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REPORT

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An appraisal of methods used in coral recruitment studies

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Abstract A new method for attaching individual artificial settlement plates directly to the reef surface using small stainless steel base plates is described. Recruitment of corals to settlement plates attached to the reef substratum and to steel mesh racks is compared. The effects of differences in depth, settlement plate angle, and local topography on recruitment of corals were also investigated. No significant difference in mean recruit density was found between settlement plates deployed using the two attachment methods. Small differences in depth and plate angle among replicate plates explained less than 6% of the variability in coral recruitment on replicate settlement plates. The direct-attachment method is less obtrusive, more cost and time efficient, and settlement plates can be deployed at precise locations. Additionally, because settlement plates are deployed individually rather than grouped on racks or frames, the direct-attachment method avoids complications associated with assumptions of independence implicit in most statistical procedures.

Key words Coral · Recruitment · Settlement plates · Larvae

Introduction

Recruitment of corals to artificial settlement plates is often used to provide a measure of the relative abundance of coral recruits in time and space (Harrison and Wallace 1990). Since the early studies of Vaughan (1912), a wide variety of methods for fixing settlement plates to the reef substratum have been utilised, including concrete blocks (Birkeland et al. 1981; Tomascick 1991), PVC pipe frames (Baggett and Bright 1985; Hunte and Wittenberg 1992; Smith 1997), steel mesh racks (Sammarco and Carleton 1981; Harriott and Fisk 1987); plastic bases (Rogers et al. 1984); iron frames (Gleason 1996; Nzali et al. 1998) and oceanographic moorings (Sammarco and Andrews 1989).

Previously, variability in recruitment rate associated with settlement plate size (Birkeland et al. 1981) and settlement plate type (Harriott and Fisk 1987) have been considered. The angle of settlement plates relative to the substratum is also an important source of variability in studies of coral recruitment (Sammarco 1991). Surprisingly, the effect of the method of attaching settlement plates to the reef substratum on coral recruitment has received little critical attention, despite the potential differences in physical parameters among methods that might influence settlement of coral larvae.

The most common method for plate attachment that has been used in recruitment studies on Western Pacific coral reefs is the steel mesh rack method (e.g. Sammarco and Carleton 1981; Wallace and Bull 1981; Wallace 1985; Harriott 1985; Harriott and Fisk 1987; Babcock 1988; Fisk and Harriott 1990; Sammarco 1991; Harriott 1992; Baird and Hughes 1997; Dunstan and Johnson 1998). The conditions encountered by coral larvae contacting settlement plates attached to raised structures such as steel mesh racks probably differ from conditions encountered on nearby natural substrata. These differences include light conditions, sediment accumulation, grazing intensity, and the assemblage of other encrusting organisms. The effect of raised structures on water flow can also introduce "trapping artefacts" (Butman 1987), influencing the supply of larvae to settlement plates on raised structures, or the accumulation of sediment on settlement plates. However, whether the variable conditions presented by different attachment methods bias estimates of coral recruitment rate or affect the

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taxonomic composition of recruits is unknown. Similarly, it is uncertain if recruitment data obtained from settlement plates attached to the reef substratum by different methods are comparable.

In a recent study of small-scale spatial patterns in coral recruitment (Mundy 1996), a method for attaching a large number of artificial settlement plates within a small area (10 m × 20 m) was required. The study required the deployment of settlement plates at a density of 2 plates/m^2 throughout the site, without impacting upon the corals or the aesthetics of the site. The use of racks or frames in a study of this intensity undoubtedly would have altered flow patterns across the site and may have modified patterns of recruitment (Keough 1983). Consequently, a new method of attaching individual settlement plates directly to the reef substratum using a fixed base plate was developed (Mundy 1996). The new method (direct attachment) also better simulates conditions encountered by coral larvae on natural substrata, and thus is more likely to give representative information that reflects natural recruitment patterns.

Because of the small-scale topographic complexity of most coral reefs, individual settlement plates attached directly to the substratum may differ in terms of depth, plate angle and also in surrounding topography (sunken, raised). Small-scale differences in surrounding topography (Birkeland et al. 1981; Snelgrove 1994) could also influence supply of larvae, and therefore recruitment of corals to replicate settlement plates. Consequently, the effect of these physical variables on coral recruitment when using the new direct-attachment method was considered.

