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Spatial and temporal variation of coral recruitment in Taiwan

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Introduction

The effect of recruitment on the structure and dynamics of marine populations and communities has received much attention in recent years (e.g., Caley et al. 1996). Even for long-lived corals, recruitment plays a critical role in the distribution and abundance of species (Connell et al. 1997).

Most research on coral recruitment has been conducted in the last three decades (e.g., Birkeland 1977; Hughes et al. 1999). Research has now shown that coral larvae are sensitive to microhabitats, e.g., substrate composition (Benayahu and Loya 1984), neighbors (Maida et al. 1995), light conditions, and orientation of substrates (Babcock and Mundy 1996). Densities and composition of coral recruits also differ among seasons and between years, often by several orders of magnitude (e.g., Wallace 1985).

The patterns of recruitment are known to change with different spatial scales (Dunstan and Johnson 1998). The scale of spatial distribution of coral recruitment has been explored mostly on the Great Barrier Reef (GBR) and its neighboring reefs (e.g., Hughes et al. 1999). It has been suggested that the pattern found in this 2,000-km stretch differs from reefs that are relatively isolated from one another (Harriott and Banks 1995). For example, a larva in the GBR has a good chance, after drifting for 2 weeks and for 200 km, to settle on the GBR. This scale of self-seeding is unlikely for many other reefs that are relatively isolated and small (Kojis and Quinn 2001).

In this study, we report on recruitment rates in Taiwan and, in particular, spatial variation in recruitment within and between areas in Taiwan.

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Materials and methods

The data used to analyze scale in spatial patterns were based on recruitment to plates simultaneously set out in 1997 through 2000. In an effort to increase the number of recruits, the methodology was changed several times over the course of the study. This is due to the results of a concomitant investigation of the effect of microhabitats on recruit densities of corals (Fan 1998). Horizontal ceramic tiles were used in 1997. Then vertical PVC plates were adopted in 1998 and 2000 since they attract higher densities of coral recruits (see Results and discussion). Vertical carbonic plates were used in 1999. (Carbonic plates were used in the electronic industry to hold integrated circuits and accessories in one piece.) All tiles and plates were of the same dimension, 15×15 cm, and a panel is defined as one side of a plate or a tile with an area of 225 cm^2. When horizontal plates/tiles were used, only the densities on the lower surface were used, since the upper surface had much fewer coral recruits. Although there were modifications in procedures between the years, all conditions, e.g., the orientation, the depth, number of plates per rack, and the material of plates, were kept constant between sites in each year.

In 1997 and 1998, plates were placed only in the Hengchun Peninsula area, on well-developed fringing reefs in Southern Taiwan (Fig. 1). A total of four "Areas" (several kilometers apart) were designated, and in each "Area" there were two "Sites," about 1 km apart from each other. Two racks, about 10 m apart, were placed in each of the eight sites, and this level (racks) was designated "Locations." In 1999 and 2000, the experiment was expanded to five additional "Regions" covering all the major reefs around Taiwan, i.e., Hsiaoliuchiu, Penghu, Northeast, Green Island, and Orchid Island, as well as two non-reef "Regions," i.e., Shitzwan and Yungan (see Fig. 1). In this Taiwan-wide study, the whole of the Hengchun Peninsula in southern Taiwan was treated as a "Region" with eight sites, i.e., combining "Area" and "Site" into the "Area/Site" level, with a scale of 1–5 km between each. All sites in the reef regions were fringing reefs. The two non-reef sites, Shitzwan and Yungan, were located along the sandy west coast of Taiwan. A few species of corals were present on hard or artificial substrates, but there were no reefs at these two localities. Plates were set at a depth of about 5 m at all the sites.

The plates were placed 1–2 weeks before the spawning dates and retrieved 4–8 weeks later. In 1998, most late-spring plates were lost, although data of another period in January–February were available. Very few coral recruits were observed in 2000, and retrieval of plates was delayed until September for Orchid Island.

After collection, the plates were air-dried and brought back to the laboratory for analysis using a magnifying glass and a dissecting microscope. Identification of coral spat was based on backtracking corals 1–2 years old in a separate study (Kuo 2001).

