

THE BEHAVIOR OF PAGURIDS IN SYMBIOTIC ASSOCIATIONS WITH ACTINIANS IN JAPAN¹⁾

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With Text-figures 1-2

Abstract

Six Japanese species of symbiotic pagurids (5 *Dardanus* spp. and *Diogenes edwardsi*) displayed active behavior patterns towards their symbiotic actinians. Amongst these pagurids which were freshly collected, 5 species of nonsymbiotic pagurids, including one species of *Dardanus*, showed no activity towards anemones. It was noted that *Dardanus* spp. in placing *Calliactis polyypus* on their shells, locates the first anemone to the right and the second to the left of the shell aperture. *D. edwardsi* showed two different behavior patterns: it always placed *S. paguri* on the claw and never on the shell; it placed other anemones only on the shell and never on the claw. Symbiotic pagurids, when brought into contact with nonsymbiotic actinians, were either indifferent or they broke off contact after displaying activity for a short period only.

Introduction

Interest has revived in recent years in the behavioral interactions of animals in symbioses and this has stimulated studies on sea anemones and crabs that live as species-pairs. The well-known behavior of the Mediterranean pagurid, *Dardanus arrosor* (Herbst), which actively detaches and resettles the anemone *Calliactis parasitica* (Couch) on its shell, first described by Brunelli (1910) and Faurot (1910) has been reexamined by Ross and Sutton (1961b). It had been shown earlier that the Atlantic pagurid, *Pagurus bernhardus* (L.) did not display an active behavior pattern towards *C. parasitica* with which it is commonly associated. In that case, *C. parasitica* established the association by a behavior pattern of its own which was triggered by contact with a molluscan shell (Ross and Sutton, 1961a). Later these studies were extended to associations of actinians with Caribbean and Hawaiian pagurids and other crabs (Ross, 1970; Cutress, Ross and Sutton, 1970). It became evident from these studies that considerable variation exists in the behavior patterns found in the different associations. Thus there is some value in extending the number of associations from which data are available for the information they provide on behavioral variations at different taxonomic levels. A number of these associations occur in Japanese waters. This paper gives an account of observations of the activities of pagurids in

1) Contributions from the Seto Marine Biological Laboratory, No. 600.

those species-pairs that were available for study.

Material and Methods

The work was carried out at the Misaki Marine Biological Laboratory of the University of Tokyo, at the Seto Marine Biological Laboratory of the University of Kyoto at Shirahama and at the Amakusa Marine Biological Laboratory of Kyushu University, Tomioka. Specimens of anemones with crabs were collected, mostly by fishermen, usually at a considerable distance from the laboratory site. Information about the distribution and general ecology of the animals is unfortunately scanty and the specimens obtained may not be truly representative of those that would be obtained in the immediate neighborhood of these laboratories.

On being received in the laboratory, the specimens were transferred to running sea-water and the numbers of anemones on the shells along with other relevant details were noted. Individual animals were labelled and kept in separate containers when possible. Records of the behavior of individuals are available in many cases. The anemones were usually separated from their hosts as soon as convenient and allowed to settle on plates and stones. Still photographs and moving picture films were taken to assist the study and description of the behavior patterns.

The Animals

The Japanese fauna is exceptionally rich in symbiotic pagurids and anemones. I obtained 6 species of pagurids whose normal mode of life involved living with one or more of 4 actinian species in symbiotic associations. The 6 species were: *Dardanus arrosor* (Herbst), *D. diogenes* (DeHaan), *D. gemmatus* (H. Milne Edwards), *D. haani* Rathbun, *D. impressus* (DeHaan) and *Diogenes edwardsi* (DeHaan). Missing from this list is *D. deformis* which was not collected. At least three other species of *Dardanus* occur in Japan but are not reported to carry anemones. Two of these, *D. megistos* and *D. sanguinolentus*, were not collected but the other, *D. cressimanus*, was available at Misaki and Shirahama in large numbers. Two of the species named above, *D. arrosor* and *D. gemmatus*, have been studied by me already in the Mediterranean and in Hawaii respectively (Ross and Sutton, 1961b; Ross, 1970).

The Japanese pagurid named above as *D. gemmatus* has been widely known in Japan by the name *D. tinctor* (Forskål) (= *D. varipes* [Heller]). My opinion that this crab was identical with *D. gemmatus* previously seen in Hawaii corresponded with the opinion of Dr. Jacques Forest who was consulted on this point by Dr. Katsushi Sakai of Kyushu University.