This paper describes the direct-attachment method and compares it to the popular steel mesh rack method in order to determine if the attachment method affects recruitment rate and taxonomic composition of corals on artificial settlement plates. The direct-attachment method is then applied in a study of the effects of the physical environment (depth, plate angle, topography) on recruitment of corals to artificial settlement substrata. No significant differences in recruit density were found among the plate attachment methods tested. Initial concerns that small differences in depth, plate angle and surrounding topography among replicate plates would contribute additional unexplained variance to estimates of recruit density were also unfounded.

Materials and methods

Study site

The study was carried out on the north slope of Heron Reef (23°26′S, 151°57′E), southern Great Barrier Reef, at two sites separated by approximately 500 m. The settlement plates used in the experiments were unglazed terracotta tiles (110 mm × 110 mm × 10 mm). Numerous pits and grooves (up to 1 mm deep and 1 mm wide) covered the upper and lower tile surfaces, providing a rough texture. All settlement plates were placed on the reef in late September 1994 and were retrieved in early February 1995. After retrieval, plates were rinsed gently to remove sediment, bleached overnight in a chlorine solution to remove algae and soft tissue animals, and then rinsed in fresh water and dried. The plates were examined microscopically and coral recruits on the upper, lower and vertical sides of the plates were counted and placed in one of six taxonomic categories; acroporids (ACR; not including isoporans), isoporans (ISO), pocilloporids (POC), poritids (POR), other taxa (OT), and unidentifiable/damaged (UI). Recruitment was standardised to recruits/100 cm^2 in comparisons of attachment methods.

Description of the direct-attachment method

Settlement plates were attached directly to the reef using a small stainless steel base plate (100 mm × 50 mm × 0.6 mm), with a stainless steel bolt secured to the centre of the plate (Fig. 1). The base plate is attached to the substratum with two nylon expansion plugs (10 mm × 30 mm; Panduit product code MPMH-38LO), inserted through holes in the steel base plate into holes (10 mm diameter by 20 mm deep) which have been drilled into consolidated non-living reef substratum using a pneumatic drill. The settlement plate (which has a hole drilled through the centre) is secured to the base plate with a stainless steel wing nut (Fig. 2). The base plate lies flush with the substratum and the heads of the nylon plugs provide a gap of 8 mm between the settlement plate and the base plate, creating a "gap habitat" (Harriott and Fisk 1987). The direct-attachment method described here is similar in concept to that used

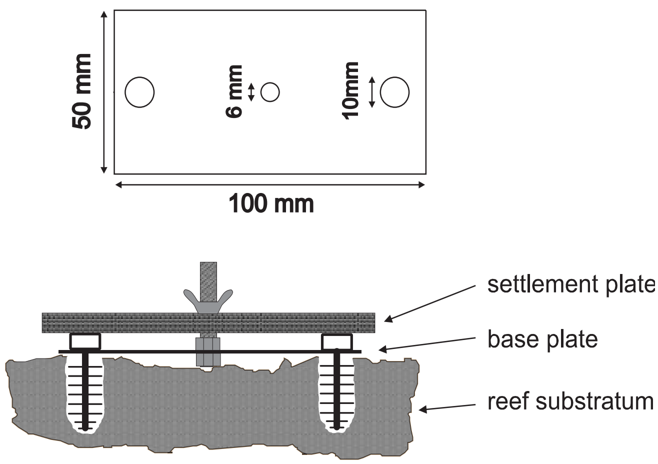

Fig. 1 Illustration of base plate with attached settlement plate

Fig. 2 Photograph of settlement plate attached to a base plate 3 months after deployment

in some previous studies (Birkeland et al. 1981; Rogers et al. 1984), but differs in the materials used and/or the use of a fixed base plate.

