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Distribution Patterns of Five Zoanthid Species at Okinawa Island, Japan

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Yuka Irei, Yoko Nozawa, and James D. Reimer (2011) Distribution patterns of five zoanthid species at Okinawa Island, Japan. *Zoological Studies* **50**(4): 426-433. Zoanthids (Anthozoa, Hexacorallia) are distributed worldwide, especially in shallow tropical and subtropical waters. In fringing reefs of Okinawa I., southwestern Japan, zoanthids are common benthic organisms. Despite their abundance, even basic ecological information such as favorable habitats based on quantitative surveys is still lacking. Accordingly, we investigated the distribution patterns of 5 common zooxanthellate zoanthid species in shallow reef waters (< 10 m) of Okinawa I.: *Palythoa tuberculosa*, *P. mutuki*, *Zoanthus sansibaricus*, *Z. kuroshio*, and *Z. gigantus*. The survey was conducted using the belt transect method in 3 reef environments (moat, reef crest, and reef slope) at 10 reef sites in 2008. As a result, 2404 zoanthid colonies were observed, and *Z. sansibaricus* and *P. tuberculosa* were the 2 most dominant species, respectively comprising 52% and 41% of the total zoanthids observed. The environment where the highest numbers of colonies were observed was the reef crest (1615 colonies) followed by the reef slope (687 colonies), while zoanthids were rare in the moat environment (102 colonies). There were significantly more *Z. sansibaricus* colonies on reef crests than reef slopes, but no significant difference was seen in the frequencies of the other 4 species between the reef crest and reef slope. As to the zoanthid colony size, most colonies (> 86%) of the 5 zoanthid species were < 10 cm in diameter, and only 2 colonies of > 50 cm in diameter were observed in the survey. The absence of zoanthids in moats suggested that sedimentation or weak currents may be factors limiting zoanthid distribution; however, detailed investigations are necessary to confirm this. Since zooxanthellate zoanthids are a major benthic group on coral reefs, further research focusing on the relationships between zoanthid distribution and environmental conditions will foster a better understanding of coral reef ecosystems. http://zoolstud.sinica.edu.tw/Journals/50.4/426.pdf

Key words: Zoanthid, Distribution, Shallow reef environment, Belt transect.

Zoanthids (Anthozoa, Hexacorallia) are an order of cnidarians characterized by having 2 rows of tentacles and 1 siphonoglyph, and are generally colonial with polyps linked by common tissue (a coenenchyme). Additionally, most zoanthids incorporate grains of sand from their environment into their body structure. Due to these unique characters, zoanthids are often referred to as encrusting anemones. Zoanthids are distributed in most marine environments, from temperate to tropical areas and from the intertidal zone to the deep sea below 5000 m, and are particularly common in tropical and subtropical seas (Fosså and Nilsen 1998, Reimer and Miyake 2009). In total, 354 zoanthid species were reported worldwide (Fautin 2010); however, the number of proper species is likely much less due to inadvertent re-descriptions (Burnett et al. 1997, Reimer et al. 2004). In shallow waters surrounding Okinawa I., southwestern Japan, there are at least

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13 species (including undescribed species) of brachycnemic zoanthids from 5 genera: *Palythoa*, *Zoanthus*, *Sphenopus*, *Isaurus*, and *Neozoanthus* (Reimer 2010).

The genera *Palythoa* and *Zoanthus* are common benthic taxa in coral reefs and have large influences on other benthos by covering them or limiting space availability (Suchanek and Green 1981). Several studies related to zoanthid population dynamics, dispersal strategies, and possible influences on coral reef ecosystems were conducted in the Atlantic (Acosta 2005, Mendonça-Neto et al. 2008) and Caribbean (Sebens 1982, Karlson 1983, Bastidas and Bone 1996). In the Indo-Pacific; however, quantitative surveys focusing on zoanthid distributions are almost nonexistent despite the general abundance of zoanthids. Ono et al. (2003) performed long-term monitoring of the coverage of *Zoanthus sansibaricus* in Kagoshima, Japan. However, their monitoring area was quite limited as only 1 transect (1 × 50 m) was examined. As to distribution patterns of zoanthids in Japan, *P. tuberculosa* being able to inhabit a wide depth range from the intertidal zone to over 30 m in depth at Okinawa was only briefly mentioned (Reimer et al. 2007b), and *Z. sansibaricus* has mainly been reported on reef crests (Reimer 2008). To verify such observations and gain additional information, this study examined distribution patterns of 5 common zooxanthellate zoanthid species on 3 typical coral reef environments (moat, reef crest, and reef slope) at 10 locations around Okinawa I., southwestern Japan.

