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Relationships between *Manicina areolata* (Cnidaria: Scleractinia), *Thalassia testudinum* (Anthophyta) and *Neogoniolithon* sp. (Rhodophyta)

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ABSTRACT: The free-living coral *Manicina areolata*, the seagrass *Thalassia testudinum*, and the coralline algae *Neogoniolithon* sp. co-occur in the reef lagoon of Xahuayxol, Quintana Roo, in the Mexican Caribbean. The distribution and abundance of these organisms was measured. In order to study why the coral was distributed only within the medium-density stands of *T. testudinum*, but not in the high- or low- density stands of the seagrass, 3 size classes of *M. areolata* were transplanted into 3 naturally occurring seagrass densities. Mortality, displacement, righting reaction, zooxanthellae, mitotic index, and chlorophyll *a* were evaluated for the transplanted colonies. High mortality of *M. areolata* was recorded in the low-density zone of *T. testudinum*, attributable to siltation and predation, whereas in the high-density zone of this seagrass, the coral was under stress, as indicated by a lowered zooxanthellae density. The fragile, arborescent algae *Neogoniolithon* sp. was found distributed only within the medium-density zone of *T. testudinum*, and *M. areolata* selectively recruited onto that algae. Experiments in which the coral and algae were separated in the medium-density seagrass zone demonstrated that *Neogoniolithon* sp. offers *M. areolata* adaptive and ecological advantages: its survivorship was significantly higher when attached to the algae than when this substrate was not available. Because of the natural distribution of *Neogoniolithon* sp., the coral did not recruit in zones that would cause it stress, or even death. *M. areolata* and *Neogoniolithon* sp. eventually separate because of the increase in size (and weight) of the coral, and the fragility of the algae. Thus, the distribution of *Neogoniolithon* sp. explained the distribution of *M. areolata* instead of the high negative correlation found between the density of *T. testudinum* and the coral.

KEY WORDS: Recruitment · Corals · Coralline algae · Seagrasses · Caribbean · Mexico · Yucatan Peninsula

INTRODUCTION

The free-living colonies of *Manicina areolata* (Linnaeus), a zooxanthellate scleractinian, are found in the Caribbean Sea, mainly associated with seagrass beds, especially *Thalassia testudinum* Banks ex König (Johnson 1988). Diverse aspects of its biology, ecology and evolution have been studied (Goreau & Goreau 1960, Peters et al. 1981, Johnson 1988, 1992a,b, Johnson et al. 1995). However, it is not known what ecological factors control its relationship with seagrasses.

The larval settlement of sessile organisms requires solid surfaces with precise physical and biological characteristics, such as substrate angle, wave exposure and surface area, which in turn can clearly affect juvenile survivorship and morphogenesis. In contrast, free-living organisms (such as *Manicina areolata*) require a firm substrate only for initial growth stages; hence, sur-

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face characteristics are almost circumstantial and do not control their morphogenesis (Hadfield 1986). However, in several laboratory- and field-oriented studies it has been found that the settlement and larval metamorphosis of different marine organisms occur in response to specific chemical signals produced by marine macroalgae (Kato et al. 1975, Switzer-Dunlap 1978, Trapido-Rosenthal & Morse 1986, Pawlik 1989). For example, a complex polysaccharide found in the crustose coralline rhodophyte *Hydrolithon boergesenii* (Foslie) Foslie specifically induces larval settlement and metamorphosis in the scleractinian corals *Agaricia humilis* Verril and *A. tenuifolia* Dana (Morse 1992, Morse & Morse 1996).

In the current work, the distribution, density, and size of *Manicina areolata* and *Thalassia testudinum* were studied at Xahuayxol, a coral reef area of the Mexican Caribbean. Three size classes of the coral (juvenile, and 2 presumed adult classes) were transplanted into 3 density zones of *T. testudinum* (low, medium, and high density), in order to determine the mortality and displacement of *M. areolata* in each zone. Zooxanthellae density, along with mitotic indices and chlorophyll *a* (chl *a*) concentrations in isolated zooxanthellae were measured to evaluate the responses of *M. areolata* to the transplantation. Such measurements have been used to describe changes in the general condition of corals (Brown & Howard 1985, Brown 1988, Grigg & Dollar 1990, Jones 1997, Mattia 1997). Another experiment was designed to evaluate the righting reaction of 3 size classes of *M. areolata*. Finally, the importance of the coralline algae *Neogoniolithon* sp. for the survivorship of *M. areolata* was investigated after it became evident that this coral recruits preferentially on *Neogoniolithon* sp.

MATERIALS AND METHODS

Study area. Xahuayxol is located at 18° 30′ 15″ N, 87° 45′ 32″ W, in the southern region of Quintana Roo, Mexico. It is bordered by a reef that is divided into 6 zones. These include a reef lagoon that is 250 to 300 m wide and has a maximum depth of 2.3 m (Fig. 1). A seagrass meadow of approximately 100 m width is located immediately seaward of a 1 to 2 m wide band of *Halodule wrightii* Ascherson along the shore. The meadow starts with a seagrass belt 30 to 35 m wide, which is mainly composed of *Thalassia testudinum* and *Syringodium filiforme* Kützing. Here, *T. testudinum* is larger and higher in density than in the rest of the seagrass meadow (Figs. 1 & 2, Table 1). Seaward of this a 25 m wide belt of *T. testudinum* with small blades and medium shoot density occurs (Figs. 1 & 2, Table 1). The population of *Manicina areolata* occurs only in this seagrass belt. From 62 to 115 m offshore, *T. testudinum* increases in density but not in size (Fig. 1, Table 1). After this seagrass belt, *T. testudinum* does not change in size but exhibits a noticably low shoot density (Figs. 1 & 2, Table 1).

