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A sea anemone symbiotic with gastropods of eight species in the Mariana Islands

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Abstract—Fifty-two specimens of the small sea anemone *Neoaiptasia morbilla* Fautin and Goodwill, 2009, were collected attached to shells of gastropods living in shallow subtidal sand on Saipan and Tinian, Mariana Islands, in 1988 and from 2003 through 2007. The anemones were associated with gastropods of eight species belonging to five families. Relative abundance of gastropods in an area where the anemones occurred was the same as the relative abundance of gastropods to which anemones were attached, from which we conclude that the anemones had no preference among the species of gastropods. A gastropod typically carried one to two anemones, but a few with three and four were collected. The anemone was generally located antero-dorsally on cerithiids and terebrids, postero-dorsally on cones, and in an intermediate position on strombids. The position on the shell minimizes the distance between anemone and substrate surface.

Introduction

Ates (1997) summarized much of what was known about actiniarians attached to shells of live gastropods as of his writing. They had been reported predominantly from the north-eastern Atlantic, the Caribbean, Japan, and New Zealand in shallow water, and the western Caribbean, western Africa, and the south-western Atlantic in deep water. Since then Mercier & Hamel (2008) have published a detailed study of such a relationship in the north-western Atlantic. Although these associations may be more host-specific than symbioses of actiniarians on shells occupied by hermit crabs, most symbiotic anemones attach to the shell of more than a single species of gastropod (Ates 1997; Mercier &

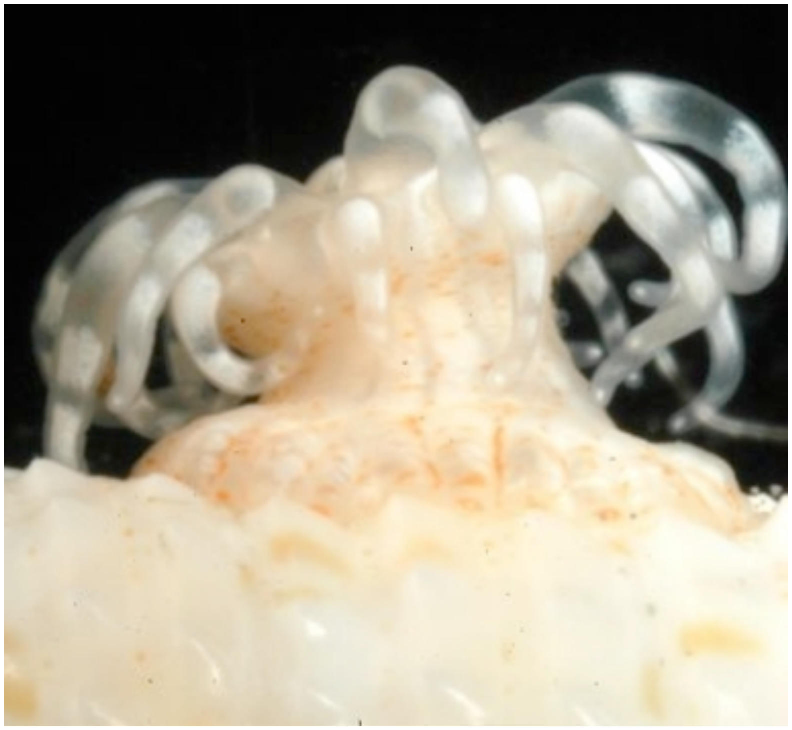

Figure 1. Sea anemone of the species *Neoaiptasia morbilla* attached to the second whorl of a specimen of the gastropod *Rhinoclavis articulata*.

Hamel 2008). The number of anemones attached to a single shell can vary from one to several (Smith 1971, Ross & Kikuchi 1976, Pastorino 1993, Riemann-Zürneck 1994, Ates 1997, Mercier & Hamel 2008).

Compared to what is known about the symbiosis between hermit crabs and the sea anemones that attach to their shells, little is known about the gastropod-sea anemone symbiosis (Ross & Kikuchi 1976). A great proportion of the reports of the gastropod-sea anemone symbiosis are from single observations, and even for the better-known relationships, the degree of specificity between the partners is poorly documented (Ates 1997). Having found individuals of a small sea anemone, *Neoaiptasia morbilla* Fautin & Goodwill, 2009, attached to shells of eight species of gastropods representing five families living in sand in shallow water on Saipan and Tinian (Figure 1), we sought to understand if the shells of any species of snail were preferred over those of others. Although we were unable to do preference experiments in the laboratory, from our samples, we infer that the anemones are not host-specific, but opportunistically associate with available snails.