MATERIALS AND METHODS

Five zooxanthellate zoanthids, *Palythoa tuberculosa* Klunzinger 1877, *P. mutuki* Haddon and Shackleton 1891, *Zoanthus sansibaricus* Carlgren 1900, *Z. kuroshio* Reimer and Ono 2006, and *Z. gigantus* Reimer and Tsukahara 2006 (Fig. 1), were examined in this study. Species identifications were sensu Reimer et al. (2006a 2007b). All 5 species possess endosymbiotic *Symbiodinium* spp. dinoflagellates (Reimer et al. 2006b 2007a b) and form colonies attached to hard substrates such as rocks or compacted coral of coral reefs.

This study was conducted at 10 coral reef sites around Okinawa I., southern Japan (Fig. 2A). The environment of shallow coral reef sites on Okinawa I. generally differ between the east and west coasts. In contrast to well-developed coral reefs on the west coast, ocean floors of many sites on the east coast are muddy and/or sandy, and zooxanthellate zoanthids are generally uncommon. Therefore, the 10 study sites were chosen mainly from the west coast of Okinawa I. (Fig. 2A). Surveys were performed between 14 Apr. and 4 Dec. 2008. Okinawan coral reefs are largely fringing reefs with developed moats, and thus in this study, we conducted surveys in 3 different reef environments at each site: moat, reef crest (the elevated area located outside of the moat), and reef slope (the area located outside the reef edge) (Fig. 2B). The depth range of each reef environment we surveyed was 1-3 m in the moat, 0-2 m on the reef crest, and 5-10 m on the reef slope. In this study, we utilized 10 × 1-m belt transects and counted the number of colonies of the 5 zooxanthellate zoanthid species. First, a 10-m line was randomly set parallel to the reef edge. Then a 0.5-m width was defined on each side of the line by the length of the observer's outstretched arms. Nine transects were set at each study site, with 3 transects for each reef environment (moat, reef crest, and reef slope). In three (Maeda-west, Mizugama, and Sunabe) of the 10 studied reef sites where the moat was not well developed, only the reef crest and reef slope were surveyed. In general, percentage coverage is often calculated in quantitative surveys of sessile benthic organisms using photography or video. However, in this study, colony numbers were utilized instead because analyzing photographic images was very difficult due to the generally small sizes of the colonies and choppy conditions on the reef crests. Observations and counts of colonies were performed in situ by scuba diving or snorkeling. The data obtained were recorded on waterproof paper.

To determine the size frequency distributions of the species, the general colony size was also recorded using 5 size categories at eight of 10 study locations, with the exception of Zanpa and Minatogawa. The 5 categories (SS, S, M, L, and LL) were defined as follows: SS, fewer than 10 polyps; S, more than 10 polyps of 10 × 10 cm; M, 10 × 10-25 × 25 cm; L, 25 × 25-50 × 50 cm; and LL, > 50 × 50 cm. Each colony size was estimated with a ruler and assigned to a size class.

From previous studies, asexual reproduction by fragmentation is known for some *Zoanthus* and *Palythoa* species (Karlson 1986, Acosta et al. 2001). Their fission processes and triggers inducing fragmentation were previously studied, especially for mat-like *Palythoa* species such as *P. caesia* on the Great Barrier Reef (Tanner 1997) and *P. caribaeorum* in the Atlantic (Acosta 2005). Those 2 species have very similar morphologies to *P. tuberculosa*, in possessing a thick and well-developed coenenchyme. In shallow reefs of Okinawa I., large aggregations of small *P. tuberculosa* colonies exist, implying that fragmentation may often occur. Numerous small polyp-clusters forming large aggregations may be genetically identical. However, it is impossible to distinguish clone colonies in the field. Thus, the definition of an "identical colony" was defined as "all polyps connected by a continuous coenenchyme" in this study. However, in some cases, the juncture of the polyps could not be observed due to the complexity of the substrate and small stoloniferous connections of the polyps. In such a situation, zoanthid polyps within a 5-cm radius were defined as being identical. However, adjoining zoanthid polyps were defined as belonging to different colonies when their oral disk colors obviously differed from each other. Considering the colony size, morphological characters of the 5 zoanthid species in this study were noted. Unlike the mat-

