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Susceptibilities of Brackish Small Crustaceans to Potential Predations

潜在的捕食に対する汽水性小型甲殻類の被食率の検討

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Abstract

Based on the previous studies on the distributions and abundances of small crustaceans in a brackish Gamo Lagoon, we hypothesized that a small crustacean species with the lowest susceptibility to predations by coexisting consumers would become the most abundant species in a habitat. This simple hypothesis was tested by a laboratory experiment pairing a single prey with a single predator without refuges in this study. The results revealed that the susceptibility of the small crustaceans to predators varied with the combination of preys and predators. The hypothesis seemed to be supported for a free-living amphipod *Melita setiflagella* to the predation by a grapsid crab *Hemigrapsus penicillatus* in oyster beds and boulder habitats. On the other hand, two small crustacean species which live in/on the bottom sediment abundantly (a benthic tube-dwelling amphipod *Grandidierella japonica* and a benthic-plankton *Neomysis intermedia*) were susceptible to the predation by a flounder, *Kareius bicoloratus*, a predator typical of the bottom sediment. In particular, the small *Grandidierella* (ca. 5mm in body length) was the most susceptible to any predations. The life styles and the escape behavior observed indicated that the presence of sediment and the water depth reduce the susceptibilities of *Grandidierella* and *Neomysis*, respectively, in the field.

Introduction

It is widely recognized that effects of predation are of central importance in ecology (e.g., see Begon *et al.*, 1986). Predators play roles in determining community structure as well as population dynamics by affecting the distribution and abundance of things which they consume selectively or randomly. The effect of predation on the composition of prey species may reflect the differences in susceptibility among preys. It is considered that the prey species with a susceptibility lower than the other preys predominates in the prey assemblage, although the intensity of predation is also an important determinant of the structure of prey assemblage. Both behaviors of predator (e.g., searching, pursuit, and capture of prey) and of prey (e.g., avoidance and escape from predator)

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influence susceptibilities of preys to predators. In addition, physical structures of habitat which act as refuges from predators may affect prey susceptibility to predations. Previous marine studies involving structures of small crustacean assemblages have tested how the efficiency of predators changes as a function of refuge abundances (e. g., Van Dolah, 1978; Nelson, 1979; Stoner, 1982; Lewis & Stoner, 1983) or of refuge structures (e. g., Edgar, 1983; Holmlund *et al.*, 1990). However, the general rule of this problem has not been unified yet.

In the brackish Gamo Lagoon in Sendai, Japan, small peracarid crustaceans segregate their habitats according to primary and secondary substrates (Matsumasa & Kurihara, 1988; Matsumasa *et al.*, 1992; Matsumasa & Kikuchi, 1993; Matsumasa, in press). Based on results of previous field and laboratory experiments examining the effects of substrates on the small crustaceans, it has been concluded that the types of substrates determine the most abundant species of small crustaceans. In particular, the physical structure specific to each substrate supplies the micro-habitats for each small crustacean which has a species-specific life style. On the other hand, each type of physical structure is also inhabited by the habitat-specific potential predators (e. g., decapod crustaceans and fishes), so that predatory effects on the small crustaceans have to be examined in addition to direct relationships between the small crustaceans and habitat structures. In the course of studies on the relationships between the small crustaceans, the predators, and the habitat structure, we hypothesized that the small crustacean species with the lowest susceptibility to its coexisting predators would be the most abundant. In order to test this hypothesis, this study investigated the susceptibilities of three species of small crustaceans to predations by four potenial predators in a simple laboratory experiment pairing a single prey species with a single predator species in the absence of physical structures as refuges.

Materials and Methods

The small crustaceans and the potential predators were all collected from the brackish Gamo Lagoon in Sendai, Japan (38° 15' N: 141° 01' E) on 20 Aug. 1993. The three species of small crustaceans used were a tube-dwelling amphipod *Grandidierella japonica* Stephensen, a free-living amphipod *Melita setiflagella* Yamato, and a mysid *Neomysis intermedia* (Czerniavsky). *Grandidierella* constructs its tube with sand particles and dominates the bottom sediment. Another amphipod *Melita* dominates oyster beds and boulder habitats and prowls on the substrate surfaces. *Neomysis* is a benthic-plankton which perches on the sediment surface and swims into water column. A grapsid crab *Hemigrapsus penicillatus* (de Haan), a prawn *Palaemon serrifer* (Stimpson), juveniles of a goby *Acanthogobius flavimanus* (Temminck et Schlegel), and juveniles of a flounder *Kareius bicoloratus* (Basilewsky) were used as potential predators. The juvenile of the flounder is abundant on the bottom sediment of the lagoon, and the other potential predators inhabit oyster beds and boulder habitats using the crevices of these habitats for their hiding places.

