Zoological Studies **50**(1): 53-60 (2011)

Zoological Studies

Reconsideration of the Surface Structure of Settlement Plates Used in Coral Recruitment Studies

Yoko Nozawa[1,*], Kouki Tanaka[2], and James D. Reimer[3,4]

[1]*Biodiversity Research Center, Academia Sinica, Nankang, Taipei 115, Taiwan*
[2]*Biological Institute on Kuroshio, 560 Nishidomari, Otsuki, Kochi 788-0333, Japan*
[3]*Rising Star Program, Transdisciplinary Research Organization for Subtropical and Island Studies, University of the Ryukyus, Senbaru 1, Nishihara, Okinawa 901-0213, Japan*
[4]*Research Program for Marine Biology and Ecology, Extremobiosphere Research Center, Japan Agency for Marine-Earth Science and Technology (JAMSTEC), 2-15 Natsushima, Yokosuka, Kanagawa 237-0061, Japan*

(Accepted September 1, 2010)

Yoko Nozawa, Kouki Tanaka, and James D. Reimer (2011) Reconsideration of the surface structure of settlement plates used in coral recruitment studies. *Zoological Studies* **50**(1): 53-60. Plain-surface settlement plates are widely used in coral recruitment research to the almost complete exclusion of plates with other surface types. This study examined whether the surface structure of settlement plates used in coral recruitment studies influences the resultant coral recruits observed on the plate surfaces. Settlement plates with artificially produced micro-crevices (MCs) on the plate surfaces were examined and compared to settlement plates without MCs (plain surfaces). Replicates of the 2 types of settlement plates were deployed side by side at 3 replicate locations for 4 mo during the coral recruitment period, and the number and taxonomic composition of coral recruits on the plate surfaces were compared. Settlement plates with MCs had significantly more coral recruits with a higher variety of species than those without MCs at all 3 locations. There was approximately an order of magnitude difference in the total number of coral recruits between settlement plates with (59-144 recruits/location) and without MCs (1-6 recruits/location). Pocilloporids dominated coral recruits on both types of settlement plates (86%-100%). These results indicate the need to consider the surface structure of settlement plates as a significant factor, along with plate materials and methods of deployment, that influences the resultant coral recruit assemblies observed on settlement plates in coral recruitment studies. http://zoolstud.sinica.edu.tw/Journals/50.1/53.pdf

Key words: Settlement plate, Refuge structure, Scleractinian coral, Recruit, Method.

In coral recruitment studies, settlement plates are extensively used to examine the relative abundances of coral recruits just after settlement in monitored coral assemblages, because their microscopic size makes it almost impossible to examine them directly in the field (English et al. 1997, Mundy 2000, Hill and Wilkinson 2004, Field et al. 2007). Although various plate materials (Harriott and Fisk 1987), methods of plate deployment (Birkeland et al. 1981, Mundy 2000), and a combination of both factors (Field et al. 2007) have been considered in a search for improved settlement, the shape of settlement plates has so far not been adequately examined (but see Wallace 1985, Harriott and Fisk 1987), and settlement plates with plain surfaces are normally used in coral recruitment studies (Rogers et al. 1984, Harriott 1992, English et al. 1997, Hughes et al. 2000, Hill and Wilkinson 2004, and many others).

However, most natural substrata in the field have numerous grooves, crevices, and gaps that

*To whom correspondence and reprint requests should be addressed. Tel: 886-2-27871581. Fax: 886-2-27855059. E-mail:nozaway@gate.sinica.edu.tw

offer complex surface structures for potential coral recruits. Previous studies highlighted the importance of this complex surface structure on settling substrata as refuges protecting minute coral recruits from the abrasive feeding activity of grazers such as grazing fishes, sea urchins, and gastropods, thereby enhancing coral recruit survivorship (Brock 1979, Sammarco 1980 1982, Carleton and Sammarco 1987, Nozawa 2008). In coral recruitment studies, settlement plates are usually deployed in the field for several months to cover the major recruitment period in targeted coral assemblages. Therefore, during such deployment periods there is a high possibility that coral recruits settling on the plain plate surfaces, which are directly exposed to grazing activities, may suffer higher post-settlement mortality than on natural substrata. If this is true, the resultant coral recruits observed on the plain plate surfaces might not reflect the relative abundances of actual coral recruits in the field, depending on the density of grazers around the settlement plates at each study location.

This study examined the performance of settlement plates with artificially-made micro-crevices (MCs) compared to settlement plates without MCs (i.e., with plain surfaces) at 3 replicate locations. Replicates of the 2 types of settlement plates were deployed side by side for approximately 4 mo during the recruitment period, and the number and taxonomic composition of coral recruits on the plates were compared. In addition, coverage extents of dominant benthic invertebrate taxa with calcified tissues observed on the 2 types of settlement plates were also compared.