Effect of different attachment methods on coral recruitment

Three different plate configurations were compared; (1) settlement plate pairs on mesh racks – a pair of tiles bolted to a steel mesh rack as described by Harriott and Fisk (1987); (2) settlement plates attached to base plates as described above; and (3) single settlement plates bolted to mesh racks. Because the direct-attachment method uses a single plate rather than a plate pair, the last configuration (single settlement plates on racks) was included to separate effects due to the method of attachment from effects due to using plate pairs. The racks were bent into an 'A' frame shape, to provide an angle of approximately 37° to 45°, as recommended by Sammarco (1991).

Five racks were anchored to the substratum with steel pegs at each of the two sites. The racks were placed 2- to 3-m apart, at approximately 9 m depth. One plate pair and one single plate were attached to each half of each rack, giving a total of ten replicates each of plate pairs and single plates on racks at each site, and 20 replicates overall. The available surface area for settlement in the plate pair treatment is also twice that of the other two treatments. The plate pairs were attached to racks with one tile above and one tile below the mesh and secured with a stainless steel bolt. The upper and lower tiles of tile pairs were considered as a single unit in all analyses. The single plates were placed above the mesh and held to the mesh racks with a narrow strip of Perspex (110 mm × 30 mm) in place of the lower plate. At each site, ten settlement plates were attached to the reef substratum using the direct-attachment method described above. These plates were located among the mesh racks, and were spaced 1–2 m apart.

A potential problem associated with attaching multiple settlement plates to each rack is that due to their close proximity, recruitment to replicate plates on a rack or frame may be influenced by common factors, resulting in similar, correlated estimates of recruitment. Therefore studies which consider multiple plates grouped on racks or frames as independent replicates may violate the assumption of independence that is implicit in parametric and non-parametric statistical analyses (Sokal and Rohlf 1981). In order to test for correlation in recruitment between replicate plates located on the same rack, Pearsons correlation coefficients were calculated between the two sets of plate pairs on each rack, and for pairs of single plates on each rack separately. Data used in these analyses were recruitment of acroporids, pocilloporids and total recruits (taxa pooled). Data from the two sites were pooled for these analyses. Because some data from plates located on the same rack were autocorrelated, a conservative approach was taken and all plates of a particular attachment method on each rack were pooled, giving $n = 5$ replicates per site for plate pair and single plate treatments and $n = 10$ replicates/site for the base plate treatment.

Comparisons of coral recruitment to settlement plates attached using the different configurations were done using a two-way ANOVA, with planned comparisons. The main effects were 'method' with three levels ('double plates', 'single plates', 'base plates') and 'site' with two levels ('site 1', 'site 2'). Site was considered as a random effect. The a priori planned comparisons were double plates versus base plates and single plates versus base plates. Data were analysed separately for acroporids, pocilloporids and total recruits. Insufficient numbers of recruits from the other taxonomic categories were recorded to be included separately in the statistical analyses. Levenes test for homogeneity of variances was used to ensure assumptions of homogeneity of variances were met (variances were homogeneous in all cases, $P > 0.1$).

The precision of the sample mean was calculated for each of the three attachment methods (Andrew and Mapstone 1987, p. 52). Because replicate plates located on the same rack were not considered to be independent, calculations of precision for the two rack methods (plate pairs and single plates) were carried out on the pooled data from replicates on the same rack. Thus for plate pairs there were five replicate racks at each site giving a total sample size of ten for calculations of precision (from 40 plates deployed). Similarly, for single plates on racks a sample size of ten was used in calculations of precision (from a total of 20 plates deployed). All 20 replicate settlement plates attached to base plates were used in precision calculations.

Effect of depth, plate angle and local topography on recruitment

Data are presented from 228 plates at site 1 and 206 plates at site 2. For this part of the study, the plates were located in an area approximately 10 m across by 20 m down the reef slope (between 3 m and 8 m below MSL). The depth of each plate was measured to the nearest 5 cm using a digital depth gauge, adjusted for tide, and expressed as depth below MSL. The angle of each plate relative to the sea surface was measured to the nearest degree using a protractor with a wire suspended by a float. The topography surrounding each plate was recorded as one of four topography categories; (1) level – the substratum within approximately 30 cm surrounding the plate was flat; (2) raised – the plate was located on a mound or knob and raised at least 10 cm above the surrounding substratum; (3) protected – the plate was located in a depression or hollow at least 5 cm below the surrounding substratum; and (4) stepped – the plate was located on one of a series of cascading ledges (see Fig. 3).

