THE DISTRIBUTION AND ABUNDANCE OF THREE SPECIES OF PEBBLE CRABS (BRACHYURA: GRAPSIDAE) IN THE NORTH JAPAN BOULDER SHORE IN RELATION TO THEIR FEEDING HABITS AND ENVIRONMENTAL FACTORS

著者	TAKEDA SATOSHI
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THE DISTRIBUTION AND ABUNDANCE OF THREE SPECIES OF PEBBLE CRABS (BRACHYURA: GRAPSIDAE) IN THE NORTH JAPAN BOULDER SHORE IN RELATION TO THEIR FEEDING HABITS AND ENVIRONMENTAL FACTORS[1]

SATOSHI TAKEDA[2]

Marine Biological Station, Tôhoku University, Asamushi, Aomori 039-35, Japan

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The distribution patterns of three species of grapsid crabs were investigated in the boulder shores of north Japan, and the morphology of their mouth parts was analyzed in relation to feeding habit. *Hemigrapsus penicillatus* inhabited estuarine shores where small creeks flowed continuously. On the other hand, *Hemigrapsus sanguineus* and *Gaetice depressus* inhabited marine boulder shores, the latter occupying shores more frequently exposed to wave action, compared with the former. *G. depressus* captured suspended solids using long setae with evenly spaced lateral spines on the second and third maxillipeds, and fed on the solids. The other two species, however, possessed smooth and plumose setae on their second and third maxillipeds, and showed no behaviour for capturing suspended solids. The distribution patterns of these three crab species are discussed in relation to their feeding habits and environmental factors, including salinity condition and exposure to wave action.

INTRODUCTION

The crabs of the Grapsidae (Brachyura: Decapoda) occupy various habitats, such as tidal flats, boulder shores, rocky shores, land and trees. Although their habitats vary, some investigators have dealt with their ecology, e.g., the relationships between their distributions and environmental factor(s), or among species (e.g., GOSHIMA *et al.*, 1978; FUKUI and WADA, 1983; TAKAHASHI *et al.*, 1985; TAKEDA and KURIHARA, 1987), unlike ocypodid crabs, which inhabit mainly tidal flats (e.g., TEAL, 1958; ONO, 1965; WADA and TSUCHIYA, 1975; RINGOLD, 1979; WADA, 1982; BERTNESS and MILLER, 1984).

In the inter- and infra-littoral boulder shores of Japan, three species of grapsid crabs, *Hemigrapsus sanguineus* (DE HAAN, 1835), *Hemigrapsus penicillatus* (DE HAAN, 1835) and *Gaetice depressus* (DE HAAN, 1833), are found commonly (e.g., KIKUCHI *et al.*, 1981; FUKUI and WADA, 1983; TAKAHASHI *et al.*, 1985). The distributions and abundances of these three species have been investigated in the

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1) Contribution from the Marine Biological Station, Tôhoku University, No. 615.

2) 武田 哲

shores of south, southeast and north Japan (Kikuchi *et al.*, 1981; Fukui and Wada, 1983; Takahashi *et al.*, 1985). Nevertheless, there is insufficient knowledge of the relationships between their distributions and environmental factor(s), or among the species.

It has been reported that *H. penicillatus* feeds upon sessile matter on stones, algae attached to stones, deposited materials, and small animals by handling with its chelipeds (Okamoto and Kurihara, 1989; Toba, 1989). On the other hand, Depledge (1989) has reported that *G. depressus* feeds upon suspended matter captured by elongated setae on the third maxillipeds, in addition to deposited and/or attached materials using its chelipeds. However, there has been no investigation on the relationships among their feeding habits, distribution patterns and environmental factor(s), although in ocypodid crabs the relationships existing among the morphology of mouth parts, feeding behaviour, distribution patterns and physical condition(s) of the substratum have been studied (Ôno, 1965; Wada, 1982).

In the present study, I attempted to analyze the distribution patterns of the above three species of grapsid crabs in relation to their feeding habits and environmental factors. For this purpose, the distributions and abundances of the crabs were initially investigated in relation to environmental factors on boulder shores in north Japan. Moreover, the morphology of the mouth parts and feeding habits were observed in the laboratory.

Materials and Methods

The distribution patterns of three species of grapsid crabs were investigated on the shores near the Marine Biological Station, Tôhoku University, Asamushi, Aomori city (40°54′ N; 140°51′ E) (Fig. 1). The area investigated is located on the west side of the Natsudomari Peninsula, which projects from the middle part of the south shore of Mutsu Bay. In the area, boulder and rocky shores are present alternately, and the three species of grapsid crabs inhabit the boulder shores.