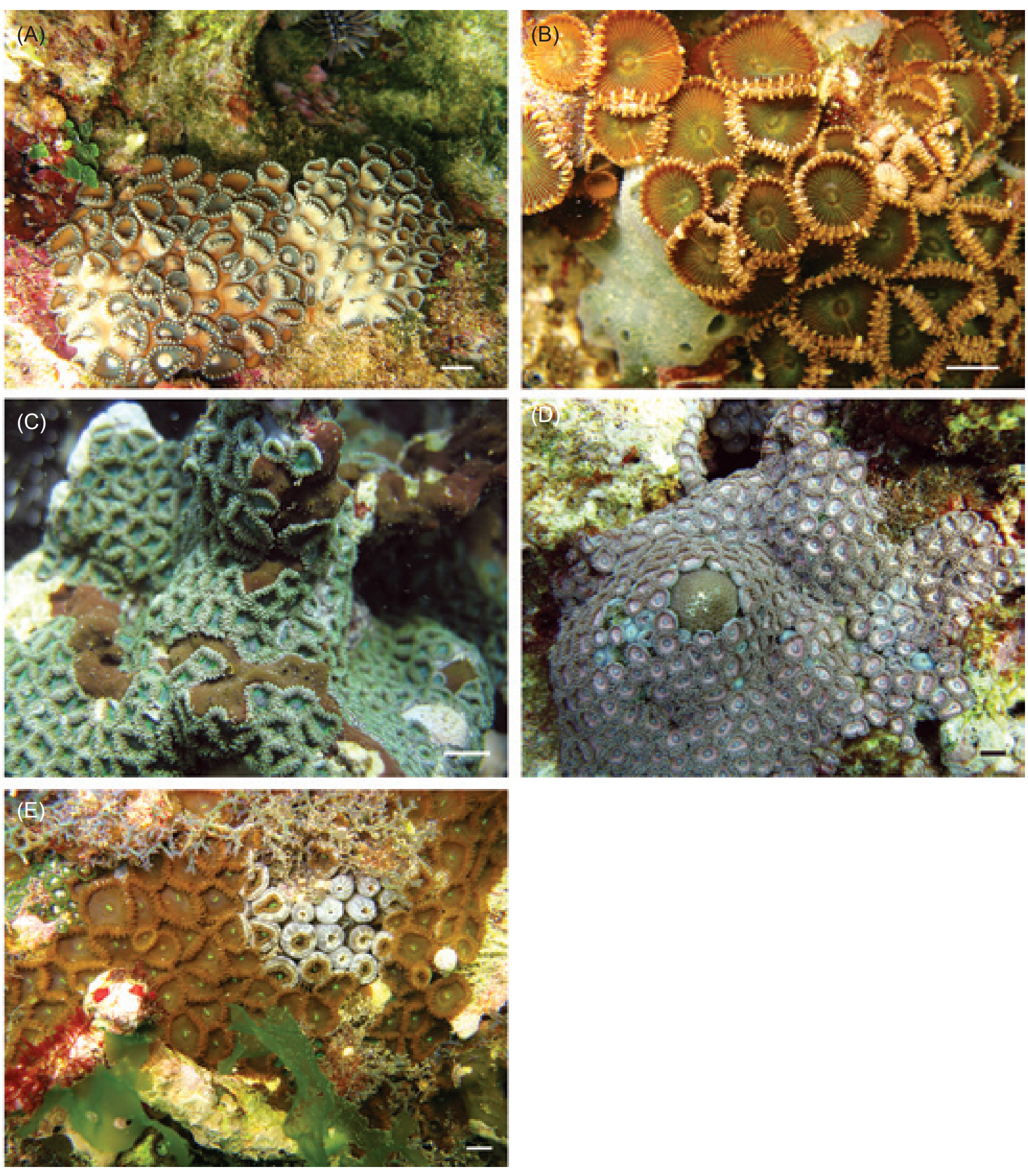

Fig. 1. Five zoanthid species investigated in this study. (A) *Palythoa tuberculosa* (at Sunabe), (B) *P. mutuki* (at Odo), (C) *Zoanthus sansibaricus* (at Oyama), (D) *Z. kuroshio* (at Maeda-east), (E) *Z. gigantus* (at Oyama). Scale bar = 1 cm.