MATERIALS AND METHODS

A comparative experiment on the performance of settlement plates with and without MCs was repeated at 3 replicate locations (Nishidomari, Shirigai, and Tatsukushi) in Kochi, southwestern Shikoku, Japan (Fig. 1). Although the study locations are in a high-latitude region (32°N), there are well-developed reef coral assemblages (Japanese Coral Reef Society and Ministry of the Environment 2004), and 127 reef coral species are reported from this region (Veron 1993, Nishihira and Veron 1995).

Fiber-reinforced cement slate boards with a plain surface (simply called “slate board” in Japan) were chosen as the material for the settlement plates in this study. The material has some advantages over commonly used terracotta tiles (i.e., indestructible, lightweight, readily available in Japan) and has been used in previous coral studies (e.g., Nozawa et al. 2006, Nozawa 2008). A hole was drilled in the center of each settlement plate (10 × 10 × 0.5 cm) for fixation. Settlement plates with MCs were made by drilling 255 micro-crevices (5 mm in diameter, 3-4 mm in depth) at intervals of 1-2 mm over the entire area of 1 side of the 2 plain surfaces of each settlement plate (Fig. 2).

The experimental layout at each study location followed a matched-pairs design, a special case of a randomized complete block design with 15 blocks, each separated by a distance of 1-2 m, established at approximately a 5-m depth (Fig. 2). In each block, a pair of settlement plates with MCs and a pair of settlement plates without MCs were placed side by side within a distance of 10 cm from each other on rocky substratum (Fig. 2). Each plate pair with or without MCs was put together with the surfaces with the MCs facing outward (for plates with MCs). The plate pair was then fixed with stainless-steel nuts and washers by putting a stainless-steel threaded rod through the center holes of the plates, approximately 2 cm above the rocky substratum. The stainless-steel threaded rod was anchored in advance to the rocky substratum by being half-embedded in a hole drilled in the rocky substratum and glued with underwater epoxy. The settlement plate pairs with or without MCs were set at a steep angle of approximately 10°-30° using the vertical surface

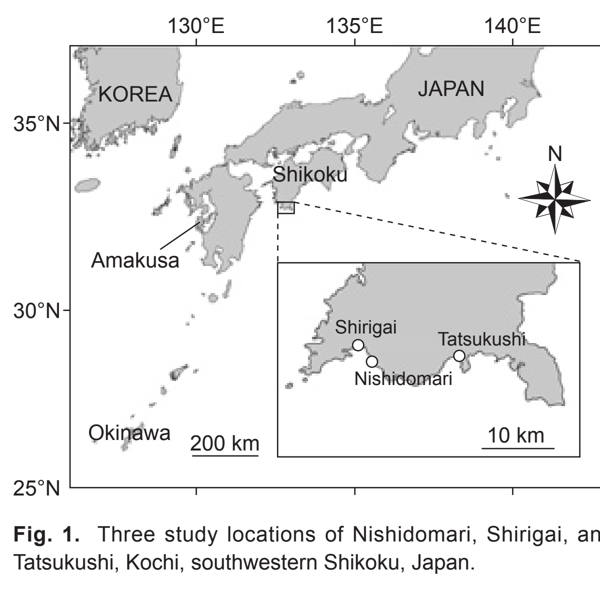

Fig. 1. Three study locations of Nishidomari, Shirigai, and Tatsukushi, Kochi, southwestern Shikoku, Japan.

of the rocky substrata to reduce the influence of sedimentation that might negate the effects of MCs on coral recruit survivorship (Sammarco 1980, Sato 1985, Nozawa 2008) and provide an optimal angle for coral settlement (Carleton and Sammarco 1987).

All settlement plates were put in place approximately 1 mo before the predicted main reproductive season of reef corals in the region (late June to Aug.) for conditioning and were retrieved approximately 1 mo after the spawning season (van Woesik 1995, Y. Nozawa. unpubl. data). Fifteen pairs each of settlement plates with and without MCs (i.e., a total of 30 settlement plate pairs/location) were put in place on 24 May 2007 at Tatsukushi, on 31 May at Nishidomari, and on 1 June at Shirigai. All settlement plate pairs, except 2 with MCs and 2 without MCs at Shirigai and 2 with MCs at Tatsukushi, were successfully retrieved on 26 Sept. 2007 at Tatsukushi and on 17 Oct. at Nishidomari and Shirigai. When the settlement plates were retrieved, the number of pocilloporid colonies (> 5 cm in diameter) within a distance of approximately 1 m from the settlement plate pairs was counted, as these colonies were theorized to have potentially influenced the number of pocilloporid recruits found on the plates (see Tioho et al. 2001, Underwood et al. 2007).

