THE ECOLOGY OF SETTLING ORGANISMS ON THE CORAL REEF AT HERON ISLAND, QUEENSLAND.

R. W. DAY

FRONTICE PIECE: The arborescent ectoproct _Idmidronea_ sp,
alias AB1

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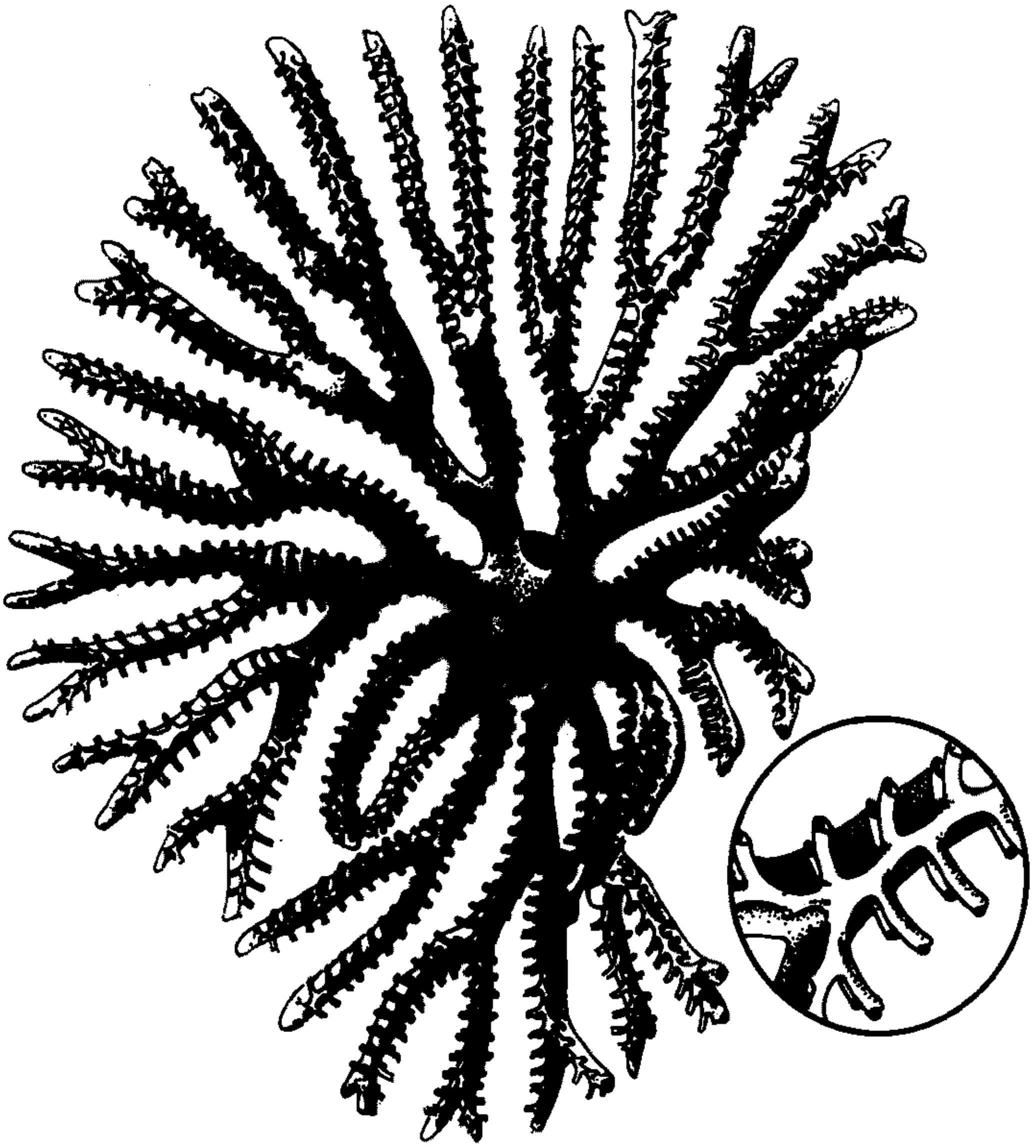

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CHAPTER 1

INTRODUCTION

This thesis is concerned with the sessile species which settle on the limestone surfaces of the coral reef at Heron Island, Queensland. Various factors which might determine the distribution and abundance of sessile species were investigated in order to find out which factors determine the species that will be present on any particular patch of surface, and what determines the diversity of species which live together on a patch of surface.

Sessile species use a common resource, space to settle and grow. The coexistence of species which appear to use the same limited resources has long been of interest to ecologists (Slatkin 1974). The niche concept, as proposed by Grinnell (1928) and elaborated by Hutchinson (1958) includes the idea that different species would be expected to use different resources. Most studies of the way in which different species use different resources have been on groups of closely related species (Schoener 1974). On Heron Reef very little of the natural surface is bare at any one time, and cleared areas are recolonised fairly quickly, so space to settle and grow appears to be a limiting resource for many different sessile species.

Two other resources that are essential for sessile organisms are light for algae, and planktonic food for sessile animals. However, the light energy and food available to sessile organisms on a patch of surface are supplied from outside the patch; and cannot be exhausted by the sessile organisms in the same way that the available surface in a patch may be used up. The rate of supply of light energy is determined by the level of illumination and the orientation of the surface. The concentration of plankton in the surrounding water and the rate at which the water moves over the surface determine the supply of food to sessile animals. Except insofar as one species may shade another, or reduce the flow of water over another species, the supply of light energy and food to a surface is not affected by the organisms on the surface. The resources of food and light energy are not limited in an absolute sense, whereas space to settle and grow may be so limited.

The distribution of sessile species.

Various components of environment may be important in determining which species will be found on a particular surface. For example, it might be expected that brightly illuminated surfaces would be occupied by algae, whereas only animals would be present in caves. If this is so, then algae and animals differ in the types of surface they occupy. Similarly some species may occupy places exposed to fast flowing currents, while others occupy places with slow water-movement. Settlement panels, suspended in dark places, brightly lit places, and so forth, were used to obtain samples of the species that settle and grow under various conditions, so as to find out how the species differ from one another in the places they occupy. I did not, however, attempt to determine how each species differed from every other species.

Seven components of environment which might be important in influencing species' abundances were chosen. These were season of the year, depth, illumination, wave action (sudden surges of water as a result of waves), water-movement (the average amount of water moving past a surface), predatory or herbivorous fish, and other sessile organisms present on the same surface.

The development of the idea that the local distribution of marine animals is largely determined by behavioural responses to various components of environment has been reviewed by Meadows and Campbell (1972). Predation or grazing may control the distribution and abundance of marine sessile organisms in various ways. Experiments were carried out to determine the effects of fish predators or herbivores on the abundances of sessile organisms, and whether grazing or predation by fish varied from place to place on the reef. Fish have been shown to be important grazers and predators on coral reefs by Stephenson and Searles (1960), Randall (1961, 1965), Bakus (1964, 1966, 1967) and Earle (1972). Predation and grazing by invertebrates may also be important but this was not studied.

Organisms which grow on the same surfaces may affect each other in many different ways. Evidence for the way in which one species might affect the abundance of another species was sought by investigating species which occurred together on the settlement panels. I was unable, however, to investigate how species of algae might affect each other.

Diversity of associations of sessile species

Many authors (Dayton and Hessler 1972, Janzen 1970, 1973, Paine 1966, Spight 1967, Williamson 1957) have argued that predation may result in a greater diversity of prey species. The effects of predation or grazing by fish on associations of algae, and of sessile animals, was investigated.