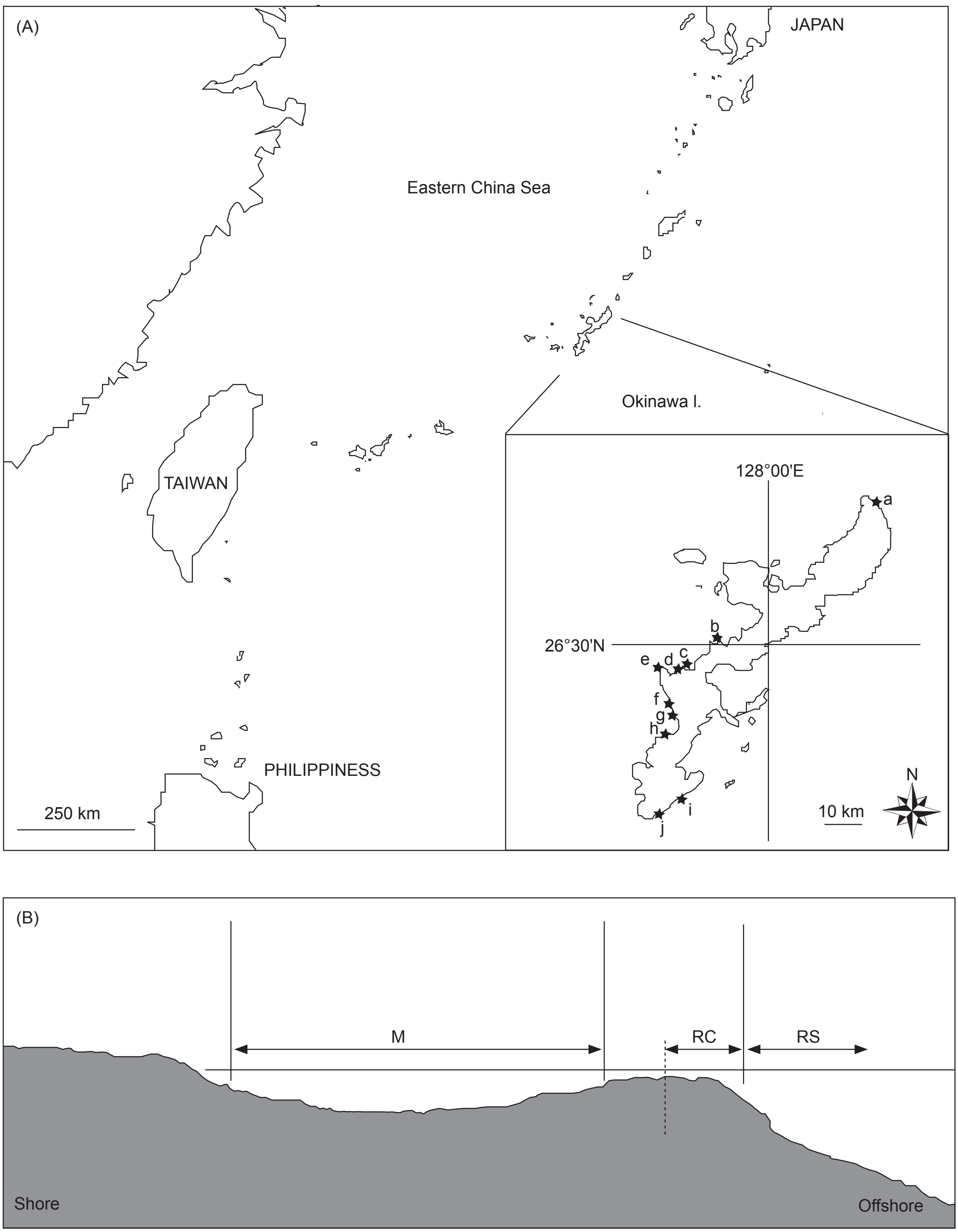

Fig. 2. Study locations investigated in this study. (A) Locations investigated at Okinawa I.: (a) Oku (26°50'58.53"N, 128°16'54.48"E), (b) Manza (26°30'06.93"N, 127°50'32.86"E), (c) Maeda-east (26˚26'42.29"N, 127°46'07.75"E), (d) Maeda-west (26°26'36.40"N, 127°46'22.80"E), (e) Zanpa (26°26'29.56"N, 127°42'44.04"E), (f) Sunabe (26°19'46.97"N, 127°44'35.14"E), (g) Mizugama (26°21'34.28"N, 127°44'20.13"E), (h) Oyama (26°17'08.07"N, 127°44'22.40"E), (i) Minatogawa (26°07'11.65"N, 127°45'41.97"E), (j) Odo (26°05'13.11"N, 127°42'36.72"E). (B) Typical geographical structure of a fringing reef and the 3 topographic zones investigated in this study: M, moat; RC, reef crest; RS, reef slope.

like *P. tuberculosa* with tightly joined polyps, the other 4 species in this study and particularly *P. mutuki* had thinner coenenchymes and less densely packed polyps, and this may have enhanced colony diameter sizes. However, this likely did not affect the results of this study since colony size categories were relatively roughly estimated with wide-ranging size classes.

Although data (number of colonies) were collected using 3 replicate transects in each of the 3 reef environments, resultant data from the 3 replicate transects were pooled and used in subsequent analyses due to the large variation among the replicates and the occurrence of many 0 values (i.e., no colony observed on the transect) in the data. When analyzing distribution patterns among the 3 reef environments, comparisons were only made between the reef crest and reef slope, because few colonies were observed in the moat environment (Table 1). Distribution patterns of the 5 zooxanthellate zoanthid species in the 2 reef environments were analyzed using the Wilcoxon matched-pairs test. Because the same analysis was employed for all 5 zoanthid species, the significance level was adjusted by dividing the original significance level by 5 according to the Bonferroni method. Size-frequency distributions were compared between the 2 dominant species, *P. tuberculosa* and *Z. sansibaricus*, using the Kolmogorov-Smirnov test. Size-frequency distributions of *P. tuberculosa* found on the reef crest and reef slope were also compared using the Kolmogorov-Smirnov test, as sufficient numbers of colonies were present in both environments. All size data recorded for each of the categories in this study were pooled and used for comparisons. STATISTICA (vers. 9.0) software (StatSoft, Tulsa, OK, USA) was used for the statistical analyses.