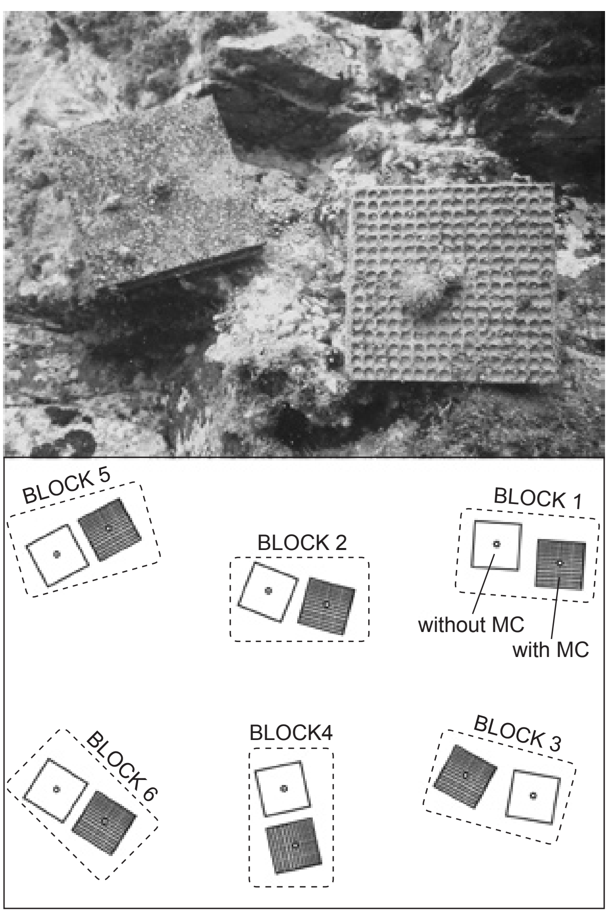

Fig. 2. (Upper) Close-up image of an experimental block showing the settlement plates with micro-crevices (MCs) and without MCs deployed side by side on rocky substratum. Some grazers (gastropods) can be seen on the plate surfaces. (Lower) Schematic diagram of a matched-pair design. Fifteen blocks were deployed at a distance of 1-2 m from each other in each study location.

Retrieved settlement plates were bleached for 24 h in a 10% chlorine solution to remove soft-tissue organisms. Settlement plates were then gently rinsed in fresh water to remove sediments and dried. The settlement plates were examined under a stereomicroscope (magnification: × 10-15). Coral recruits on the 2 outer surfaces of the plate pairs, i.e., the upper surface facing seaward and the lower surface facing the rocky substratum, were counted and classified into 4 taxonomic categories; acroporids, pocilloporids, poritids, and other taxa (Babcock et al. 2003).

In addition to examining coral recruitment, the coverage (%) of dominant benthic invertebrates with calcified tissues that left traces on the 2 surfaces of each settlement plate pair after bleaching was examined using the program, CPCe vers. 3.5 (Kohler and Gill 2006). For each plate surface, a close-up digital photograph was taken and overlaid with 100 random points on a computer screen, and underlying benthic invertebrates were classified into 4 categories: barnacles, bryozoans, polychaetes, and other organisms. Although coralline algae were also the dominant benthos on the plate surfaces, this category was not included in this examination because the presence or absence of coralline algae under each random point was vague in many cases, due to their weak development and numerous scars left by sea urchins on the plate surfaces.

The total number of coral recruits and coverage (%) of each of the 4 benthic invertebrate taxa with calcified tissues on the 2 plate surfaces were compared between settlement plate pairs with and without MCs. Data at each study location were analyzed separately by the non-parametric Wilcoxon matched-pairs signed-rank test with the significance level adjusted using the Bonferroni procedure. Because the surface area of the settlement plates with MCs was approximately 2.4 times larger than that of plates without MCs due to the addition of 255 MCs per plate (each MC increased the surface area by 62.8 mm^2), the total numbers of coral recruits on settlement plates with MCs were standardized to values per unit area (200 cm^2) by dividing them by 2.4 before the analysis. As some settlement plates were lost during the experimental period, the numbers of blocks, or pairs of settlement plates with or without MCs, used for the statistical analysis were 15 at Nishidomari, 12 at Shirigai, and 13 at Tatsukushi.

