Effects of some natural and artificial substrata on sessile marine organisms at Galeta Reef, Panama

Keith A. McGuinness*

Galeta Marine Laboratory, Smithsonian Tropical Research Institution, Apartado 2072, Balboa, Republic of Panama

ABSTRACT: Despite the potential importance of substratum type to the sessile assemblage developing, few field experiments have examined the effects of this factor in marine habitats. Three types of hard substrate are common in the shallow waters near Galeta Point on the Caribbean coast of Panama: coral, on intertidal reef-flats, rock, more common in lagoonal areas, and wood, most abundant in the nearby mangrove forest. There were significant differences in the number of alga species, and the abundances of some of these species, colonizing plates of these 3 natural substrata and of 2 artificial substrata (perspex and concrete) in 4 habitats (front and back reef-flat, lagoon and mangrove forest). Effects of substrata varied among habitats. In the lagoon, for example, plates of rock, concrete and perspex were colonized by more species than were plates of coral or wood. Further, at some times on the reef-flat, algae occupied less space on perspex plates than on plates of the other 4 types of substrata. In contrast, the coralline crust *Lithothamnion* sp. was most abundant on perspex and concrete in the lagoon. Results demonstrate that type of substratum plays an important role in determining the abundance of sessile species in some marine habitats. Reasons for these effects are not clear but may include differential grazing by invertebrates or differential retention of spores, water or heat. Using artificial substrata to follow the development of sessile assemblages may give misleading results, particularly if comparisons are made among habitats.

INTRODUCTION

Despite early suggestions as to the potential importance of the type of substratum to the settlement, and perhaps survival, of marine organisms (Hatton 1938, Meadows & Campbell 1972, Crisp 1974, Lewis 1977), few field studies on intertidal shores have considered its effects. Compared to other factors affecting organisms on hard intertidal habitats, type of substratum has received relatively little attention and only a handful of field experiments have been done (e.g. Caffey 1982, McGuinness & Underwood 1986).

There are 3 major reasons for this neglect. First, much of the research on the effects of type of substratum on the settlement of marine organisms has been done in the laboratory. Doubts have, however, been expressed that such simple effects would carry over to the field where larvae are exposed to the profusion of settlement cues in the maelstrom of surge and currents found on most rocky shores (Underwood 1979, Caffey 1982). The

results of an experiment by Caffey (1982), using plates of each of 4 naturally occurring rock types on each of 4 shores on the coast of New South Wales, reinforced this impression: he found 'no consistent trend for settlement density or proportional survival'.

A second reason for neglect may lie in the spatial scale of studies, particularly experimental studies. Many, and probably most, rocky intertidal experiments are done on a single shore. Rock type is usually similar within a shore (e.g. Caffey 1982, McGuinness & Underwood 1986), so questions about its influence may never arise. Among exceptions is the study of McGuinness & Underwood (1986) of organisms on intertidal boulders on 2 shores, also on the coast of New South Wales. In contrast to the work of Caffey (1982), they found striking differences in the abundances of an alga and 2 species of sessile invertebrates colonising boulders of different types transplanted between the 2 shores.

A third reason why effects of substrata are ignored stems from the prolific use of artificial substrata in marine biology. As several authors have noted, many studies in both the field and laboratory make extensive use of artificial substrata as settlement surfaces (e.g. Risk 1973, Harlin & Lindbergh 1977, Caffey 1982). The

---

* Present address: Institute of Marine Ecology, Zoology Building A08, University of Sydney, New South Wales 2006, Australia

reason given for the use of such materials is usually the ease of obtaining many, replicate uniform experimental units (e.g. McGuinness & Underwood 1986, Todd & Turner 1987). If, however, substratum influences the settlement and survival of organisms, then the results of studies using artificial surfaces may be extremely misleading.

At least 3 types of substratum are common in intertidal and shallow subtidal areas on the Caribbean coast of Panama: coral, rock and wood. Approximately 15 % of the reefs in the Caribbean have reached the water surface, so exposed coral is a common substratum in the region (Macintyre & Glynn 1976). As with most coasts, the bedrock has been exposed in some places creating rocky shores and boulder fields. Finally, wood is present either as the trunks and roots of mangrove trees, or in the form of logs driven onto the shore. The first aim of this work was to determine the effect of these types of substratum on the colonisation of hard surfaces by marine organisms. A second aim was to examine the validity of using artificial substrata – specifically perspex and concrete – to study colonisation in sessile assemblages.