Multiple regression analyses were used to examine the proportion of the total variance in recruitment (dependent variable) which was explained by depth and plate angle (independent variables). A G-test for goodness of fit (Sokal and Rohlf 1981) was used to determine if proportionally more or fewer recruits than expected were found on plates located in different topography categories (level, raised, sunken, stepped). To determine whether local topography influenced the taxonomic composition of recruits found on plates, a G-test of independence (Sokal and Rohlf 1981) was used to test whether the relative proportion of taxa found on plates was independent of local topography. Data were analysed separately for each site.

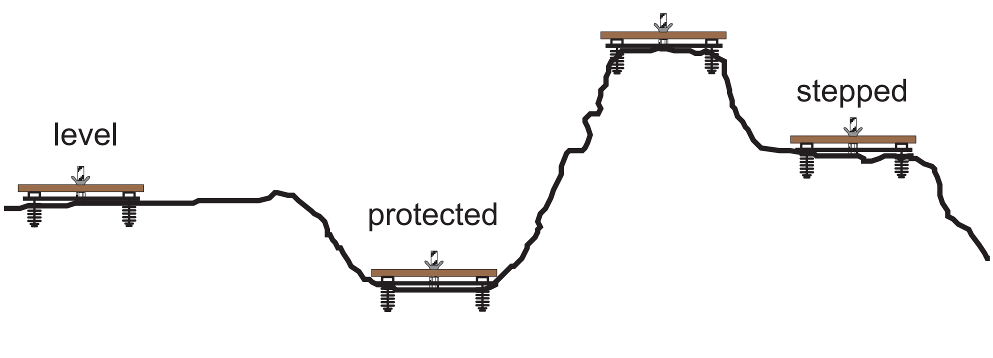

Fig. 3 Illustration of local topography categories (level substratum surrounding plate level, protected surrounding substratum higher than plate, raised surrounding substratum lower than plate, and stepped plate located on a ledge)

Results

Effect of attachment method on coral recruitment

The method of plate attachment had little effect on either coral recruit density or taxonomic composition of coral recruits. No significant differences in mean density of coral recruits (acroporid, pocilloporid or total recruits) were found in planned comparisons of the three methods ($P > 0.24$ in all tests; Fig. 4). Because recruit density (recruits/100 cm^2) in the plate pair treatment was similar to recruit density on the two single plate treatments, coral recruitment in this study was proportional to the available area for settlement. The precision of the three attachment methods was also similar. Sample precision ranged from 0.26 to 0.27 for acroporids, 0.17 and 0.22 for pocilloporids, and 0.17 and 0.20 for total recruits (all taxa pooled; n = 10 for plate pairs and single plates on racks, and n = 20 for base plates).

Pocilloporids were the most common coral recruits found on all settlement plates, followed by non-isoporan acroporids and poritids, while recruits from other taxonomic groups (OT) accounted for 5% or less of all coral recruits (Table 1). The proportion of coral recruits on different plate surfaces (top, bottom, and vertical sides) was also similar among the three attachment methods. Coral recruits were mostly on the lower surface of settlement plates in all three methods with 69% and 62% of recruits on lower surfaces in the base plate and single plate methods respectively, and 54% on the lower surface of the bottom plate in the plate pair treatment (Table 2). Approximately 20% of recruits were on the vertical sides of plates in all three methods, while the upper surface of plates in all three treatments had the lowest recruitment (Table 2). Recruitment to the interior surfaces between the upper and lower plate of the tile pair (plate pair) accounted for 21% of recruits to plate pairs. There were no differences among taxa in preference for a particular plate surface in the three attachment methods tested.