CHAPTER 2

GENERAL METHODS

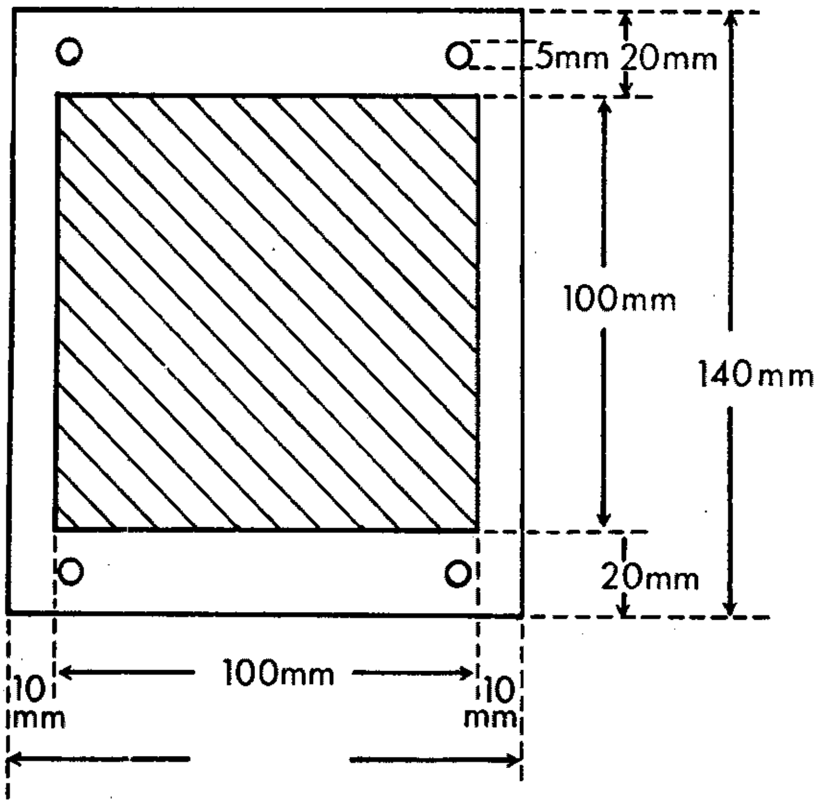
Settlement panels:

As natural surfaces on coral reefs are seldom flat and uniform it is difficult to find replicate surfaces on a reef. Instead, settlement panels were suspended vertically at various sites for three month periods. The panels were made of 3mm. thick sheets of a material called Novasteen. Novasteen consists of a canvas cloth impregnated with plastic. As a result of the weave of the canvas the surface of the plastic is minutely textured. This is important because some settling organisms are known to avoid very smooth surfaces (Pomerat and Weiss 1946). The Novasteen was cut into panels of a standard design shown in Figure 2:1. Novasteen is made by the British Zylonite Company.

Settlement panels have long been used to study the fouling organisms that settle on ship's bottoms. It is well known from such work that the organisms at the edges of the panels may grow larger, settle more densely, or be of different species from those in the centre of the panel. Previous unpublished work I have done on fouling organisms suggested that such edge effects could be minimised by suspending the panels vertically and allowing them to rotate. This method was apparently first used by Johnson and Miller (1935) to minimise the loss of settlement panels in strong currents. To reduce the edge effect further the areas of the panels within 20mm of the top and bottom edges of the panels, or within 10mm of the side edges were not used in censuses. The area of 10^4 mm^2 (0.01 m^2) used in censuses is indicated by the shaded area in Figure 2:1.

FIGURE 2:1.

The design and dimensions of the settlement panels used, and the area of the panels which was censused.


5mm
20mm
100mm
140mm
20mm
10 mm
100mm
10 mm

Panels were mounted in two types of cages to investigate the effects of predation by fish. One type of cage was closed, and the other open at the end which would face downstream in a current; so that fish could gain access to the panel inside. The design and dimensions of these cages are shown in Figure 2:2. The cages were constructed of half inch (12.7mm) mesh galvanised iron "chicken wire", reinforced with 4mm diameter baling wire. The panels were mounted inside these cages using thin galvanised iron wire twisted through each hole in the panel.

The cages were attached to swivels near one end, and suspended on monofilament nylon lines so that invertebrates such as crabs could not gain access to the panels. The nylon lines were attached to steel reinforcing rod frames. These were constructed at a number of sites by hammering four long stakes into the coral at the corners of a rectangle, and then binding crossbars to the top and bottom pairs of stakes. Care was taken to ensure that the bottom crossbar was vertically below the top crossbar, and that the attachment points of the cages were one above the other, so that the panels in their cages would hang vertically and swivel freely. In most cases this was done with a plumb line of thin nylon attached to a large lead fishing sinker.

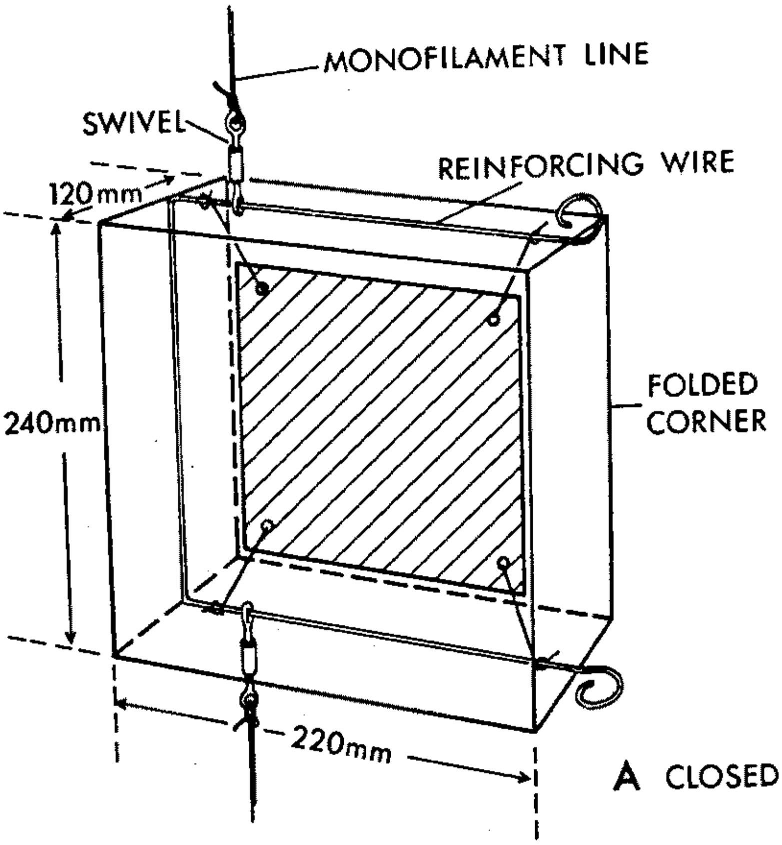
The panels were wiped before use with alcohol to remove any grease or other chemicals. They were collected after three months immersion, brought back to the research station at Heron Island, and placed in an aquarium. They were photographed in seawater, then fixed in 8 percent formaldehyde in seawater, and finally each panel was placed in a sealtop plastic bag.

FIGURE 2:2.

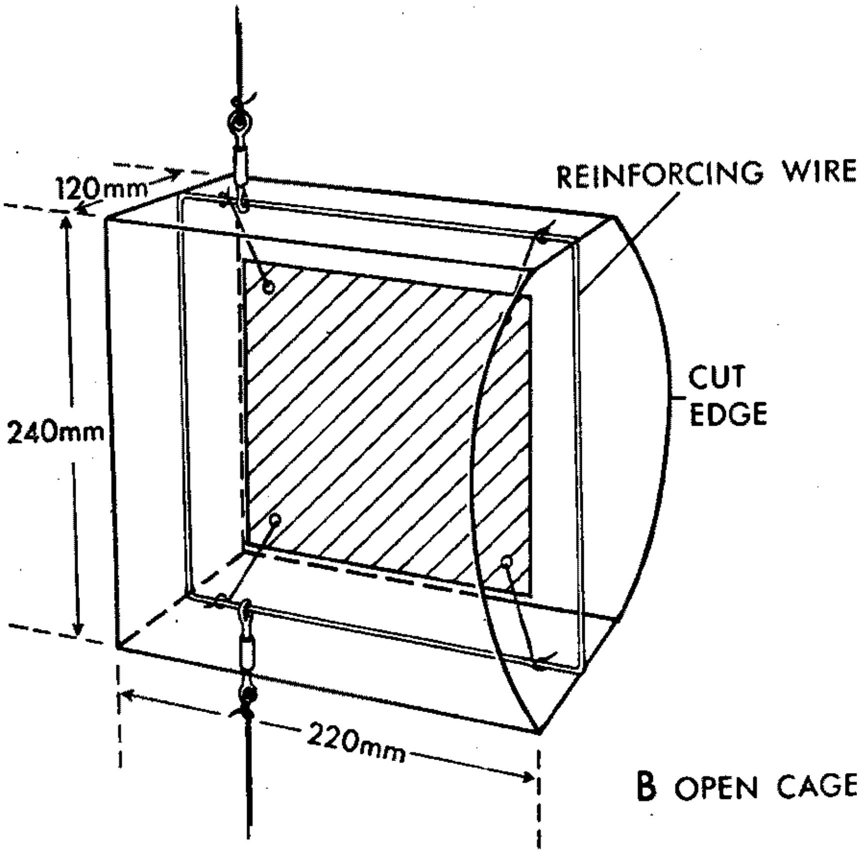
The design and dimensions of the wire mesh cages in which the settlement panels were mounted.