MATERIALS AND METHODS

Study sites. This work was done on an extensive intertidal reef-flat at the Galeta Marine Laboratory of the Smithsonian Tropical Research Institute on the Caribbean coast of Panama. Four habitats were studied: the front and back of the reef-flat itself; the lagoon behind the reef-flat; and an intertidal sand flat near the mangrove forest to the east of the laboratory.

The reef-flat was dominated visually by foliose algae, though the zoanthid *Zoanthus sociatus* was patchily abundant (see also Hay 1981, Sebens 1982). The common algae were *Laurencia papillosa*, *Halimeda opuntia*, *Acanthophora spicifera* and *Gelidiella acerosa*. Coralline crusts, predominantly *Lithothamnion* sp., occupied much space amongst the foliose algae. The most obvious mobile species were sea urchins, with *Echinometra lucunter* being the most common. The cover of foliose algae generally declined towards the back of the reef (author's unpubl. data, Sebens 1982) and the space was occupied by a mixture of filamentous forms (predominantly *Cladophora* sp. and *Enteromorpha* sp.), blue-green algae and diatoms (referred to as 'microalgal mat' following Cubit et al. 1987a) and *Z. sociatus*.

The majority of the lagoon floor was occupied by the seagrass *Thalassia testudinum*, though patches of *Syringodium filiforme* were also present. Amongst the seagrass were sea urchins, primarily *Lytechinus variegatus*, and hermit crabs, usually *Paguristes cadenati.*

The same hermit crab was abundant on sand flats near the mangroves. Algae were present epiphytically on nearby seagrasses, on logs, and on the roots and trunks of mangroves.

The Panamanian climate is strongly seasonal with a pronounced dry season from December to April and a wet season from May to November (Cubit et al. 1987b). During the dry season winds blow strongly from the north and the resulting swell means that the reef is rarely exposed (Cubit et al. 1987b). In the wet season winds are light and the reef may be exposed for the entire day. These exposures usually coincide with mass mortalities of plants and animals on the reef-flat (Glynn 1968, 1972, Cubit et al. 1987b, Hendler 1977).

Experimental design. Sixteen rectangular plates ca 10×13 cm, and 3 cm thick, were cut from each of 5 substrata – coral, wood, rock, concrete and perspex. Most of the substrata used were obtained from flotsam and rubble on a nearby beach. Coral plates were cut from pieces of *Porites* rubble and rock plates from natural siltstone boulders. Wooden plates came from a large beam which had been on the beach for at least 3 mo. I could not use natural mangrove wood in the experiment because the roots and trunks of the trees at the water's edge (which were the appropriate ones to use) were too small to cut into plates (results, therefore, do not apply to mangrove roots or trunks). Concrete plates were cut from 'besser' building blocks (6 mo) and perspex plates from a 5 mm thick sheet. All plates, except perspex, had one uncut, weathered surface and it was this surface which was exposed for settlement. The exposed surface of the perspex was roughened with sandpaper in an attempt to compensate for the fact that it was not weathered like the other plates.

Ten plates (2 replicates of each type) were attached with nylon fishing line (to avoid possible effects of glues or metal fastenings) to each of 8 sheets of plastic mesh. The plates were arranged, 1 plate distance apart, in 2 rows, each row having one of each type of substratum arranged in random order. Perspex plates had a wooden 'spacer' placed between the plate and the mesh in order to make their upper surface level with that of the other, thicker plates. One mesh unit was placed in each of 2 haphazardly selected sites in each of the 4 habitats – front reef, back reef, lagoon and mangrove forest. Units on the reef were anchored with stainless steel spikes; others with wooden stakes.

Plates in the lagoon and mangrove forest mimicked the orientation of natural hard substrata in those habitats; that is, they sat on the sediment with their upper surface a few centimetres above it. Plates on the reef-flat were not countersunk into the coral so their orientation was unnatural in this habitat. In order to determine the effects of the extra few centimetres elevation in this habitat, small patches of similar size to the

plates were cleared on the reef-flat at the same time that experimental plates were put out.