The above named 6 species of pagurids were found living with 4 species of symbiotic actinians: *Calliactis polyopus* (Forskål), *Paracalliactis japonica* (Carlgren), *Sagartia paguri* Verrill²⁾ and an unidentified anemone which will be referred to as "Actinian A"³⁾. A general description of this unnamed anemone will be supplied in another paper dealing with the behavior of actinians in these associations (Ross and Wada, MS).

Some other pagurids, mollusks and anemones were used in certain experiments. These were collected on the shore or in shallow dives in the neighborhood of the laboratories. The Japanese fauna also includes some other interesting associations between crabs and anemones, specimens of which could not be obtained, e.g. *Dorippe granulata* and *Carcinactis ichikawai* (Uchida, 1960) and *Leptomithrax edwardsi* (T. Sakai, personal communication). Thus this study by no means exhausts this field of enquiry.

Identification of pagurids and actinians was carried out with the aid of the "Illustrated Encyclopedia of the Fauna of Japan" (1971, Uchida, ed.). Examples of the pagurids were sent to Professor Miyake of Fukuoka to check the identifications. The two largest anemones, *Calliactis polypus* and *Paracalliactis japonica* were well-known and easily identified. The third actinian, *Sagartia* (?*Adamsia*) *paguri*, the small anemone found living on the claw of the hermit crab *Diogenes edwardsi*, cannot yet be assigned to a genus with any certainty, but it is always easily recognised because of its unique and consistent symbiotic association.

Results

The Associations

Table 1 summarises the data on pagurids collected with actinian associates at Misaki, Shirahama and Amakusa. No conclusions can be drawn from these data about the numbers of crabs in these locations which carry anemones. Fishermen collected hermit crabs with sea anemones and they probably discarded those without. I did not find *Dardanus arrosor* at the two southern laboratories at Shirahama and Amakusa but this may be due to the animal's habits or to differences in the depths or temperatures at which the animal lives in different locations. I did note that *Dardanus haani* occurred only once at Misaki and was very common at Shirahama and that *D. gemmatus* was collected only at Shirahama. On the other hand, *D. cressimanus* was very common in shallow water at all three locations. The data in Table 1 on the occurrence of certain species-pairs do not indicate choices by the members of such pairs because distribution and ecology enter into such associations. For instance, *Paracalliactis japonica* is apparently a more northern species and so it was found only at Misaki and there only on hermit crabs reaching a large size, especially *D. arrosor* and *D. diogenes*. With one exception, all *D. haani* in our collection came from the laboratory at Shirahama where *P. japonica* did not occur. Possibly the ranges of

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- 2) Verrill's name for the actinian on the chela of *D. edwardsi*, *Sagartia paguri*, is now suspect since the virtual suppression of the genus. Carlgren (1949) listed this actinian as ?*Adamsia paguri*, adding the note "possibly an *Anthothoe*". According to Mr. C.E. Cutress (personal communication), my specimens do not fit descriptions of *S. paguri* so both name and identity are doubtful. (*Note added in proof*).
 - 3) Specimens of "Actinian A" fell into two groups, small white and large striped individuals. The latter were used for most experiments and in the opinion of Mr. C.E. Cutress (personal communication) these will be assigned eventually to a new species and genus of the Family Sagartiomorphae. (*Note added in proof*).

D. haani and *P. japonica* overlap and one might find them living as associates north of Shirahama.

Table 1. Occurrence of 4 symbiotic species of actinians on pagurid hosts at 3 Japanese locations.

Pagurids		Locations	Actinians			
Species	No. Collected		<i>Calliactis polypus</i>	<i>Paracalliactis japonica</i>	<i>Sagartia paguri</i>	"Anemone A"
<i>Dardanus arrosor</i>	12	M	8	4	0	4
<i>D. cressimanus</i>	20+	MSA	1	1	0	0
<i>D. diogenes</i>	5	MSA	2	3	0	1
<i>D. gemmatus</i>	8	S	8	0	0	0
<i>D. haani</i>	20	MS	18	0	0	0
<i>D. impressus</i>	14	MSA	7	1	0	10
<i>Diogenes edwardsi</i>	*10	MA	0	0	7	8

N.B. Counts under actinians are occurrences in associations, not numbers of individuals.