A: Closed cage used to exclude fish.

B: Open cage which allowed fish to enter from the downstream end.



A CLOSED CAGE



B OPEN CAGE

Census of sessile organisms:

The census of organisms on the panels was done by placing the panels in a dish of water under a 10 mm mesh grid of coloured cotton strands. A dissecting microscope on a field stand was used to traverse the area to be censused on each side of the panel, using the cotton grid as a guide. For the ectoprocts, molluscs, sponges, ascidians, some polychaetes, and some algae, the size of each colony or individual was estimated by comparing its size with a square or squares of the cottom grid suspended over the panel. Care was taken to avoid parallax errors. The number of colonies, and the total area covered by each species was recorded. For the common species of algae the percentage cover on the entire panel was estimated by eye. Comparisons of such whole panel estimates with estimates based on the sizes of individual clumps of algae showed that the whole panel estimates tended to overestimate the percentage cover of the algae slightly, but the two estimates were almost always within fifteen percent of each other.

When the panels were covered with a dense growth of algae or ectoprocts the organisms were often covered with silt. I removed the silt with a jet of water to uncover the attached organisms. I took care not to wash off any of the organisms to be censused, but mats of diatoms and blue-green algae were often washed away.

Many algae and ectoprocts project upwards from the surface and then branch outwards. Rather than estimate the small area of attachment of these organisms, I estimated the area of surface they would shade. However encrusting species may grow beneath the projecting ones, so that the total percentage cover of all organisms censused may theoretically exceed 100%.

In the case of encrusting ectoprocts and ascidians one colony may grow over, and smother its neighbours. The smothered colonies may be identified by prising off the colony on top. In estimating the area covered by each species I considered only colonies or parts of colonies which were not smothered, but I included smothered colonies when counting the number of colonies of each species on each sample, as I wished to obtain an estimate of the numbers of each species settling at each site.

Identification of species:

The organisms in this study generally belonged to one of three groups: ascidians, ectoprocts, and filamentous algae. It is difficult to identify species of all three groups. The taxonomy of many groups of ectoprocts and filamentous algae is confused, and although Kott (1964, 1966) has published very useful papers on the taxonomy of northern Australian ascidians, much taxonomic work remains to be done on the species of the Great Barrier Reef in all three of the groups under discussion.

I divided the organisms I found on the panels into what I considered to be species on the basis of large numbers of specimens. Reference collections of algae mounted on slides, preserved specimens of the animals, and drawings and photographs were used to ensure that my classification scheme was consistent for all the samples. The reference specimens were given to taxonomists during the course of the study. Discussions with these taxonomists have convinced me that the categories I have used usually represent taxonomic species. A few groups of algae, however, such as the '*Lophosiphonia*' group are particularly difficult to split into species, and a few species in these groups may have been lumped together.

The ectoproct species were given numbers, and tentative generic names were used for the ascidians and algae, often with numbers to denote different species. For example AB1 is a species of arborescent ectoproct; EB1 is a species of encrusting ectoproct; and *Ceramium* sp. 1 is a species of filamentous alga. Among the algae in particular the tentative genus used may include species of allied genera.

Appendix 2 contains a list of the species which have been identified by taxonomists, and the preliminary names or numbers I used for these species.

CHAPTER 3

PRELIMINARY EXPERIMENTS

The experiments described in this chapter were designed to determine: 1) Whether organisms which occurred on the settlement panels were distributed at random, or were aggregated.

2) Whether any species was concentrated near the edges, or towards the centre of settlement panels.

3) Whether any species settled or grew less profusely (or more profusely) on the artificial settlement surface I used than on a more natural calcium carbonate surface.

4) Whether the number and proportions of species on the settlement might change with the area of the panels used.

This information was needed to formulate satisfactory methods, and for correct interpretation of results.

3.1 DISPERSION OF SETTLING ORGANISMS.

Wisely (1958), Knight-Jones (1951, 1953), and Meadows and Campbell (1972) have shown that the settling larvae of a number of sedentary organisms choose to settle close to individuals of their own species. Such gregarious behavior might affect the results of this investigation. Gregarious species might occur densely on one panel and infrequently on nearby panels. A large number of replicates would then be required for each treatment in an experiment to ensure that differences between the treatments are not due to chance effects.

The point of settlement of algae and colonial ascidians is usually impossible to determine. Thus it is difficult to test whether these organisms are gregarious. An analysis of the distribution of species' numbers in a large number of replicate samples is impossible because conditions on the reef may vary within a few meters: samples taken some distance apart are poor replicates.

The point of settlement of ectoprocts however, can be determined easily. A test for aggregated settlement was carried out as follows: Thirty-four panels, collected from a number of sites at various times of the year were censused. Each side of a panel was divided into two equal areas; and the number of colonies of each species which had settled in each half was recorded. For this study I did not ignore the areas near the edges of the panels as described in chapter 2. Only the areas near the holes used to mount the panel (Figure 2:1) were omitted, so that each censused half was 80 cm^2.

Taking each species in turn, the frequencies observed on the two halves were compared with the frequencies expected for randomly distributed colonies. Where a species occurred only once in both halves the data were not used. The chi-squared values for differences between the observed and expected values were summed for each species over all the panels, each value being allotted one degree of freedom. The results are shown in Table 3:01. The ectoproct species have been given numbers as described in chapter 2.

Six out of twenty-eight encrusting ectoproct species were found to be significantly aggregated at $p=0.05$ (Table 3:01). If all twenty-eight species were distributed at random then only one or two species might be expected to have shown an aggregated distribution by chance. Thus a few species appeared to be gregarious.

TABLE 3:01

CHI-SQUARED VALUES CALCULATED FROM THE FREQUENCIES OF ECTOPROCTS ON EITHER HALF OF EACH SAMPLE

Species	Observed χ^2	Degrees of Freedom	Significance*
Encrusting Species:			
EB 1	62.145	43	S
EB 1A	39.788	20	S
EB 2	38.967	48	n.s.
EB 6	34.981	34	n.s.
EB 7	50.014	47	n.s.
EB 8	57.065	37	S
EB 9	48.860	39	n.s.
EB10	41.914	44	n.s.
EB11	32.559	34	n.s.
EB12	42.196	28	S
EB12A	26.787	24	n.s.
EB12B	15.467	17	n.s.
EB12C	21.333	13	n.s.
EB14	62.025	47	n.s.
EB15	24.367	22	n.s.
EB15A	18.867	12	n.s.
EB15B	6.333	8	n.s.
EB16	80.350	34	S
EB18	49.690	42	n.s.
EB18A	9.333	8	n.s.
EB20	11.667	12	n.s.
EB26	4.143	10	n.s.
EB29	92.084	29	S
EB30	5.000	8	n.s.
EB31	3.000	7	n.s.
EB31A	7.143	11	n.s.
EB40	10.810	12	n.s.
EB43	6.800	11	n.s.

TABLE 3:01 Continued

(ANALYSIS OF AGGREGATION)

Species	Observed χ^2	Degrees of Freedom	Significance*
Arborescent Species:			
AB 1	45.365	37	n.s.
AB 3	208.679	47	S
AB 3A	11.933	12	n.s.
AB 4	30.717	26	n.s.
AB 5	106.653	33	S
AB 6	35.938	19	S
AB 7	36.843	20	S
AB 8	11.455	9	n.s.
AB 9	111.339	29	S
AB12	17.863	13	n.s.
AB13	47.922	32	S
AB14	69.486	33	S
AB17	52.760	36	S
AB21	50.909	19	S
AB22	17.467	12	n.s.