The plates were put out on 27 February 1985 and were sampled 4 times over the following 7 mo (13 March, 10 April, 5 June and 12 September). On each occasion the percentage cover and identity of all sessile species present was recorded using a 5×5 cm perspex quadrat with 25 randomly placed points. At each time of sampling, each plate was sampled by 2 haphazardly placed quadrats (to give 2 replicate readings on each plate at each time). Only occupation of primary space was recorded, but species on plates did not form a canopy. The numbers of any mobile species (e.g. hermit crabs) on the plates were also recorded.

Statistical analyses. Percentage covers and numbers of species in the major experiment were analysed by 5-factor analyses of variance (ANOVA) with the factors: Times (random), Substratum (fixed), Habitats (fixed), Sites (random and nested in Habitats) and Plates (random and nested in Substratum × Sites). The inclusion of Times in analyses was valid because replicate, independent observations were made on each plate at each time. The procedures of Winer (1971) were used to derive expected mean squares for this (and subsequent) designs and construct appropriate F-ratios for testing the significance of interactions and main effects. Again following Winer (1971), interaction terms were dropped from the model only if the appropriate F-ratio was non-significant at the 25 % level (see Winer 1971 and Underwood 1981 for discussions of the rationale of this procedure). On some occasions the complexity of the ANOVA model meant that valid F-ratios could not be formed for tests of some main effects and interactions, but in all analyses in which this problem arose higher order interactions were significant, making interpretations of simple main effects uninteresting (main effects and their lower order interactions were, therefore, not examined if a higher order interaction with that factor was significant). Assemblages developing on coral plates and in cleared patches on the reef-flat were compared using 5-factor analyses of variance (ANOVA) with the factors: Times (random), Location (fixed), Habitats (fixed), Sites (random and nested in Habitats) and Plates (random and nested in Location × Sites).

The numbers of hermit crabs on plates were analysed with 3-factor analyses of variance, with the factors: Substratum (fixed), Habitats (fixed), Sites (random and nested in Habitats). Times could not validly be included in analyses in this instance because only 1 observation was made on each plate (a total count of all individuals present). Between June and September, 2 plates were lost from the front reef (a perspex plate from Site 1, and wooden one from Site 2) and one from the lagoon (perspex from Site 1). In order to balance the design for analyses, the means of the other plate of that type at the site were substituted for the missing values and the degrees of freedom for tests adjusted (Winer 1971, Underwood 1981). The effects of this on the overall analysis are slight (a loss of 3 df out of 639) but no conclusions about these substrata at the affected sites should be drawn because the observations there are essentially unreplicated (only 1 plate of the type present).

Data were transformed to stabilise variances for analyses if necessary. On some occasions this proved impossible so a conservative significance level of 0.1 % was used. A posteriori comparisons of means were made using Ryan's test, a method which avoids some of the problems found with other multiple comparisons (Begun & Gabriel 1977, Day & Quinn 1988). Multiple comparisons methods are sensitive to heterogeneity of variances (Day & Quinn 1988), so a posteriori tests were only done when variances could be satisfactorily stabilised.

RESULTS

Comparison of coral plates and cleared patches on the reef-flat

There were some differences between the assemblages of sessile species colonising coral plates and cleared patches on the reef-flat itself (Table 1). The number of sessile species present varied with time, and between the coral plates and the cleared patches on the reef-flat, with, in general, more species on the reef-flat (Time × Location × Site interaction in Table 1, and see Table 2). The total percentage of the patch or plate occupied also varied with time and location of patch (Time × Location interaction in Table 1): with the exception of March, cover was always greater on the reef-flat (Table 3). Variances in analyses of *Laurencia papillosa* could not be stabilised, but in this case the results were unequivocal: the alga was only ever present on the reef-flat (average in September of 0 % on plates and 25 % on the reef-flat). Not all components of the flora were affected. Percentage cover of the microalgal mat varied greatly among times, sites and patches (Time main effect, and Time × Site and Time × Plate interactions in Table 1) but was similar on plates and the reef-flat (no main effect of, or interaction with, Location in Table 1).