Results and discussion

In 1997, pocilloporids were the dominant recruits (95%), while acroporids constituted the rest (5%). In 1998, the only year when data outside the broadcasting season were used, only pocilloporids were found. In 1999 and 2000, pocilloporids were still the dominant group (90 and 95%, respectively); in addition, acroporids were found in Penghu, a region in the Taiwan Straits. In 4 years, only two recruits belonging to groups other than pocilloporids or acroporids were discovered.

Densities of recruits were low except at the Hobihu site (Site 5 in Hengchun Region; Fig. 1) in 1997 and 1998, where more than 10 coral spat were recorded per panel. Densities of coral recruits were low in Taiwan; the highest averages at a site were all below three per panel from 1999 to 2000. This was especially pronounced in the broadcasting species and when compared with results on the GBR [up to 700/panel; see quotes in Harriott (1992)]. Whereas mass spawnings have been observed by both scientists and amateur divers over the past 10 years, in southern Taiwan (personal observations), successful recruitment of broadcasting species in our study was extremely limited. Similar phenomena have also been observed around the high latitude (30°S) islands south of the GBR (e.g., Harriott and Banks 1995).

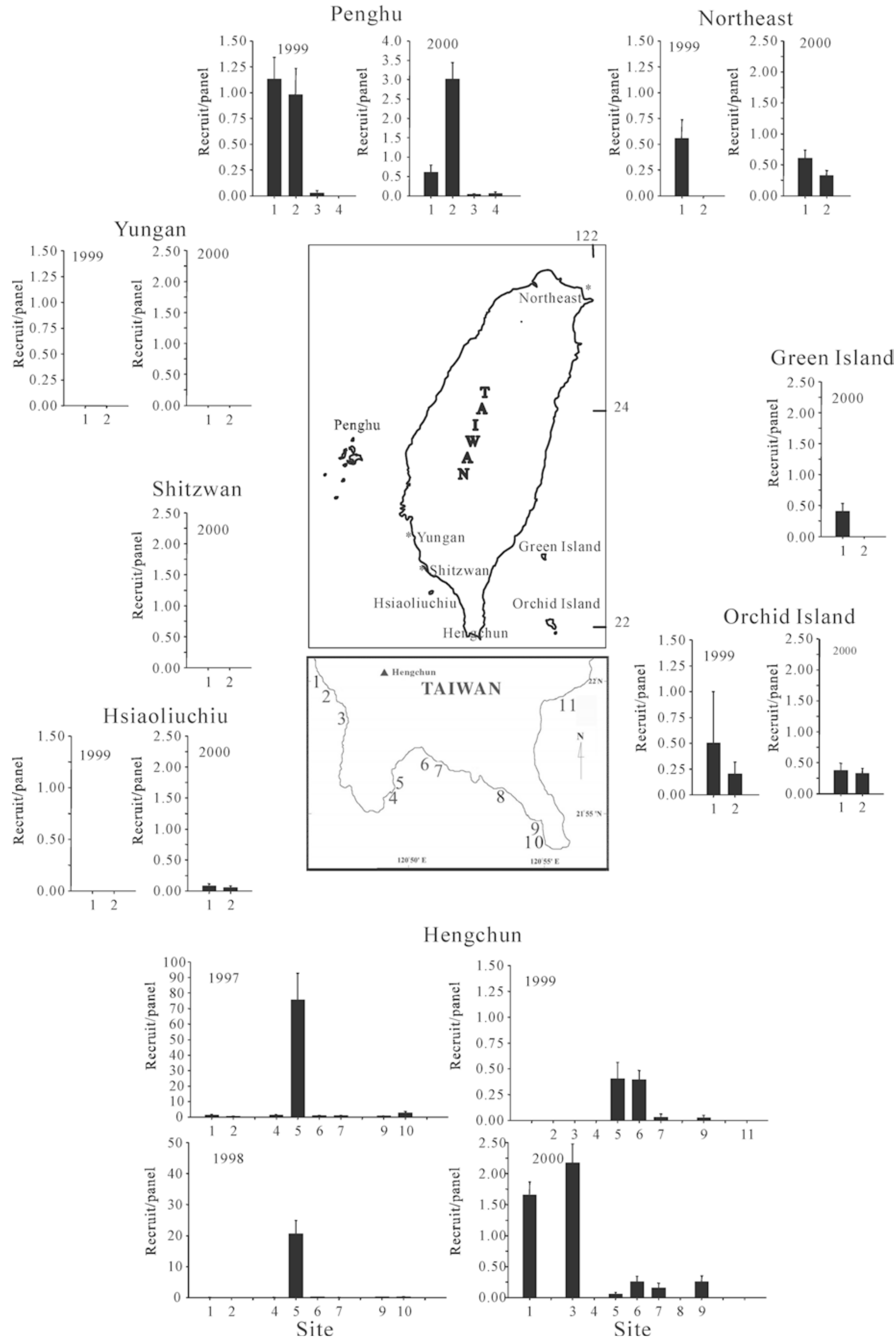
High rates of recruitment may occur several months after mass spawning for broadcasting species on Bowden Reef, GBR (Babcock 1988). Most planktonic larvae might have traveled hundreds to thousands of kilometers away from the reefs producing them (Williams et al. 1984). Thus inter-reef dispersal may be the main source of recruitment for these species (Harriott and Fisk 1988). The results of an independent study with new plates placed every 2 months in southern Taiwan did reveal that new settlement of spawning corals might occur several months after the mass spawning time in April–May, but the densities were nevertheless low (Kuo 2001). Despite their very low recruitment densities, broadcasting corals dominated the coral communities in all our study sites (Dai 1991). Rates of coral recruitment are known to vary greatly among years (e.g., Hughes 1985; Wallace 1985); thus one cannot rule out the possibility that a low rate of recruitment is natural in most years for isolated reefs like those around Taiwan.