As many as four anemones can occupy a single shell, but typically there are only one or two. We analyzed the position of anemones on shells to understand the forces that position them as they are. We conclude that the position on the shell minimizes the distance between anemone and substrate surface.

Methods

RHG and JF collected specimens of *Neoaiptasia morbilla* and their live gastropod hosts from Saipan and Tinian in the Commonwealth of the Northern Mariana Islands; gastropods with attached anemones were collected haphazardly (as opposed to systematically) in 1988, 2003, 2004, 2005, and 2007. In 2004 and 2006 gastropods with and without attached anemones were systematically collected from transects. All collections and shipments of specimens were made in accordance with permits issued by the Commonwealth of the Northern Mariana Islands Division of Fish and Wildlife. Repositories of many of the anemone specimens are listed by Fautin and Goodwill (2009).

The number of anemones, their position on the shell, and length, height, and width of each shell collected from 2003 thru 2007 were documented. Most gastropods were identified from photographs by Gustav Paulay (Florida Museum of Natural History, University of Florida); others were identified by RHG and JF.

The search for anemones was done by excavating trails left in the sand by gastropods and by inspecting hard surfaces, such as rocks and buoys, for specimens. Most were found on the southern side of Managaha Island, a small island at the entrance to Tanapag Lagoon (approximately 15°14'N, 145°43'E), by students instructed in searching for the animals and by RHG and JF. The substrate and water depth at the collection sites were documented by RHG and JF. Anemones and gastropods were kept alive for two weeks in aquaria for observation and photography. The length and pedal disc diameter of 18 anemones that appeared to be fully relaxed after fixation were measured by RHG.

In 2004, RHG and JF laid five 100 m by 1 m transects to assess relative abundance of gastropods from the southern side of Managaha Island, which is at the center of a recently established marine sanctuary and is now not subject to shell collecting by humans without agency permission. Four transects were perpendicular to the shoreline from the water's edge to a depth of 1 m, and one transect was parallel to the shoreline at a depth of 4.6 m. In 2006, a 100 m by 2 m transect was laid by JF in the same area, perpendicular to the shoreline from the water's edge to a depth of 1 m. Every trail in a transect was followed to its terminus where an excavation was made in the sand for gastropods. Gastropods were identified and measured by RHG and JF.

Statistical analyses were by TexasSoft, WINKS SDA Software, 6th Edition. Random distribution of anemones among the collected mollusks was tested by chi-square, using the 2004 transects as expected values and the haphazardly collected gastropods from the same area as observed values. The 2004 data were tested with and without *Rhinoclavis articulata*; the 2006 data were analyzed alone and in combination with the 2004 data that included *R. articulata*.

Table 1. Locations on Saipan and Tinian where sea anemones and gastropods were collected.

Island: location	depth (m)	# gastropods	# attached anemones
Saipan: Managaha Island – south side	1-5	30	44
Saipan: Tanapag Lagoon – center area	9	1	4
Saipan: Tanapag Lagoon, Tanapag Park	1	2	3
Tinian: Tachnogna Beach, Sunharon Park	0.5	1	1
Totals		34	52

To determine preferences for shell size, Student's t-test was used to compare the means for length, height, and width of the three most numerous gastropod hosts (*R. articulata*, *Conus pulicarius*, and *Terebra affinis)* against the means of the same species not supporting anemones. Student's t-test was used to determine if the dimensions of *R. articulata* and *T. affinis* with a single anemone versus those with more than one anemone differed. No similar comparisons could be made for other snails.

Table 2. Living gastropods collected from all areas on Saipan and Tinian, and the number of specimens of *Neoaiptasia morbilla* attached to them.