Effects of type of substratum

The sessile assemblage colonising plates was affected by the type of substratum (Table 4). Significant effects of type of substratum were detected even

Table 1. Analyses of variance of colonisation of cleared patches on the reef-flat and coral plates (Location). F-ratios from analyses of variance are given, with their significance, and the source of variation used as the denominator (in parentheses for each organism; see text for further details). A dash indicates that a valid F-ratio was not possible. Two degrees of freedom were subtracted from the Ti × Pl interaction because of lost plates. Lower rows of table list transformations used and significance of Cochran's test for homogeneity of variance (after transformation). In this and all following tables: ns, non-significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Source	df	No. of species	Total cover	Microalgal mat	Laurencia
1 Time (Ti)	3	4.6 (8)ns	27.3 (9)***	9.2 (8)*	1.5 (8)ns
2 Location (Lo)	1	–	–	1.7 (6)ns	1.3 (11)ns
3 Habitat (Ha)	1	–	–	2.7 (11)ns	1.2 (4)ns
4 Site (Si)	2	–	1.1 (5)ns	0.0 (8)ns	3.4 (8)ns
5 Plate (Pl)	8	11.0 (14)***	1.6 (9)ns	1.2 (9)ns	0.2 (9)ns
6 Ti × Lo	3	10.7 (13)***	27.6 (9)***	2.4 (13)ns	1.5 (13)ns
7 Ti × Ha	3	1.9 (8)ns	2.9 (9)ns	1.2 (8)ns	1.5 (8)ns
8 Ti × Si	6	6.7 (14)***	0.7 (9)ns	3.0 (9)*	5.6 (9)**
9 Ti × Pl	22	1.0 (13)ns	13.7 (14)***	105 (14)***	40.8 (14)***
10 Lo × Ha	1	–	–	2.3 (13)ns	1.2 (11)ns
11 Lo × Si	2	–	0.7 (5)ns	1.2 (13)ns	3.4 (13)ns
12 Ti × Lo × Ha	3	1.2 (13)ns	2.9 (9)ns	1.0 (13)ns	1.5 (13)ns
13 Ti × Lo × Si	6	11.3 (14)***	0.7 (9)ns	1.5 (9)ns	5.6 (9)***
14 Residual	64				
Total	125				
Transformation		None	ArcSin	None	None
Cochran's Test		ns	ns	*	*

Table 2. Results of Ryan's test comparing mean number of species on plates and the reef-flat at different times and sites (at $p = 0.05$)

Time	Site	Front		Back	
		Plate	Reef	Plate	Reef
1	1	1.0 = 1.0		1.0 = 1.0	
	2	1.0 = 1.0		1.0 = 1.0	
2	1	1.0 < 3.0		1.0 = 1.0	
	2	1.0 < 2.5		1.0 = 1.0	
3	1	1.0 < 2.5		0.0 < 1.0	
	2	0.0 < 2.0		0.0 < 2.5	
4	1	2.0 > 1.5		1.0 = 1.0	
	2	1.0 < 1.5		1.0 = 1.0	

Table 3. Results of Ryan's test comparing total percentage cover on plates and the reef-flat at different times and sites (at $p = 0.05$)

Time	Plate		Reef
1	99.5	=	98.5
2	81.5	<	99.9
3	9.0	<	99.7
4	75.0	<	100.0

using the conservative level of 0.1 % (Table 4). Further, Substratum and its interactions accounted for from 12 to 46 % of the variability in the numbers and abundances of species (calculated as the percentage of the Total Sums of Squares which was due to these factors).

The number of sessile species varied with Substratum and Time (Time × Substratum × Site interaction in Table 4), but variances could not be stabilised so Ryan's tests were not done. The differences did, however, appear to be in the number of encrusting species (Lithothamnion sp., other coralline crusts and Ralfsia sp.) colonising plates in the lagoon, so a smaller analysis was done considering just these species in September when they were most common (Table 5). Again, Substratum interacted with Site. With the exception of concrete (mean of 1.0 species), plates at Site 1 had no encrusting species (but there was only one perspex plate at this site at this time). At Site 2, concrete and perspex plates had most species (3.8), rock had slightly fewer (3.0), coral fewer again (1.0) and wood had none.