* S = significant at p=0.05, n.s. = not significant at p=0.05

If more data had been available, some of the remaining species might have been shown to be aggregated, since a non-significant result may occur as a result of insufficient data. The "average encrusting species" has a significantly aggregated distribution at p=0.05, since the sum of χ^2 values for all the encrusting species is 903.7 with 701 degrees of freedom; and this value is significant at p=0.05. This is a very sensitive test however, and the significant result is a consequence of the six species with markedly aggregated distributions. If these species are omitted the sum of the chi-squared values becomes 530.1 with 510 degrees of freedom. This value is not significant at p=0.05. I conclude that some encrusting species have aggregated distributions but most of them probably do not.

Most of the arborescent ectoprocts are significantly aggregated at p=0.05 (Table 3:01). Furthermore, of the six results which are not significant, four are associated with the four lowest degrees of freedom. This suggests that if further information had been available an aggregated distribution might have been detected for these species.

The sum of chi-squared values for all the arborescent ectoprocts is significant at p=0.05. When the species which show significant aggregation are omitted, the sum of the remaining six chi-squared values is 134.8 with 109 degrees of freedom, which is significant at p=0.05, the critical value being $\chi^2 = 134.1$. Three random samples of six species of encrusting ectoprocts were chosen, and the sum of χ^2 values for these species were computed. None of the three χ^2 values computed in this way were significant at p=0.05.

It appears, therefore, that arborescent species in general, and some encrusting species, have aggregated distributions. Since this may affect the results of the main sampling study, the arborescent species, and those encrusting species showing an aggregated distribution were investigated further. The number of individual colonies of each species on the censused area (Figure 2:1) on each side of settlement panels were compared using the methods outlined above. The results are shown in Table 3:02. Although there is less information for each species, ten of the twenty one species were significantly aggregated at $p=0.05$ with respect to the two sides of settlement panels.

Caution is required therefore, in interpreting the results of studies of the distribution of these species with respect to other factors, and there is also the possibility that species of algae and ascidians which were not investigated here, were aggregated in their distributions. The possible ecological significance of such aggregation is discussed later.

TABLE 3:02

CHI-SQUARED VALUES CALCULATED FROM THE FREQUENCIES OF ECTOPROCT SPECIES ON EITHER SIDE OF EACH PANEL.

Species	Observed χ^2	Degrees of Freedom	Significance*
AB 1	18.329	16	n.s.
AB 3	54.581	21	S
AB 4	25.992	14	S
AB 5	77.933	12	S
AB 6	17.717	8	S
AB 7	19.644	12	n.s.
AB 8	7.933	6	n.s.
AB 9	55.294	14	S
AB12	7.800	6	n.s.
AB13	22.075	15	n.s.
AB14	31.770	18	S
AB17	20.917	16	n.s.
AB21	18.167	8	S
AB22	1.267	5	n.s.
EB 1	22.294	17	n.s.
EB 1A	18.239	10	n.s.
EB 8	39.625	14	S
EB12	10.105	8	n.s.
EB14	25.843	18	n.s.
EB16	60.750	20	S
EB29	59.921	10	S

* S = significant at $p=0.05$, n.s. = not significant at $p=0.05$.

3:2 EDGE EFFECTS ON PANELS

As described in chapter 2, settling organisms may settle preferentially towards the edges of panels, or may grow more rapidly there. I attempted to minimise such effects by suspending the panels so that they could rotate freely in currents, and by not censusing areas near the edges of the panels. However, edge effects, if they exist, may be in the form of gradients from the center to the edges of the panels.

Furthermore, natural surfaces are usually sharply contoured, with ridges, pits, and other relief. They are, in effect, full of edges. Such edges would be exposed to more water movement, turbulent eddies, and perhaps higher illumination. Thus a preference for edges might be an ecologically important characteristic of a species. By not censusing the edges of panels I should have obtained more homogenous samples, but I might also have omitted important species from consideration.

Unfortunately, it is difficult to test for edge effects for many species of algae. The algae may project well beyond the edge of the panel so that estimates of percentage cover are difficult. Furthermore most algal species cannot be counted as a number of individuals. I have therefore examined the importance of edge effects only in ectoprocts and the oyster Patro australis. Thirty two panels from caves were used. Each side of each panel was divided into equal areas: a central one, and an area near the edge of the panel. For each species the number of colonies (or individual oysters) in each area was recorded.

The procedure used in the analysis of aggregation is not applicable here, as such aggregation may affect the results.

Instead a non-parametric procedure was used. If the area near the edges of a panel contained most colonies of species A, for example, this was scored as +1 for species A, and the converse situation was scored as -1. The series of scores was analysed using a procedure adopted from Armitage (1960 page 27). With each successive panel the score was accumulated on a graph as shown in Figure 3:1 for species AB1. The abscissa shows the number of samples investigated. The ordinate shows the cumulative total of the plus and minus scores. The procedure is stopped when the plotted line has crossed one of the outer boundaries marked, or entered the region between the inner boundaries.

If the plotted line crosses the upper boundary then the species shows a significant preference for the edge areas at $p=0.05$. If the plotted line crosses the lower boundary then the species shows a significant preference for the central areas at $p=0.05$. If the plotted line enters the region between the inner boundaries no preference is shown for either area. Should the plotted line not cross any boundary the question of preference is left unresolved.

The results are shown in Table 3:03 for thirty seven species. Because each species is tested separately, two significant results might be expected by chance if all the species were randomly distributed between the center and edge areas. Table 3:03 shows that five of the thirty seven species were significantly concentrated in the edge areas at $p=0.05$, and three were significantly more common (at $p=0.05$) in the central areas.

The possible ecological significance of such preferences will be discussed later. Most species of both arborescent and

FIGURE 3:1

SEQUENTIAL TESTING OF EDGE-EFFECT SCORES

Positive and negative edge-effect scores were obtained from each sample as described in the text. The cumulative score was plotted against the number of samples examined. The cumulative scores for species AB1 are shown by the thick solid line. The broken lines show the boundaries used to decide whether a significant edge effect exists, and are taken from Armitage (1960). The boundaries are defined by the equations shown in the figure.