Table 1. Colony numbers of 5 zoanthid species belonging to the genera *Palythoa* and *Zoanthus*, observed in a 30-m^2 area of 3 coral reef zones (M, moat; RC, reef crest; RS, reef slope) at 10 sites around Okinawa I. Sites are listed in order of latitude from north to south. *The moat was not surveyed due to the lack of the zone at these sites

Palythoa	*P. tuberculosa* (*n* = 988)				*P. mutuki* (*n* = 86)			
Sites	M	RC	RS	Total	M	RC	RS	Total
Oku	1	124	61	186	65	17	0	82
Manza	2	1	27	30	0	0	0	0
Maeda-east	0	3	5	8	0	0	0	0
Maeda-west*	-	58	69	127	-	1	0	1
Zanpa	0	15	27	42	0	1	0	1
Mizugama*	-	91	63	154	-	0	0	0
Sunabe*	-	37	5	42	-	1	0	1
Oyama	0	2	0	2	0	0	0	0
Minatogawa	0	8	216	224	0	1	0	1
Odo	1	17	155	173	0	0	0	0
Total	4	356	628	988	65	21	0	86

Zoanthus	*Z. sansibaricus* (*n* = 1253)				*Z. kuroshio* (*n* = 54)				*Z. gigantus* (*n* = 23)			
Sites	M	RC	RS	Total	M	RC	RS	Total	M	RC	RS	Total
Oku	5	38	1	44	0	0	1	1	0	8	2	10
Manza	27	58	1	86	0	0	9	9	0	0	1	1
Maeda-east	1	176	0	177	0	0	5	5	0	1	0	1
Maeda-west*	-	230	11	241	-	2	15	17	-	0	1	1
Zanpa	0	41	0	41	0	8	5	13	0	2	0	2
Mizugama*	-	94	0	94	-	0	0	0	-	3	0	3
Sunabe*	-	21	0	21	-	0	0	0	-	0	0	0
Oyama	0	70	0	70	0	1	2	3	0	4	0	4
Minatogawa	0	224	0	224	0	0	4	4	0	0	1	1
Odo	0	255	0	255	0	2	0	2	0	0	0	0
Total	33	1207	13	1253	0	13	41	54	0	18	5	23

RESULTS

In total, 2404 zoanthid colonies were observed from the 81 transects (with a total surveyed area of 810 m^2) recorded in this study. *Zoanthus sansibaricus* was the most dominant species (1253 colonies), making up 52% of the total colony number, followed by *Palythoa tuberculosa* (988 colonies; 41%) (Table 1). The 3 remaining species combined to make up < 7% of the total colony number. There were large variations and no obvious trend in colony numbers of each zoanthid species among the 10 study sites (Table 1). Large variations were also seen in the number of zoanthid colonies among the 3 replicate transects in each reef environment, resulting in many 0 values recorded in the replicate transects (data not shown). Among the 3 reef environments at Okinawa I. examined in this study (moat, reef crest, and reef slope), most zoanthid colonies were observed on the reef crest and reef slope (Table 1). In the moat environment, the density of each zoanthid species was 0-5 colonies/30 m^2, except for *P. mutuki* at Oku (65 colonies/30 m^2) and *Z. sansibaricus* at Manza (27 colonies/30 m^2). Of the 5 zooxanthellate zoanthid species examined, only *Z. sansibaricus* showed a significant difference in the number of colonies between the reef crest and reef slope environments. There were significantly more colonies of *Z. sansibaricus* on the reef crest than reef slope (pre-adjusted $p < 0.01$, adjusted by the Bonferroni method $p < 0.05$, $n = 10$ sites) (Table 1). Although the same trend was also seen with *P. mutuki* (i.e., more colonies on the reef crest), the result was not statistically significant after adjusting the significance level by the Bonferroni method (cf. pre-adjusted $p < 0.05$, $n = 5$ sites).