The relationship between the number of adult brooding pocilloporid colonies in the vicinity of the settlement plates and the number of pocilloporid recruits observed on the settlement plates was examined by the Chi-square test for independence. The total number of adult pocilloporid colonies at each study location and the total number of pocilloporid recruits on the settlement plates at each study location were used for the analysis. The settlement orientation of coral recruits on the 2 outer surfaces of the settlement plates (facing upwards or downwards) was analyzed by the Chi-square test for goodness of fit. The total number of recruits in each orientation at each location was used for the analysis. Equal proportions of coral recruits were expected on the 2 orientations in the analysis (i.e., up: down = 1: 1). As for the settlement plates without MC treatment, the total number of recruits was too small to use the Chi-square test (most observed values were < 5). Hence the exact test for goodness of fit (Zar 1999) was used instead by pooling the total numbers of recruits on each orientation among the 3 study locations. STATISTICA (vers. 9.0) software (StatSoft, Tulsa, OK, USA) was used for all statistical analyses conducted in this study, except the exact test.

RESULTS

The settlement plates with MCs had significantly more coral recruits than those without MCs at all 3 study locations ($p < 0.01$) (Fig. 3). There were up to 7.1-9.2 coral recruits/unit area (200 cm^2)/location observed on settlement plates with MCs compared to only a few coral recruits on plates without MCs (up to 1-2 recruits/unit area/location) (Fig. 3). On settlement plates with MCs, only a few coral recruits were observed outside the MCs: 0 (at Shirigai), 2 (at Nishidomari), and 5 (at Tatsukushi) (all pocilloporids). In other words, 97%-100% of the coral recruits were observed within the MCs at the 3 study locations.

The difference was more evident in the total number of coral recruits at each study location, in which there was approximately an order of magnitude difference between settlement plates with (59-144 recruits/location) and without MCs (1-6 recruits/location) (Table 1). Pocilloporids dominated the coral recruits (86%-100%), whereas no acroporid recruits were observed on the settlement plates (Table 1). Coral recruits of taxonomic groups other than pocilloporids were observed on settlement plates with MCs, but none was seen on plates without MCs. Most coral recruits (75%-90%) were observed on the upward-facing surfaces of the settlement plate pairs with MCs ($p < 0.001$), whereas smaller numbers of coral recruits observed on plates without MCs were found mostly on the downward-facing plate surfaces ($p < 0.05$) (Table 1).

The number of pocilloporid corals (> 5 cm in diameter) within a distance of 1 m from the settlement plate pairs at each study location was 9 colonies of *Pocillopora damicornis* at Nishidomari, 7 colonies of *P. damicornis* and 9 colonies of *Stylophora pistillata* at Shirigai, and 2 colonies of *P. damicornis* and 62 colonies of *S. pistillata* at Tatsukushi. The total number of pocilloporid recruits at each study location showed a significant positive relationship with the number of pocilloporid colonies ($p < 0.01$).

As to the coverage of benthic invertebrate taxa with calcified tissues, positive effects of MCs on settlement plates were also detected at some locations on barnacles ($p < 0.05$ at Shirigai), bryozoans ($p < 0.05$ at Nishidomari and Shirigai), and polychaetes ($p < 0.05$ at Shirigai and Tatsukushi) (Fig. 4). In contrast to coral recruits, there were more benthic invertebrates with calcified tissues on the downward- than on the upward-facing plate surfaces irrespective of the presence or absence of MCs on the plate surfaces (Table 2).

DISCUSSION

This study demonstrates that the surface structure of settlement plates has a significant influence on both the number and species composition of the resultant coral recruits observed on the plate surfaces. In this study, settlement plates with MCs had more coral recruits with a higher variety of species compared to plates without MCs. A similar trend was also seen with some other benthic invertebrate taxa with calcified tissues, which showed higher coverage on settlement plates with MCs than on plates