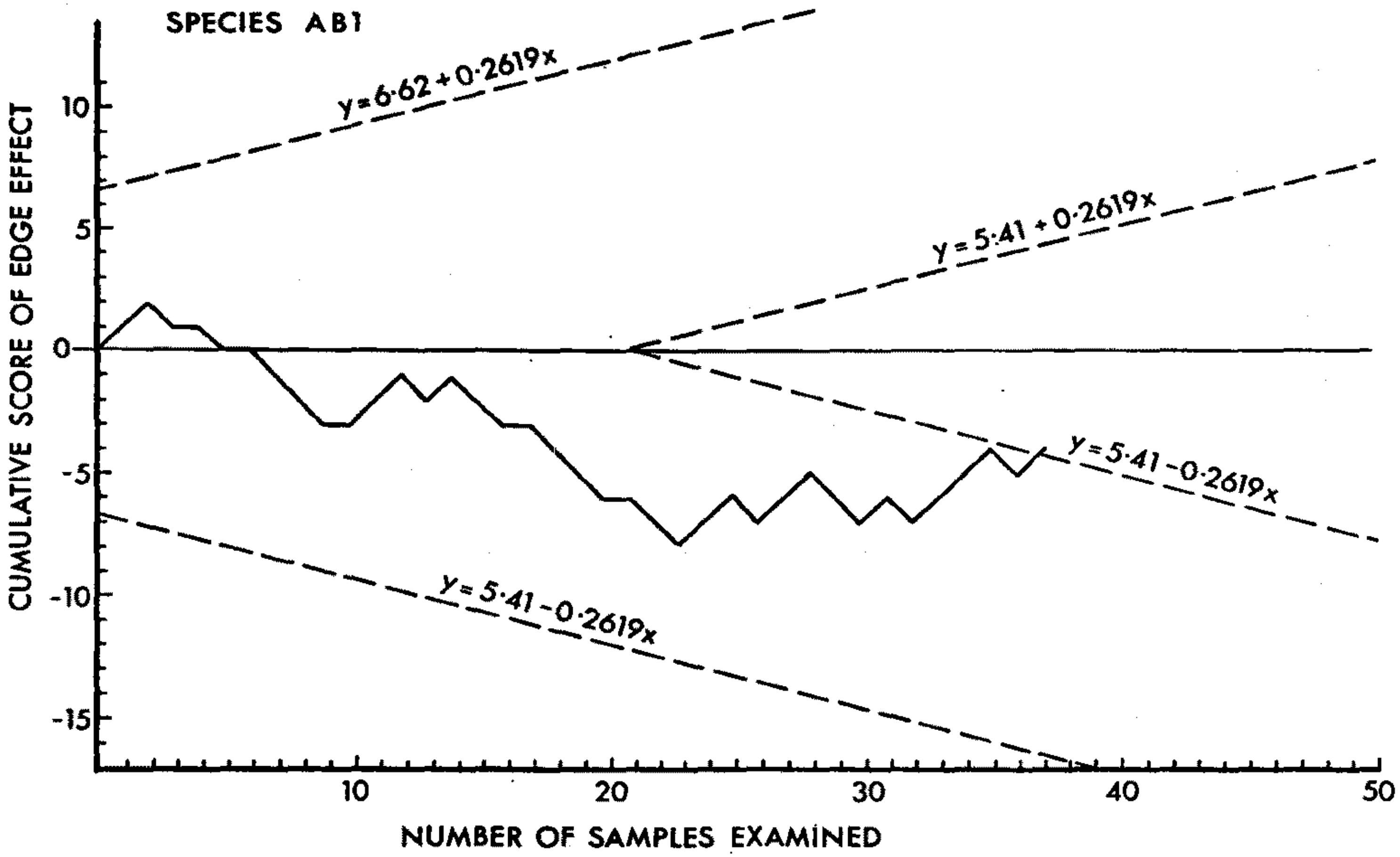

SPECIES AB1
y=6·62+0·2619x
y=5·41+0·2619x
y=5·41−0·2619x
y=5·41−0·2619x
10
5
0
-5
-10
-15
10
20
30
40
50
CUMULATIVE SCORE OF EDGE EFFECT
NUMBER OF SAMPLES EXAMINED

TABLE 3:03

EDGE EFFECTS

E: Significantly concentrated near the edges of panels at $p=0.05$

C: Significantly concentrated in the central areas of panels at $p=0.05$

R: Not significantly concentrated in either area.

Species	Conclusion	Species	Conclusion
Encrusting Ectoprocts		Encrusting Ectoprocts	
EB 1	R	EB 30	R
EB1A	R	EB 31	R
EB 2	E	EB 40	E
EB 6	E	EB 43	R
EB 7	R	Arborescent Ectoprocts	
EB 8	R	AB 1	R
EB 9	C	AB 3	R
EB10	R	AB 4	R
EB11	R	AB 5	C
EB12	R	AB 6	R
EB12A	R	AB 7	R
EB14	R	AB 9	C
EB15	R	AB 13	R
EB15A	R	AB 14	R
EB16	R	AB 17	R
EB18	R	AB 21	R
EB20	R	Other Species	
EB26	R	*Amathea* sp.	E
EB29	R	*Patro australis*	E

encrusting ectoprocts appear to be randomly distributed between central and edge areas, or at least do not show strong preferences towards either area. The procedure of censusing the central area described earlier will, however lead to an overestimate of three species and an underrepresentation of five other species. Since the oyster _Patro australis_ and the encrusting ectoproct _Thalamoporella granulata_ (EB6), which are concentrated at the edges, are common and fast growing species they may markedly influence other species in areas near edges.

The results presented here do not include any information on the relative size of organisms near the edges. My observations indicate that the oyster _Patro australis_ and the ectoproct _Thalamoporella_ are usually larger when they occur near the edges of panels than when near the center. Many species of algae also appear to occur as larger plants at the edges of the panels. This effect is probably due to more rapid growth near the edges of the panels.

3:3 THE NATURE OF THE SUBSTRATUM

The larvae of many sedentary marine organisms are known to settle on some types of surface more readily than on others. The texture of the surface may be important; or its chemical nature, its colour or reflective properties, or its orientation (Meadows and Campbell 1972). The larvae may also respond to the contours of the surface or the film of microorganisms which develop on the surface when it is immersed (Williams 1964, Meadows and Campbell 1972).

Different species may settle on different surfaces (Crisp and Ryland 1960). Thus the nature of the available surfaces may be an important component of environment, controlling the distribution of many sedentary organisms. For example Stephenson (1961) found that the sedentary species present on intertidal rocks at Heron Island appeared to vary with the hardness of the substratum.

In the experiments described in other sections of this thesis Novasteen surfaces were used throughout, and all the panels were oriented vertically. Thus these experiments were not subject to the effects of varying types or orientation of substratum. However, the set of species which settle rapidly on Novasteen surfaces at Heron reef might be different from the set of species which settle rapidly on the natural surfaces of the reef. To apply the results of experiments with Novasteen panels to the natural environment it was necessary to determine whether the panels provide an unbiased sample of the species which settle on the natural surfaces.

Almost all the natural surfaces on the reef are composed of calcium carbonate. I therefore compared the abundances of species on calcium carbonate and on Novasteen surfaces to determine whether any of the sedentary species showed any marked preference for, or avoidance of, the artificial surface. Thin slices cut from giant clam shells were used to provide a calcium carbonate surface. This surface is white, whereas Novasteen is brown. The effects of the colour and chemical nature of the surfaces are not separated in the following experiment. However the experiment remains a good comparison of the Novasteen surface with a more natural surface, as most of the natural calcium carbonate surfaces are light in colour.

The experiment was carried out at two sites: in a cave and at a well-illuminated site, so as to obtain data on as wide a range of species as possible. Similarly, since some species predominate in the presence of grazing by fishes while others predominate in the absence of grazing, some panels were mounted with fish exclusion cages. Because the species present at the two sites were very different the data from each site was treated separately.

Methods

Two large dead shell valves of the giant clam *Tridacna maxima* were cut into slices about 4mm thick with a geological saw. The saw marks were then ground off the surfaces of the slices, leaving a flat, roughened surface. The slices of shell were glued to one side of each of eight Novasteen settlement panels. Thus a flat calcium carbonate surface was formed on one side of each panel, to be compared with the other Novasteen side.

Four of these panels were suspended at the well-illuminated site (site 1) which was 7m below the reef crest, and four panels were suspended in a cave at the same depth (site 2). Two of the panels at each site were caged. The panels were immersed for three months.

For the panels from site 1 the central area of each side of each panel was divided into four. The percentage cover of each species was then estimated for each quarter. Thus for site 1 there were eight replicates per treatment, and four treatments: caged and uncaged calcium carbonate surfaces, and caged and uncaged Novasteen surfaces. If a species was absent from more than three quarters of the samples it was not considered. The mean abundances of each of the remaining species for each treatment are shown in Table 3:04. The arrangement of species into groups as shown in the table is explained later.

For site 2 (the cave site) the number of individuals of each species which settled on the panels was low, and the procedure outlined for site 1 could not be used. Instead the central area on each side of each panel was used as one sample, and the number of colonies of each species on each sample was recorded as shown in Table 3:05.

Analysis of results from site 1.

An arcsine transformation of the data was used: $x' = \text{arcsine}\sqrt{x}$ where x' is the transformed data and x is the raw data. This transformation is recommended (Snedecor and Cochran 1967) where the data are percentages. In spite of this transformation Cochran's test (Winer 1971, p.208) showed that the variances were significantly heterogeneous at $p=0.05$. This was partly the result of zeros in some cells: some species were absent under some treatments. Also, some species were rare

TABLE 3:04

THE MEAN PERCENTAGE COVER OF SESSILE SPECIES AT SITE 1 ON NOVASTEEN AND CALCIUM CARBONATE SUBSTRATA UNDER TWO CAGING TREATMENTS

Groups:		
	A1:	Rare on uncaged samples, > 0.3% mean abundance on caged samples
	A2:	Rare on uncaged samples, < 0.3% mean abundance on caged samples
	B1:	Not rare on uncaged samples, > 1% mean abundance
	B2:	Not rare on uncaged samples, < 1% mean abundance.