Distribution, density, and size of *Manicina areolata* and *Thalassia testudinum*. Nine transects were placed at Xahuayxol, from September 29 to October 2, 1996. Each transect ran parallel to the shore and was sepa-

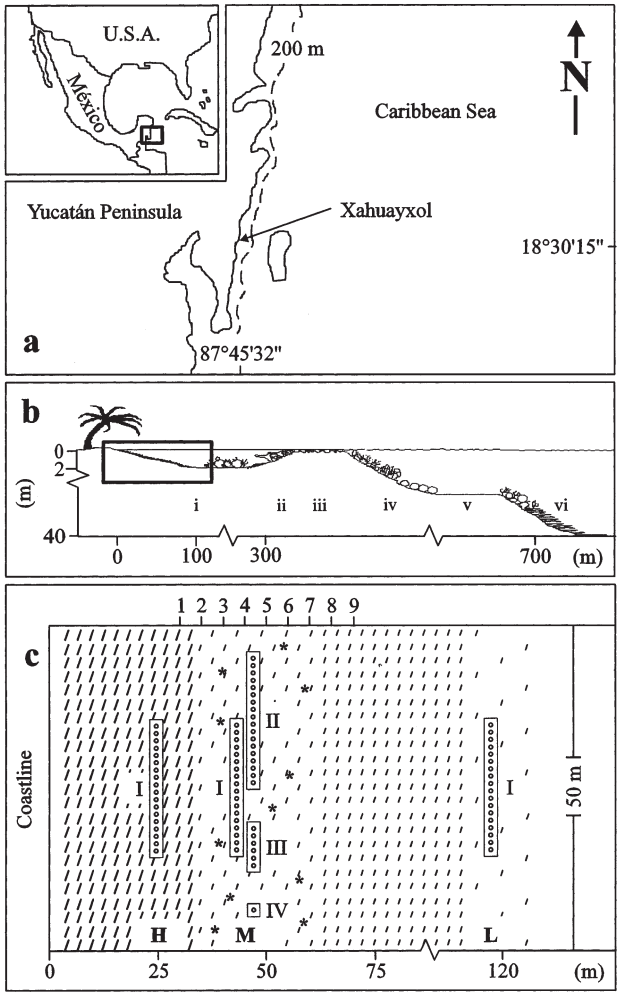

Fig. 1. (a) Location of Xahuayxol in the southern region of the Mexican Caribbean. (b) Diagrammatic profile perpendicular to the shoreline showing reef zonation at Xahuayxol: i, reef lagoon; ii, rear zone; iii, breaker zone; iv, fore reef; v, sand platform; vi, buttress zone (spur and grove). (c) Diagram of the study zone, in the reef lagoon of Xahuayxol: the Arabic numerals 1 to 9 represent the transects, parallel to the coastline, where the population measurements of *Manicina areolata* and *Thalassia testudinum* were carried out. The Roman numerals I to IV correspond to the position where the 4 experiments were performed on the high (H), medium (M), and low (L) densities of *T. testudinum*. (/) *T. testudinum*, according to its density and size, (*) *M. areolata* colonies. See text for details. Note the difference in scale between the 2 axes

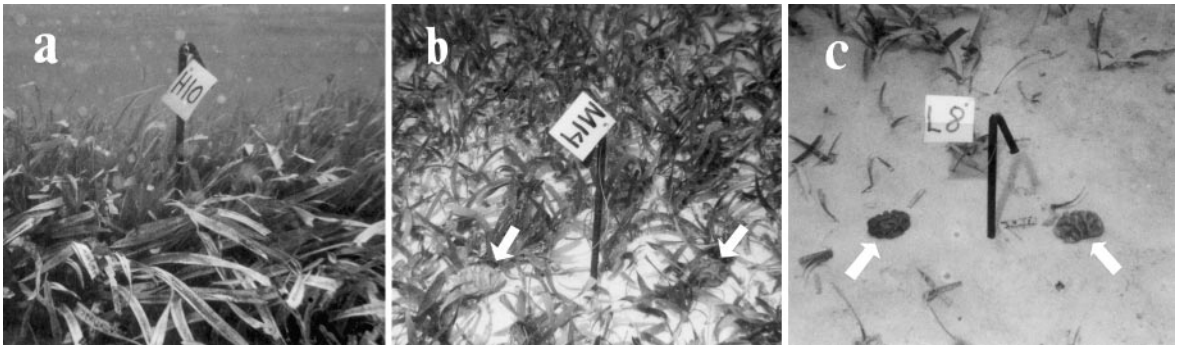

Fig. 2. Experimental zones within (a) high, (b) medium, and (c) low densities of *Thalassia testudinum*. *Manicina areolata* colonies (arrows) were placed at both sides of numbered metal stakes (see text for details). Photos by H. Bahena-Basave

rated from adjacent transects by 5 m. Transects were 30 to 70 m from the coastline, at water depths of 0.83 to 1.50 m (Table 1). Each transect was further subdivided into 25 quadrants of 1 m^2. Within each transect, the density of *M. areolata* and the length and width of each colony was measured. The shoot density and the length of 5 of the largest blades of *T. testudinum* and *Syringodium filiforme* was obtained from seven 0.0625 m^2 quadrats, placed every 3 m along the 25 m transects.

The surface area (cm^2) of each colony of *Manicina areolata* was calculated assuming an elliptic shape for the corallum tissue portion ($A = \pi$[length/2][width/2]). Area cover (cm^2 m^{-2}) of *M. areolata* was also calculated. An analysis of spatial pattern of colonies was made using the local quadratic variance of 2 terms method (Ludwig & Reynolds 1988).

The length, width, height, and surface area of 73 colonies of *Manicina areolata* were compared in a preliminary survey. A redundant relation was found between height and length ($r = 0.94$, $p < 0.0001$), and between height and surface area ($r = 0.96$, $p < 0.0001$). If *M. areolata* starts sexual reproduction when it reaches a height of 15.0 to 20.0 mm (Johnson 1992b), the corresponding surface area is between 3.0 and 5.8 cm^2, and its length is between 2.5 and 3.5 cm, near the 4.0 cm considered by Bak & Engel (1979) and Chiaponne & Sullivan (1996) as the limit in length for a juvenile coral colony. Accordingly, a juvenile colony of *M. areolata* was considered as those ≤3.5 cm in length. These sizes do not necessarily correspond to sexual stages since we did not look for gonad development.