Results of tests for correlation in recruitment among replicate plates located on the same rack were mixed. The density of recruits found on replicate plates on the same rack was highly correlated in the single plate method for pocilloporids ($r = 0.90$, $P < 0.001$) and for total recruits ($r = 0.74$, $P < 0.02$), but not for acroporids ($r = 0.18$, $P > 0.90$). No significant correlations in recruit density of acroporids, pocilloporids or total taxa were found among replicate plates attached with the plate pair method ($r < 0.2$ in all cases).

Table 1 Total number of recruits and percentage of recruits from six taxonomic groups on settlement plates from different plate attachment methods. (*ACR* non-isoporan acroporids, *ISO* isoporan acroporids, *POC* pocilloporids, *POR* Poritids, *UI* unidentifiable spat, *OT* other taxonomic group). Data are pooled across sites

	Total no. recruits	ACR	ISO	POC	POR	UI	OT
Plate pairs	173	25.4	1.7	66.5	2.9	1.7	1.7
Single plates	80	23.8	2.5	58.8	7.5	2.5	5
Base plate	72	19.4	0.0	69.4	5.6	1.4	4.2

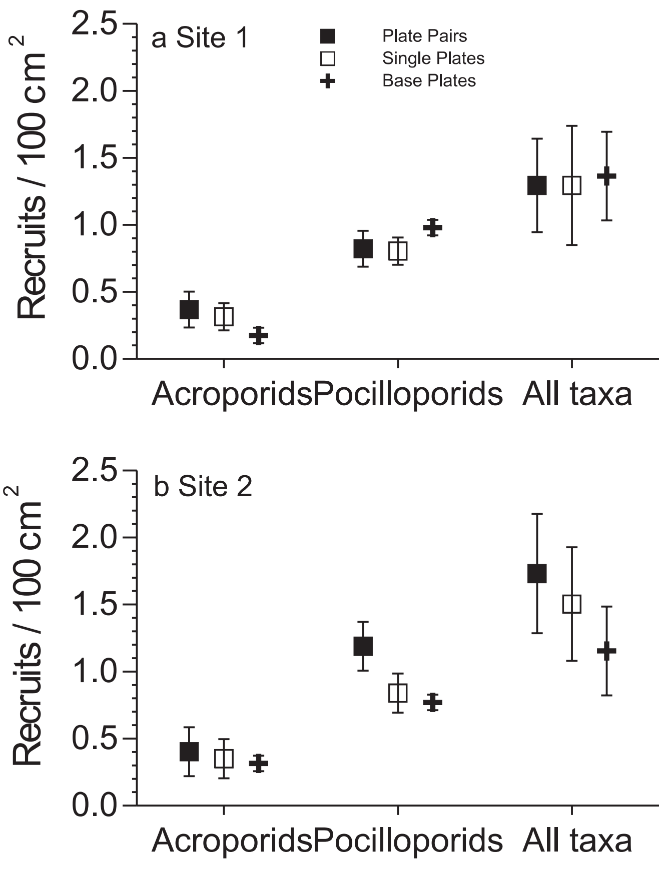

Fig. 4 Comparison of mean recruitment to settlement plates deployed with alternative methods at **a** site 1, and **b** Site 2. Data for the double plate and single plate on racks methods are pooled for each rack. Data shown are mean recruit density (recruits/100 cm^2). *Error bars* indicate standard errors

Effect of depth, plate angle and local topography on coral recruitment

The three environmental variables that were considered as potential factors affecting recruitment had little measurable effect. Depth of plate (below MSL) and plate angle (degrees from horizontal) explained little of the variability (r^2 < than 0.06) in recruit density among replicate settlement plates, for all taxa at both sites (Figs. 5, 6).