The sizes of the small crustaceans (mean body length ± 1SE) used were 4.7 ± 0.06 mm for *Grandidierella*, 5.2 ± 0.61 mm for *Melita*, and 11.0 ± 0.12 mm for *Neomysis* (sex was not distinguished). In addition, large *Grandidierella* males with well-developed gnathopod 2 (body length; 7.7 ± 0.07 mm) were also used. A predator *Hemigrapsus* was divided into two size classes:

small crabs with a carapace width below 15 mm (mean ± 1SE, 11.6 ± 0.63 mm) including 3 males and 5 females, and large crabs with a carapace width above 15 mm (mean ± 1SE, 18.5 ± 1.20 mm) including 3 males and 3 females. Two size classes of *Palaemon* were also used (mean body length ± 1SE, 19.4±0.85 mm for small prawns, and 49.6 ± 1.09 mm for large ones), but the effect of sex was not examined (all prawns were female). The mean body length ± 1SE of *Acanthogobius* and *Kareius* was 48.6 ± 2.50 and 66.1 ± 2.19, respectively; the sexes were not identified. An individual of each predator was put into a plastic aquarium containing 50% sea water with a 1.5 cm depth. An aquarium with a basal area of 12 cm × 24 cm was used for *Kareius*, and a smaller one (basal area, 8 cm × 12 cm) for the other predators. After withholding food from the predators for 24 hr, 30 prey were put into the aquarium with *Kareius* and 10 prey were put into another aquarium with the other predators. The number of surviving prey was counted 24 hr after the start of the experiment. The above procedures were all carried out in a constant-temperature room at 23℃ on a 14:10 hr light:dark cycle.

The effect of treatment on the proportion of prey survival was examined by ANOVA (analysis of variance), using SYSTAT (Wilkinson, 1992). The proportions of survivals were transformed using the arcsine square root transformation to make the variances homogeneous. If the ANOVA indicated a significant treatment effect ($p < 0.05$), the Tukey HSD test was used for the pairwise comparisons between means.

Results

A three-way ANOVA for the *Hemigrapsus* predation shows the significant effects of the prey item and the crab size[1)] (**Table 1**). Post hoc pairwise comparisons show that the susceptibility of prey to the small *Hemigrapsus* was significantly lower in *Melita* than the others ($p < 0.001$), and in

Table 1

Predation by *Hemigrapsus* on the small crustaceans. Results of a three-way ANOVA; dependent variables are the arcsine square root transformations of the proportion of survival. Asterisks show the significance of F: ** = $p < 0.001$, * = $p < 0.05$.

Source	SS	df	MS	F	p
Prey item (PI)	8.192	3	2.731	37.516	< 0.001**
Crab size (CSI)	0.362	1	0.362	4.976	0.031*
Crab sex (CSE)	0.001	1	0.001	0.019	0.892
PI × CSI	0.309	3	0.103	1.417	0.252
PI × CSE	0.006	3	0.002	0.026	0.994
CSI × CSE	0.033	1	0.033	0.460	0.502
PI × CSI × CSE	0.080	3	0.027	0.368	0.777
Error	2.911	40	0.073		

[1)] The effects of treatment on the susceptibility of prey to predations were also examined by a non-parametric method (Friedman test). The Friedman test indicated the same significant effects as ANOVAs for all treatments but the crab size ($p = 0.134$). Therefore, the effect of the crab size tended to be significant.

Neomysis than *Grandidierella* ($p < 0.005$) (**Fig. 1**). On the other hand, the susceptibility of prey to the large *Hemigrapsus* was significantly lower only in *Melita* than the others ($p < 0.005$).