Mutsu Bay is frequently exposed to the southwest wind in winter, and to the northeast wind in summer (Hoshiai, 1965; Kyozuka *et al.*, 1981, 1982, 1983). The area investigated is hardly exposed to the waves produced by the northeast wind, because the area is located on the west coast of the peninsula. On the other hand, the waves produced by the southwest wind wash the area. In general, the area investigated was divided into three parts according to the difference in the degree of exposure to wave action; the area to the south of a small islet, Hadakajima, which is directly washed by waves (Stns. 1–7), the area to the east of Hadakajima, where wave action is weaker than at the former location (Stns. 8–13 and 17) because the area runs parallel with the direction of wave propagation, and the area where there is hardly any exposure to waves due to a protecting breakwater (Stns. 14–16).

The distribution and abundance of the crabs were investigated at the low water of the spring tide between 8 and 13 April 1985, because the study area is emerged enough to investigate the distribution pattern of grapsid crabs only the low water of the spring tide in spring. At each station, all grapsid crabs were collected within a 1-m^2 quadrat near the low water level of the neap tide, while all the boulder stones were removed. At the same time, the number of layer(s) of boulder stones and the texture of the bottom under the stones were recorded, because grapsid crabs conceal themselves in the apertures created between boulder stones, and between the stones and the bottom under the stones (Tanaka *et al.*, 1981; Kurihara and Okamoto, 1987; Kurihara *et al.*, 1989). The crabs collected were recorded for sex, and the

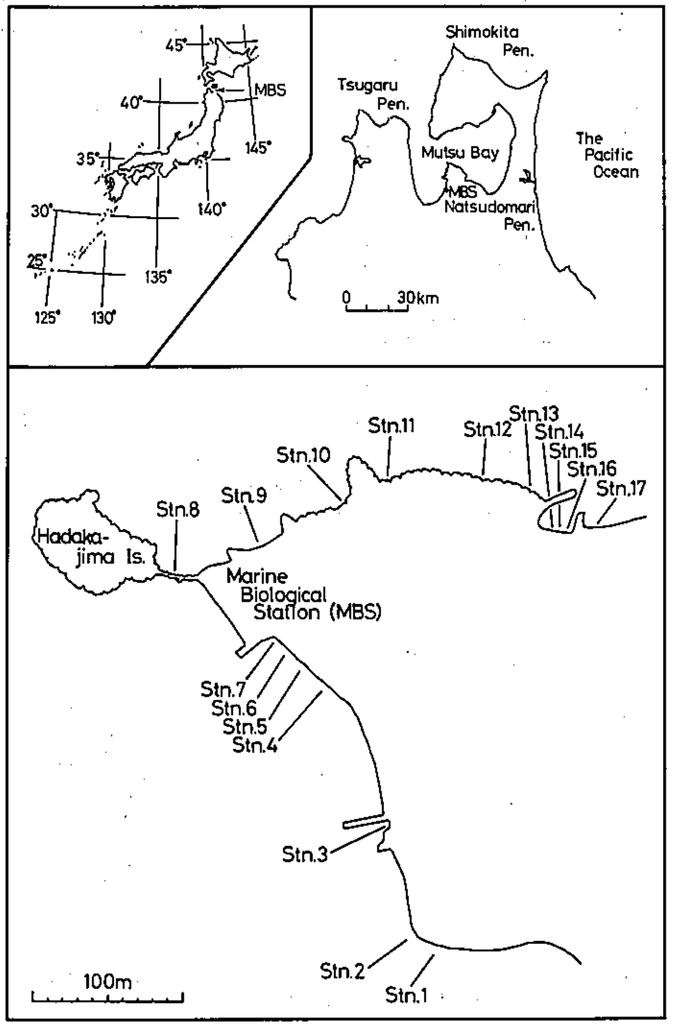

Fig. 1. Maps of the area around the Marine Biological Station (MBS) with the sampling stations indicated.

maximum carapace width was measured as an index of body size. Salinity was measured at high water on 8 and 16 May 1985.

The grapsid crabs collected were fixed and stored in 70% ethanol, and the general morphology of their mouth parts and the distribution and morphology of the setae were observed under a binocular microscope.

Results

Field investigation

The substratum conditions were divided into four types based on combinations of the amount of boulder stones and the texture of the bottom under the stones (Table 1). Stations 14, 15 and 16, which were located in the cove sheltered by a breakwater had sand or muddy sand under a single layer of stones, and the stones were smaller than those at other stations. At Stns. 11, 12 and 13, a single layer of stones lay on rocks partly covered by gravel and pebbles. One layer or two layers of boulder stones lay on gravel and pebbles at Stns. 1, 2, 4, 5, 6, 7 and 17, and at Stns. 3, 8, 9 and 10.

Table 1. Substratum condition at each station. The substratum condition was categorized into four types according to the combination of the amount of boulder stones and the nature of the bottom under the stones.