Locations are Misaki (M), Seto (S) and Amakusa (A) Laboratories.

*Count excludes Amakusa collection (see text).

Behavior Patterns of Pagurids in Interaction with Symbiotic Actinians

(a) *Dardanus spp.* Single pagurids from all 6 species were placed in containers with single specimens of each of the 4 actinian species named above. These trials lasted for not less than 15 min and besides the pagurid species named above, 5 other pagurids which do not normally carry actinians were tested under the same trial conditions. 31 different species-pairs were brought together in these experimental presentations. Disproportionate sizes, premature deaths or shortages of animals made some pairings inappropriate or impossible. The initial aim was to set up at least 10 encounters for each species-pair but this was reduced to 5 encounters or less in cases where the pattern was clear or where animals died before the program could be completed. Table 2 summarises the results of these tests.

The columns headed "Active" in Table 2 record the occasions on which a particular species of crab performed stroking movements leading to attempts to dislodge the anemone. In most cases, this behavior pattern was concluded by the transfer of the anemone to the shell (bracketed figures in "Active" column). Successful transfers depend, however, on cooperating behavior patterns in the anemone but Table 2 shows that "active" crabs were usually "successful". Four stages in the transfer of *C. polypus* by *D. gemmatus* are shown in Figure 1. The series begins with the first contacts of the crab with the anemone (Fig. 1-a), continues with the relaxation of the anemone (Fig. 1-b) and with the detachment of the anemone (Fig. 1-c) and ends with the crab lifting the anemone to a position on the right of the aperture of the shell (Fig. 1-d).

Sometimes the anemone transferred itself successfully to an "inactive" individual but such transfers are not included in the bracketed figures. Table 2 shows that only those crabs belonging to the 6 symbiotic species (Group 1) displayed active behavior patterns towards these anemones. In one species, *Dardanus diogenes*, this

Table 2. Activity of pagurids in encounters with symbiotic actinians. Results of trials in which actinians, settled on glass, stones, etc., were brought into contact with pagurids.

Actinian presented	<i>Calliactis polypus</i>		<i>Paracalliactis japonica</i>		<i>Sagartia paguri</i>		"Anemone A"		
	Active	Inactive	Active	Inactive	Active	Inactive	Active	Inactive	
Group 1	<i>Dardanus arrosor</i>	10(10)	0	2(1)	3	2(0)	3	8(7)	2
	<i>Dardanus diogenes</i>	3(0)	7	4(1)	6	—	—	—	—
	<i>Dardanus gemmatus</i>	10(8)	0	—	—	—	—	4(4)	1
	<i>Dardanus haani</i>	20(17)	0	—	—	—	—	7(7)	0
	<i>Dardanus impressus</i>	20(18)	0	8(6)	2	2(0)	8	13(10)	2
	<i>Diogenes edwardsi</i>	1(1)	14	—	—	8(8)	*2	9(9)	*6
Group 2	<i>Aniculus aniculus</i>	0	10	0	5	—	—	—	—
	<i>Dardanus cressimanus</i>	0	20	0	5	0	4	0	20
	<i>Paguristes barbatus</i>	0	10	—	—	—	—	0	10
	<i>Pagurus japonicus</i>	0	10	0	5	—	—	0	15
	<i>Pagurus similis</i>	0	10	—	—	0	3	0	5

N.B. Figures in brackets are numbers of times in which anemones were successfully transferred to shells as a result of the crab's activity.

* Exclude occasions when crab hyper-excitable and avoided encounters. — Not tested.

activity was not impressive and was seldom successful. It is unfortunate that more specimens of this species were not available. Tests on this animal came to an abrupt end when the specimens died so perhaps the lack of success in transferring anemones was due to a deterioration in their condition.

With the exception of *D. diogenes*, the 5 *Dardanus* species in group 1 showed almost 100% activity and over 90% success in transferring *Calliactis polypus* and Actinian A to their shells. But activity was very low and success very poor with *Paracalliactis japonica*, surprisingly so with *D. arrosor* on which it was frequently found living in nature (Table 1). It was suspected that *P. japonica*, like *C. parasitica* in Europe, possessed a response to shell by which it could detach and resettle on pagurid shells with or without the help of a crab. Yet the anemone, when offered shells, showed no tendency to relax and cling to them as might be expected if this were an important factor in its association with pagurids.