Coral reefs at the southern portion as well as in other regions of Taiwan are under threat from both natural and anthropogenic sources (Dai et al. 1998). Eutrophication and high sediment load are known to adversely affect coral recruitment (e.g., Hodgson 1990; Wittenberg and Hunte 1992). These factors, however, cannot explain the low rates of coral recruitment in all our study sites, since the offshore islands, Green Island and Orchid Island, are apparently affected neither by eutrophication nor by excessive sediment loads (personal observation). Taiwanese coral reefs are, on average, 150 km from one another (our estimation); thus isolation may explain the domination of recruitment by brooding corals (see Harriott 1992; Harriott and Banks 1995; Dunstan and Johnson 1998).

The Hobihu site recorded the highest recruitment in the southern region of Taiwan (with at least eight sites each year) for three consecutive years. Two hypotheses are likely explanations. First, a model, using surface current data and topographical features of the Hobihu area predicts a cyclonic eddy in the west side of the bay (where Hobihu is) during ebb (Lee et al. 1999). This could concentrate settling planulae at that site.

The second hypothesis assumes that larvae of the brooding pocilloporids do not travel far after planulation; thus high local recruitment may simply reflect high local abundance of fecund colonies (Harrison and Wallace 1990). This is supported by the results of a 1998 survey of *Seriatopora hystrix*, the dominant pocilloporid in the region. Hobihu site had the highest number of colonies, largest mean colony diameters, as well as the highest estimated coverage (three times that of the second highest site, and more than 10 times that of the rest) of *S. hystrix*, among the eight sites investigated in the region (unpublished data).

In southern Taiwan, significant variation occurred at the "Site" level (1 km apart) in both 1997 and 1998, and at the "Location" level (10 m apart) from 1998 to 2000 (Table 1). "Area" level spatial variation was significant only in 2000. As to the comparison for the whole of Taiwan, significant spatial variation occurred at the "Location" level in both 1999 and 2000, and at the "Area/Site" level (1–5 km) only in 2000. No significant difference was found at the "Region" (100 km) level in either year (Table 2). No coral recruits occurred at Yungan and Shitzwan, the two non-reef sites of the study in 1999 and 2000. The phenomenon of significant variation at low levels seems to suggest that the source of coral recruits is very local. This is compatible with the hypothesis that most larvae of brooding pocilloporids do not disperse far upon settlement.