Identification of the coralline algae. During the census of *Manicina areolata*, and while collecting colonies for the transplantation experiments (see below), it was observed that remains of a coralline alga were attached to the aboral portion of the majority of juvenile colonies. In a later sampling, it was found that 92% of 48 recruits (<10 mm) were attached to a free-living

Table 1. Average values of population parameters of juvenile (J) and adult (A) *Manicina areolata*, and of seagrasses *Thalassia testudinum* (*Tt*) and *Syringodium filiforme* (*Sf*) at the nine 25 m transects parallel to the coastline of Xahuayxol, Mexico. DC = distance of each transect from coastline. Beyond 115 m off the coastline, the density of *T. testudinum* decreased to 35 shoots m^{-2} (see 'Materials and methods' and Fig. 1)

Transect	DC (m)	Depth (m)	*Manicina areolata* Density (colonies m^{-2}) J	A	Total	Cover (cm^2 m^{-2}) J	A	Total	Seagrasses Density (shoots m^{-2}) *Tt*	*Sf*	Height (cm) *Tt*	*Sf*
1	30	0.8	0.0	0.0	0.0	0.0	0.0	0.0	541.7	1291.4	20.1	21.1
2	35	0.9	0.2	1.0	1.2	0.8	15.0	15.8	317.7	393.1	11.5	11.2
3	40	1.1	0.4	1.5	1.9	1.5	25.7	27.2	246.9	196.6	12.1	8.7
4	45	1.1	0.6	1.2	1.8	1.5	20.9	22.4	230.9	331.4	10.6	10.9
5	50	1.1	0.1	1.2	1.4	0.1	27.3	27.5	306.3	347.4	11.7	11.4
6	55	1.2	0.1	0.6	0.7	0.6	14.8	15.3	406.9	276.6	12.8	10.6
7	60	1.2	0.0	0.4	0.4	0.0	7.0	7.0	377.1	176.0	12.3	9.8
8	65	1.4	0.0	0.0	0.0	0.0	0.0	0.0	409.1	374.9	14.0	11.5
9	70	1.5	0.0	0.0	0.0	0.0	0.0	0.0	420.6	260.6	12.9	9.1
	Average:		0.2	0.7	0.8	0.5	12.3	12.8	361.9	405.3	13.1	11.6

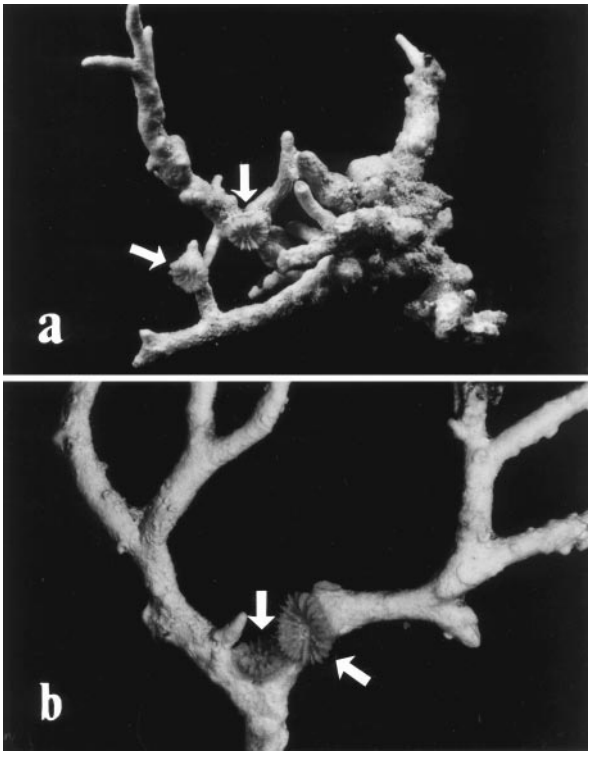

Fig. 3. Recruits of *Manicina areolata* (arrows) attached to *Neogoniolithon* sp. (a) ×0.5 (catalog number ECOCHBC-0148), (b) ×0.4 (catalog number ECOCHBC-0146). Photos by H. Bahena-Basave

branched nongeniculated coralline alga (Fig. 3). The remaining recruits were affixed to a fragment of a stony coral, a crustose coralline algae, a bivalve shell or a piece of wire. These alternative substrates for *M. areolata*, with the exception of wire, were abundant at the study site.

The nongeniculated coralline algae that we found at Xahuayxol was consistent with species included in *Neogoniolithon* (Taylor 1960, Wynne 1998), but it was not possible to identify the algae to species level because the uniporated sporangial conceptacles were empty. The thallus of the species from Xahuayxol is free-living, with an agglomerated habit, up to 6 cm in height, and rounded tips, and is fragile, with an unclear basal structure. The branches are terete to a little complanated, with branching mainly dichotomic, generally of 1 order. Internally, a core of coaxial filaments is found, formed by elongated cells with lengths 2–3 times their width. The filaments are joined by cell fusion with no evident secondary pit-connections. No trichocytes were observed, and the cortical cells are rather quadrangular in shape.

Characterization of the experimental zones with different *Thalassia testudinum* density. Three seagrass-density zones were selected to perform the experiments (Fig. 1): high (542 shoots m^{-2}, Zone H), medium (239 shoots m^{-2}, Zone M), and low (35 shoots m^{-2}, Zone L). The distance to the shore of each experimental zone was 25, 45 and 118 m, with depths of 0.5, 1.1 and 2.3 m, respectively. A Tukey's HSD test indicated significant differences between the mean *T. testudinum* shoot density in the 3 experimental zones ($p < 0.001$). The measurements indicated below were carried out for each experimental zone.

Sediment: On June 15, 4 cores of sediments were collected in each zone, using a 4.4 cm diameter PVC tube that was inserted 10 cm into the substratum or sandy bottom. Different grain sizes were separated by sieving the sample (Folk 1969), and the software of Vargas-Hernández (1991) was used to calculate granulometric parameters.

Irradiance and temperature: On June 28, 1997, 15 instantaneous readings of irradiance were obtained in each zone, with a Li-Cor® LI-1000 irradiometer, by placing the spherical sensor on the bottom. It was a cloudy day. The water temperature was obtained by placing a thermometer on the substratum.

Plant biomass: Plant biomass was measured by haphazardly placing three 0.0625 m^2 quadrats within each experimental zone and collecting all the enclosed plant material. Weight was obtained after drying the seagrasses and seaweeds at 60°C for 3 d.