An apparent solution to the problem came to light when it was observed that pagurids which encountered detached *P. japonica* sometimes seized the anemones and squeezed and stroked them with their walking legs and claws. Before this, *P. japonica* had been tightly closed and quite unresponsive and intractable. Under the influence of the crab's manipulations the anemone opened up, its column lengthened and its tentacles extended and the entire animal became limp and flexible. Often the crab did little more than hold the anemone and scratch it gently. On a number of occasions the scratching was applied directly to the pedal disk which was hidden in a deep concavity. This caused the pedal disk to emerge and to assume the convex shape associated with settling on a shell. After this, if the tentacles of *P. japonica* made contact with a shell, the anemone developed a special behavior pattern leading to settlement on the shell as will be described elsewhere (Ross and Wada, MS). I was never able to elicit this behavior pattern except when the anemone had been palpated and manipulated by a crab.

The results of encounters between *P. japonica* and *D. impressus* in Table 2 are somewhat misleading if it is concluded that only *D. impressus* has the capacity to transfer the anemone successfully to its shell. The capacity of *D. impressus* to induce a state of relaxation in *P. japonica* was discovered late in the series of trials when some other *Dardanus* species were not available for comparable tests. Indeed, most of the *D. impressus* which showed this behavior were so small in comparison to the large *P. japonica* that they could not have served as permanent hosts, though sometimes the anemone did settle, completely engulfing the shell with the pedal disk and dwarfing the pagurid.

While all the pagurids in Group 1 (Table 2) displayed active behavior patterns towards their anemone partners, the pagurids in Group 2 failed completely to show any signs of activity towards these anemones. Although this might have been expected, it shows clearly that this activity is not just an extension of normal exploratory behavior which one might find in any pagurid in a chance encounter. It is interesting that this group includes one species, *D. cressimanus*, belonging to a genus to which the most active species belong, not only in Japan but throughout the whole Indo-Pacific

region, and also in the Caribbean and Mediterranean Seas. *D. cressimanus* is an inshore species which was only twice found carrying anemones though several dozen individuals were examined. The occasional occurrence of anemones living on shells of inactive pagurids is no evidence for activity by that pagurid since some anemones can attach to shells unaided and there is nothing to prevent an inactive pagurid sometimes occupying a shell with anemones in place after it has been vacated by a member of