There appeared to be an effect of local topography on the number of coral recruits on settlement plates attached to base plates. At site 1, slightly more recruits were found on plates located on level sites and slightly fewer recruits were found on plates located in protected sites, than was expected under the null hypothesis of equal recruitment among locations (G-test, $P < 0.05$). However, at site 2 the proportion of recruits on settle-

Table 2 Percentage of total recruits found on different surfaces of settlement plates attached using three methods of attachment (plate pairs and single plates on racks, and base plate). Data are pooled across sites

Plate surface	Plate pair		Single plate		Base plate
	Available space (cm^2)	% of recruits	Available space (cm^2)	% of recruits	
Upper surface	121	2.9	121	8.8	12.5
Plate sides	88	22.5	44	28.8	18.1
Lower surface	121	53.8	121	62.5	69.4
Interior surfaces	242	20.8		–	–
Total no. of recruits		173		80	72

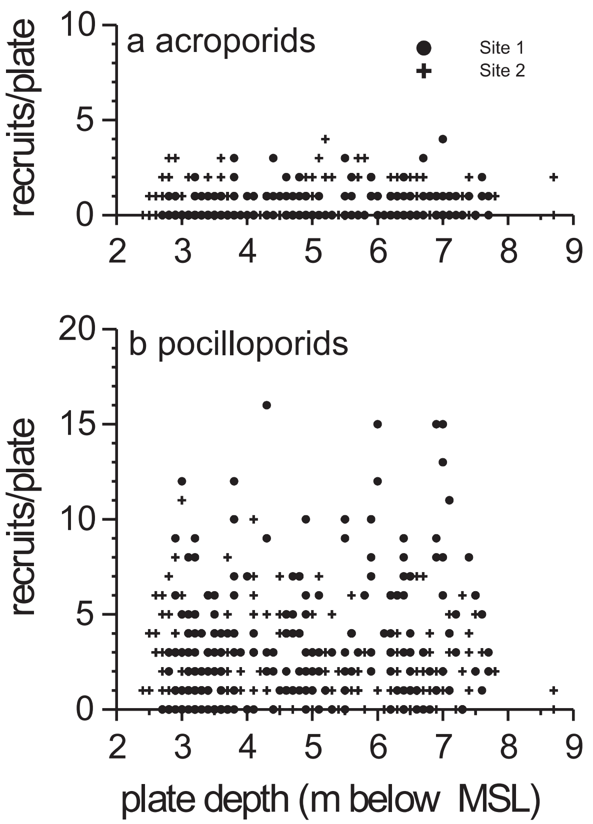

Fig. 5 Relationship between number of coral recruits and depth of settlement plate

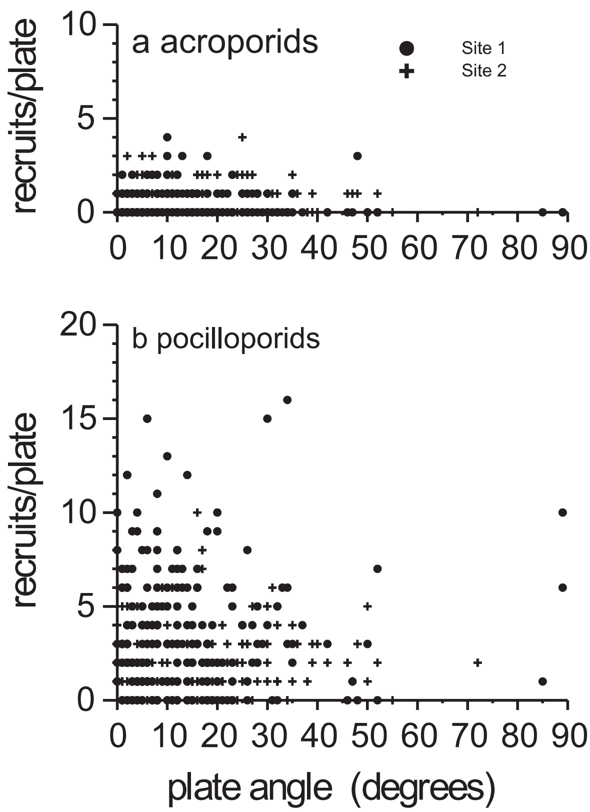

Fig. 6 Relationship between number of coral recruits and angle of settlement plate

ment plates located in different topographies did not depart significantly from expectation (G-test, $P > 0.05$). At site 1, the observed number of recruits was within 5% of the expected number in each topography category. The statistically significant result at this site is most likely due to the high number of observations ($n = 228$). However, the magnitude of the difference is not considered to be ecologically significant.