Substratum condition	Stn.
One layer of boulder stones on sand or muddy sand	14, 15, 16
One layer of boulder stones on gravel and pebbles	1, 2, 4, 5, 6, 7, 17
Two or more of layers boulder stones on gravel and pebbles	3, 8, 9, 10
One layer of boulder stones on rocks partly covered by gravel and pebbles	11, 12, 13

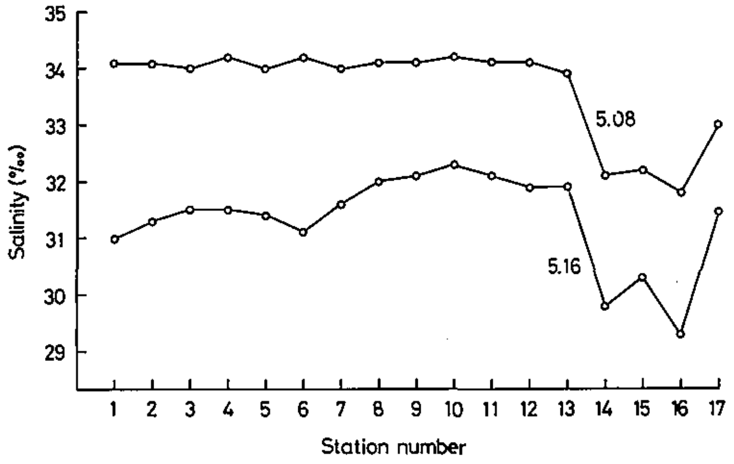

Fig. 2. Changes in salinity at the sampling stations.

In general, salinity was lower at Stns. 14-16 than at other stations (Fig. 2). The low salinity was caused by the inflow of a small creek into the sheltered cove.

In this area, the distribution and abundance of grapsid crabs differed among the three species (Fig. 3). That is, *H. sanguineus* was found at all stations, and its density was high at Stns. 10, 11 and 12. On the other hand, *H. penicillatus* and *G. depressus* were distributed locally; the former was found densely at Stns. 14, 15 and

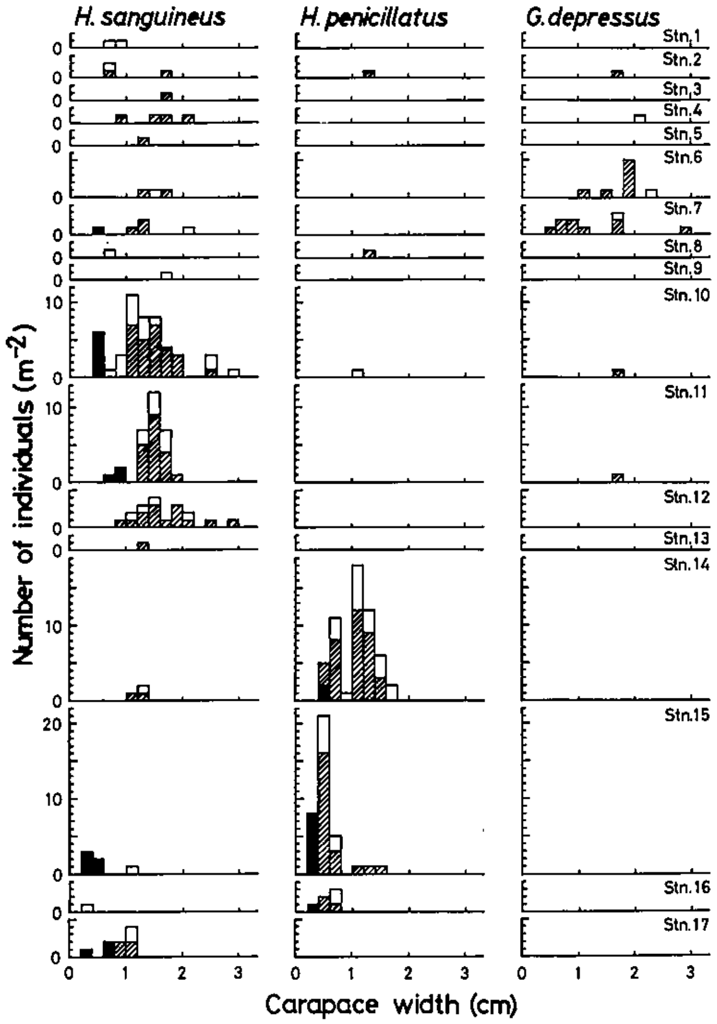

Fig. 3. Density (1 m^{-2}) and size-frequency distribution of three species of grapsid crabs at each sampling station. Open bar: males; hatched bar: females; solid bar: juveniles.

16, and the latter was frequently found at Stns. 6 and 7. Mainly, *H. sanguineus* was distributed to the north of Hadakajima, *H. penicillatus* in the sheltered shore, and *G. depressus* to the south of Hadakajima. *H. penicillatus* and *G. depressus* collected from stations other than in the main distribution area were large (*H. penicillatus* : male = 1.17 cm, females = 1.34 and 1.40 cm ; *G. depressus* : male = 2.07 cm, female = 1.70, 1.75 and 1.75 cm). On the other hand, the size of *H. sanguineus* individuals varied.