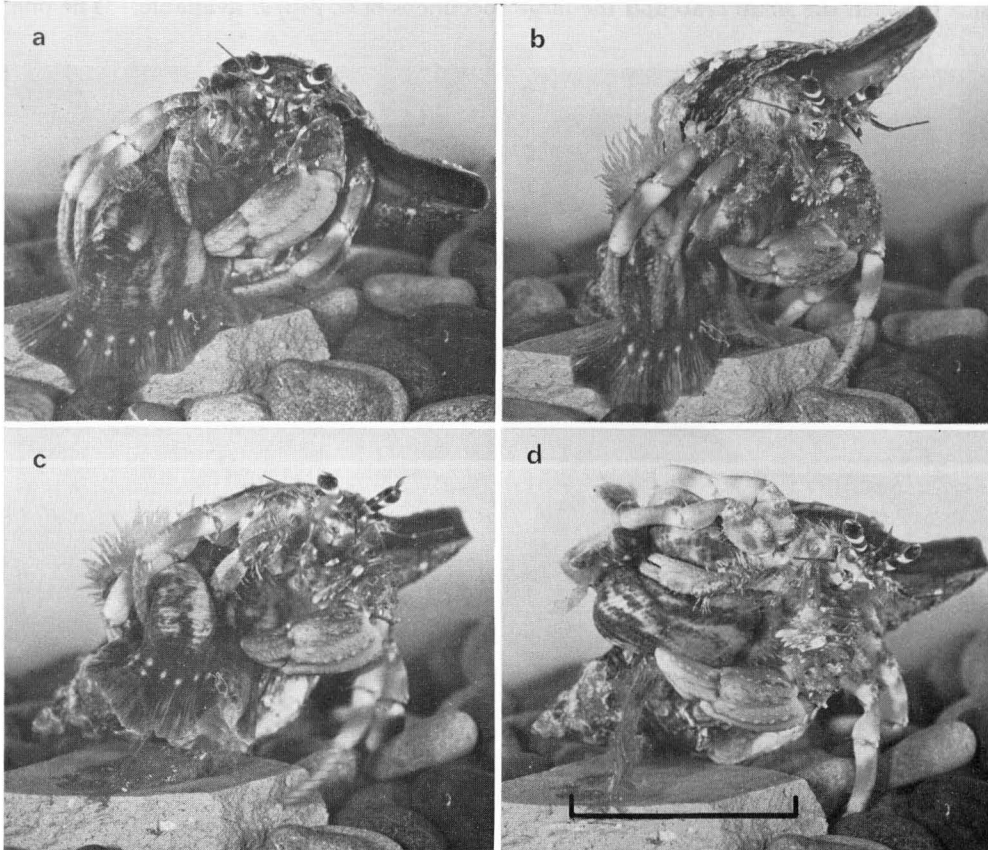


Fig. 1. *Dardanus gemmatus* detaching *Calliactis polypus* from a stone and placing the detached anemone on its shell. **a.** *C. polypus* beginning to relax after first contacts (2 min.); **b.** column extending and pedal disk beginning to lift (4.5 min.); **c.** anemone immediately after detachment (6.0 min.); **d.** anemone held by crab so that pedal disk will settle on right side of shell (7.5 min.). Note mucous deposits being sloughed off in **c** and **d**. Times are from beginning of crab's activity. Scale: 5 cm.

an active species. The failure of *D. cressimanus* to display activity shows that active behavior patterns towards anemones are strictly associated with the symbiotic habit. They are not even inherent or latent in non-symbiotic species of *Dardanus*, ready to appear if the crab should encounter a symbiotic anemone. This is in keeping with the general experience that modes of life and behavior patterns are features that

should not be assumed to be characteristic of taxa beyond the level of a species. Indeed, one might expect behavioral variation in different populations within a species that has an extensive geographical distribution and whose ecological niches are not the same in different locations.

The numbers of experimental animals available were too small for meaningful comparisons of the activity of individual crabs in Group 1. The inactivity of *Diogenes edwardsi* in encounters with *C. polyopus* is explained simply by the vast discrepancy in size between the small crab and the large specimens of *C. polyopus* available. The one