The relative abundance of recruits from the three major taxa (acroporids, pocilloporids and poritids) was dependent on local topography at site 1 (G-test, $P < 0.05$), but not at site 2 (G-test, $P > 0.05$). The result at site 1 reflects a shift in the proportion of poritid and pocilloporid recruits in the stepped category. In this category, 46% of recruits were poritids compared with between 31% and 36% in level, protected and raised categories. Conversely, 45% of recruits found in the stepped category were pocilloporids compared with 62% in all other categories. Many of the plates in the stepped category were located within a high-density patch of poritid recruits (Mundy 1996), rather than a systematic and consistent effect of stepped environments on taxonomic composition of recruits.

Discussion

Comparison of settlement plate attachment methods

The new method of attaching individual settlement plates directly to the reef substratum using small base plates proved to be highly successful, providing comparable estimates of coral recruitment to the steel mesh rack method. (Tables 1, 2; Fig. 4). The patterns of recruitment to different plate surfaces of settlement plates were also similar among the three attachment methods, although slightly fewer recruits were found on the lower surface of the lower plate in plate pair treatments than the other two methods (Table 2).

The number of recruits on the sheltered interior plate surfaces (gap habitat) of plate pairs was low compared with that found by Harriott and Fisk (1987). In this study, only 21% of recruits were found on interior surfaces, whereas Harriott and Fisk (1987) found between 31% and 79% of recruits in these surfaces, depending on plate type and reef zone. Surprisingly, recruit density on single plates on racks, which do not provide a sheltered habitat, was not significantly different from recruit density on plate pairs. A possible explanation for this result is that the steel mesh racks used in this study were reasonably small, arranged in an 'A' frame shape, with the settlement plates held approximately 10- to 15-cm above the substratum. This may have provided a more sheltered and darker environment for settlement than provided by racks which hold settlement plates further off the substratum (e.g. Harriott and Fisk 1987). Similarly, settlement plates attached to base plates provide a sheltered habitat between the base plate and the lower surface of the settlement plate, although larvae that settle on the base plate itself or the substratum covered by the settlement plate would not be recorded in this method.

Several specific advantages of using the new direct-attachment method were apparent. Firstly, because the number of recruits on replicate plates grouped on the same rack may be correlated, use of the direct-attachment method avoids problems associated with the violation of the assumption of independence required by most parametric and non-parametric statistical analyses (Sokal and Rohlf 1981). If recruitment is significantly correlated among plates within racks, it may be necessary to pool the data from these plates to avoid violation of the assumption of independence, resulting in fewer true replicates in statistical analyses. There are some exceptions to this, for example in hierarchical designs that are concerned with estimating variability in recruitment at multiple spatial scales (e.g. Baird and Hughes 1997; Dunstan and Johnson 1998).

The second advantage of the direct-attachment and single plate methods over the plate pair method is that comparable estimates of recruit density can be obtained with 50% fewer settlement plates, without sacrificing sample precision. As microscopic examination of each settlement plate may take up to 45 min, a considerable time saving can be obtained by using either of the single plate methods. Harriott and Fisk (1987) clearly showed, however, that recruits in the sheltered interior surfaces provided by plate pairs may represent a significant proportion of the total recruitment at some sites. A similar sheltered habitat is provided by the direct-attachment method, whereas plates attached singly to mesh racks raised above the substratum do not provide a sheltered habitat. Methods of attaching settlement plates that do not provide a sheltered habitat may under-estimate recruitment of taxa that prefer interior surfaces.

An additional advantage of the direct-attachment method is that settlement plates can be located at precise locations on the substratum (e.g. next to potential competitors for space, in caves, or on vertical walls). This may be desirable in studies investigating the effects of specific factors on recruitment such as proximity to soft corals (e.g. Maida et al. 1995) or effect of overstory corals (Fisk and Harriott 1993), without substantially altering the environmental conditions (light, water flow) at the point of interest. Small discrete structures may also avoid confounding effects such as experienced by Sammarco and Carleton (1981), who found that damselfish territories were established around and under some control racks in their study of the effects of defended territories on coral recruitment.

