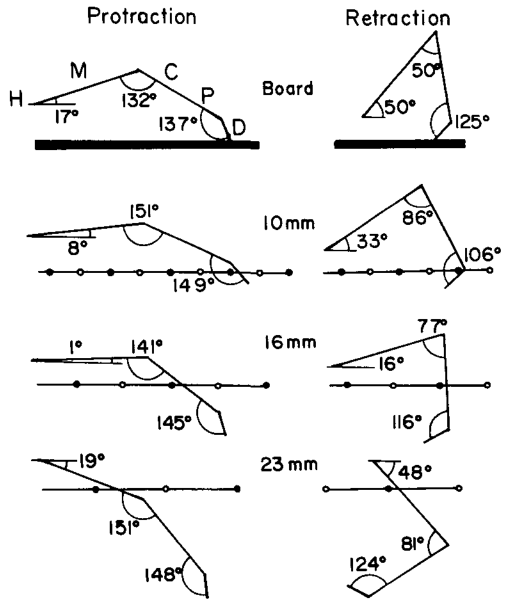

Fig. 8. Joint angles between segments of the walking legs at protraction and retraction under the four substrates.

trated in Fig. 8. A comparision of the lateral position in the walking crabs showed that the joint angles of the legs on the flat board were significantly different from those on the nettings due to the passing through and to entangling segments.

The H-M angle was decreased approximately from 20° to −20° below horizon at protraction and from 50° to −50° at retraction in accordance with the flat board and mesh size of the nettings. The M-C angle was varied less from 130° to 150° at protraction rather than from 50° to 90° at retraction, while the P-D angle contained relatively constantas about 140-150° at protraction and about 110-125° at retraction under the four substrates.

The change of joint angles between protraction and retraction on the flat surface in this results was similar to the results from obtaining electro-physiological methods. Otherwise, the joint angles on the nettings were different from those of walking in abnormal conditions of the crabs such as fixing the legs and organ ablations, because of an absence of mechanical contact with the uneven netting substrate (Miyamoto and Yamaguchi, 1977; Evoy and Ayers, 1982).

Summary

The sideways walking movements of the grass crabs on the flat board and the nettings 10, 16, 23 *mm* in mech size, were investigated on the stepping positions and times in air by using the video camera and recorder. It was concluded that the irregular movements of the walking crabs were revealed more on the nettings than on the flat board due to an absence of mechanical contact with the subatrates.

1. The lengh of the 3rd and 4th walking legs (L. L, *mm*) was increased with the carapace width (C. W, *mm*) as follows;

$$L.L=1.4\ C.W-1.0$$

2. The stride length (S. L, *mm*) on the flat board was as follows;

$$S.L=1.7\ C.W+1.6$$

and greater than those values on the nettings where the mean strdide length was about 20 *mm* regardless the mesh size.

3. The mean phase difference about 0.4 ± 0.2 on the flat board was definitely dissimilar to those values on the nettings which varied from about 0.4 ± 0.3 to 0.2 ± 0.6 with the mesh size.

4. The mean velocity (V, *mm*/sec) of the walking crabs on the flat surface was increased with the carapace width as a following regression line;

$$V=2.1\ C.W+1.3$$

and faster than on the nettings where slightly reduced from 30 to 10 *mm*/sec with incresing mesh size.

5. The joint angles of the walking legs were changed in the H-M joint from 20° to below horizon −20° at protraction and from 50° to −50° at retraction, and in the M-C joint from 50° to 90° at retraction with the four substrates, while the other joints remained virtually constant angles.

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망지에 대한 풀게(*Hemigrapsus penicillatus*)의 보행운동

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통발과 자망 등에 어획되는 게류의 측면적인 보행운동은 매우 특이하여 어획 메카니즘을 밝히는데 매우 중요한 요소가 된다. 여기서는 해운대 동백섬의 조간대에서 채집한 풀게를 사용하여 망지위에서의 직선적인 운동과 회전 운동 등을 관찰하고 다리의 보행위치와 시간적인 변화를 분석하였다.

그 결과 망지위에서의 보행운동은 착지위치에 따라 그물코 사이로 다리가 빠지게 되는 불규칙적인 움직임이 대부분이므로 여러가지 보행 요인들의 편차가 게의 크기에 관계 없이 크게 나타났다. 풀게의 망지위에서의 보폭, 보행속도, 다리간의 위상차 등은 평면에서 보다 훨씬 작았으나, 보행주기, 다리마다간의 각도 등은 평면에서 보다 약간 증가하였다. 따라서 게가 자망에 걸리는 현상은 게의 크기에 따른 다리의 보행운동과 망지의 망목크기 등을 고려하여 세밀하게 조사되어야 할 것이다.