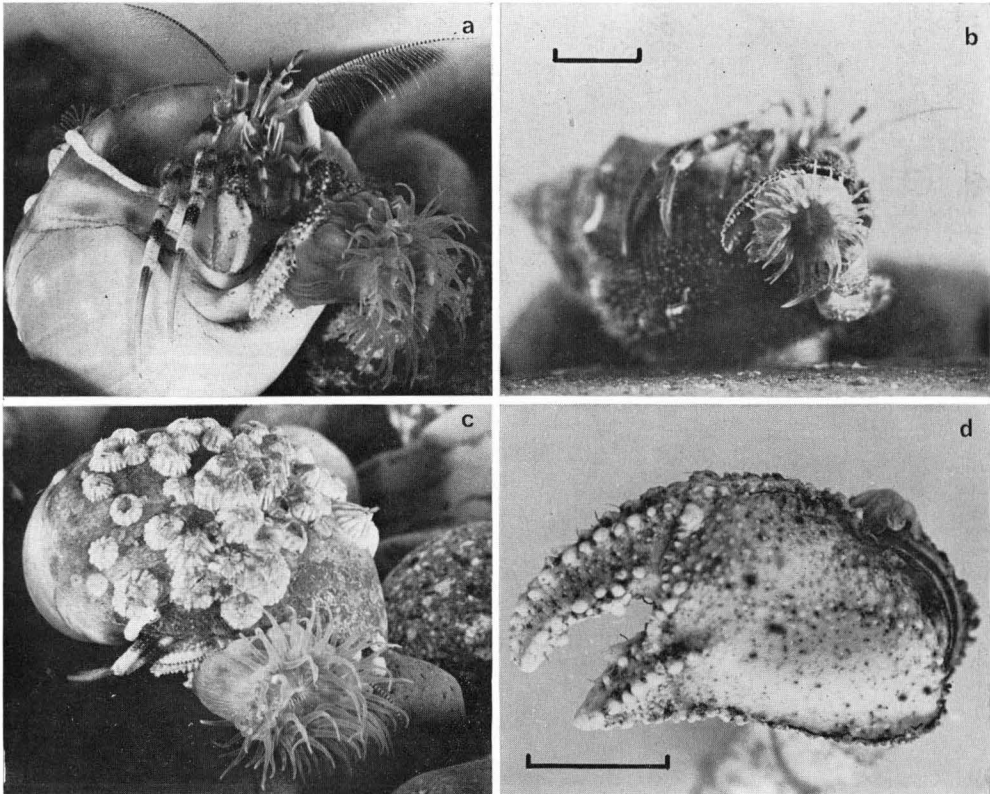


Fig. 2. *Diogenes edwardsi*. **a** and **b**. *Sagartia paguri* on chela of crab emerging from shell. **c**. On claw of crab withdrawn into shell. **d**. Chela of *D. edwardsi* showing smooth area usually occupied by *S. paguri*. Scale: **a**, **c** **b**,—0.5 cm; **d**—0.5 cm.

active transfer with these two species occurred with a small *C. polyopus*.

Non-performing individuals were very rarely found amongst the active species in this collection. This contrasts with my experience in two other laboratories (Ross and Sutton, 1961b; Cutress and Ross, 1969) but recent work by Balasch (personal communication) has shown that non-performing crabs generally come from stock held in aquaria under crowded conditions for a considerable time. My work in Japan was done with fresh animals mostly held in separate containers.

Films provide information on the methods employed by the Japanese pagurids in detaching anemones. Much depended on the relative sizes of crab and anemone. As described above, *D. impressus* used very gentle movements in relaxing the much larger and tough-skinned *P. japonica* but the same crab detached the small thin-skinned Actinian A by holding it tightly with its claws and pulling the anemone roughly from its anchorage almost before it had time to relax. The large *D. haani* possesses a heavy and seemingly clumsy cheliped. Its relaxing and detaching activities were aggressive and rough compared with other species of *Dardanus* in Japan and in other places, e.g., *D. venosus* in Puerto Rico. It was interesting to compare the behavior pattern of *D. arrosor* in Japan with *D. arrosor* in the Mediterranean. *D. arrosor* in the Mediterranean when relaxing *Calliactis paraitica* frequently place themselves in such a way that the shell is brought close to the tentacles, the behavior pattern that assists the anemone in clinging to the shell and conducting its own transfer. This feature in the behavior pattern was not apparent when *D. arrosor* was relaxing and detaching *C. polypus* in Japan. Indeed, such behavior would not appreciably assist the transfer of *C. polypus* since it has been shown already that the response of *C. polypus* to shells prior to detachment is much less well-developed than in *C. parasitica* (Ross, 1970).

It was noted both in films and in visual observations that these Japanese pagurids that have picked up anemones did not place them at random on their shells. In 20 trials with *D. haani*, the first anemone being placed on a bare shell was placed to the right and slightly above the shell aperture in 19 of the trials. These same pagurids later detaching the second *Calliactis* in 16 trials, without any exploratory behavior or hesitation of any kind, lifted the anemone to the left and away from the apex of the shell. After these positions were occupied further anemones, as they became available, were placed directly above the shell opening. No definite patterns could be seen in any subsequent settlements but data are scanty on this point. An interesting observation was that even after removal of the first anemone from its position on the right the next anemone picked up by *D. haani* was placed at the left as if the first one was still in position. It seemed as if the crab possessed some memory of having recently placed *C. polypus* to the right. This memory persisted for at least half an hour but in the 2 experiments that I was able to carry out after a lapse of 2 hrs between the removal of a recently settled anemone on the right and the presentation of the second anemone, the crab behaved towards the second as if it were the first and placed it on the right.

(b) *Diogenes edwardsi*. The small pagurid, *Diogenes edwardsi*, was usually found at Misaki with the outer surface of the claw occupied by a single *Sagartia paguri* (Fig. 2-a & b). When the crab withdraws into its shell, the anemone is pulled back to the aperture facing the outside (Fig. 2-c). As the crab emerges from its shell the anemone comes out first, usually fully expanded. *Diogenes edwardsi* at Misaki usually carried a number of small specimens of the so-called Actinian A on the shell.