Effect of depth, plate angle and topography on coral recruitment

Initial concerns that small differences in depth, angle of settlement plate and surrounding topography among replicate plates attached to base plates may introduce additional variance to estimates of coral recruitment proved to be unfounded. The combined effects of depth and settlement plate angle explained less than 6% of the variability in recruitment (Figs. 5, 6 see also Mundy 1996). On this basis I conclude that small differences in depth and differences in settlement plate angle among replicate plates deployed using the direct-attachment method will not introduce additional unwanted variability to estimates of coral recruitment.

The absence of an effect of plate angle on coral recruit density in this study (Fig. 6) contrasts strongly with the results of Carleton and Sammarco (1987), who found a significant correlation between plate angle and coral recruit density, and significantly more recruits than expected on substrata angled between 61 and 90°. The results presented here also disagree with the suggestion by Sammarco (1991, p 497) that the optimum angle of artificial settlement plates for coral recruitment was between 37 and 45°. Differences in the type of settlement plates used and the scale of measurement may explain the differences between this study and the findings of Carlton and Sammarco (1987). The terracotta settlement plates used in this study have a flat uniform surface, whereas plates used by Carleton and Sammarco were cut from colonies of *Pachyseris speciosa*, and had complex irregular surfaces. Carleton and Sammarco (1987) measured the angle of the plate at the location of each recruit, and consequently, measured the angle of the microhabitat rather than the angle of the settlement plate. Coral larvae may prefer particular angles within microhabitats at settlement and/or survival of recruits may be dependent on the angle of the microhabitat. However, the extrapolation of the importance of the angle of microhabitat at settlement to the optimum angle of settlement plate for recruitment (a scale one order of magnitude greater) is not supported by this study.

Settlement plates located in protected locations were expected to have higher settlement than plates in level or exposed locations simply as a result of passive deposition of planulae (Hannan 1984; Butman 1987; Mullineaux and Garland 1993; Snelgrove 1994). Contrary to these a priori expectations, local topography as categorised in this study (e.g. level, protected, exposed or stepped) did not strongly influence the number or taxonomic composition of recruits in this study. Carlon and Olson (1993) reported that initial contact of *Favia fragum* planulae appeared to be a random process occurring as planulae were 'tumbling' in the near-bottom turbulence. Most coral planulae show substratum searching behaviour, and continue searching if a site is unsuitable for settlement (Harrison and Wallace 1990). Factors affecting post-settlement survival such as predation of larvae and recruits, competitive interactions with other sessile taxa (e.g. sponges, ascidians, bryozoans), and grazing herbivores, could substantially modify any patterns determined at the time of settlement. Although local topography may have influenced the rate of initial deposition of coral planulae at small spatial scales (10^{-1} m), this did not translate to predictable effects on recruitment rate at this scale.

The absence of a predictable effect of local topography on recruitment in this study differs from the observations of Sakai and Yamazato (1984), who found significant differences in abundance of recruits between exposed and sheltered microhabitats. Sakai and Yamazato found greater recruitment of acroporids and pocilloporids in sheltered habitats than in open habitats, whereas the reverse pattern was found for poritids. This is consistent with suggestions by Carleton and Sammarco (1987) that coral larvae may select a particular micro-topographic feature at the time of settlement. The patterns observed by Sakai and Yamazato may also have resulted from differential mortality. The differences between the present study and Sakai and Yamazato (1984) probably relate to the scale at which the microhabitat was considered, 10^{-3} m to 10^{-2} m in the latter, and 10^{-1} m in this study.

In summary, the new direct-attachment method using small discrete base plates has proved to be an efficient and reliable method of obtaining recruitment data. This method provides comparable estimates of recruitment and sample precision, using 50% fewer plates than methods that group replicate plate pairs on structures such as steel racks or frames. Furthermore, statistical complications associated with violations in the assumption of independence that can affect methods which group several plates are avoided. Small differences in depth, plate angle and surrounding topography among replicate plates within each site did not contribute additional unexplained variance to estimates of recruit density. Settlement plates deployed using base plates are also less obtrusive than steel racks, resulting in a lower visual impact of recruitment experiments on reef sites, and use non-corrosive, reusable materials.

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