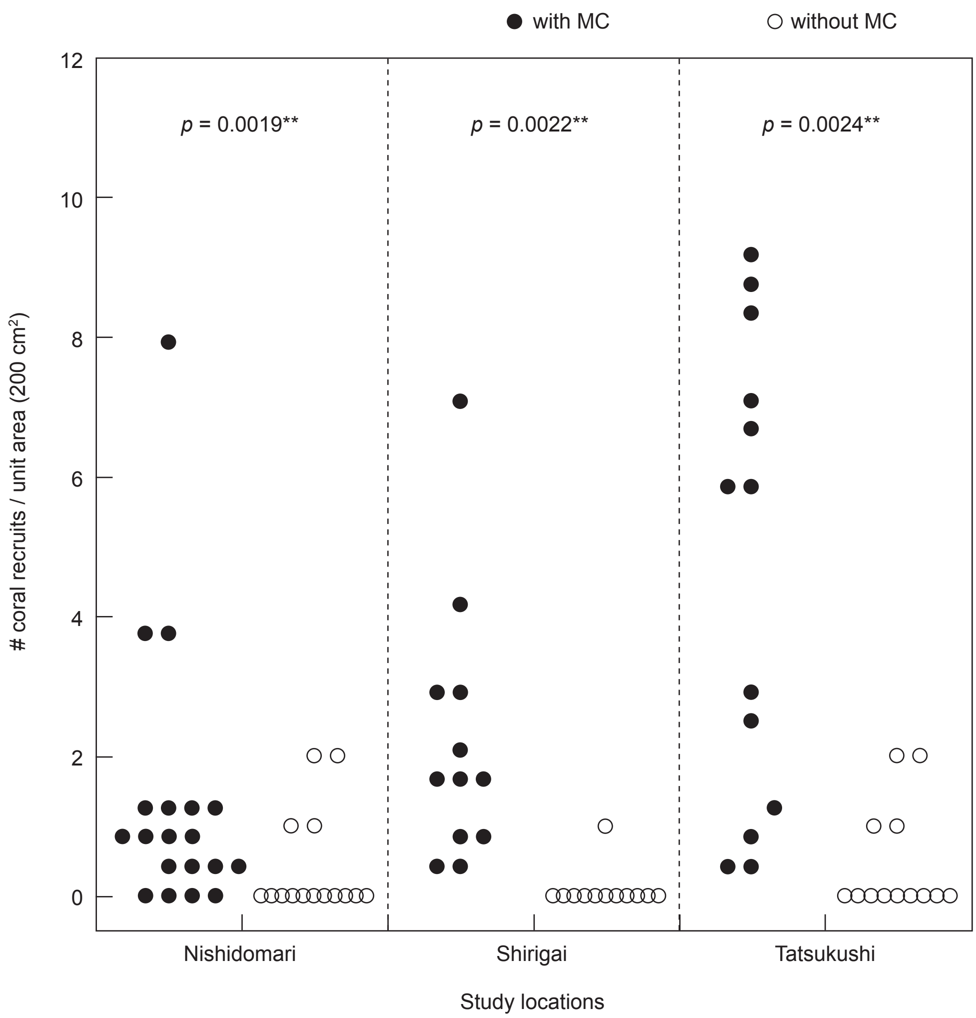

Fig. 3. Total number of coral recruits on the 2 outer surfaces of each stacked settlement plate pair with or without micro-crevices (MCs) at each study location (*n* = 15 each at Nishidomari, *n* = 12 each at Shirigai, and *n* = 13 each at Tatsukushi). Note that as the surface area of settlement plates with MCs was about 2.4 times larger that of plates without MCs, the total number of coral recruits on settlement plate pairs with MC was standardized to the unit area (200 cm^2) by dividing it by 2.4. Data at each study location were analyzed separately by the Wilcoxon matched-pairs signed-rank test. **Denotes $p < 0.01$ after being adjusted using the Bonferroni procedure.

Table 1. Taxonomic composition of coral recruits and their settlement orientation on 2 outer surfaces (upward or downward) of stacked settlement plate pairs with or without micro-crevices (MCs) at each study location (*n* = 15 each in Nishidomari, *n* = 12 each in Shirigai, and *n* = 13 each in Tatsukushi). Note that the surface area of settlement plates with MCs was ca. 2.4 times larger than that without MCs

		Taxon				Orientation		
	Location	Pocilloporids	Poritids	Acroporids	Others	Up	Down	Total no. recruits
With MC	Nishidomari	56	1	0	2	53	6	59
	Shirigai	63	0	0	1	48	16	64
	Tatsukushi	124	16	0	4	114	30	144
Without MC	Nishidomari	6	0	0	0	2	4	6
	Shirigai	1	0	0	0	0	1	1
	Tatsukushi	6	0	0	0	0	6	6