S. paguri were obtained for presentation tests with *D. edwardsi* and other crabs by preventing the crab's withdrawal and holding the claw while removing the anemone. This treatment seemed to affect the behavior of some of the crabs, rendering them useless for tests. These animals withdrew into their shells or ran into the corners of

the tanks on being handled or when moved close to the anemones. The figures on inactivity by *D. edwardsi* in Table 2 do not include these abortive trials in which it was impossible to set up encounters. With less excitable *D. edwardsi* the activity patterns were very clear. Crabs without an anemone on the claw immediately responded when they encountered *S. paguri* on a stone or a plate. On such surfaces this anemone was never firmly fixed. On contact, the crab pulled or pushed the anemone off the plate sometimes within a few seconds. The released anemone was manipulated and held by legs and mouth parts for a short time. The crab's claw then came into action and was held close to the detached anemone. Settlement followed very quickly. The entire performance in one case was accomplished in less than 2 minutes.

6 of the specimens of *D. edwardsi* moulted during their period in the laboratory. It was noted that *S. paguri* was never to be found on the claw of the moult. In 4 of the 6 cases the anemone was back in its normal position on the claw of the new exoskeleton. Apparently the crab had recovered the anemone and placed it there.

Table 3 gives the results of trials in which *S. paguri* and Actinian A were presented to *D. edwardsi* sometimes when *S. paguri* occupied the claw and other times when it did not. It was clear that once *S. paguri* was in position on the claw, the crab failed to respond to a different *S. paguri* on the plate. It showed no tendency to place a second *S. paguri* on the shell when the claw was occupied. Specimens of Actinian A were picked up quickly and placed on the shell whether or not the claw was occupied by *S. paguri*. The crab never placed Actinian A on the claw.

Table 3. Activity of *Diogenes edwardsi* in encounters with *Sagartia paguri* and "Anemone A".

Actinian presented	No. of Trials			
	<i>S. paguri</i>		"Anemone A"	
Crab behavior	Active	Inactive	Active	Inactive
<i>D. edwardsi</i> Claw unoccupied	8(8c)*	2	4(4s)*	2
<i>D. edwardsi</i> Claw with <i>S. paguri</i>	0	7	5(5s)	4

* "c" and "s" in brackets refer to settlements on claw and shell, respectively.

The results in Table 3 were obtained from 5 animals only, all at the Misaki Laboratory. At the Amakusa Laboratory, *D. edwardsi* was available in fair numbers but it never carried anemones, neither *S. paguri* nor Actinian A, though the latter occurred there living on some other pagurids. There are color differences between those two populations, the Misaki *D. edwardsi* being predominantly brown, those from Amakusa grey. We noticed, however, that the spine-free area on the cheliped which provided a smooth seat for *S. paguri* in the Misaki specimens (Fig. 2-d) was lacking in the specimens that were collected at Amakusa. This emphasises once again that the symbiotic habit with its associated behavior patterns and possibly some minor morphological adaptations, may be confined only to certain populations within a species.

(c) *Trials with non-symbiotic actinians.* Encounters were set up between 3 species of active anemones that carry pagurids, *Dardanus arrosor*, *D. haani* and *D. impressus* and 3 species of non-symbiotic actinians, *Actinia aquina*, *Anthopleura japonica* and *Diadumene (Haliplanella) luciae*. It could be assumed that such anemones do not appear in symbiotic associations because they lack the response to shells shown by such anemones as *C. parasitica* and because they do not elicit an active behavior pattern from the active crabs. The occasional occurrence of some of these anemones living on shells of mollusks, pagurids and other crabs can be explained as the result of chance settlements on any available surface. But the existence of several species of active crabs in Japan provided a good opportunity to find out what happens when such crabs encounter actinians with which they are not normally associated.