The total percentage of the surface of the plates occupied by sessile organisms varied with Substratum, and Habitat and Time (Time × Substratum × Habitat interaction in Table 4). Colonisation of plates on the front reef was rapid. within only 3 wk virtually all the space on the plates was occupied (Fig. 1). Cover remained great until after low-tide exposures in April when the plates became almost completely bare. Subsequent recovery was slowest on perspex, with an average of 12 % cover in September compared to 79 % for the other 4 substrata. The pattern was essentially similar on the back reef, though no differences among substrata developed (Fig. 1). In the lagoon, cover was constant throughout the year and did not vary with substrata (Fig. 1). The means for this habitat are some-

Table 4. Analyses of variance comparing colonisation on different substrata. F-ratios from analyses of variance are given, with their significance, and the source of variation used as the denominator (in parentheses for each organism). Three degrees of freedom were subtracted from the Ti × Pl interaction because of lost plates. Analyses of *Lithothamnion* were done only for 2 times, so degrees of freedom were lower for some tests (indicated in parentheses in df column). A dash indicates that a valid F-ratio was not possible. Lower rows of table list transformations used and significance of Cochran's test for homogeneity of variance (after transformation)

Source	df	No. of species	Total cover	Microalgal mat	*Lithothamnion*
1 Time (Ti)	3(1)	3.3 (8)ns	24.1 (8)···	26.6 (8)···	0.2 (8)ns
2 Substratum (Su)	4	–	2.8 (6)ns	4.6 (6)·	–
3 Habitat (Ha)	3	–	–	–	–
4 Site (Si)	4	6.7 (8)·	16.4 (8)ns	8.1 (8)··	–
5 Plate (Pl)	40	0.8 (9)ns	1.1 (9)ns	0.9 (9)ns	4.3 (14)···
6 Ti × Su	12(4)	4.3 (13)···	3.2 (9)···	1.5 (13)ns	4.3 (13)·
7 Ti × Ha	9(3)	0.9 (8)ns	4.0 (8)ns	4.3 (8)·	2.8 (8)ns
8 Ti × Si	12(4)	16.0 (9)···	6.4 (9)···	6.8 (9)···	61.9 (14)···
9 Ti × Pl	117	4.0 (14)···	34.6 (14)···	38.4 (14)···	1.0 (14)ns
10 Su × Ha	12	–	0.8 (12)ns	1.1 (12)ns	–
11 Su × Si	16	2.2 (13)·	0.7 (9)ns	0.8 (13)ns	–
12 Ti × Su × Ha	36(12)	1.8 (13)ns	2.3 (9)···	1.8 (13)·	2.2 (13)ns
13 Ti × Su × Si	48 (36)	1.9 (9)·	0.8 (9)ns	1.2 (9)ns	35.8 (14)···
14 Residual	320(160)				
Total	636(316)				
Transformation		None	ArcSin	ArcSin	Log$_e(x+1)$
Cochran's Test		··	ns	·	·

Table 5. Analyses of variance of numbers of encrusting species on different substrata at the 2 sites in the lagoon. Number in parentheses after the F-ratio gives the source of variation used as the denominator. Degrees of freedom for Plates were reduced by 1 due to the loss of a plate

Source	SS	df	F-ratio	
1 Substratum (Su)	30.75	4	1.61	(3)ns
2 Site (Si)	44.10	1	294.00	(5)···
3 Su × Si	19.15	4	31.92	(5)···
4 Plates	0.50	9	0.37	(5)ns
5 Residual	3.00	20		
Total	97.50	38		

what deceptive: cover at one site was consistently close to zero, but at the other site it was consistently close to 100 %. Total cover in the mangrove forest was always lower than in other habitats (Fig. 1). The plates were completely bare in April and June and in March cover averaged only 49 %. In September cover was even smaller (34 %) but was affected by substratum being greatest on concrete (98 %) and less on other surfaces (overall average of 18 %).

Not all species responded similarly. The microalgal mat was unaffected, or perhaps only slightly affected, by substratum (Substratum main effect, and Time × Substratum × Habitat interaction significant at $p = 0.05$ in Table 4 but variances heterogeneous). The abundance of *Lithothamnion* sp., in contrast, varied with Substratum, Time and Site (Time × Substratum

× Site interaction in Table 4). Because of heterogeneous variances, Ryan's tests were not done but the crust appeared to be most abundant on perspex and concrete (Fig. 2). Only one mobile species was common, the hermit crab *Paguristes cadenati*, but only in the lagoon and mangrove forest. Its abundance varied with Site at all times and with Substratum in April and September. The only consistent difference was for more crabs at mangrove Site 2 than Site 1.