Family: Species	# snails (% total)	# anemones (% total)	anemones per shell: one	two	three	four	av.
Cerithiidae:							
Rhinoclavis articulata	17 (50.0)	26 (50.0)	9	7	1	0	1.5
Rhinoclavis aspera	1 (2.9)	2 (3.8)	0	1	0	0	2.0
Conidae:							
Conus pulicarius	7 (20.7)	10 (19.3)	6	0	0	1	1.4
Conus tessellatus	1 (2.9)	1 (1.9)	1	0	0	0	1.0
Pyramidellidae:							
Otopleura mitralis	1 (2.9)	1 (1.9)	1	0	0	0	1.0
Strombidae:							
Strombus gibberulus	1 (2.9)	2 (3.8)	0	1	0	0	2.0
Terebridae:							
Terebra affinis	5 (14.8)	9 (17.4)	3	1	0	1	1.8
Terebra crenulata	1 (2.9)	1 (1.9)	1	0	0	0	1.0
Total	34 (100)	52 (100)	21	10	1	2	1.5
% of snails (34) supporting one, two, three, or four anemones:			61.8	29.4	2.9	5.9	
% of anemones (52) found one, two, three, or four per snail:			40.4	38.5	5.8	15.3	

Results

Fifty-two specimens of the sea anemone *Neoaiptasia morbilla* attached to 34 living gastropods were collected from Saipan and Tinian (Table 1). On Saipan, specimens of this sea anemone occurred only in Tanapag Lagoon, with the largest concentration on the southern side of Managaha Island; on Tinian it occurred in Sunharon Bay (14°57'N, 145°37'E) and Harbor. In both, it was found only in sandy subtidal habitats from 0.5 to 9.0 m deep; however, we did not search below 10 m. We failed to find it on shipping lane buoys, WWII debris, coral-rubble reef flats, mixed rubble/sand flats, wave-cut benches, and coral outcrops.

In aquaria, gastropods burrowed into the sand so that only the extended tentacles of the attached anemones were exposed on the sand surface. No anemone changed position on the shell to which it was attached nor did any change shells during the two weeks they were observed in aquaria.

The subtidal, sand-dwelling gastropods to which anemones were attached belong to eight species in five families. An average of 1.5 anemones occurred per shell. Only three gastropods supported more than two anemones, and most (61.8%) carried a single one; 40.4% of anemones occurred singly on a shell (Table 2). Specimens of *N. morbilla* were the only anemones we found on the snail shells.

Single anemones were consistently located on the antero-dorsal or lateral surface of the first whorl of cerithiids and terebrids, and on the postero-dorsal or lateral surface of cones (Table 3). Six of the 28 anemones on cerithiids were just behind the siphon in the notch formed where the siphonal canal and first whorl join. On cerithiids and terebrids with two anemones, in seven of nine instances, one was in an antero-dorsal position on the first whorl and the other was immediately behind in an antero-dorsal position covering the second whorl or more than one whorl. One cerithiid had three and one terebrid had four anemones. In both cases the anemones were arranged one behind another, from antero-dorsal to postero-dorsal, their pedal discs touching or nearly so. On the single strombid collected, both anemones were on one side of the shell, one mid-laterally on the second whorl, the other adjacent postero-laterally on the third whorl. One cone shell had four anemones, one in a postero-dorsal position and the other three grouped together dorsally, spread from slightly anterior to the middle of the shell.

Table 3. Position of single anemones on gastropod shells.

host family (N)	anterior N (%)	middle N (%)	posterior N (%)	Dorsal N (%)	lateral N (%)
Cerithiidae (9)	8 (88.9)	1 (11.1)	0 (0)	8 (88.9)	1 (11.1)
Conidae (7)	0 (0)	0 (0)	7 (100)	4 (57.1)	3 (42.9)
Pyramidellidae (1)	1 (100)	0 (0)	0 (0)	1 (100)	0 (0)
Terebridae (4)	3 (75.0)	1 (25.0)	0 (0)	4 (100)	0 (0)

Table 4. Managaha gastropods collected from transects in 2004 and 2006, and gastropods collected haphazardly from the same area hosting anemones of the species *Neoaiptasia morbilla*. "Others" indicates members of the family for which only one or two specimens per species were collected and that did not host an anemone. (n/a = not applicable; no anemones were found in the 2004 transects).