Morphology of mouth parts

It was observed that *G. depressus* captured suspended solids using its third maxillipeds, and sometimes second maxillipeds, as observed by Depledge (1989).

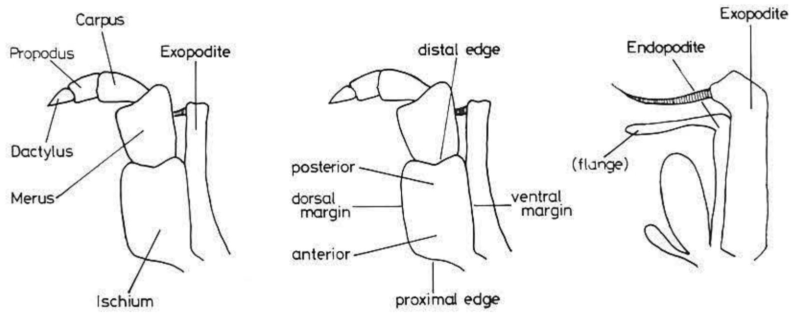

Fig. 4. Schematic drawings of outer views of the left third (left and center) and first maxillipeds (right), except for epipodite and gills.

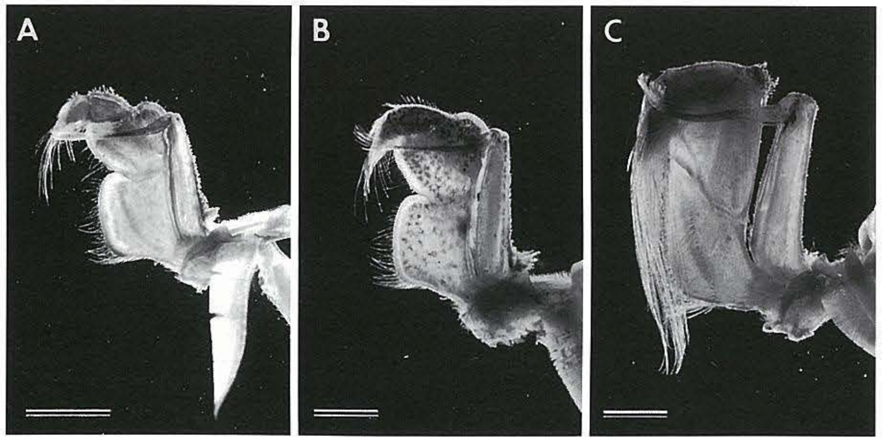

Fig. 5. Inner view of left third maxillipeds, except for epipodite and gills, of *Hemigrapsus sanguineus* (A), *Hemigrapsus penicillatus* (B) and *Gaetice depressus* (C). Scale bars indicate 2 mm.

The crab extended its third and second maxillipeds, and captured the suspended solids with the setae on the distal edge of the merus, the dorsal margin of the carpus, the postero-inner surface (facing the mouth) of the propodus, and the dorsal and ventral margins of the dactylus of third maxillipeds, the setae on the ventral margin of the carpus, the postero-outer surface (facing away from the mouth) of the propodus, and the postero-outer surface and tip of the dactylus of the second maxillipeds (Fig. 4). Subsequently, it raked up the solids captured on the third maxillipeds using the second and first maxillipeds (Fig. 4). Therefore the morphologies of the three pairs of maxillipeds and setae were compared among the three species of crabs.

The specimens using to show the morphology of the maxillipeds were females with maximum carapace widths of 14.80 mm for *H. sanguineus*, 12.85 mm for *H. penicillatus* and 17.35 mm for *G. depressus*. *G. depressus* had a longer propodus and dactylus, compared with *H. sanguineus* and *H. penicillatus* (Figs. 5 and 6). When