It is important to note that there were several differences between natural and artificial substrata. In the lagoon, concrete and perspex plates were colonised by more encrusting species than the natural substrata coral and wood. Further, the plates with the least cover were usually the perspex ones, with this difference being significant in September on the front reef and in the mangrove forest.

DISCUSSION

These results lead to several important conclusions. The first is that the algal assemblage that developed on hard surfaces in these parts of the Caribbean was influenced by the type of substratum present. There were differences among substrata in the number of species settling and/or surviving, the total area occupied and the abundances of some species. Unfortunately, because of heterogeneous variances in several analyses, it was difficult to describe precisely the
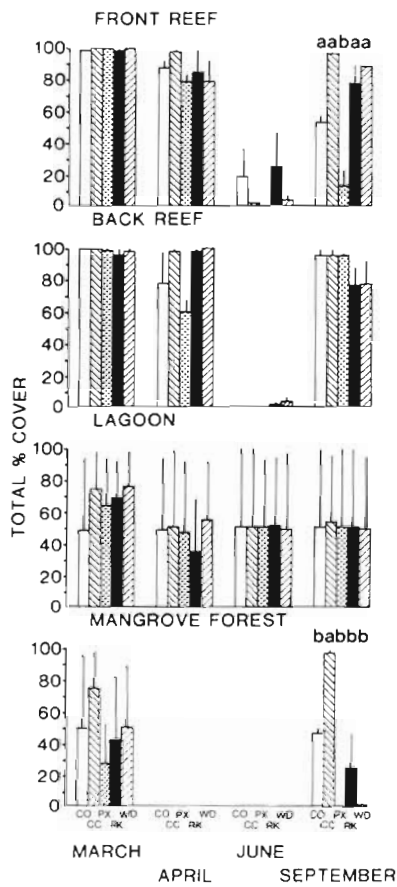
Fig. 1. Changes in total percentage cover on the different substrata (mean plus standard error). Substrata: CO, coral; CC, concrete; PX, perspex; RK, rock; WD, wood. Letters show the results of Ryan's tests: means at the same time with the same letter did not differ significantly (means also did not differ if no letters are given)
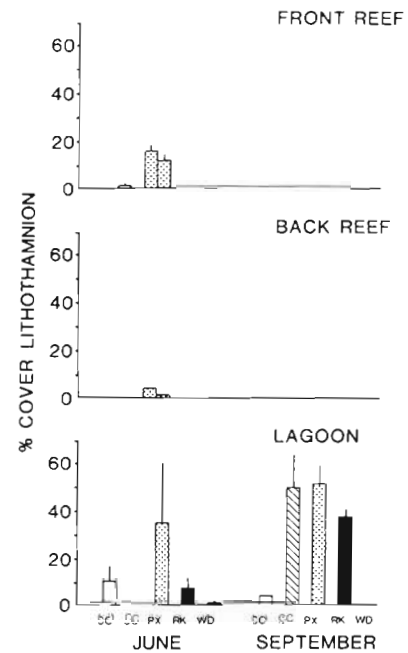

Fig. 2. *Lithothamnion* sp. Changes in cover on the different substrata (mean plus standard error). (The species was not found in the mangrove forest.) Substrata as in Fig. 1

differences that developed. It is, however, clear that differences were present and were, on occasion, substantial. Differences of more than 60 % in total cover occurred at some times and places. Further, in the lagoon an average of 3 encrusting species grew on rock, compared to only 1 on coral and none on wood; a large difference considering the small number of species present.