Family: Species	2004 transects: # snails (%)	2006 transect: # snails (%)	2006 transect: # snails (%) / # anemones (%)	haphazard: # snails (%) / # anemones (%)
Architectonicidae:				
Others: 1 species	1 (0.8)	0	n/a	0 / n/a
Cerithiidae:				
Rhinoclavis articulata	16 (13.4)	69 (75.0)	6 (54.5) / 9 (64.4)	11 (57.8) / 17 (56.7)
Rhinoclavis aspera	7 (5.9)	0	n/a	0 / n/a
Rhinoclavis fasciata	5 (4.3)	0	n/a	0 / n/a
Others: 2 species	3 (2.5)	1 (1.1)	0	0 / n/a
Conidae:				
Conus pulicarius	29 (24.4)	5 (5.4)	3 (27.3) / 3 (21.4)	1 (5.3) / 1 (3.3)
Conus tessellatus	1 (0.8)	1 (1.1)	1 (9.1) / 1 (7.1)	0 / n/a
Others: 3 species	2 (1.7)	1 (1.1)	0 / n/a	0 / n/a
Mitridae:				
Imbricaria olivaeformis	5 (4.3)	0	n/a	0 / n/a
Others: 5 species	3 (2.5)	2 (2.2)	0 / n/a	0 / n/a
Naticidae:				
Others: 1 species	1 (0.8)	0	n/a	0 / n/a
Pyramidellidae:				
Otopleura mitralis	3 (2.5)	6 (6.5)	0 / n/a	1 (5.3) / 1 (3.3)
Others: 1 species	0	1 (1.1)	0 / n/a	0 / n/a

Table 4, *cont*.

Family: Species	2004 transects: # snails (%)	2006 transect: # snails (%)	2006 transect: # snails (%) / # anemones (%)	haphazard: # snails (%) / # anemones (%)
Strombidae:				
Strombus gibberulus	2 (1.7)	0	n/a	1 (5.3) / 2 (6.6)
Others: 1 species	1 (0.8)	0	n/a	0 / n/a
Terebridae:				
Terebra affinis	20 (16.8)	4 (4.3)	1 (9.1) / 1 (7.1)	4 (21.0) / 8 (26.8)
Terebra crenulata	0	0	n/a	1 (5.3) / 1 (3.3)
Terebra maculata	10 (8.4)	1 (1.1)	0 / n/a	0 / n/a
Others: 11 species	10 (8.4)	1 (1.1)	0 / n/a	0 / n/a
Total	119 (100)	92 (100)	11 (100) / 14 (100)	19 (100) / 30 (100)

Table 5. Dimensions of gastropod shells with attached anemones collected from all areas on Saipan and Tinian.

Family: Species (N)	length: average + sd (range) mm	height: average + sd (range) mm	width: average + sd (range) mm
Cerithiidae:			
Rhinoclavis articulata (17)	26.4 ± 3.0 (21.5 – 31.5)	7.6 ± 1.0 (6.0 – 10.0)	9.6 ± 1.1 (7.4 -11.5)
Rhinoclavis aspera (1)	41.3	10.6	11.8
Conidae:			
*Conus pulicarius** (6)	35.9 ± 6.1 (26.6 – 42.5)	21.8 ± 4.3 (15.2 – 25.7)	22.0 ± 4.6 (15.9 – 26.8)
Conus tessellatus (1)	21.4	10.0	10.8
Pyramidellidae:			
Otopleura mitralis (1)	13.0	5.5	5.5
Strombidae:			
Strombus gibberulus (1)	32.0	12.5	16.4
Terebridae:			
Terebra affinis (5)	32.9 ± 9.6 (23.5 – 48.0)	6.9 ± 1.7 (5.0 – 9.3)	7.2 ± 1.9 (5.3 – 10.1)
*Terebra crenulata***	113.0	24.0	25.0

*Six snails were measured; one collected in 1988 was not

**These measurements are not from the single specimen collected in 1988, but from an average-size museum specimen collected that year in Saipan; for comparative purposes only.

Table 6. Dimensions of gastropod shells lacking anemones collected from the Managaha transects in 2004 and 2006.