	Uncaged Panels		Caged Panels	
Substratum	Novasteen	Calcium Carbonate	Novasteen	Calcium Carbonate
SPECIES				
Group A1				
?*Diplosoma* sp	0	0	1.310	1.605
Callithamnion sp 5	0	0.030	1.110	2.850
Ceramium sp 5	0	0	3.078	1.975
Gelidella sp 1	0	0	0.535	2.100
Laurencia sp 1	0.030	0.030	0.103	0.575
Laurencia sp 3	0.010	0.015	1.683	2.145
Polysiphonia sp 1	0.043	0.038	9.210	5.370
Polysiphonia sp 2	0.028	0.035	2.110	2.870
Polysiphonia sp 3	0	0	0.335	1.080
Zanardinia sp	0	0	0.283	1.038
Group A2				
Ascidian B	0	0	0.108	0.045
Spirorbid 2	0	0	0.050	0.255
cf *Colpomenia*	0	0.003	0.085	0.260
Jania sp	0	0	0	0.130
Peyssonelia sp 2	0	0	0.040	0.023

TABLE 3:04 (Continued)

Group B1:				
Ralfsia sp 2	52.625	52.375	41.125	44.000
Ectocarpus sp 2	28.500	31.250	3.415	9.890
Ectocarpus sp 3	4.500	3.750	0.516	1.125
Enteromorpha sp	1.211	0.898	28.375	14.400
Lophosiphonia sp 1	6.440	4.520	0.960	2.513
Group B2:				
Hydroid 1	0.055	0.065	0.225	0.570
Coralline 1	0.100	0.043	0.148	0.025
Coralline 3	0.093	0.075	0.060	0.075
Ceramium sp 1	0.060	0.030	0.478	0.525
Cladophora sp	0.675	0.450	0.983	1.355
?*Colpomenia* sp	0.013	0.060	0.518	1.245
Lophosiphonia sp 2	1.235	0.345	0.130	0.270
Lyngbya sp	0.033	0.213	0	0.395
Sphacelaria	0.375	0.553	0.003	0.183
Pseudobryopsis sp	0.604	0.189	0	0.020

TABLE 3:05

THE NUMBER OF COLONIES OF EACH SPECIES IN EACH SAMPLE AT SITE 2.

	Uncaged Panels				Caged Panels			
Substratum	Novasteen		Calcium Carbonate		Novasteen		Calcium Carbonate	
Replicates	1	2	1	2	1	2	1	2
SPECIES:								
Ectoprocts:								
AB1	15	8	4	9	8	17	10	14
AB3	1	4	1	0	7	6	5	2
AB4	1	0	4	0	2	4	2	4
EB1	4	4	2	1	1	3	3	1
EB2	13	6	3	5	1	2	3	2
EB6	10	5	4	4	5	3	4	7
EB7	5	2	7	1	9	2	3	1
EB8	2	0	2	3	0	1	3	2
EB10	2	3	4	0	0	6	6	2
EB12A	1	2	2	6	1	0	9	2
EB14	3	1	4	2	3	3	1	0
EB16	3	1	1	0	0	3	3	2
EB18	3	3	0	1	1	1	1	0
EB29	4	2	4	1	4	1	3	3
EB30	6	6	5	0	3	3	3	6
EB31A	0	2	1	0	1	0	2	4
EB34	1	2	1	3	1	3	3	1
EB40	0	2	3	0	1	2	2	4
EB45	2	2	3	3	0	0	5	4
Amathea sp	0	1	3	0	5	0	5	1
Other species:								
?*Echinoclinum* sp	0	2	0	0	1	1	2	1
Patro australis	0	3	0	2	3	6	3	1
Vermetid	1	0	3	1	1	0	3	1
Filograna implexa	2	0	0	0	2	6	0	0

throughout, whereas other species were very common, but with more variable abundances.

To overcome these difficulties the species were divided into groups as shown in Table 3:04. Species which were absent or very rare on uncaged samples were put into category A. Only the data from caged samples was analysed for these species. Species which occurred frequently on uncaged samples were put into category B, and all the data was used for these species. Categories A and B were subdivided on the basis of the mean abundances of the species as shown in the table. The data for each group of species were analysed separately.

Analysis of group A1:

Cochran's test showed no significant heterogeneity of variance at $p=0.05$ in the data for this group of species. I carried out a two-way analysis of variance on the data, with substratum type as a fixed factor, and species as a random factor (Table 3:06).

The interaction between species and substratum type is not significant at $p=0.05$, nor is the main effect of substratum type. Thus the species as a group do not show any marked preference for either substratum, and the species in the group do not differ markedly in their substratum preferences. The significant result at $p=0.05$ for the effect of species merely indicates that the species differ markedly in their mean abundances.

Analysis of group A2:

Cochran's test showed no significant heterogeneity of variance at $p=0.05$ in the data for group A2; and I carried out the same analysis as for group A1 (Table 3:07). As the interaction

TABLE 3:06

ANALYSIS OF VARIANCE OF THE ARCSINE TRANSFORMATION OF ABUNDANCE OF SPECIES IN GROUP A1

Source of Variation	Mean Square	Degrees of Freedom	F Ratio	Significance*
Substratum type	56.113	1	1.80	n.s.
Species	191.432	9	6.44	S
Interaction	25.027	9	0.84	n.s.
Residual	29.705	140		

* S = significant at p=0.05,   n.s. = not significant at p=0.05

TABLE 3:07

ANALYSIS OF VARIANCE OF THE ARCSINE TRANSFORMATION OF ABUNDANCE OF SPECIES IN GROUP A2.

Source of Variation	Mean Square	Degrees of Freedom	F Ratio	Significance*
Substratum type	13.187	1	2.45	n.s.
Species	5.790	4	6.17	S
Interaction	5.374	4	5.72	S
Residual	0.939	70		

* S = significant at p=0.05,   n.s. = not significant at p=0.05.

between species and substratum type was significant at p=0.05 the main effect of substratum type could not be interpreted directly. I have therefore compared the means for the substrata for each species (Table 3:08) using the least significant difference statistic (L.S.D.) described by Snedecor and Cochran (1967, p. 269). A similar comparison of the means for species in group A1 was not carried out as Snedecor and Cochran recommend against such a comparison when the analysis of variance shows no significant result.

Table 3:08 shows that three of the five species in the group were significantly more abundant (p=0.05) on the calcium carbonate surface. The remaining two species showed no significant preference for either substratum (at p=0.05) although they were both, on average, more abundant on the Novasteen surfaces.

Analysis of group B1:

Cochran's test showed that the variances between replicates in this group were significantly heterogeneous at p=0.05. As an arcsine transformation of the data had been used, no further transformation of the data was carried out. Instead I carried out an analysis of variance using the p=0.01 level of significance rather than p=0.05. Winer (1971) states that the F test is not markedly affected by heterogeneity of variance, so that the precaution of increasing the significance level should be sufficient. In the three factor analysis of variance 'species' was treated as a random factor, and the caging and substratum treatments as fixed factors. The results are shown in Table 3:09. Comparisons of the means were planned to test, for each species

TABLE 3:08

SUBSTRATUM PREFERENCES OF SPECIES IN GROUP A2, AS SHOWN BY THE MEAN FOR NOVASTEEN SAMPLES MINUS THE MEAN FOR CALCIUM CARBONATE SAMPLES OF THE ARCSINE TRANSFORMATION OF ABUNDANCE.

Species	Difference Between Means	Significance*
Ascidian B	+ 0.789	n.s.
Spirorbid 2	- 1.760	S
cf *Colpomenia*	- 1.266	S
Jania sp	- 1.829	S
Peyssonelia sp 2	+ 0.007	n.s.
	L.S.D. = 0.808	

*S = significant at p=0.05, n.s. = not significant at p=0.05.