Expt 1: Effect of *Thalassia testudinum* density on *Manicina areolata*. Colonies of *M. areolata* from the naturally occurring population were transplanted into the 3 zones (H, M, and L). The colonies in the Zone M, with a medium density of *T. testudinum*, functioned as a control. Eighteen numbered metal stakes were driven into the sand bottom in each zone in a north-south-oriented row 1 m apart from each other (Fig. 1). One colony of *M. areolata* was placed 10 cm away from each side of the stakes (Fig. 2), following a north-south orientation. Three size classes of *M. areolata* were transplanted to each experimental zone: juvenile (≤3.5 cm in length), small adults (SA, 3.6 to 6.5 cm in length), and large adults (LA, >6.5 cm in length). A total of 36 colonies per size class (12 per experimental zone) were transplanted. Healthy colonies were selected for transplantation according to their color (light to dark brown) and absence of visible injuries, and by eliminating those with the presence of crab cavities (10% of naturally occurring colonies). During handling, *M. areolata* was continuously maintained in seawater, using a floating rectangular metallic basket. The same precautions were utilized during the survival experiments with juveniles and recruits of *M. areolata* as described below.

A 2-color code was assigned to each numbered stake. Side (N/S) and position of each *Manicina areolata* was indicated by coloring its aboral portion with

wax colors. Transplantation experiments were initiated on June 6, 1997. Measurements of displacement and survival of *M. areolata* colonies were obtained on June 9, 14, 20 and 28, July 11, and September 3, 1997. The displacement, or change from the original position, of the colonies of *M. areolata* was measured using a metric band, and the angle of movement (from the N-S oriented row) with a plastic protractor. After each measurement, displaced colonies were returned to their original position. The angle and displaced distance were calculated following Rees & Sparks (1970). The percentage of displaced colonies in each zone was calculated as the proportion between the sum of the position changes by all the colonies within each size class and the total number of potential moving colonies during the experiment (for each size class: 12 colonies multiplied by 6 observation dates = 72, except in Zone L, where the numbers were low because of mortality of colonies; see below). The mean proportion of displaced colonies was compared for differences using 2-way ANOVAs. Descriptive statistical parameters for circular distributions, such as vector, mean angle of displacement and distribution range for each size class in each zone, were obtained. The Rayleigh test was applied to these data with H_0 = there is no mean population direction of movement (Zar 1984).

Zooxanthellae, chl a, and mitotic index: On September 3, 3 of the *Manicina areolata* colonies of each size class that had been transplanted on June 6 to the H, M, and L zones were collected, and each was maintained separately in 1 l plastic containers with seawater. The plastic containers were placed into an insulated box containing seawater in order to eliminate the possibility of zooxanthellae expulsion caused by rapid changes in temperature (Gil-Turnes & Corredor 1981). Eight hours after collection, live tissue was extracted from each colony following Johannes & Wiebe (1970). The blastate was homogenized and the volume measured. Three aliquots of 10 ml of blastate for each colony were separated for chl *a* determination, following Lorenzen & Jeffrey (1978). The extractions were filtered through a Whatman 40 filter paper to eliminate skeletal residues (Carricart-Ganivet & Beltrán-Torres 1993). A Spectronic® 1001+ spectrophotometer was used and chl *a* concentrations were calculated according to the equations of Jeffrey & Humphrey (1975).

For measurements of zooxanthellae density and mitotic index, 100 ml of blastate in each sample was fixed by adding 4 ml of formalin. To determine the density of zooxanthellae of each sample, 10 replicate cell counts were made using an hemocytometer after gentle homogenization of the fixed blastate (Carricart-Ganivet & Beltrán-Torres 1993). To quantify the mitotic index, the fixed blastate of each sample was centrifuged (5 ml at 5000 rpm [3920 × *g*]), the supernatant was eliminated, and the pellet was resuspended in 5 ml of distilled water. Two replicate 1000 zooxanthellae counts were made using an hemocytometer to register the number of cells that were dividing (Wilkerson et al. 1983). The skeletal portion of each colony was thoroughly washed in running water, and its surface area later determined using the aluminum foil procedure (Marsh 1970). The zooxanthellae cm^{-2}, chl *a* cm^{-2} and chl *a* zooxanthella^{-1} were calculated from these data.

Expt 2: Righting reaction of *Manicina areolata*. On June 6, 1997, another experimental setting was placed in Zone M, parallel to the ones used in the former experiment (Fig. 1). Here, 36 colonies of *M. areolata* (12 juveniles, 12 SA and 12 LA), all with their oral portion placed on the substrate, were positioned alongside 18 numbered metal stakes as in the previous experiment. The date that each colony returned to its normal position was recorded. The observation dates were June 8, 9, 14, 20 and 28 and July 11, by which time all the colonies had become righted. As a control, we used the *M. areolata* colonies placed in a normal position for Expt 1.

Expt 3: Importance of *Neogoniolithon* sp. to the survival of juvenile *Manicina areolata*. We tested the hypothesis that the branching architecture of the coralline algae *Neogoniolithon* sp. functioned as an 'anchor' for juveniles of *M. areolata*, thereby increasing their survival. To test this hypothesis, another experiment was set up within Zone M. On June 6, 1997, 12 juvenile colonies of *M. areolata*, each between 0.8 and 3.5 cm in length and each adhering to a branched coralline algae, were collected. Attached algae were removed from all colonies, and each colony was placed beside 6 stakes, in a 5 m long row as in previous experiments (Fig. 1). The control was the 12 juvenile colonies (with attached algae) of Expt 1. The survival of colonies was recorded on the same dates as Expt 1.

Expt 4: Importance of *Neogoniolithon* sp. for *Manicina areolata* recruits. *Distribution and biomass of Neogoniolithon sp.:* During a preliminary survey it was determined that the coralline algae on which juvenile colonies attached had a patchy distribution. To quantify patches, on June 9, 4 transects of 70 × 2 m were placed parallel to the shoreline in Zones H, M, and L. All patches located along the transects were classified as small (0.2 to 1.0 m in diameter), and large (>1.0 m in diameter). Coralline algal biomass was measured from 2 haphazardly chosen patches, one small and one large, by collecting all specimens of this species in three 0.0625 m^2 quadrats at each patch. In the laboratory, the samples were dried at 60°C for 3 d. Total and individual weights of 10 specimens were obtained for each sample, using a Sartorius® PT600 balance.

Survival of recruits of Manicina areolata: Once the patches of coralline algae were located, we found that recruits of *M. areolata* of millimeter size (<10 mm) were relatively easy to see with the unaided eye. We prepared an additional experiment within Zone M (Fig. 1) in order to measure the survival of recruits, with and without attached algae. This test was important because the recruits of *M. areolata* were not represented in Expt 3 (in that experiment, only 1 colony measured less than 10 mm in length).