Family: Species (N)	Length: average + sd (range) mm	height: average + sd (range) mm	width: average + sd (range) mm
Architectonicidae:			
Philippia radiata (1)	11.5	6.7	10.5
Cerithiidae:			
Cerithium columna (2)	23.0 ± 3.3 (20.6 – 25.3)	8.0 ± 2.5 (6.2 – 9.8)	10.2 ± 2.0 (8.8 -11.6)
Cerithium nodulosum (1)	79.5	27.1	35.4
Rhinoclavis articulata (79)	24.8 ± 2.7 (16.5 – 30.6)	7.4 ± 0.8 (6.3 – 9.7)	9.1 ± 1.2 (6.1 – 11.8)
Rhinoclavis aspera (7)	30.3 ± 1.9 (28.3 – 33.0)	8.8 ± 0.7 (8.0 – 9.9)	10.3 ± 0.7 (9.6 – 11.7)
Rhinoclavis fasciata (5)	22.6 ± 3.8 (16.8 – 27.3)	6.1 ± 0.4 (5.5 – 6.4)	6.5 ± 0.3 (6.2 – 6.8)
Rhinoclavis sinensis (1)	43.7	14.4	16.6
Conidae:			
Conus ebraeus (1)	17.1	9.8	10.1
Conus eburneus (1)	39.9	22.5	24.6
Conus flavidus (1)	38.6	19.7	21.7
Conus pulicarius (31)	32.9 ± 6.0 (25.0 – 48.7)	18.5 ± 3.6 (13.0 – 27.2)	20.2 ± 3.9 (14.2 – 30.2)
Conus tessellatus (1)	20.2	10.0	11.0
Mitridae:			
Cancilla praestantissima (1)	17.6	6.4	6.8
Imbricaria olivaeformis (5)	14.4 ± 1.6 (13.0 – 17.1)	5.9 ± 1.1 (4.8 – 7.6)	6.3 ± 1.1 (5.2 – 8.1)
Imbricaria punctata (1)	13.2	6.2	6.6
Mitra mitra (2)	61.4 ± 1.7 (60.3 -62.6)	16.1 ± 0.6 (15.7 – 16.6)	17.9 ± 0.2 (17.8 – 18.1)
Neocancilla papilio (1)	15.1	6.4	6.7
Naticidae:			
Natica gualtieriana (1)	7.0	7.0	10.1

Table 6, *cont.*

Family: Species (N)	Length: average ± sd (range) mm	height: average ± sd (range) mm	width: average ± sd (range) mm
Pyramidellidae:			
Otopleura mitralis (9)	12.9 ± 1.7 (10.7 – 15.4)	5.2 ± 0.7 (4.5 -6.3)	5.3 ± 0.6 (4.6 – 6.3)
Otopleura nodicincta (1)	20.8	8.2	8.8
Strombidae:			
Strombus gibberulus (2)	31.0 ± 0.7 (30.5 – 31.5)	11.8 ± 0.2 (11.6 – 12.0)	15.5 ± 0.9 (14.9 – 16.2)
Strombus mutabilis (1)	17.0	7.4	9.3
Terebridae:			
Hastula albula (1)	9.9	3.8	3.9
Hastula lanceata (1)	23.8	5.7	5.7
Hastula solida (1)	14.7	4.4	4.6
Terebra affinis (23)	23.7 ± 7.0 (15.5 – 43.2)	5.5 ± 1.2 (3.7 – 9.2)	5.6 ± 1.3 (3.9- 9.9)
Terebra argus (1)	58.9	10.0	10.2
Terebra cerithina (1)	40.7	9.0	9.1
Terebra chlorata (1)	71.4	15.3	15.7
Terebra dimidiata (1)	79.1	14.1	14.4
Terebra felina (1)	45.7	10.4	10.4
Terebra funiculata (1)	32.3	5.7	5.7
Terebra maculata (11)	103.9 ± 23.6 (79.3 – 166.7)	28.1 ± 6.1 (21.1 – 44.7)	28.8 ± 6.3 (21.5 – 45.8)
Terebra subulata (1)	131.4	22.1	22.7
Terebra sp. juvenile (1)	24.2	5.0	5.2

Of the 119 gastropods belonging to 29 species in eight families collected on the Managaha transects in 2004, none bore anemones, although five of the species were represented in the haphazard collections from Managaha (Table 4). The 2006 transect yielded 92 gastropods in five families; 14 anemones were attached to 11 snails representing four of the 12 species collected (thus 12% of the snails bore at least one anemone). *Rhinoclavis articulata* was the gastropod found most often with attached anemones, representing 57.8% of the haphazardly collected gastropods and 54.5% of those collected along the 2006 transect (Table 4).

The size of specimens of *R. articulata*, *C. pulicarius*, and *T. affinis* with anemones did not differ significantly from the dimensions of specimens of the same species collected from the transects not hosting anemones (Tables 5, 6). There was no significant difference in size of those specimens of *R. articulata* and *T. affinis* supporting one or multiple anemones.