These results cannot, however, be applied uncritically to organisms on the reef-flat itself. The assemblages developing on the plates were less diverse, and covered less space, than those on cleared patches on the reef-flat. Further, the dominant alga on the reef-flat, *Laurencia papillosa*, did not become abundant on the plates in this study (it did, in fact, colonise the plates in late October but was killed by unseasonal exposures in November). These differences may have been caused by the slightly greater time for which the plates were exposed at low tide. Alternatively, scraping the

reef-flat to remove sessile organisms may have changed the surface texture in some way. Changes in water flow around the plates, or a slightly greater distance from sources of propagules, may have reduced the number of spores arriving. Whatever the reason, studies attempting to compare assemblages developing on coral and rocky intertidal shores would have to use plates sunk into the shore (as in Caffey 1982).

There are several ways in which the substrata could affect the sessile assemblage which develops. McGuinness & Underwood (1986) suggested that algae might grow or survive better on some kinds of rock because of differences in the retention of heat or water. In this study, the wood clearly remained damper for longer when exposed than the coral, rock, concrete or perspex plates. The latter plates dried out very quickly and this may be the reason that they often had least cover. This explanation is plausible for the intertidal habitats – the front and back reef-flat and the mangrove forest – but not for the lagoon, since here plates were rarely exposed. It is possible that the different textures of the substrata retained different numbers and types of spores (Den Hartog 1972). Alternatively, animals may have grazed on some substrata more than others, though no consistent differences among substrata at a site in the numbers of hermit crabs were seen. Other animals (e.g. the decorator crab *Microphrys bicornutus*) occasionally grazed on the plates but they were uncommon in the day or night.

The effects did not occur at all times or in all places.

This is perhaps not surprising. The habitats differed markedly in important ways. As noted above, the plates in the lagoon were rarely, if ever, exposed at low-tide. Cover on these plates quickly reached a maximum and remained constant thereafter, though species composition did change (also see below). Plates in other habitats were exposed during some low tides throughout the year and, importantly, were out of water for long periods during the wet season. At this time, the organisms on the plates would have experienced considerable desiccation stress (Glynn 1968, 1972, Cubit et al. 1987b, Hendler 1977) and this was probably the cause of the small abundances seen in June. There were also differences among the habitats in the abundance of grazers. Hermit crabs were not seen near the plates on the reef-flat but were common in the lagoon and mangrove forest. Further, fish could have grazed on plates in the lagoon but were less likely to do so in intertidal habitats. All this implies that some effects of type of substratum may only occur when agents of mortality (physical stress, grazing or disturbance) are neither so severe as to kill all individuals, nor so mild as to allow all to survive.

Some of the differences among times and places are difficult to explain. The most perplexing is the profound difference between the 2 lagoon sites. Cover on the plates at the first site was almost always nil, but at the second site was almost always total. At this second site there was a great effect of substrata on the algal assemblage developing, but there was little effect at the first site. Plates at the first site were in slightly shallower water and may have been exposed occasionally, but no substantial cover developed even when there was good growth on intertidal plates. Nor were there consistent differences between the sites in the abundance of hermit crabs, which might have been grazing on the plates. The reason for the difference remains obscure.

Altogether, the results of this study and those of McGuinness & Underwood (1986) show that substratum can affect organisms in different ways in many habitats. The topic warrants further study. It is important to note here that Caffey (1982) did not say that he found *no* effects of rock-type on the barnacle *Tesseropora rosea*; he said that he found no *consistent* effects. Analyses of settlement at one time showed a significant Rock-type by Shore interaction; at the second time there was a Rock-type by Site within Shore interaction (Table 1 in Caffey 1982). Subsequent analysis of the order of the means for the 4 different types found no consistent ranking. Another interpretation of his results is that the effects of rock-type varied with time and place, as in the present study. Caffey (1982) himself noted that physical conditions were particularly severe at 2 shores, with nearly all of the barnacles dying, and particularly mild at the others, with nearly all individuals surviving.

A significant conclusion of this work is that the use of artificial substrata in studies of settlement or colonisation may give totally erroneous results. This is clearly shown by the many interactions in this study between Times, Types of Substratum and Zones or Sites. Further, the artificial substrata, perspex and concrete, were in some ways the most aberrant of those examined. Assemblages developed on these which were significantly different, at some times and in some places, from those on the natural surfaces of coral, rock and wood. The spatial and temporal variation in the differences between natural and artificial surfaces is particularly worrying because it means that any bias arising from their use is unlikely to be consistent and predictable. It seems clear that artificial substrata should be used with great caution.