TABLE 3:09

ANALYSIS OF VARIANCE OF THE ARCSINE TRANSFORMATION OF ABUNDANCE OF SPECIES IN GROUP B1

Source of Variation	Mean Square	Degrees of Freedom	F Ratio	Significance*
Substratum type	1.475	1	0.013	n.s.
Caging treatment	421.615	1	0.242	n.s.
Species	6622.250	4	429.180	S
Substratum-Species interaction	112.082	4	7.264	S
Caging-Species interaction	1745.640	4	113.133	S
Substratum-Caging interaction	11.472	1	0.134	n.s.
Three factor interaction	85.390	4	5.534	S
Residual	15.430	140		

*S = significant at p=0.01, n.s. = not significant at p=0.01.

in turn, whether the effects of substratum type, caging treatment, and the interaction of these treatments were significant; and to test for significant differences between the species with respect to the effects of the treatments.

As the three factor interaction of substratum, caging treatment, and species was significant at $p=0.01$, no general conclusion can be made for all the species in the group. Each species needs to be examined in turn.

Comparisons of the means for each species in turn were carried out using the following formulae:

1 Substratum type comparison:

$$C=-\tfrac{1}{2}(\overline{X}_{c1,s1}) + \tfrac{1}{2}(\overline{X}_{c1,s2}) - \tfrac{1}{2}(\overline{X}_{c2,s1}) + \tfrac{1}{2}(\overline{X}_{c2,s2})$$

2 Caging treatment comparison:

$$C=-\tfrac{1}{2}(\overline{X}_{c1,s1}) - \tfrac{1}{2}(\overline{X}_{c1,s2}) + \tfrac{1}{2}(\overline{X}_{c2,s1}) + \tfrac{1}{2}(\overline{X}_{c2,s2})$$

3 Interaction:

$$C= \tfrac{1}{2}(\overline{X}_{c1,s1}) - \tfrac{1}{2}(\overline{X}_{c1,s2}) - \tfrac{1}{2}(\overline{X}_{c2,s1}) + \tfrac{1}{2}(\overline{X}_{c2,s2})$$

where: c1 denotes caging treatment one = uncaged; c2 denotes caging treatment two: caged; s1 denotes the Novasteen substratum; and s2 denotes the calcium carbonate substratum. Thus $\overline{X}_{c1\ s1}$ is the mean for the species on uncaged Novasteen samples.

A significance level of $p=0.01$ was used because the L.S.D. criterion was calculated using the residual mean square from the analysis of variance (Table 3:09), and this mean square is based on a heterogenous set of variances.

The results (Table 3:10) show that the interaction of substratum and caging treatments was significant at p=0.01 only for *Enteromorpha*. An inspection of the means (Table 3:04) shows that *Enteromorpha* was more common on Novasteen surfaces than on calcium carbonate surfaces under both caging treatments, but this difference is much more marked in the caged samples, where *Enteromorpha* was more abundant. The overall effect of substratum was significant at p=0.01, as was the overall effect of caging treatment. *Enteromorpha* was very much more common on the caged surfaces. It appeared to be markedly affected by grazing by fish.

Zoospores of *Enteromorpha* species have been found to be negatively phototactic after a few hours motility by Kapraun (1970) and Evans and Christie (1970) so that possibly the dark colour of the Novasteen surface is attractive to settling *Enteromorpha* spores. It seems unlikely that a species of *Enteromorpha* in a coral reef habitat where almost all the available substrata are calcium carbonate should avoid calcium carbonate surfaces on settlement. There are however, many dark settlement surfaces available, particularly in small crevices where the algae may be somewhat protected from grazing by fish. I suggest therefore, that the preference shown by *Enteromorpha* for Novasteen surfaces was probably due to preferential settlement on dark surfaces.

Of the remaining species in group B1 only one: '*Ectocarpus*' sp 2, was significantly affected (at p=0.01) by the substratum type. This species was significantly more abundant on calcium carbonate surfaces than on Novasteen surfaces, and also significantly more abundant on uncaged than on caged samples. Thus

TABLE 3:10

THE EFFECT OF SUBSTRATUM TYPE, CAGING TREATMENT, AND THE INTERACTION OF THESE EFFECTS, ON EACH SPECIES IN GROUP B1, AS SHOWN BY DIFFERENCES BETWEEN THE MEANS OF THE ARCSINE TRANSFORMATION OF ABUNDANCE FOR EACH SET OF SAMPLES.

Species	Comparison	Difference between means	Significance*
'*Ectocarpus*' sp 2	Substratum effect	+ 4.701	S
	Caging effect	-18.962	S
	Interaction	+ 2.918	n.s.
'*Ectocarpus*' sp 3	Substratum effect	+ 0.534	n.s.
	Caging effect	- 6.730	S
	Interaction	+ 1.288	n.s.
Enteromorpha	Substratum effect	- 5.725	S
	Caging effect	+21.242	S
	Interaction	- 5.107	S
'*Lophosiphonia*' sp1	Substratum effect	+ 0.663	n.s.
	Caging effect	- 5.990	S
	Interaction	+ 2.646	n.s.
Ralfsia sp 2	Substratum effect	+ 0.788	n.s.
	Caging effect	- 5.794	S
	Interaction	+ 0.934	n. s.

L.S.D. = 3.261

---

*S = significant at p=0.01, n.s. = not significant at p=0.01.

its behavior is exactly opposite to that of Enteromorpha. The effect of substratum type on 'Ectocarpus' sp. 2 was most marked on caged surfaces (Table 3:04), where Enteromorpha was most abundant. If Enteromorpha tends to exclude 'Ectocarpus' sp 2 in some way, then the reduced abundances of 'Ectocarpus' sp 2 on caged and on Novasteen samples might be a result of the increased abundance of Enteromorpha on these samples. Some planktonic algae are known to produce chemicals which inhibit the growth of other algal species (Accorinti 1964), and benthic algae probably produce such chemicals too (Whittaker and Feeny 1971).

The behavior of Enteromorpha was very different from the other species in group B1. The behavior of the remaining species appears to be very similar with respect to both caging and substratum effects. I therefore repeated the analysis of variance on group B1 omitting Enteromorpha, in the hope of gaining more information about these species. In this case Cochran's test showed no significant heterogeneity of variance at p=0.05, so that I could use a significance level of p=0.05 for the analysis. 'Species' was treated as a fixed factor for this analysis, since the species had been selected on the basis of their behaviour.

The results (Table 3:11) show that the three factor interaction was not significant at p=0.05, and no significant difference between the substratum preferences of the species (the substratum-species interaction) was found at p=0.05. However the species differed significantly in their response to the caging treatments.

Since the substratum-caging interaction was significant at p=0.05, the four species as a group showed significantly different responses to substratum type on the uncaged and the

TABLE 3:11

ANALYSIS OF VARIANCE OF THE ARCSINE TRANSFORMATION OF ABUNDANCE OF SPECIES IN GROUP B1, OMITTING *ENTEROMORPHA*.

Source of Variation	Mean Square	Degrees of Freedom	F Ratio	Significance*
Substratum type	89.586	1	6.202	S
Caging treatment	2807.714	1	194.381	S
Species	8603.655	3	595.640	S
Substratum-species interaction	32.843	3	2.274	n.s.
Caging-species interaction	328.113	3	22.716	S
Substratum caging interaction	121.441	1	8.408	S
Three factor interaction	7.750	3	0.537.	n.s.
Residual	14.444	112		

*S = significant at $p=0.05$, n.s. = not significant at $p=0.05$.

caged samples. On the uncaged samples all the species except 'Ectocarpus' sp 2 were more abundant on Novasteen than on calcium carbonate surfaces. In contrast, on the caged samples all the species were more abundant on the calcium carbonate than on the Novasteen surfaces. This result is discussed further after the description of the results from species group B2.

Analysis of group B2:

The two encrusting coralline species in this group (Table 3:04) were omitted from the analysis. They are very hard to see on the calcium carbonate surfaces, and the data for these species may therefore be biased. Cochran's test showed no significant heterogeneity of variance at $p=0.05$ in the data for the remaining species. I therefore carried out a three factor analysis of variance as for group B1, using a significance level of $p=0.05$.

The results are shown in Table 3:12. The three factor interaction was not significant. The substratum-caging interaction was significant, which indicates that the response to substratum type was different under different caging treatments. in this group of species, as for group B1 with Enteromorpha omitted.