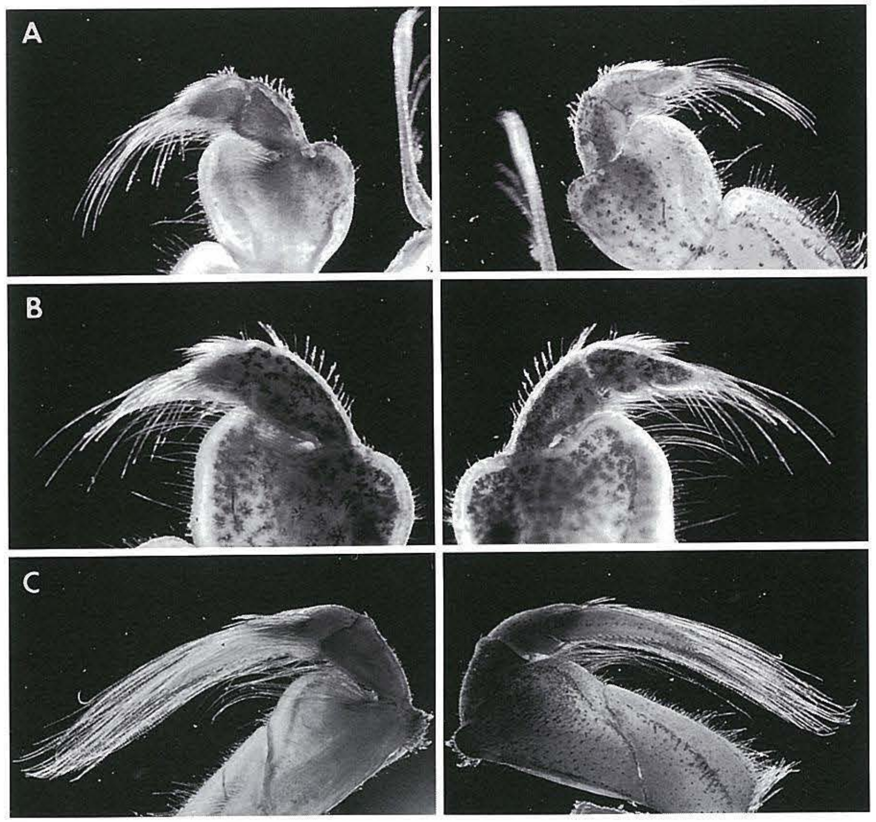

Fig. 6. Inner (left) and outer (right) views of endopodite of left third maxillipeds of *Hemigrapsus sanguineus* (A), *Hemigrapsus penicillatus* (B) and *Gaetice depressus* (C).

the third maxillipeds were flexed in front of the mouth, the tip of the dactylus extended beyond the middle point of the ischium on *G. depressus*, but never reached the distal edge of the ischium on *H. sanguineus* and *H. penicillatus* (Fig. 6). Moreover, the setae on the tip of the dactylus extended beyond the proximal edge of the ischium on *G. depressus*, hardly reached the middle point of the ischium on *H. sanguineus*, and almost reached the proximal edge of the ischium on *H. penicillatus* (Figs. 5 and 6).

Generally, *G. depressus* possessed long setae with evenly spaced lateral spines (Fig. 10A) on the carpus, propodus and dactylus of the third maxillipeds, except for a few serrate setae on the postero-inner surface of the propodus (Fig. 6 and Table 2). When the third maxillipeds were extended, each bundle of spined setae on the carpus, propodus and dactylus, used to capture the suspended solids, formed a net-like structure, like that in *Porcellana longicornis* (Galatheidea; Anomura) (Nicol, 1932). These long spined setae and long propodus and dactylus may make it possible to capture a wide range of suspended solids.

On the other hand, *H. sanguineus* and *H. penicillatus* principally possessed smooth (Fig. 10B) and plumose setae, except for several serrate setae on the inner

Table 2. Distribution and morphology of the setae on the carpus, propodus and dactylus of the third maxillipeds.

	Carpus			
	outer-dorsal margin	inner-dorsal margin	ventral margin	
H. sanguineus	plumose	smooth	plumose, short	
H. penicillatus	plumose	smooth, long	plumose	
G. depressus	spined, long	spined, long	—	
	propodus			
	postero-inner surface	postero-dorsal margin	antero-ventral margin	postero-ventral margin
H. sanguineus	smooth, dense*	smooth, long	plumose, shors	smooth, short, dense
H. penicillatus	smooth, dense*	smooth, long	plumose, short, sparse	smooth, short, dense
G. depressus	spined, long, dense**	spined, long	—	—
	dactylus			
	dorsal and ventral margin			
H. sanguineus	smooth, short (on the tip, few with short spines and few serrated)			
H. penicillatus	smooth, short (on the tip, few with short spines and few serrated)			
G. depressus	spined, long			

*few serrate setae on the distal edge
**few serrate setae on the upper half

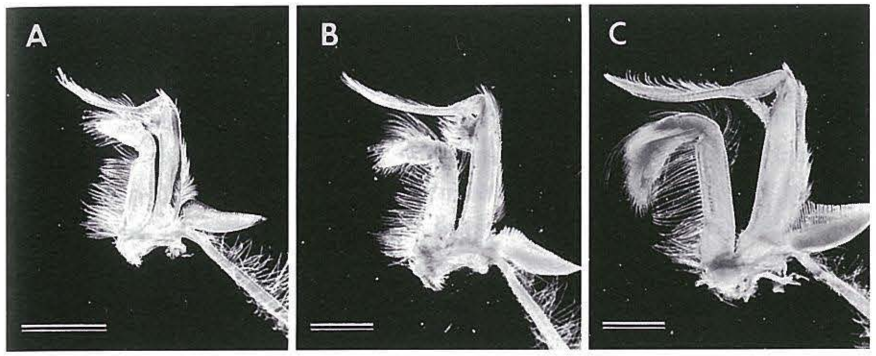

Fig. 7. Inner view of left second maxillipeds, except for epipodite and gill, of *Hemigrapsus sanguineus* (A), *Hemigrapsus penicillatus* (B) and *Gaetice depressus* (C). Scale bars indicate 2 mm.