Small (S)-sized colonies were the most frequent for all 5 zooxanthellate zoanthid species (Fig. 3). For *P. mutuki* and *Z. gigantus*, frequencies of SS colonies were also high (Fig. 3). In terms of the 2 dominant species (*P. tuberculosa* and *Z.*

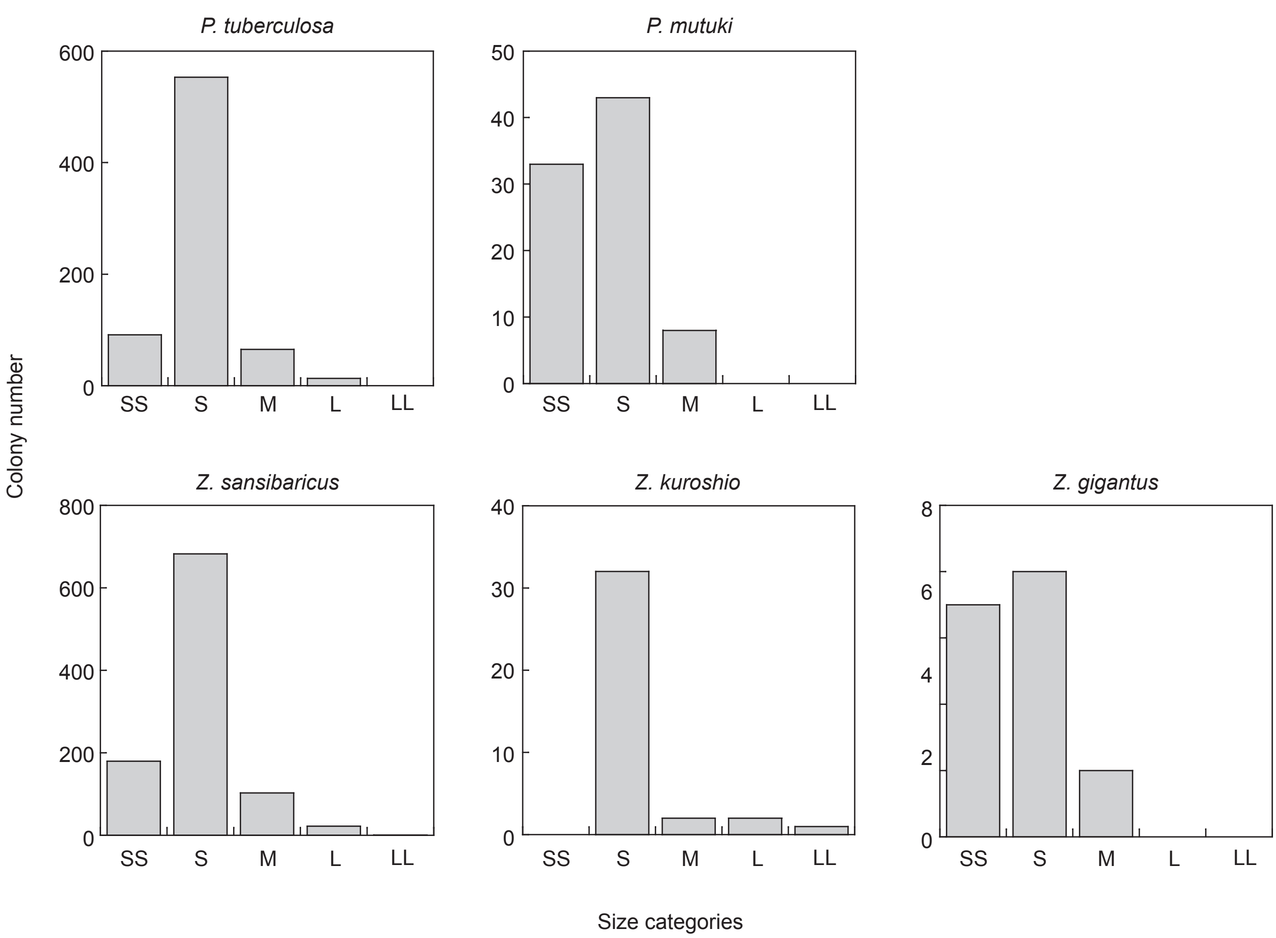

Fig. 3. Size-frequency distributions of 5 zooxanthellate zoanthid species observed in this study. Size categories: SS, fewer than 10 polyps; S, more than 10 polyps at 10 × 10 cm; M, 10 × 10-25 × 25 cm; L, 25 × 25-50 × 50 cm; LL, > 50 × 50 cm.

sansibaricus), we found no significant difference in size class ratios between the 2 species ($p > 0.1$) (Figs. 3A, C). In addition, colony sizes of *P. tuberculosa* found on the reef crest and reef slope were compared, since sufficient numbers of colonies were present in both environments. Again, no significant differences were seen between the 2 reef environments ($p > 0.1$) (Fig. 4).