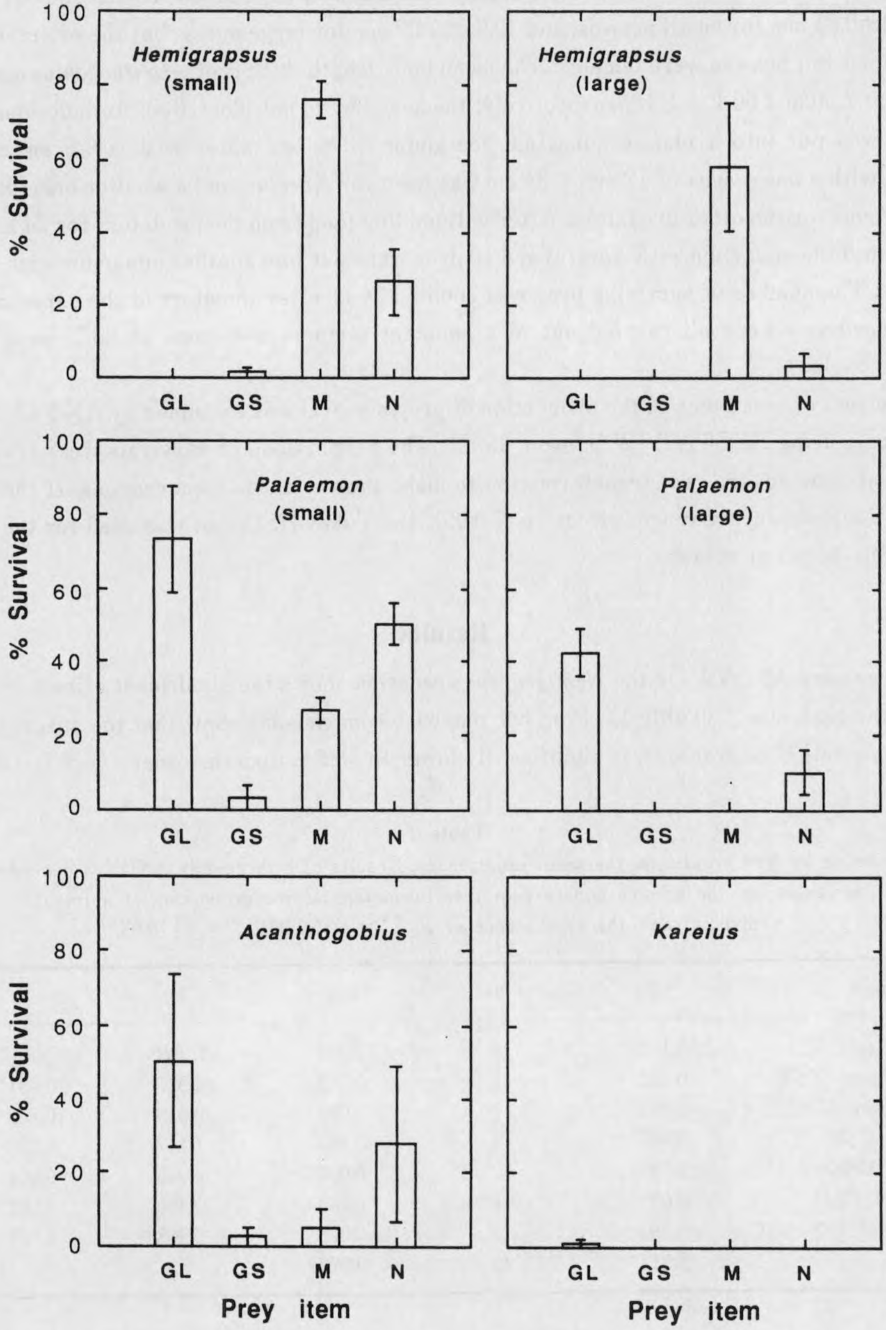

Fig. 1 Predation effects on mean % survival of the small crustaceans. Bars indicate ± 1SE. GL, *G. japonica* (large males); GS, *G. japonica* (small individuals); M, *M. setiflagella*; N, *N. intermedia*. The results of the pairwise comparisons between means were shown in the text.