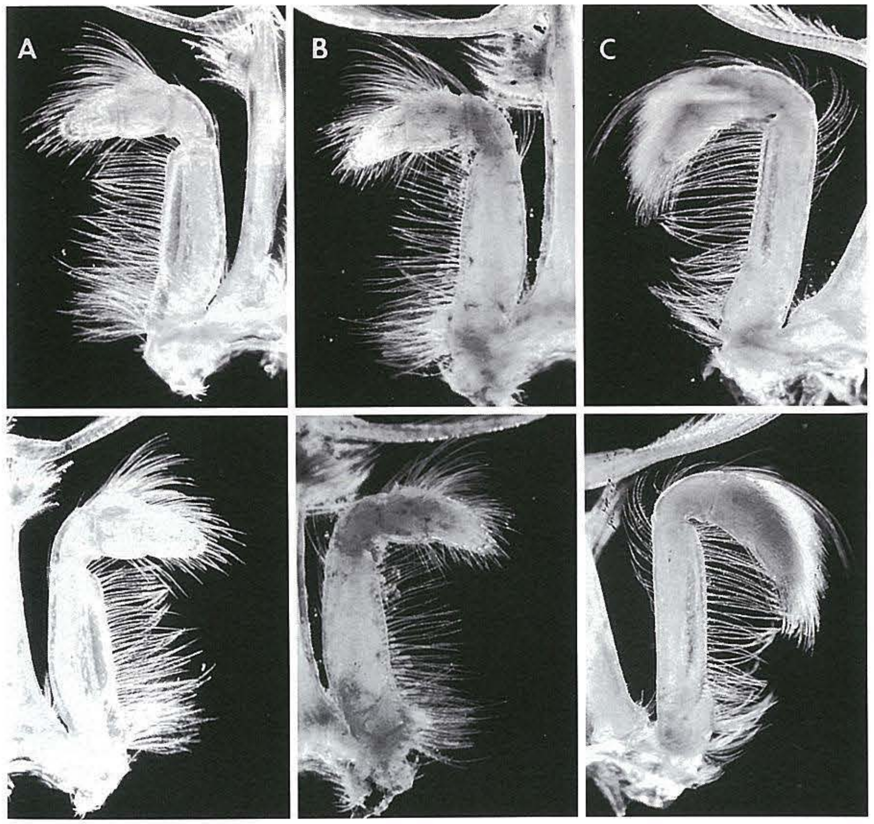

Fig. 8. Inner (upper) and outer (lower) views of endopodite of left second maxillipeds of *Hemigrapsus sanguineus* (A), *Hemigrapsus penicillatus* (B) and *Gaetice depressus* (C).

distal edge of the propodus, and few serrate setae and setae with short spines on the tip of the dactylus (Fig. 6 and Table 2). The setae on the tips of the third maxillipeds of these two species were shorter than those of *G. depressus*, indicating that the third maxillipeds are unsuitable for capturing suspended solids.

The general morphology of the second maxillipeds was similar among the three species (Fig. 7). In principle, *G. depressus* possessed spined setae, except for serrate setae on the tip of the dactylus (Fig. 8 and Table 3). Serrate setae (Fig. 10C) are considered to be useful for raking up the suspended solids captured on the spined setae of the third maxillipeds. On the other hand, *H. sanguineus* and *H. penicillatus* principally had smooth setae, except for the serrate setae on the ventral postero-outer surface of the propodus of *H. sanguineus*.

Table 3. Distribution and morphology of setae on the carpus, propodus and dactylus of second maxilipeds.

	carpus	propodus	dactylus	
	ventral margin	postero-outer surface	postero-outer surface	tip
H. sanguineus	smooth, long, few	smooth (outer surface) serrate (ventral margin)	smooth	smooth
H. penicillatus	smooth, long, few	smooth	smooth	smooth
G. depressus	spined, long	spined	spined	serrate