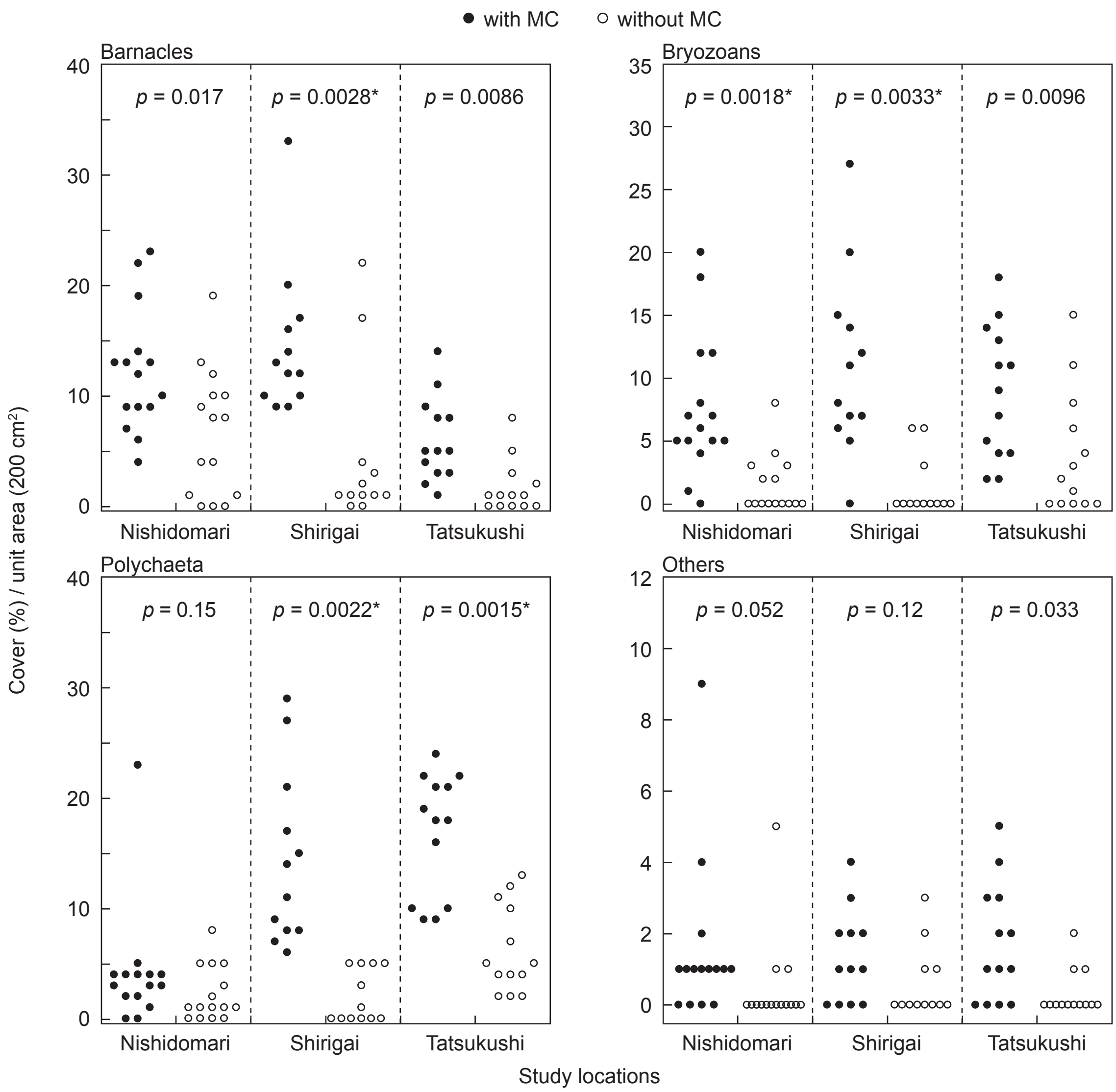

Fig. 4. Total cover (%) of 4 benthic invertebrate taxa with calcified tissues on the 2 outer surfaces of each stacked settlement plate pair with or without micro-crevices (MCs) at each study location (n = 15 each at Nishidomari, n = 12 each at Shirigai, and n = 13 each at Tatsukushi). Data at each study location were separately analyzed by the Wilcoxon matched-pairs signed-rank test. *Denotes $p < 0.05$ after being adjusted using the Bonferroni procedure.

Table 2. Accumulated covers (%) of 4 benthic invertebrate taxa with calcified tissues observed on 2 outer surfaces (upward or downward) of stacked settlement plate pairs with or without micro-crevices (MCs) at each study location (n = 15 each in Nishidomari, n = 12 each in Shirigai, and n = 13 each in Tatsukushi)

	Barnacles		Bryozoans		Polychaeta		Others	
	up	down	up	down	up	down	up	down
with MC								
Nishidomari	39	144	5	110	9	53	12	11
Shirigai	55	120	1	131	20	152	8	8
Tatsukushi	36	42	2	113	30	189	10	12
without MC								
Nishidomari	5	94	0	22	3	30	0	7
Shirigai	0	53	0	15	0	24	0	7
Tatsukushi	1	21	0	50	0	81	0	4

without MCs. There may be 2 possible factors involved in and causing these results. Pre-settlement factors: recruits of corals and some benthic invertebrate taxa may have been attracted by the MC structures that provide a higher variety of microenvironments for settlement than the plain plate surfaces (Petersen et al. 2005). Post-settlement factors: the mortality of recruits that settled in the MC structures may have been reduced because of the refuge effects from grazers, while recruits on the plain plate surfaces may have suffered higher mortality due to being exposed to chronic disturbances of abrasive feeding activities by grazers. In the present study and other studies (Nozawa 2008 2010) that were conducted at the same study location, the plain surfaces of settlement plates had numerous fresh scratch marks made by sea urchins (see Nozawa 2010), and many coral recruits showed signs of having been scraped off, in particular in tissues and corallites that were not in the MCs. Although the pre-settlement factors have not been fully examined yet, the post-settlement factors are supported by sufficient experimental evidence (Brock 1979, Sammarco 1980 1982, Carleton and Sammarco 1987, Nozawa 2008).