A two-way ANOVA for the *Palaemon* predation shows the significant effects of the prey item and the prawn size (**Table 2**). Post hoc pairwise comparisons show that the susceptibility of prey to the small *Palaemon* was significantly lower in the larger male of *Grandidierella* ($p < 0.01$) and in *Neomysis* ($p < 0.05$) than in the small *Grandidierella* (**Fig. 1**). On the other hand, the susceptibility of prey to the large *Palaemon* was significantly lower only in the large *Grandidierella* male than in the others ($p < 0.05$).

ANOVAs show that the effect of the prey item was not significant for either the *Acanthogobius* ($F_{3/12} = 2.08$, $p > 0.1$) or *Kareius* ($F_{3/8} = 1.00$, $p > 0.1$) predations. However, mean percent survivals of the large male of *Grandidierella* and *Neomysis* tended to be higher than those of the small *Grandidierella* and *Melita* (**Fig. 1**). *Kareius* ate almost all of the small crustaceans, and its predation was the severest among predators in this experiment.

The effect of six predator types (*Hemigrapsus* and *Palaemon* of large and small sizes, the juvenile *Acanthogobius*, and the juvenile *Kareius*) was significantly as well as the effect of prey item (**Table 3**). The interactional effect was also significant.

Table 2

Predations by *Palaemon* on the small crustaceans. Results of a two-way ANOVA; dependent variables are the arcsine square root transformations of the proportion of survival. Asterisks show the significance of F: ** = $p < 0.001$.

Source	SS	df	MS	F	p
Prey item (PI)	2.440	3	0.813	22.938	< 0.001**
Prawn size (PRS)	0.938	1	0.938	26.469	< 0.001**
PI × PRS	0.181	3	0.060	1.705	0.206
Error	0.567	16	0.035		

Table 3

Predations by the predators on the small crustaceans. Results of a two-way ANOVA; dependent variables are the arcsine square root transformations of the proportion of survival. Asterisks show the significance of F: ** = $p < 0.001$.

Source	SS	df	MS	F	p
Prey item (PI)	2.514	3	0.838	11.393	< 0.001**
Predator type (PDT)	2.835	5	0.567	7.708	< 0.001**
PI × RDT	8.999	15	0.600	8.156	< 0.001**
Error	6.179	84	0.074		

Discussion

The result of this study shows susceptibility of the small crustaceans to the *Hemigrapsus* predation changes with the prey item (**Table 1**). The susceptibility of prey was low in *Melita* and high in *Grandidierella* for both the small and large crab sizes, although it differed in *Neomysis* for the two crab sizes (**Fig. 1**). The oyster bed and the boulder habitat in the Gamo Lagoon harbor the small crustaceans, *Grandidierella japonica*, *Corophium uenoi* Stephensen, *Sinelobus* (*Tanais*) *stanfordi* (Richardson), and *Gnorimosphaeroma rayi* Hoestland abundantly, but another amphipod *Melita setiflagella* is the most abundant species (Okamoto & Kurihara, 1989; Matsumasa, 1988; 1992; 1993). The potential predators, *Hemigrapsus penicillatus*, *Palaemon serrifer*, and juveniles of *Acanthogobius flavimanus* also inhabit these habitats using the crevices for their hiding places. Among these potential predators, *Hemigraopsus* is the most abundant species. In addition, the crab population consists of two age classes coexisting in the field (Okamoto & Kurihara, 1987) which correspond to the two crab size classes tesed in this study. Therefore, the crab predation may be a cause for the small crustacean assemblage dominated by *Melita* in the oyster bed and the boulder habitat. The low susceptibility of *Melita* to the crab predation seems to be due to its ability to swim faster than *Grandidierella*. When the crab attacked *Melita*, the amphipod swam away quickly and avoided being caught. *Neomysis* is also a good swimmer; however, its susceptibility to the crab predation was lower than *Melita*. This may be due to the difference in avoidance behaviors of these small crustaceans rather than to those in swimmimg abilities. When *Neomysis* was attacked by the crab, it swam quickly upwards to escape. Since the water was shallow in this experiment (1.5 cm deep), this avoidance behaviour of the mysid may be disadvantageous. This effect of water depth on *Neomysis* susceptibility is also expected for the other predators, and has to be examined.