DISCUSSION

In this study, distribution patterns of 5 zoanthid species were surveyed among 3 different reef environments (moat, reef crest, and reef slope) at 10 sites around Okinawa I. Colony numbers of each zoanthid species greatly varied from site to site, suggesting a patchy nature of distribution for the 5 zoanthid species. Despite this, distribution patterns among the 3 reef environments were generally consistent and clear for all 5 species among different sites. *Palythoa tuberculosa* and *Z. sansibaricus* were numerous on coral reefs of Okinawa. From the frequency in each environment, the main habitat of *Z. sansibaricus* was the reef crest, while *P. tuberculosa* was observed on both reef crests and reef slopes. Thus, in general, it appears that *P. tuberculosa* has a vertically wider distribution than *Z. sansibaricus* around Okinawa I. These results are similar to the theory proposed by Reimer et al. (2006b), in which *P. tuberculosa* was surmised to be a “generalist” based on observations of *P. tuberculosa* in various environments in southern Japan as well as on the presence of subclades C1 and C3 *Symbiodinium* within *P. tuberculosa* colonies, which are relatively common among various zooxanthellate anthozoans in the Indo-Pacific and Atlantic-Caribbean (LaJeunesse 2005). It was difficult to conclusively determine the habitats of the 3 remaining species; *P. mutuki*, *Z. kuroshio*, and *Z. gigantus*, between the reef crest and reef slope (but clearly not the moat), due to their low total numbers observed in this study.

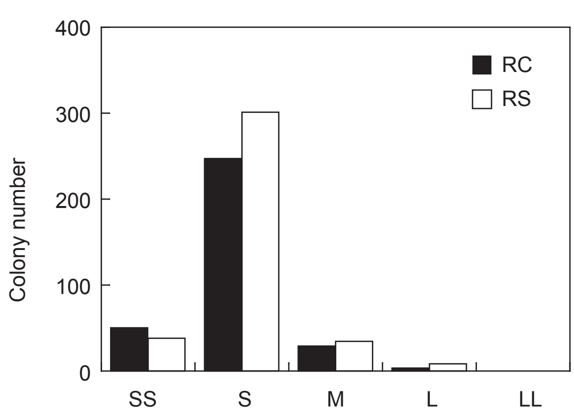

Fig. 4. Size-frequency distributions of colonies of *Palythoa tuberculosa* observed in 2 reef environments (RC, reef crest; RS, reef slope). Size categories: SS, fewer than 10 polyps; S, more than 10 polyps at 10 × 10 cm; M, 10 × 10-25 × 25 cm; L, 25 × 25-50 × 50 cm; LL, > 50 × 50 cm.

There are likely various environmental factors that determine the distribution patterns of zoanthid species. It was shown that water temperature (Ono et al. 2003), sedimentation (Sebens 1982, Ono et al. 2003), predation (Sebens 1982), and desiccation stress during low tides (Sebens 1982) affect zoanthid distributions. In moats, only a few colonies were recorded, and sedimentation or unfavorable salinity could have been cause of this. For example, due to generally weak currents in moats, the substratum was often covered by drifted sand (Takahashi 1988, Nakai 2007), making survival of zoanthids and other benthic cnidarians difficult. Moreover, moats are often affected by runoff of fresh water from terrestrial ecosystems, which lowers the salinity and in Okinawa, causes red clay/sand sedimentation particularly after heavy rains. As the water circulation in moats is relatively poor (Nakai 2007), such unfavorable low-salinity conditions can persist for a relatively longer period than on the reef crest or reef slope. Thus, such harsh conditions may limit the number of colonies of zoanthids in moats. At Oku and Manza; however, relatively large numbers of zoanthid colonies were observed in the moats. The moats at these 2 sites have relatively higher water flow, and thus they may be similar environments to reef crests (e.g., more favorable for zoanthids).

In this study, the frequency of zoanthid species was determined from colony numbers on the transects. Although we did not investigate coverage, the frequency may be able to be assumed to roughly correspond to the relative cover of each zoanthid species, as most of the colonies were in the SS and S categories. Studies similar to the research performed here with more-quantitative investigations of zoanthids are needed in other regions of the world to better understand the fundamental ecology of these important coral reef organisms. Moreover, these zooxanthellate zoanthids can be utilized as environmental indicators for coral reef health since they are common and abundant in coral reefs. Additional research in future studies, such as detailed environmental investigations and rearing experiments of zoanthids, will help elucidate which environmental factors control the observed distributional patterns of zoanthids.

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REFERENCES

Acosta A, PW Sammarco, LF Duarte. 2001. Asexual reproduction in a zoanthid by fragmentation: the role of exogenous factors. Bull. Mar. Sci. **68:** 363-381.

Acosta A, PW Sammarco, LF Duarte. 2005. New fission processes in the zoanthid *Palythoa caribaeorum*: description and quantitative aspects. Bull. Mar. Sci. **76:** 1-26.

Bastidas C, D Bone. 1996. Competitive strategies between *Palythoa caribaeorum* and *Zoanthus sociatus* (Cnidaria: Anthozoa) at a reef flat environment in Venezuela. Bull. Mar. Sci. **59:** 543-555.