Coral recruits observed in the present study reflected typical features of coral recruit assemblies observed on settlement plates in previous studies conducted at high-latitude locations, i.e., a low number of recruits and a high proportion of brooding species compared to spawning species (mainly pocilloporids) (see Harriott 1992, Harriott and Banks 1995, Hughes et al. 2002, Nozawa et al. 2006). This pattern is hypothesized to occur due to the different pre-settlement competency periods caused by different sexual reproduction modes (i.e., spawning and brooding) (Harriott 1992). Spawning corals release eggs and sperm for external fertilization, and subsequent larval development takes a few days in the water column before larvae become settlement-competent. In contrast, brooding corals are characterized by internal fertilization and development, and release settlement-competent larvae. The significant relationship found in the brooding pocilloporid corals between recruits and adult colonies around the settlement plates in the present study may have been caused by brooded larvae being settlement-competent just after being released (see Tioho et al. 2001, Underwood et al. 2007), and suggests a need to consider adult brooding pocilloporid colonies around settlement plates when conducting coral recruitment studies. In a similar coral recruitment study conducted in a neighboring high-latitude region, Amakusa, Kumamoto, southwestern Japan (32°N) (see Fig. 1), where brooding pocilloporid colonies were rare, there were only 1 or 2 non-pocilloporid recruits observed on a total of 50-100 settlement plates (with plain surfaces) deployed every year from 2001 to 2003 (Nozawa et al. 2006).

Most coral recruits were observed on the upper surfaces of settlement plates with MCs, whereas this pattern was reversed on plates without MCs in the present study (Table 1). The reverse pattern is most likely to have been caused by a lack of coral recruits on the upward surfaces of settlement plates without MCs. Given the complex surface structure of natural substrata, the pattern seen on the plates with MCs may more closely reflect actual settlement patterns in the field.

The results of the present study indicate a need to consider the surface structure of settlement plates in future coral recruitment studies, which influences the resultant coral recruits on settlement plates, along with the plate materials (Harriott and Fisk 1987) and methods of plate deployment (Birkeland et al. 1981, Mundy 2000). The use of settlement plates with a complex surface structure (e.g., MCs used in the present study) is highly recommended, as the complex surface structure may attract and promote the settlement of coral larvae, and prevent post-settlement mortality of coral recruits from grazers during the deployment periods. Another advantage of using settlement plates with a complex surface structure is that community development of fast-growing algae and fouling organisms on plate surfaces is controlled by grazers. Periodic grazing activities remove or weaken fast-growing organisms on more-exposed plate surfaces (i.e., plain or projecting areas), preventing coral recruits in depressions from being completely overgrown by such organisms and hence enhancing the survival of coral recruits in refuges. Other methods such as making a gap of a few centimeters using 2 settlement plates or using a cage to exclude macro-grazers often allow fast-growing algae and fouling organisms to dominate available plate surface space that was intended for coral settlement (Sato 1985, Harriott and Banks 1995, Banks and Harriott 1996, Wilson and Harrison 2005, Glassom et al. 2006).

Acknowledgments: The authors thank the Kuroshio Biological Research Foundation and the staff of the Biological Institute on Kuroshio, and in particular J. Fukada and F. Iwase, for support of this study. J.D. Reimer was supported in part by the 21st Century Center of Excellence (COE) Program and the Rising Star Program for Subtropical Island Sciences at the Univ. of the Ryukyus, Okinawa, Japan.

REFERENCES

Babcock RC, AH Baird, S Piromvaragorn, DP Thomson, BL Willis. 2003. Identification of scleractinian coral recruits from Indo-Pacific reefs. Zool. Stud. **42:** 211-226.

Banks SA, VJ Harriott. 1996. Patterns of coral recruitment at the Gneering Shoals, southeast Queensland, Australia. Coral Reefs **15:** 225-230.

Birkeland C, D Rowley, H Randall. 1981. Coral recruitment patterns at Guam. Proc. 4th Int. Coral Reef Symp. **2:** 339-344.

Brock RE. 1979. An experimental study on the effects of grazing by parrotfishes and role of refuges in benthic community structure. Mar. Biol. **51:** 381-388.

Carleton JH, PW Sammarco. 1987. Effects of substratum irregularity on success of coral settlement: quantification by comparative geomorphological techniques. Bull. Mar. Sci. **40:** 85-98.

English S, C Wilkinson, V Baker. 1997. Survey manual for tropical marine resources, 2nd ed. Townsville, Australia: Australian Institute of Marine Science, 390 pp.