Although *Palaemon* catches the small crustaceans using their pereopods the same as *Hemigrapsus* does, the susceptibilities of the small crustaceans to the prawn was quite different from that to the crab (**Table 2, Fig. 1**). The lower survival rate of *Melita* to *Palaemon* than to *Hemigrapsus* indicates that *Palaemon* is a good hunter. On the other hand, the cheliped of *Palaemon* is smaller than that of *Hemigrapsus*, and this seems to be related with the highest survival rate of the large male of *Grandidierella* with developed gnathopods. It was observed that the large male *Grandidierella* escaped from the grasp of the prawn. However, it was also observed that the small *Palaemon* often did not show predatory behavior toward the large *Grandidierella*. Therefore, the prey selection by small *Palaemon* might cause a high survival rate of the large *Grandidierella*, as well as the escape behavior of the prey.

In this study, the susceptibility of the small crustaceans to the juvenile *Acanthogobius flavimanus* did not differ significantly among preys, but the pattern resembled that to the small *Palaemon* (**Fig. 1**). Kikuchi & Yamashita (1992) revealed that small crustaceans were the most frequent food items for *A. flavimanus* inhabiting a mudflat in Amakusa, Kyushu by analyzing its digestive tract content. Since this goby inhabits the Gamo Lagoon abundantly (Omori *et al.*, 1976), more detailed examinations on its predation have to be carried out.

The effect of predation on the small crustaceans by a flounder *Kareius bicoloratus* was the severest among the predators, and did not differ significantly among preys under this experimental condition (**Fig. 1**). *Kareius* is a typical predator of the sandy sediment, and is an abundant benthic fish in the Gamo Lagoon. Omori *et al.* (1976) have reported that amphipods have been observed in the stomach of the juvenile flounders (body length, > 15 mm) at about 5–10% in occurrence in the lagoon. However, because their investigations were carried out in April and May when the amphipod densities are the lowest (Matsumasa & Kurihara, 1988), the seasonal changes in the food habits of *Kareius* as well as the abundance of the fish must be investigated in the field. Although

Grandidierella is the most abundant small crustacean in the bottom sediment inhabited by *Kareius*, it was susceptible to *Kareius* predation (**Fig. 1**). Since *Grandidierella* builds its U-shaped tube in the sediment, it is expected that the presence of sediment lowers the susceptibility of this amphipod to flounder predation by offering the sites of refuge in the field.

As the results of above-mentioned relationships between the small crustaceans and the predators, the susceptibility of the small crustacean to predators differed as a function of the combination of prey items and predator types (**Table 3**). This indicates that it is important to consider the distributions and abundances of the predators as well as the prey for evaluating the effect of predation on the prey assemblage in the field. As mentioned above, *Kareius* is a predator typical of the bottom sediment, and *Hemigrapsus*, *Palaemon*, and *Acanthogobius* inhabit oyster beds and boulder habitats using the crevices as their refuges. However, it is reported that *Hemigrapsus* migrates between these refuges across the surrounding bottom sediment (Goshima *et al.*, 1978; Ogura & Kishi, 1985; Okamoto & Kurihara, 1987). In addition, the individuals of *Palaemon* and *Acanthogobius* which are foraging on the bottom sediment around their refuges are also observed in the field. Therefore, these three predators may also affect the small crustacean assemblage of the bottom sediment, so that their feeding behaviors, especially the feeding sites, have to be investigated, as well as their distributions and abundances. In particular, the low susceptibility of the large male *Grandidierella* to *Palaemon* and *Acanthogobius* predations is interesting, because adult males of this tube-dwelling amphipod cruise on the sediment surface searching for tubes of the adult females (Nakajima, 1991; pers. obs.), and males of the other tube-dwelling amphipods such as *Corophium volutator* (Pallas), *C. arenarium* Crawford (Fish & Mills, 1979), *Lembos websteri* Bate (Moore, 1981), *Microdeutopus gryllotalpa* (Costa) (Borowsky, 1983a), *Jassa falcata* (Montagu), and *Amphithoe valida* Smith (Borowsky, 1983b) also show the similar behaviors.

In conclusion, the pattern in susceptibility of the small crustacean to *Hemigrapsus* predation supports the hypothesis that the most abundant species of the small crustacean has the lowest susceptibility to the predation. On the other hand, the behaviors of small crustaceans indicate that the presence of sediment and the water depth may affect the susceptibilites of a tube-dwelling *Grandidierella* and a benthic-plankton *Neomysis*, respectively, in the field.

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