On June 14, 1997, 40 recruits without visible signs of damage were collected from the coralline algae patches and placed within a radius of 5 cm from 4 metal stakes. Twenty recruits with attached algae were placed at 1 pair of stakes, while the other 20 recruits, without algae, were placed at the other 2 stakes. The separation of recruits and algae was accomplished by carefully breaking only the algae, never the coral, and using a pincer when necessary to break remaining parts of the algae. The number of live recruits was counted on June 28. Our observations of the movement of colonies suggested that it was possible that recruits were lost due to displacement, not mortality, so on June 28 we repeated the experiment, but now using enclosures. Twenty-four recruits with algae and 20 recruits without algae were placed inside an enclosure 20 × 20 cm, 5 cm in height, made with 4 stakes and a fence of plastic window screen. For this trial, the percentage of surviving recruits was determined on July 11. The same experiment was repeated starting on June 2, 1998, placing 24 recruits with algae and 23 without algae in 2 enclosures, and ending on June 30, 1998. The length of all transplanted recruits used in the preceding 3 experiments was 2 to 8 mm.

RESULTS

Distribution, density, and size of *Manicina areolata* and *Thalassia testudinum*

The mean total density and cover values of *Manicina areolata* (juveniles + adults), and the mean density and height values of the seagrasses *Thalassia testudinum* and *Syringodium filiforme* on all transects are given in Table 1.

The distribution of juvenile colonies of *Manicina areolata* was slightly more restricted (in Transects 2 to 6) than adult colonies (in Transects 2 to 7). The spatial distribution of all colonies (juveniles + adults) was aggregated on Transects 2, 4, and 5 (Fig. 4). However, only on Transect 4 did the clump pattern present a high definition and intensity, with a mean distance of 16 m between groups (twice the size of the block associated with the peak; Ludwig & Reynolds 1988). A random distribution was found for the colonies at Transects 6 and 7.

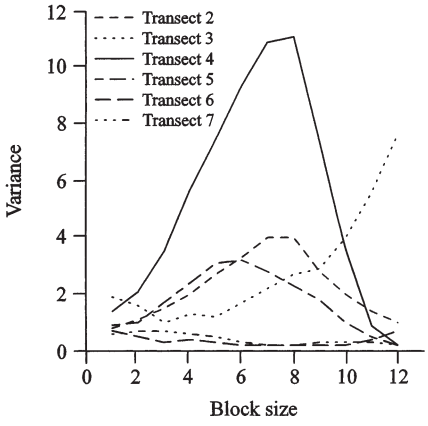

Fig. 4. *Manicina areolata.* Spatial distribution pattern within 6 transects at Xahuayxol, according to the local quadratic variance of 2 terms method. *M. areolata* colonies were not found on Transects 1, 8, and 9 (see Table 1)

The correlation coefficients and linear regressions indicated a significant negative relationship between the density of *Thalassia testudinum* and the density and cover of *Manicina areolata* juveniles and adult colonies (Fig. 5). On the other hand, the size of *T. testudinum* and the density and size of *Syringodium filiforme* were not significantly related ($p > 0.05$) to the population variables of *M. areolata*.

A significant positive relationship ($p < 0.01$) existed between the density of adult *Manicina areolata* colonies and the density and cover of juvenile colonies ($r^2 = 0.67$ and $r^2 = 0.64$, respectively). Similarly, adult cover exhibited a positive relationship ($p < 0.05$) with the density and cover of juveniles ($r^2 = 0.52$ and $r^2 = 0.45$, respectively).

Characterization of the experimental zones with different *Thalassia testudinum* density

Sediment

The results of the 1-way ANOVA, HSD Tukey's test indicated that Zone M contained a significantly higher percentage ($p < 0.001$) of coarse sand (24.0%) than Zones H (7.3%) and L (9.0%). Zone L had a significantly higher percentage ($p < 0.001$) of medium sand (23.7%) than Zones H (9.2%) and M (11.7%). The sediment in Zone H was composed of more ($p < 0.001$) fine sand (83.4 %) than Zones M (63.5%) and L (66.0%). The percentage of very fine sand in Zone H (0.13%) was significantly lower ($p < 0.01$) only in comparison with Zone L (1.27%).

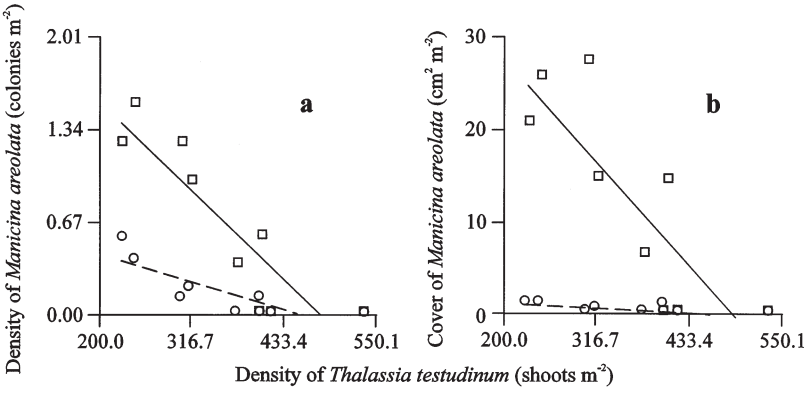

Fig. 5. Relationships between density of *Thalassia testudinum* and (a) density and (b) cover of juveniles (○) and adults (□) of *Manicina areolata*. Regression lines are: $y = 0.77 - 0.002x$ ($r^2 = 0.69$, $p = 0.006$), $y = 2.65 - 0.006x$ ($r^2 = 0.79$, $p = 0.001$), $y = 2.32 - 0.005x$ ($r^2 = 0.61$, $p = 0.01$), and $y = 46.27 - 0.094x$ ($r^2 = 0.69$, $p = 0.006$), respectively

Irradiance and temperature

Mean bottom irradiance in Zone H was 138 µmol m^{-2} s^{-1}, in Zone M 657 µmol m^{-2} s^{-1}, and in Zone L 637 µmol m^{-2} s^{-1}. The temperature was similar in all 3 zones, between 28.5 and 28.7°C.