Field SN, D Glassom, J Bythell. 2007. Effects of artificial settlement plate materials and methods of deployment on the sessile epibenthic community development in a tropical environment. Coral Reefs **26:** 279-289.

Glassom D, L Celliers, MH Schleyer. 2006. Coral recruitment patterns at Sodwana Bay, South Africa. Coral Reefs **25:** 485-492.

Harriott VJ. 1992. Recruitment patterns of scleractinian corals in an isolated sub-tropical reef system. Coral Reefs **11:** 215-219.

Harriott VJ, SA Banks. 1995. Recruitment of scleractinian corals in the Solitary Islands Marine Reserve, a high latitude coral-dominated community in eastern Australia. Mar. Ecol. Progr. Ser. **123:** 155-161.

Harriott VJ, DA Fisk 1987. A comparison of settlement plate types for experiments on the recruitment of scleractinian corals. Mar. Ecol. Progr. Ser. **37:** 201-208.

Hill J, C Wilkinson. 2004. Methods for ecological monitoring of coral reefs, vers. 1. Townsville, Australia: Australian Institute of Marine Science, 117 pp.

Hughes TP, AH Baird, EA Dinsdale, VJ Harriott, NA Moltschaniwskyj, MS Pratchett et al. 2002. Detecting regional variation using meta-analysis and large-scale sampling: latitudinal patterns in recruitment. Ecology **83:** 436-451.

Hughes TP, AH Baird, EA Dinsdale, NA Moltschaniwskyj, MS Pratchett, JE Tanner, BL Willis. 2000. Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. Ecology **81:** 2241-2249.

Japanese Coral Reef Society, Ministry of the Environment. 2004. Coral reefs of Japan. Tokyo: Ministry of the Environment, 356 pp.

Kohler KE, SM Gill. 2006. Coral Point Count with Excel extensions (CPCe), a Visual Basic program for the determination of coral and substrate coverage using random point count methodology. Comput. Geosci. **32:** 1259-1269.

Mundy CN. 2000. An appraisal of methods used in coral recruitment studies. Coral Reefs **19:** 124-131.

Nishihira M, JEN Veron. 1995. Hermatypic corals of Japan. Tokyo: Kaiyusha Publisher, 439 pp. (in Japanese)

Nozawa Y. 2008. Micro-crevice structure enhances coral spat survivorship. J. Exp. Mar. Biol. Ecol. **367:** 127-130.

Nozawa Y. 2010. Survivorship of fast-growing coral spats depends less on refuge structure: the case of *Acropora solitaryensis*. Galaxea JCRS. **12:** 31-36.

Nozawa Y, M Tokeshi, S Nojima. 2006. Reproduction and recruitment of scleractinian corals in a high-latitude coral community, Amakusa, southwestern Japan. Mar. Biol. **149:** 1047-1058.

Petersen D, M Laterveer, H Schuhmacher. 2005. Innovative substrate tiles to spatially control larval settlement in coral culture. Mar. Biol. **146:** 937-942.

Rogers CS, HC Fitz III, M Gilnack, J Beets, J Hardin. 1984. Scleractinian coral recruitment patterns at Salt River Marine Canyon, St. Croix, U.S. Virgin Islands. Coral Reefs **3:** 69-76.

Sammarco PW. 1980. *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. J. Exp. Mar. Biol. Ecol. **45:** 245-272.

Sammarco PW. 1982. Echinoid grazing as a structuring force in coral communities: whole reef manipulations. J. Exp. Mar. Biol. Ecol. **61:** 31-55.

Sato M. 1985. Mortality and growth of juvenile coral, *Pocillopora damicornis* (Linnaeus). Coral Reefs **4:** 27-33.

Tioho H, M Tokeshi, S Nojima. 2001. Experimental analysis of recruitment in a scleractinian coral at high latitude. Mar. Ecol. Progr. Ser. **213:** 79-86.

Underwood JN, LD Smith, MJH van Oppen, JP Gilmour. 2007. Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching. Mol. Ecol. **16:** 771-784.

Veron JEN. 1993. A biogeographic database of hermatypic corals: species of the central Indo-Pacific, genera of the world. Monograph series 10. Townsville, Australia: Australian Institute of Marine Science.

Wallace CC. 1985. Seasonal peaks and annual fluctuations in recruitment of juvenile scleractinian corals. Mar. Ecol. Progr. Ser. **21:** 289-298.

Wilson J, PL Harrison. 2005. Post-settlement mortality and growth of newly settled reef corals in a subtropical environment. Coral Reefs **24:** 418-421.

van Woesik R. 1995. Coral communities at high latitude are not pseudopopulations: evidence of spawning at 32°N, Japan. Coral Reefs **14:** 119-120.

Zar JH. 1999. Biostatistical analysis. 4th ed. Upper Saddle River, NJ: Prentice Hall.