Burnett WJ, JAH Benzie, JA Beardmore, JS Ryland. 1997. Zoanthids (Anthozoa, Hexacorallia) from the Great Barrier Reef and Torres Strait, Australia: systematics, evolution and a key to species. Coral Reefs **16:** 55-68.

Fautin DG. 2010. Hexacorallians of the world. Available at http://geoportal.kgs.ku.edu/hexacoral/anemone2/index.cfm Accessed 7 Mar. 2011.

Fosså SA, AJ Nilsen. 1998. The modern coral reef aquarium. Vol. 2. Bornheim, Sweden: Birgit Schmettkamp Verlag, 479 pp.

Karlson RH. 1983. Disturbance and monopolization of a spatial resource by *Zoanthus sociatus* (Coelenterata, Anthozoa). Bull. Mar. Sci. **33:** 118-131.

Karlson RH. 1986. Disturbance, colonial fragmentation, and size-dependent life history variation in two coral reef cnidarians. Mar. Ecol. Progr. Ser. **28:** 245-249.

LaJeunesse TC. 2005. "Species" radiation of symbiotic dinoflagellates in the Atlantic and Indo-Pacific since the Miocene-Pliocene transition. Mol. Biol. Evol. **22:** 570-581.

Mendonça-Neto JP, CEL Ferreira, LCT Chaves, RC Pereira. 2008. Influence of *Palythoa caribaeorum* (Anthozoa, Cnidaria) zonation on site-attached reef fishes. An. Acad. Bras. Ciênc. **80:** 495-513.

Nakai T. 2007. Physiographic unit for understanding the spatial structure of the coral reef ecosystem at the Yoron Island fringing reef, Ryukyu Islands. J. Geogr. **116:** 223-242. (in Japanese with English summary).

Ono S, JD Reimer, J Tsukahara. 2003. Long-term changes of *Zoanthus* spp. in the infra-littoral zone at Taisho Lava Field, Sakurajima, Kagoshima, Japan. Galaxea **5:** 21-31.

Reimer JD. 2008. Implications for different diversity levels of *Symbiodinium* spp. (Dinophyceae, Suessiales) within closely related hosts: zoanthids (Cnidaria: Hexacorallia: Anthozoa) as a case study. Galaxea **10:** 3-13.

Reimer JD. 2010. Key to field identification of shallow water brachycnemic zoanthids (Order Zoantharia: Suborder Brachycnemina) present in Okinawa. Galaxea **12:** 23-29.

Reimer JD, H Miyake. 2009. Recent research on ignored taxa: diversity of zoanthids (Zoantharia: Hexacorallia). Kaiyo Month. **41:** 302-312. (in Japanese).

Reimer JD, S Ono, A Iwama, K Takishita, J Tsukahara, T Maruyama. 2006a. Morphological and molecular revision of *Zoanthus* (Anthozoa: Hexacorallia) from southwestern Japan, with descriptions of two new species. Zool. Sci. **23:** 261-275.

Reimer JD, S Ono, K Takishita, Y Fujiwara, J Tsukahara. 2004. Reconsidering *Zoanthus* spp. diversity: molecular evidence of conspecifity within four previously presumed species. Zool. Sci. **21:** 517-525.

Reimer JD, S Ono, J Tsukahara, K Takishita, T Maruyama. 2007a. Non-seasonal clade-specificity and subclade microvariation in symbiotic dinoflagellates (*Symbiodinium* spp.) in *Zoanthus sansibaricus* (Anthozoa: Hexacorallia) at Kagoshima Bay, Japan. Phycol. Res. **55:** 58-65.

Reimer JD, K Takishita, T Maruyama. 2006b. Molecular identification of symbiotic dinoflagellates (*Symbiodinium* spp.) from *Palythoa* spp. (Anthozoa: Hexacorallia) in Japan. Coral Reefs **25:** 521-527.

Reimer JD, K Takishita, S Ono, T Maruyama. 2007b. Diversity and evolution in the zoanthid genus *Palythoa* (Cnidaria: Hexacorallia) based on nuclear ITS-rDNA. Coral Reefs **26:** 399-410.

Sebens KS. 1982. Intertidal distribution of zoanthids on the Caribbean coast of Panama: effects of predation and desiccation. Bull. Mar. Sci. **32:** 316-335.

Suchanek TH, DJ Green. 1981. Interspecific competition between *Palythoa caribaeorum* and other sessile invertebrates on St. Croix reefs, U.S. Virgin Islands. Proc. 4th Int. Coral Reef Symp. **2:** 679-684.

Takahashi T. 1988. Coral reefs. Tokyo. Kokon Publishers, 258 pp. (in Japanese).

Tanner JE. 1997. The effects of density on the zoanthid *Palythoa caesia*. J. Animal. Ecol. **66:** 793-810.