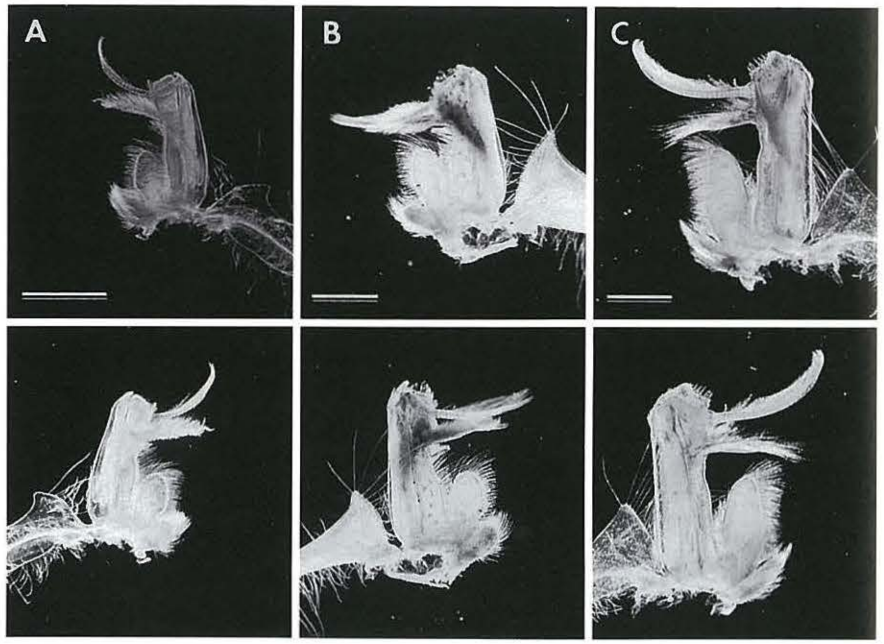

Fig. 9. Inner (upper) and outer (lower) views of left first maxillipeds, except for epipodite, of *Hemigrapsus sanguineus* (A), *Hemigrapsus penicillatus* (B) and *Gaetice depressus* (C). Scale bars indicate 2 mm.

The general morphology of the first maxillipeds hardly differed among the three species (Fig. 9). *G. depressus* principally possessed spined setae, except for plumose setae on the postero-dorsal margin of the posterior-endopodite, which is the posterior part of the endopodite flange (Fig. 4 and Table 4). In addition, the lack of setae on the antero-dorsal margin, the plumose setae on the postero-dorsal margin (Fig. 10D) and the long spined setae on the distal edge of the flange of the posterior-endopodite (Table 3) created a space between the posterior- and anterior-endopodite useful for guiding the suspended solids captured into the mouth. On the other hand, no space was recognized on *H. sanguineus* and *H. penicillatus*, due to the presence of spined or plumose setae on the antero-dorsal margin of the endopodite (Fig. 9).

DISCUSSION

On the boulder shores of Asamushi, Aomori city, the main distribution areas differed among the three species of grapsid crabs studied (Figs. 1 and 3). That is, *H. penicillatus* was concentrated in the cove sheltered by the breakwater, where there are usually brackish conditions created by the inflow of a small creek (Figs. 1, 2 and 3). On the other hand, this species was hardly collected on the shores to the south of Hadakajima, where temporarily brackish conditions are created by the inflow of melting snow in early spring (KYOZUKA *et al.*, 1981, 1982, 1983). These

Table 4. Distribution and morphology of setae on the anterior endopodite, which is the anterior part of the flange and posterior endopodite of the first maxilliped.

	anterior endopodite			
	outer surface	antero-dorsal margin	postero-dorsal margin	ventral margin
H. sanguineus	smooth	spined, dense	smooth	spined, dense
H. penicillatus	smooth	spined	smooth	spined
G. depressus	spined, dense	spined, short	spined, dense	spined (anterior)

	posterior endopodite		
	antero-dorsal margin	postero-dosal margin	distal edge of flange
H. sanguineus	spined	spined	plumose, dense
H. penicillatus	plumose	spined (plumose ?)	plumose
G. depressus	—	spined	spined, long

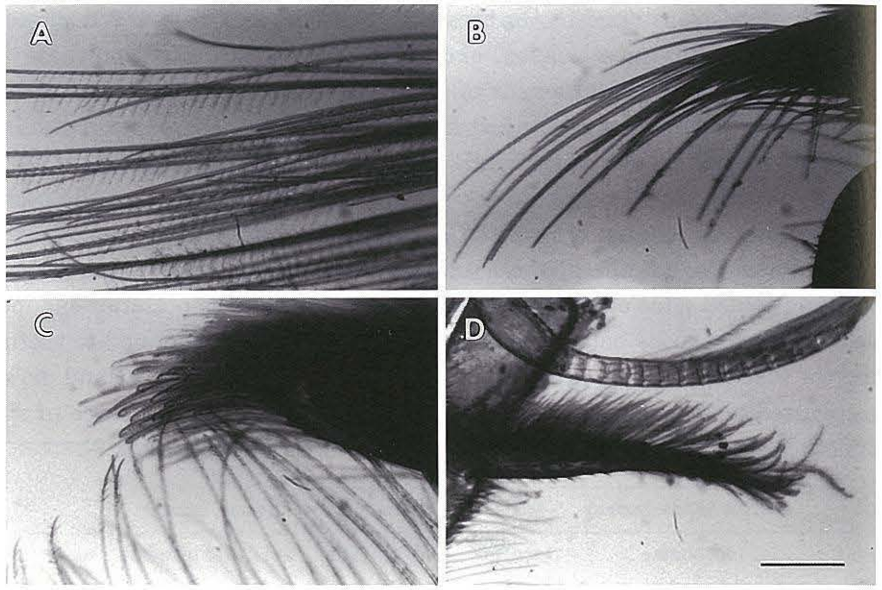

Fig. 10. Typical morphology of spined (A), smooth (B), serrate (C) and plumose (D) setae. A : setae with evenly spaced lateral spined on the dactylus of the third maxilliped of *Gaetice depressus*, B : smooth setae on the dactylus of the third maxilliped of *Hemigrapsus sanguineus*, C : serrate setae on the tip of the dactylus of the second maxilliped of *Gaetice depressus*, D : plumose setae on the postero-dorsal margin of the posterior endopodite of the first maxilliped of *Hemigrapsus sanguineus*. Scale bars indicate 0.2 mm.