Plant biomass

The most important plant component in the 3 zones was the seagrass *Thalassia testudinum*, with a biomass of 368 g m^{-2} in Zone H, 99 g m^{-2} in Zone M, and 24 g m^{-2} in Zone L. The seagrass *Syringodium filiforme* was second in importance, but it was present only in Zones H and M, with 280 and 4.8 g m^{-2}, respectively. Other plant elements were only found in Zone M: *Halimeda incrasata* (Ellis) Lamouroux (11.2 g m^{-2}), *Penicillus lamourouxii* Decaisne (3.2 g m^{-2}), *Udotea flavellum* (Ellis & Solander) Lamouroux (3.2 g m^{-2}), and *Neogoniolithon* sp. (0.5 g m^{-2}).

Expt 1: Effect of *Thalassia testudinum* density on *Manicina areolata*

Mortality and displacement

Zone L, with low densities of *Thalassia testudinum*, was different from the other 2 zones because mortality and loss of coral colonies only occurred there. By July 11, 1997, 83 % (10) of the juvenile colonies in Zone L had been registered as dead or missing; the other 2 colonies died between that date and September 3, 1997. By September 3, 50 % of the SA and 33 % of the LA of *Manicina areolata* were also recorded as dead and/or lost. The great majority of dead colonies had clear bite marks on most of their surface area (Fig. 6a), caused, possibly, by coralivorous fishes. Another cause of coral mortality was asphyxia, due to sediment burial (Fig. 6b).

The mean distance of displacement, in cm, for juvenile, SA, and LA of *Manicina areolata* colonies was 14, 5 and 0 within Zone H, 12, 10 and 35 within Zone L, and 15, 14 and 0 within Zone M, respectively. There was no significant difference in displacement between size classes in each zone, nor among zones (1-way ANOVA, $p > 0.53$, in all cases). The proportion of displaced colonies was very low (Fig. 7). Within Zone H, there was less displacement (2 %) than in Zones M (6 %) and L (8 %) but it was not significantly different (2-way ANOVA, $p > 0.05$, $1 - \alpha = 0.90$). However, in each zone, juveniles had a greater percentage of displaced colonies than SA

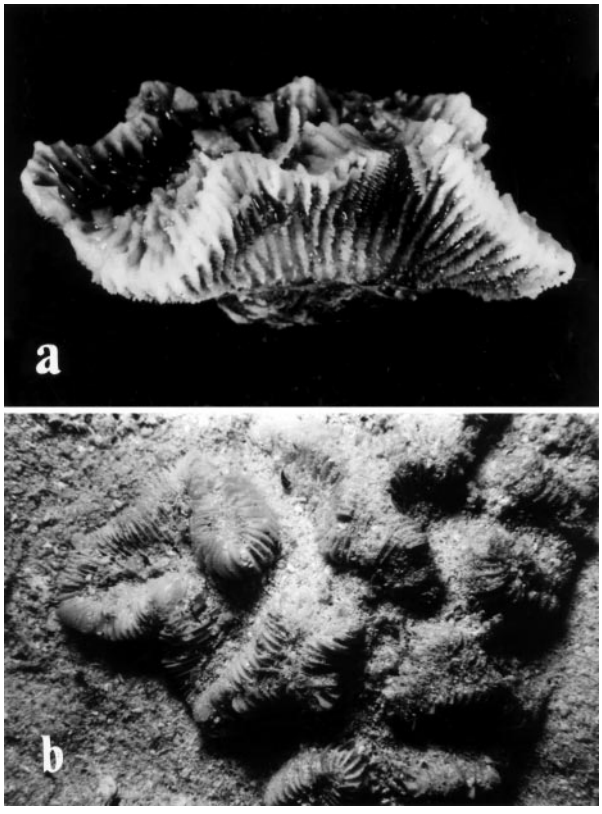

Fig. 6. *Manicina areolata*. (a) Skeleton of a juvenile found dead in the zone of low density of *Thalassia testudinum* (35 shoots m^{-2}); note the bite marks on its edges (×0.4). (b) *In situ* buried adult of *Manicina areolata* in the same zone (×0.8). Photos by H. Bahena-Basave

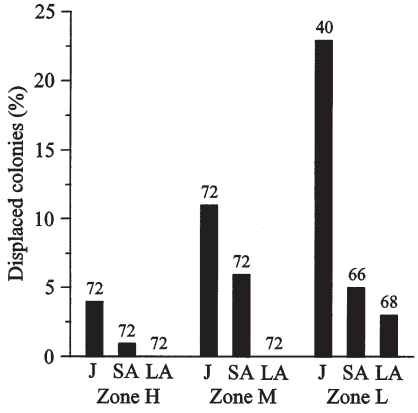

Fig. 7. *Manicina areolata*. Percentage of displacement of juveniles (J, ≤3.5 cm in length), small adults (SA, 3.6 to 6.4 cm in length) and large adults (LA, ≥6.4 cm in length) in the 3 experimental zones of *Thalassia testudinum* density (H = 542 shoots m^{-2}, M = 239 shoots m^{-2}, L = 35 shoots m^{-2}). Numbers above bars indicate the number of observations in each case. The number of observations in Zone L was lower due to the mortality that occurred within this zone (see text for details)

and LA (2-way ANOVA, $p < 0.05$, $1 - \alpha = 0.90$; LSD test, $p < 0.05$) (Fig. 7). There was no mean direction of displacement for the colonies according to Rayleigh's test ($p < 0.1$, in all cases). Thus, displacement of colonies was random.

Zooxanthellae, chl *a*, and mitotic index

The mean values of zooxanthellae cm^{-2}, chl *a* zooxanthella^{-1}, chl *a* cm^{-2}, and the mitotic index (Table 2) did not differ significantly between size classes of *Manicina areolata* in each experimental zone (1-way ANOVAs, $p > 0.05$, in all cases). Based on these results, only zones were considered in subsequent statistical analysis. The mean number of zooxanthellae cm^{-2} of *M. areolata* from Zone H (2.775×10^6) was significantly lower (Tukey's HSD test, $p < 0.001$) than those from Zones L (4.736×10^6) and M (3.486×10^6), but the latter were not statistically different. Mean values of chl *a* zooxanthella^{-1}, chl *a* cm^{-2}, and mitotic index were not significantly different among the 3 experimental zones ($p > 0.05$, in all cases).

Expt 2: Righting reaction of *Manicina areolata*

Righting reaction time increased with size/weight of the colonies, from 8 d for the juveniles to 14 d for SA to 35 d for LA. Control colonies, which were placed upright, exhibited a very low percentage of overturned colonies for all 3 size classes (Table 3).