JF made a single aquarium observation of a specimen of *T. affinis* that had been crawling forward, but abruptly changed direction and accelerated after its siphon touched the tentacles of an anemone attached to the shell of *R. articulata*.

Discussion

In 2004, haphazardly collected anemones of the species *Neoaiptasia morbilla* on Saipan were significantly more associated with *R. articulata* ($p = 0.000$) than would be predicted by the relative abundance of the eight species of gastropods from the transects. If associations with *R. articulata* were excluded from analysis, the association of anemones with gastropods did not differ significantly ($p = 0.19$) from what was expected by chance (Table 4). In 2006, anemones were randomly distributed ($p = 0.07$) among all gastropods collected from the transect, regardless of whether *R. articulata* was included in analyses. When data from 2004 and 2006 were combined, the probability of a random association was 0.020 (Table 4). We therefore conclude that anemones occur on gastropods in proportion to the abundance of the snails.

It would seem that an anemone smaller than the shell could attach anywhere on it; Ates (1997) opined that location preference would require behavioral adaptation in the actiniarian. Dales (1957) suggested that certain locations on a shell allow sedentary symbionts access to the host's feeding and respiratory currents. The anemone *Hormathia digitata* is usually found on the first whorl of the shell of *Colus gracilis* but rarely on the second whorl, even if there are two anemones (Ates 1997, 1998). Large individuals of *Allantactis parasitica* attach to the body whorl of their host *Buccinum undatum,* whereas smaller individuals are on apical whorls, from which Mercier and Hamel (2008) inferred the former are in a more stable position with greater access to food particles, whereas the latter are less subject to smothering by the mud in which the snails live or being knocked off.

By analogy, it may be that the position of *N. morbilla* on a shell minimizes the distance for the anemone's tentacles to reach the surface of the sand for feeding. On cerithiids or terebrids, an anemone was positioned antero-dorsally or laterally, but on a cone shell postero-dorsally or laterally. Such positions were occupied even when other areas on the shell were sufficiently large for attachment. A mid-dorsal position would be nearest the substratum on strombids, but on the one strombid shell that bore two anemones, both mid-lateral on one side of the shell; perhaps the narrow mid-dorsal surface does not provide enough area for attachment.

Other factors may also affect position. The siphonal canal of cerithiids, which extends upward much further than that of other sand-dwelling gastropods, might act as a plow shear for small anemones attached between it and the first whorl. Although the shell of most snails documented by Riemann-Zürneck (1994: 218) as being associated with the sea anemone *A. parasitica* was entirely enveloped by the anemone, very tiny anemones ("<1 cm," dimension unspecified) attached to the siphonal canal of the gastropod. Four of the six anemones found in the groove between the siphon and first whorl of *R. articulata*, were small, ranging from 1.1 to 2.1 mm in length as compared to an average length of 3.0 mm (Fautin & Goodwill 20**); in that position, the siphonal canal might protect them from abrasion as the snail moves through the sand.

During this research, the only specimens of *Neoaiptasia morbilla* we found were attached to shells of living gastropods, which we located by following trails left by the crawling gastropods. We could not determine if this is an obligate symbiosis for the anemones: our failure to find them on any surface except snail shells may be because the anemones are small (no more than several mm in diameter and length) and cryptically colored.

We have no explanation for the marked difference in number of snails with anemones between Managaha Island and surrounding areas where the substratum and gastropod fauna are the same, nor between the two years in which we ran transects. Mercier & Hamel (2008) reported anemones attached to snails in only three of 87 trawls. Where such a symbiosis exists, the proportion of snails in a population bearing anemones can be high (Pearce & Thorson 1967, Ross & Kikuchi 1976, Pastorino 1993, Mercier & Hamel 2008).

A mollusk shell provides an anemone a firm substratum in soft bottom habitats, and the gastropod may receive protection from predators, as suggested by our single aquarium observation. Cnidarians are commonly proposed to protect their symbionts (e.g. Whorff 1991; Riemann-Zürneck 1994; White et al. 1999). However, Ates (1997) reasoned that if the relationship of anemones with snails were highly beneficial, it should be widespread, and because it seems not to be, the benefits are lower or the costs higher than appreciated. Whether symbioses between sea anemones and gastropods are really uncommon or are simply poorly documented is unclear (Ross 1967, 1974; Ates 1997).

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