facts correspond to several investigations that have been *H. penicillatus* to be present mainly in estuaries (Goshima *et al.*, 1978 ; Pillay and Ono, 1978 ; Sato, 1979 ; Kikuchi *et al.*, 1981 ; Ogura and Kishi, 1985 ; Fukui and Wada, 1983 ; Okamoto and Kurihara, 1987). In addition, *H. penicillatus* has been revealed to be a brackish-water species through comparison of survival rates under various degree of salinity (Okamoto and Kurihara, 1987 ; Matsumasa and Kikuchi, 1993). The distribution of *H. penicillatus* may be markedly affected by its own physiological adaptation to various salinity conditions.

H. sanguineus was collected at all stations (Fig. 3), and its abundance hardly corresponded to the number of layers of stones (Fig. 3 and Table 1). The crab was more abundant on the shores of north Hadakajima than on the southern shores. In general, the shores to the south of Hadakajima are exposed to waves more frequently and strongly than the shores to the north (Hoshiai, 1965 ; Kyozuka *et al.*, 1981, 1982, 1983). These facts correspond to the results of investigations showing that *H. sanguineus* is distributed on semi-exposed and sheltered boulder shores (Kikuchi *et al.*, 1981 ; Fukui and Wada, 1983 ; Takahashi *et al.*, 1985), and appear to indicate that its density is affected by factor(s) other than the abundance of apertures created

between stones and between stones and the bottom.

On the other hand, *G. depressus* was found locally at Stns. 6 and 7 to the east of Hadakajima, which is frequently exposed to waves. This corresponds to the description by Fukui and Wada (1983). In contrast, Kikuchi *et al.* (1981) and Takahashi *et al.* (1983) reported that *G. depressus* is distributed on sheltered shores. Thus, these results indicate that *G. depressus* is able to occupy both sheltered and exposed shores.

In the laboratory, *G. depressus* captured suspended solids using the spined setae on its third maxillipeds, and slightly with its second maxillipeds, when suspended matter collected from the field was supplied in a vessel contained seawater (Figs. 5, 6, 7, 8 and Tables 2, 3). Subsequently, the solids captured on the setae of the third maxillipeds were raked up by the setae on the second maxillipeds, and then transported to the mouth one by one. In fact, Depledge (1989) demonstrated that *G. depressus* depends considerably on suspended matter as a food source.

In contrast, *H. sanguineus* and *H. penicillatus* principally possessed smooth and plumose setae on the third and second maxillipeds, these setae being unsuitable for capturing suspended solids (Figs. 5, 6, 7, 8 and Tables 2, 3). These morphological characteristics explain the fact that both species did not capture suspended solids that were supplied at a high concentration (personal observations).

In general, wave action causes water currents, and these current resuspends fine particles which have been deposited on the bottom near the shoreline (Takeda and Kurihara, 1988). The shores to the south of Hadakajima are more exposed to waves produced by wind action (Hoshiai, 1965 ; Kyozuka *et al.*, 1981, 1982, 1983), especially the shore at the base of the long quay. These facts suggest that deposited fine matter is frequently resuspended by the water current along the shores to the south of Hadakajima.

Fukui and Wada (1983) described *G. depressus* as being distributed along semi-exposed shores in southeast Japan. Their study area faced the Pacific Ocean, and there were no large rivers nearby that would have carried suspended matter from the land. In areas without a direct source of suspended matter from the land, it is presumed that the suspended matter mainly originates from deposited matter through wave action. On the other hand, Kikuchi *et al.* (1981) reported that *G. depressus* abundantly inhabited sheltered shores in southern Japan. On the sheltered shores two rivers flowed, and *Macrophthalmus japonicus* inhabiting muddy tidal flats was found at the mouths of these rivers (Omori *et al.*, 1984). These results indicate that fine particles such as silt, clay and detritus are carried from the land via rivers to the sheltered shores. Thus, the distribution of *G. depressus* may be understood to be closely related to the distribution of suspended matter, rather exposure of the shore to wave action.

The main distribution areas of the three species of grapsid crabs investigated in this study differed reciprocally in response to differences in salinity and exposure to wave action, and perhaps the amount of suspended matter. Their habitat segregation may be related to the differences in their physiological tolerance to salinity conditions and feeding habits, as is the case in ocypodid crabs.

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