18 trials were carried out, 2 individuals from each species of *Dardanus* being tested against medium sized specimens of the 3 actinian species. In 5 of the trials, the crabs displayed no activity. In the remaining 13 trials, on coming into contact with the anemone, the crabs carried out tapping and prodding movements that closely resembled their activity towards *C. polyopus*. In all cases this activity was brief, lasting about 10–15 sec; the longest recorded duration was 70 sec. The behavior declined gradually, as if the crab was testing the anemone and rejecting it. But such a test seemed to be necessary and it was not terminated by a sudden withdrawal which would have suggested the occurrence of some strong negative stimulus. For instance, *D. luciae* shot out acontia but these did not seem to act as deterrents. In 2 trials with *A. aquina*, the anemone, which was not very firmly attached, came away and was picked up by the crab and manipulated for a few seconds but then quickly dropped. In all other cases the anemones closed at the crab's first contact and remained closed during these brief periods of activity. Symbiotic actinians do the same during the short initial phase of activity by their pagurid partners. The obvious conclusion from these observations is that crabs that display active behavior patterns towards symbiotic anemones probably respond to any anemones on contact. They seem to distinguish anemones that are not potential partners by the anemone's response to these first contacts. Maybe nematocysts are discharged or some other deterrent response occurs. Another possibility, however, is that the symbiotic anemones respond positively to the first contact by relaxing very slightly. Then the anemone becomes softer and smoother as the crab's palpations continue and this change in the anemone provides the basis for the apparent recognition of the symbiotic anemone and for the continuing activity by the crab.

Discussion

This is an exploratory account of the behavior of several Japanese pagurids in their associations with actinians. It has sampled the remarkably rich assortment of species-pairs that are known to exist in Japan but the samples were collected fortuitously, not systematically. For that reason it can add little existing knowledge on the ranges and the depths characteristic of these pagurids and their actinian partners.

The general ecology of the species is still largely unknown and there is no information on seasonal migrations or on the life histories of the species and how they become associated in nature. I hope that my descriptions of the behavioral capacities of these animals will encourage other studies on their general biology as well as behavioral studies on those species that were not available to me.

One point to be noted in conclusion is the fresh evidence of the range of techniques employed by pagurids in detaching actinians and placing them on their shells. These techniques all exploit the capacity of the symbiotic actinian to respond to certain forms of mechanical stimulation by becoming relaxed and releasing the pedal disk (Ross and Sutton, 1970). But the behavior patterns of the different actinians are not identical and this is reflected in the behavior of the crabs. The intractable and large *Paracalliactis japonica* could only be relaxed by *Dardanus impressus* using gentle stroking and scratching movements and maintaining the movements sometimes for as long as an hour or two. The same crab, however, responded to a small, soft-skinned Actinian A by tapping it aggressively and as it opened pulling and stretching it far beyond its normal length while using the tip of one of its walking legs to ease the base off the surface to which it was attached.

An even sharper contrast is the difference in the technique employed by *Diogenes edwardsi* in its interaction with *Sagartia paguri* and Actinian A. On several occasions, the crab detached *S. paguri* by tapping it once or twice with its claw, then resting the claw on the tentacular crown. This caused the anemone to detach and to cling to the claw where it soon settled with the aid of some gentle manipulation from the other appendages. Yet the same crab, as described above, detaches Actinian A by the more usual stroking and lifting movements and resettles this anemone on the shell. Such examples of complex and discriminating behavior by these pagurids are important in appraisals of the behavioral capacities of the higher arthropods.

When these observations were made it was not known that the presence of actinians on the shell provided protection to two species of Mediterranean pagurids, in laboratory trials, against predation by *Octopus* (Ross, 1971). The considerable number of pagurid-actinian associations in Japan together with a large number of non-symbiotic pagurids raises an interesting question about the possible interactions between these various species and *Octopus* in Japanese waters. The actinians which grow to a larger size, *C. polypus* and *P. japonica*, would possibly provide effective protection against *Octopus*. Larger specimens of Actinian A might do the same but some of the smaller crabs, *D. edwardsi* and small *D. impressus* were often found with large numbers of small Actinian A on their shells and would not be protected against *Octopus* by these anemone partners. Protection against *Octopus* may be one of the advantages conferred upon pagurids by symbiotic anemones in some of these Japanese associations but it cannot be the explanation of all these examples.

The work of Mainardi and Rossi (1969) on the agonistic behavior between individual hermit crabs and their interactions with their anemone partners is relevant here. They showed that a dominance hierarchy existed amongst *D. arrosor* and the dominant individuals acquired *C. parasitica*. My trials were conducted with single

crabs so that the results of individual trials would not be affected by this factor. However, before their use in such trials, the crabs were frequently maintained in groups in large tanks and it is possible that under these circumstances some individuals, or the members of one species, might have developed a submissive behavior pattern. This might explain the relative inactivity of *D. diogenes*, which invariably was collected with anemones on its shell but was conspicuously unsuccessful in acquiring anemones in the laboratory.

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