Penghu
1999
2000
Northeast
1999
2000
Yungan
1999
2000
Shitzwan
2000
Hsiaoliuchiu
1999
2000
Green Island
2000
Orchid Island
1999
2000
Recruit/panel
122
24
22
Northeast
T A I W A N
Penghu
Yungan
Green Island
Shitzwan
Hsiaoliuchiu
Orchid Island
Hengchun
▲ Hengchun
TAIWAN
22°N
21°55'N
120°50' E
120°55' E
N
Hengchun
1997
1998
1999
2000
Site

◄
Fig. 1 Recruitment density (no./plate surface) of pocilloporids in Taiwan. The settlement plates were recovered at sites 1, 2, 4, 5, 6, 7, 9, and 10 in 1997 and 1998; at sites 2, 3, 4, 5, 6, 7, 9, and 11 in 1999; and at sites 1, 3, 4, 5, 6, 8, and 9 in 2000. *Site labels on the x-axis* were deleted for those sites with no plates retrieved

Variations at the various spatial scales was inconsistent over the years in this study. This differs from that of the GBR in which both brooders and spawners had a consistent pattern over 2 years (Hughes et al. 1999). In a 4-year study at Heron Island (GBR), however, spatial pattern of coral recruits was not consistent between years, and this prompted Dunstan and Johnson (1998) to suggest that coral recruitment patterns are determined by mechanisms that manifest themselves over a range of spatial scales. Wallace's (1985) discovery of reversed rank order of recruitment at sites from one year to the next is compatible with the hypothesis that the dominating factors affecting recruitment may shift over the years. Since coral recruits in Taiwan are dominated by a few brooding taxa, spatial variation may be affected by very local events. For example, dispersal of brooder larvae may be influenced by wind velocity which tends to be variable in the Hengchun Region. When wind velocity is combined with tidal current, dispersal of short-ranged brooding larvae may be highly variable from year to year. The same mechanism may make little difference on larvae of broadcasting species, since they have a long planktonic stage and small-scale variation tends to even out over a longer time period.

Table 1 Nested-ANOVA table of pocilloporid recruitment in Hengchun Peninsula, southern Taiwan. Scale of area, 2–5 km; site, 1 km; location, 10 m. All data were transformed by using $\log(n+1)$

Levels	d.f.	SS	F-value	p
(1) 10/4 to 23/5/97				
Area	3	2.696	0.83	0.54
Site	4	4.294	9.67	< 0.01
Location	8	0.889	1.82	0.10
Residual	49	2.996		
(2) 14/1 to 28/2/98				
Area	3	10.187	0.97	0.49
Site	4	13.972	40.15	< 0.01
Location	8	0.700	2.81	< 0.01
Residual	160	4.974		
(3) 22/4 to 27/6/99				
Area	3	0.131	0.76	0.57
Site	4	0.235	0.66	0.65
Location	5	0.436	8.30	< 0.01
Residual	209	2.192		
(4) 2/4 to 8/8/00				
Area	3	7.217	63.32	< 0.01
Site	4	0.154	0.43	0.78
Location	5	0.438	3.32	< 0.01
Residual	247	6.518		

Table 2 Nested-ANOVA table of pocilloporid recruitment in Taiwan. Scale of region, about 100 km; area/site, 1–5 km; location, 10 m. All data were transformed by using $\log(n+1)$

Level	d.f.	SS	F-value	p
(1) 22/4 to 27/6/99				
Region	5	0.944	0.90	0.50
Area/Site	13	2.729	0.87	0.59
Location	13	3.342	19.46	< 0.01
Residual	552	7.292		
(2) 2/4 to 8/8/00				
Region	7	2.624	0.40	0.89
Area/Site	15	14.030	11.08	< 0.01
Location	17	1.435	3.97	< 0.01
Residual	760	16.135		

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