Expt 3: Importance of *Neogoniolithon* sp. to the survival of juvenile *Manicina areolata*

We did not record mortality for juvenile colonies of *Manicina areolata* to which *Neogoniolithon* sp. was not available as a substrate.

Expt 4: Importance of *Neogoniolithon* sp. for *Manicina areolata* recruits

Distribution and biomass of *Neogoniolithon* sp.

Patches of *Neogoniolithon* sp. were found only within Zone M, with a larger number of small (16) than large patches (5). In the small patches, the mean biomasses per area (5889.6 g dw [dry weight] m^{-2}) and per individual (3.2 g dw) were greater than the corresponding mean values for the large patches (2937.6 g dw m^{-2} and 1.2 g dw, respectively).

Survival of juveniles and recruits of *Manicina areolata*

In the experiment without an enclosure, where *Neogoniolithon* sp. was manually removed from *Manicina areolata* recruits, only 25% of the recruits survived, in comparison to 85% for recruits with algae attached. In the similar experiment with an enclosure, the survival

Table 2. Average zooxanthellae density (cm^{-2}), chl *a* zooxanthella^{-1}, chl *a* cm^{-2}, and the mitotic index (%) per size class of *Manicina areolata*, in the 3 experimental zones. The measurements of juvenile colonies in Zone L are not given due to their mortality (see text for details). Acronyms as in Fig. 7

Zone	Zooxanthellae cm^{-2} ($\times 10^6$)			µg chl *a* zooxanthella^{-1} ($\times 10^{-6}$)			µg chl *a* cm^{-2}			Mitotic index (%)		
	J	SA	LA	J	SA	LA	J	SA	LA	J	SA	LA
H	2.93	3.30	2.09	2.26	2.34	2.98	6.44	7.65	9.08	8.8	8.4	6.6
M	2.96	3.77	3.73	1.63	2.42	2.21	5.04	9.08	8.20	10.7	8.9	10.3
L	–	4.52	4.95	–	1.68	1.80	–	7.59	8.41	–	9.8	9.7

Table 3. *Manicina areolata.* Percentage (%) of righting reaction of 12 colonies per size class for each observation date and number of days elapsed since the beginning of the experiment. Control refers to percentage of overturned colonies per size class in Zone M at the end of the experiment (see text for explanation). Acronyms as in Fig. 7

Date of observation	Number of elapsed days	Percentage of righting J	SA	LA
Jun 6	0			
Jun 8	2	33	42	0
Jun 9	3	58	58	17
Jun 14	8	100	92	75
Jun 20	14		100	92
Jun 28	22			92
Jul 11	35			100
Control Sep 3	89	1.2	2.4	3.6

of *M. areolata* recruits without algae was 40%, versus 75% survival of recruits with algae attached. In the replication of the latter experiment, the survival of recruits without and with coralline algae attached was 58 and 100%, respectively. Considering that there was no significant difference in survival within experiments with and without the enclosure (t-test = −0.59, $p < 0.58$), the results of the 3 experiments were grouped. Then, the survival was significantly greater (t-test = 3.77, $p < 0.03$) for recruits of *M. areolata* with *Neogoniolithon* sp. attached (87%) than for those without algae (41%).

DISCUSSION

Importance of *Thalassia testudinum* and *Neogoniolithon* sp. to the distribution of *Manicina areolata*

The mean value (0.8) and total range (0.4 to 1.9) of juvenile plus adult *Manicina areolata* colonies m^{-2} found in this study (Table 1) are similar to (Chiappone & Sullivan 1991) or greater than (Johnson 1992b, Chiappone & Sullivan 1994) other density values reported in the literature. However, the maximum density of *M. areolata* in the Caribbean Sea can be up to 12 colonies m^{-2} and under exceptional circumstances up to 70 colonies m^{-2} (Johnson 1988, 1992a,b). The cover values of *M. areolata* found here (7.0 to 27.5 cm^2 m^{-2}; Table 1) are greater than the values reported by Chiappone & Sullivan (1994) in the Florida Keys (0.1 cm^2 m^{-2}) and by Chiappone & Sullivan (1991) in the Bahamas (0.0 to 8.9 cm^2 m^{-2}).

The population of *Manicina areolata*, a brooding coral (Boschma 1929, Johnson 1992b) from Xahuayxol, was comprised mainly of adult colonies (>3.5 cm in length, Table 1). As with other brooding scleractinian species (Chiappone & Sullivan 1996), we found a strong correlation between the density and cover of adult colonies and the density and cover of juvenile colonies. This probably is indicative of a population in which the supply of larvae depends on local adult colonies, meaning that each local colony is relatively isolated from other populations. These correlations can also be a characteristic of life histories of massive brooding species of relatively small size inhabiting unstable environments, as Soong (1993) reported for several species of coral from the Indo-Pacific and the Atlantic Ocean. On the other hand, we do not know of any other study reporting the aggregated distribution of *M. areolata* such as occurs at Xahuayxol. Our data indicate that the distance between patches was between 10 and 16 m.

Thalassia testudinum, *Syringodium filiforme*, and *Halodule wrightii*, found at Xahuayxol, were also reported from the west coast of Florida and the Caribbean portion of the Yucatán Peninsula (Zieman & Zieman 1989, Espinoza-Avalos 1996). The density and height values of *T. testudinum* found at Xahuayxol are within the ranges previously recorded by other authors for the Gulf of Mexico, the Mexican Caribbean, and Florida (De la Lanza et al. 1991, Gallegos et al. 1993, Lapointe et al. 1994). However, the mean density of *S. filiforme* in this seagrass meadow is 24 and 17 times lower than in reports from the Bahamas (Short et al. 1985) and northern Quintana Roo (Gallegos et al. 1994), respectively, and its mean height at our study site is 1.5 times lower than that recorded by Short et al. (1985) in the Bahamas. These differences could be because *S. filiforme* is intermixed with *T. testudinum* at Xahuayxol, whereas at the other 2 sites it grows alone.

Manicina areolata was not normally present at high and low densities of *Thalassia testudinum* (Table 1), and at medium densities exhibited an inverse relationship with the density of seagrass (Fig. 5). It has been recognized that the biomass and cover of marine plant communities influence the distribution and ecological links of benthic fauna (Stoner 1980, Fisk 1983). However, the highly significant relationship found at Xahuayxol between *M. areolata* and *T. testudinum* did not explain the distribution of the former species in Zone M, which is better attributed to the distribution of the coralline algae *Neogoniolithon* sp., as discussed below.