LITERATURE CITED

Begun, J. M., Gabriel, K. R. (1977). Closure of the Newman-Keuls multiple comparisons procedure. J. Am. stat. Assoc. 76: 241–245

Caffey, H. M. (1982). No effect of naturally-occurring rock types on settlement or survival in the intertidal barnacle, *Tesseropora rosea* (Krauss). J. exp. mar. Biol. Ecol. 53: 119–132

Crisp, D. J. (1974). Factors influencing the settlement of marine invertebrate larvae. In: Grant, P. T., Mackie, A. M. (eds.) Chemoreception in marine organisms. Academic Press, London, p. 177–267

Cubit, J. D., Getter, C. D., Jackson, J. B. C., Garrity, S. D., Caffey, H. M., Thompson, R. C., Weil, E., Marshall, M. J. (1987a). An oil spill affecting coral reefs and mangroves on the Caribbean coast of Panama. In: 1987 Oil Spill Conference. Proceedings of the tenth biennial conference. Amer. Petrol. Inst. Publ. 4452, Washington, D. C., p. 401–406

Cubit, J. D., Windsor, D. M., Thompson, R. C., Burgett, J. M. (1987b). Water-level fluctuations, emersion regimes, and variations of echinoid populations on a Caribbean reef flat. Estuar. coast. Shelf Sci. 22: 719–738

Day, R. W., Quinn, G. P. (1988). Comparison of means after an analysis of variance in ecology. Ecol. Monogr. (in press)

Glynn, P. W. (1968). Mass mortalities of echinoids and other reef flat organisms coincident with midday, low water exposures in Puerto Rico. Mar. Biol. 1: 226–243

Glynn, P. W. (1972). Observations on the ecology of the Caribbean and Pacific coasts of Panama. Bull. biol. Soc. Wash. 2: 13–30

Harlin, M. M., Lindbergh, J. M. (1977). Selection of substrata by seaweeds: optimal surface relief. Mar Biol. 40: 33–40

Hatton, H. (1938). Essais de bionomie explicative sur quelques espèces intercotidales d'algues et animaux. Ann. Inst. oceanogr. Monaco 17: 241–348

Hay, M. E. (1981). The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. Ecology 62: 739–750

Hendler, G. L. (1977). The differential effects of seasonal stress and predation on the stability of reef-flat echinoid populations. In: Taylor, D. L. (ed.) Proceedings Third International Coral Reef Symposium. University of Miami, Miami, p. 217–223

Lewis, C. A. (1977). A review of substratum selection in free-living and symbiotic cirripeds. In: Chia, F. S., Rice, M. (ed.) Settlement and metamorphosis of marine invertebrate larvae. Elsevier, Amsterdam, p. 207–217

Macintyre, I. G., Glynn, P. W. (1976). Evolution of modern Caribbean fringing reef, Galeta Point, Panama. Am. Assoc. Petroleum Geologists Bull. 60: 1054–1072

Meadows, P. S., Campbell, J. I. (1972). Habitat selection by aquatic invertebrates. Adv. mar. Biol. 10: 271–382

McGuinness, K. A., Underwood, A. J. (1986). Habitat structure and the nature of communities on intertidal boulders. J. exp. mar. Biol. Ecol. 104: 97–123

Risk, M. J. (1973). Settling plates of cold-cure acrylic plastic replicated from natural surfaces. Limnol. Oceanogr 18: 801–802

Sebens, K. P. (1982). Intertidal distribution of zoanthids on the Caribbean coast of Panama: effects of predation and desiccation. Bull. mar. Sci. 32: 316–335

Todd, C. D., Turner, S. J. (1987). Ecology of intertidal and sublittoral cryptic epifaunal assemblages. I. Experimental rationale and the analysis of larval settlement. J. exp. mar Biol. Ecol. 99: 199–231

Underwood, A. J. (1979). The ecology of intertidal gastropods. Adv. mar. Biol. 16: 111–210

Underwood, A. J. (1981). Techniques of analysis of variance in marine biology and ecology. Oceanogr. mar. Biol. A. Rev. 19: 513–605

Winer, B. J. (1971). Statistical principles in experimental design. McGraw-Hill, Kogakusha, Tokyo

This article was submitted to the editor