Effect of *Thalassia testudinum* density on *Manicina areolata*

The mobility of some scleractinian corals represents an important adaptive feature that provides the oppor-

tunity for them to colonize different environments (Glynn 1974, Hoeksema 1988, Lewis 1989, Chadwick-Furman & Loya 1992). However, a very low displacement was registered for the 3 size classes of the free-living coral *Manicina areolata* within the 3 experimental zones of this study. Free-living species can be displaced to environments that may have fatal consequences (Hoeksema 1988). Such a possibility was evident in this study for colonies transplanted to Zone L, where all juvenile and several adult coral colonies died because of predation and siltation (Fig. 6). The sediment of this zone not only contained 90% medium and fine sand, but also was not compacted (pers. obs.). Both factors probably facilitate resuspension of the sediment and, consequently, burial and death of colonies (see Yonge 1936). A decrease in movement has been observed in unattached corals as they increase in size (Glynn 1974, Hoeksema 1988, Chadwick-Furman & Loya 1992). The same was found for *M. areolata* transplanted into 3 experimental zones, although the percentage of displaced colonies in our study was very low (Fig. 7).

The specimens of *Manicina areolata* transplanted into Zone H suffered stress caused by environmental factors; this was measured as a significant decrease in the number of zooxanthellae cm^{-2}. It is known that under stress hermatypic corals use digestion and/or expulsion mechanisms in order to regulate their number of zooxanthellae (Titlyanov et al. 1996). The quantity and quality of light is one factor causing changes in the density of zooxanthellae, photosynthetic pigments, and mitotic index of scleractinian corals (Dustan 1979, Titlyanov 1981, Wilkerson et al. 1983, Kinsie et al. 1984). Nonetheless, the chl *a* zooxanthella^{-1}, chl *a* cm^{-2}, and mitotic index of transplants did not change compared to the control colonies located in Zone M (Table 2). In our study, the irradiance in Zone H was on average 4.7 times lower than in the other 2 zones. We think that the low light level found in Zone H caused the stress, and, consequently, a lower number of zooxanthellae cm^{-2}.

Righting reaction of *Manicina areolata*

The disproportionately large surface area in relation to size (volume) found in the free-living form of *Manicina areolata* has been interpreted as an adaptive specialization to colonize sandy bottoms, and for righting ability if overturned by waves and sea currents (Goreau & Goreau 1960). Nonetheless, quantitative evaluations of these behaviors have not been studied sufficiently for this coral species.

All *Manicina areolata* of the 3 size classes returned to their normal position after 35 d, before the end of the experiment. The juveniles reached 100% righted before adult colonies (Table 3). This is similar to the findings of Johnson (1988), who mentioned that the righting reaction was limited by the size of the colony. The percentage of overturned control colonies was insignificant for the 3 size classes (Table 3), suggesting that righting ability is actively controlled by *M. areolata* (Goreau & Goreau 1960). The process, then, is not dictated by stochastic factors (i.e. sea currents, bioturbation), as was proposed by Fabricius (1964) for *M. areolata* and by Chadwick-Furman & Loya (1992) for Indo-Pacific fungiids. The low displacement distance for the 3 size classes registered within the 89 d of the experiment also confirms that the righting reaction, which is relatively rapid, is controlled by *M. areolata* and, in addition, did not play an important role in its displacement.

Importance of *Neogoniolithon* sp. to the survival of *Manicina areolata*

Differential larval settlement can be an influencing variable for recruitment, particularly on hard substrates (Pawlik 1992). In our study, 92% of the *Manicina areolata* recruits were found attached to *Neogoniolithon* sp. (Fig. 3). Pawlik (1992) stated that the recruitment of marine benthic invertebrates shows variable spatial and temporal patterns, attributable to numerous factors occurring before, during or after settlement. Although recruits and juvenile colonies of *M. areolata* were attached to *Neogoniolithon* sp., it was demonstrated that the algae was not important for the survival of the juvenile stage. However, the recruits suffered significant mortality when separated from the algae, placing importance on the arborescent structure of the algae, which provides the possibility of escaping asphyxia for recruits living in sandy environments. It has been demonstrated that coral planula avoid substrates with high sedimentation rates (Hodgson 1990). The above data and this information demonstrate that *Neogoniolithon* sp. is only important for the early stages of *M. areolata*. All adult colonies observed during this study lacked attached algae, implying that at a specific weight the growing coral eventually separates from the fragile algae, as noted previously for *M. areolata* attached to shells and other corals (Goreau & Goreau 1960). It is important to note that while decalcifying recruits of *M. areolata* attached to *Neogoniolithon* sp. for identification of the algae the organisms separated easily, without cellular modifications on the contact site, indicating that the settlement of the coral did not physically injure the algal tissue.

It is thought that the patchy spatial distribution of coralline algae and the preferential larval settlement on live substrates causes an aggregated distribution

pattern of adults (Carlon & Olson 1993). In our study, the patchy distribution of *Neogoniolithon* sp., the recruitment of *Manicina areolata* associated to those algae patches, and the relatively patchy distribution of adult *M. areolata* colonies support that notion.

In summary, the distribution of *Manicina areolata* was restricted to densities of *Thalassia testudinum* between 231 and 407 shoots m^{-2}. At these densities, a significant relationship was found between the density of *T. testudinum* and the density and cover of *M. areolata*. However, the density of *T. testudinum* does not explain the distribution of *M. areolata*. The coral distribution is explained by the distribution of *Neogoniolithon* sp., an arborescent alga here used preferentially by *M. areolata* for recruitment. The strong *Neogoniolithon* sp.–*M. areolata* relationship, and the distribution of the algae, gives adaptive and ecological advantages to *M. areolata*. *Neogoniolithon* sp. offers a recruitment substrate that increases the survival of *M. areolata* by helping to avoid siltation. On the other hand, the distribution of *Neogoniolithon* sp. may prevent *M. areolata* from settling in zones where the corals would be subject to ecological stress (i.e. low-irradiance regimes) and death by predation and/or siltation. These findings show that even though shallow reef coral zones are among the most studied communities, not all ecological relationships have been discovered.

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