The species also differed significantly from each other in their responses to caging and substratum treatments, so that it was necessary to examine the behavior of each species in turn. Comparisons of the means for each species were carried out as for group B1. The results are shown in Table 3:13. The interactions between the effects of substratum type and caging treatment were positive for all species, and significant at $p=0.05$ for three

TABLE 3:12

ANALYSIS OF VARIANCE OF THE ARCSINE TRANSFORMATION OF ABUNDANCE OF SPECIES IN GROUP B2.

Source of Variation	Mean Square	Degrees of Freedom	F Ratio	Significance*
Substratum type	26.218	1	3.129	n.s.
Caging treatment	18.279	1	0.293	n.s.
Species	37.710	7	13.047	S
Substratum-species interaction	8.378	7	2.899	S
Caging-species interaction	62.424	7	21.598	S
Substratum-caging interaction	66.319	1	32.080	S
Three factor interaction	2.067	7	0.715	n.s.
Residual	2.890	224		

*S = significant at p=0.05, n.s. = not significant at p=0.05.

TABLE 3:13

THE EFFECT OF SUBSTRATUM TYPE, CAGING TREATMENT, AND THE INTERACTION OF THESE EFFECTS ON EACH SPECIES IN GROUP B2, AS SHOWN BY DIFFERENCES BETWEEN THE MEANS OF THE ARCSINE TRANSFORMATION OF ABUNDANCE FOR EACH SET OF SAMPLES.

Species	Comparison	Difference between means	Significance*
Hydroid sp 1.	Substratum effect	1.0502	S
	Caging effect	2.2920	S
	Interaction	0.9812	n.s.
Ceramium sp 1	Substratum effect	0.0680	n.s.
	Caging effect	2.6172	S
	Interaction	0.5643	n.s.
Cladophora sp.	Substratum effect	-0.0155	n.s.
	Caging effect	2.2084	S
	Interaction	1.1380	S
?Colpomenia	Substratum effect	1.3913	S
	Caging effect	4.4597	S
	Interaction	0.8634	n.s.
'Lophosiphonia' sp 2	Substratum effect	-0.6138	n.s.
	Caging effect	-2.4804	S
	Interaction	2.1830	S
Lyngbya	Substratum effect	2.4148	S
	Caging effect	0.4150	n.s.
	Interaction	1.0055	S
Sphacelaria	Substratum effect	1.1252	S
	Caging effect	-2.5955	S
	Interaction	0.6371	n.s.
Pseudobryopsis	Substratum effect	-0.3000	n.s.
	Caging effect	-2.6411	S
	Interaction	0.7711	n.s.
	L.S.D. =	0.9888	

*S = significant at p=0.05, n.s. = not significant at p=0.05.

species. A positive interaction may be interpreted as follows: If a species showed a preference for calcium carbonate surfaces on uncaged samples, then this preference was stronger on caged samples. If a species showed a preference for Novasteen surfaces on uncaged samples then this preference was weaker or reversed on caged samples.

The fact that the interaction was positive for all the species in group B2, and all the species except *Enteromorpha* in group B1, suggests that a common factor was operating on all the species. The species which showed a significant interaction might simply have been more affected by this factor. I suggest that the caged calcium carbonate samples supported a slightly greater abundance of most algal species than the caged Novasteen samples because of the abundance of *Enteromorpha* on the caged Novasteen surfaces.

I have already suggested that *Enteromorpha* affected '*Ectocarpus*' sp 2, possibly by chemical means. Other species may have been suppressed where *Enteromorpha* was abundant. The *Enteromorpha* thalli shaded the caged Novasteen surfaces, perhaps sufficiently to reduce the growth of other algae. The calcium carbonate substratum reflected more light, so that shading effects would not have been as important on the caged calcium carbonate surfaces. Thus the substratum preferences of *Enteromorpha* might have been responsible for the substratum-caging interaction observed for many other species.

Four species of those analysed in group B2 were more common on uncaged calcium carbonate surfaces than on uncaged Novasteen surfaces (Table 3:04). The overall effect of substratum type was significant at $p=0.05$ for these species (Table 3:13).

However the differences between the means for uncaged samples were all very small (Table 3:04): the significant results may be attributed to the probable effect of Enteromorpha on caged surfaces. The significant preferences for calcium carbonate caged samples shown by three species in group A2, and the fact that eight of the ten species in group A1 were more common on calcium carbonate caged samples, may be attributed to the effect of Enteromorpha too.

The effect of Enteromorpha on other species could possibly have masked the substratum preferences of other species. Thus species which do not fit the general pattern are of interest. Two species in group A1: Ceramium sp 5 and Polysiphonia sp 1, and two in group A2: Ascidian B and Peyssonelia sp 2, were more common on the novasteen caged samples (Table 3:04). The variation between replicates for the two species in group A1 was very great so that no conclusions can be drawn from the means. Ascidian B may have settled preferentially on the dark, shaded surfaces of the caged Novasteen samples, since this species is most abundant in caves. The differences between the means for Peyssonelia sp 2 are too small to draw any conclusions about this species.

Enteromorpha could not have affected the abundance of species on uncaged surfaces greatly. A number of species in groups B1 and B2, particularly 'Lophosiphonia' sp 1 and 'Lophosiphonia' sp 2 were more abundant on the Novasteen uncaged samples than on the calcium carbonate uncaged samples. The results for the two 'Lophosiphonia' species are however, unlikely to be the result of substratum preferences, since Borowitzka et al (in preparation) found that 'Lophosiphonia' became more common on the edges of immersed glass slides, on top of coralline algae. Grazing by fishes was reduced at the edges of the slides used by Borowitzka et al. I suspect that grazing by fishes was slightly more intense on my calcium carbonate uncaged samples than on the uncaged Novasteen surfaces. The algae were more readily visible on the calcium carbonate surfaces. Differences in grazing pressure may, therefore, explain the observed results for 'Lophosiphonia' spp and other species on the uncaged samples.

Thus at site 1 the pattern of abundance of Enteromorpha and possibly, differences in grazing pressure on uncaged surfaces, may have affected the abundance of most of the species. The magnitude of these effects however, is not very great when they are compared to the abundances of the species (Table 3:04) and the difference in abundance between species. Furthermore the "Enteromorpha effect" is largely confined to caged samples, where the algae are protected from fish. On the reef slope the only natural surfaces protected from grazing are in crevices of some kind, and are therefore partly shaded. If dark surfaces are attractive to Enteromorpha spores, then many of the natural surfaces protected from fish may support large numbers of Enteromorpha plants, as the caged Novasteen samples do.

Analysis of results from site 2

At site 2 the number of individuals of each species, and the area covered by the organisms, was low. I therefore lumped together the data from the caged and uncaged samples. Totals for each substratum type were calculated from the numbers of colonies on each sample shown in Table 3:05. The lumping of the data is justified only if the effects of substratum type and caging treatment were independent. I tested for independence of the effects by means of a χ^2 test, except where the numbers were small, in which case I used Fisher's exact probability test (Siegel 1956 pp 96-104). Examples of these tests are shown in Table 3:14. Very rare species were not considered in the analysis.

As none of the tests showed any significant interdependence of the effects of caging and substratum at $p=0.05$, it was reasonable to lump the data, and use the totals for each substratum type. I calculated the binomial probability of obtaining results as extreme as those observed if the species showed no preference for either substratum: that is, if the probability of an individual larva settling on each substratum type was 0.5. The results are shown in Table 3:15.

Because 24 species were tested one significant result at $p=0.05$ could be expected by chance. Three significant results at $p=0.05$ occurred. The encrusting bryozoans EB12A and EB45 appeared to settle preferentially on the calcium carbonate surfaces. The colonial polychaete, <u>Filograna implexa</u>, appeared to settle preferentially on the Novasteen surfaces.

It is unlikely that these results for the encrusting bryozoans were affected by aggregated distributions of the species. EB12A was tested for an aggregated distribution in section 1 of this chapter, and its distribution was not found to be significantly aggregated. EB45 was not tested, but very few encrusting ectoprocts were found to have aggregated distributions. On the other hand, the individual polychaetes of <u>Filograna implexa</u> tend to settle close to each other so that their tubes eventually fuse to form a large network. Thus the observed results for <u>Filograna</u> may be due to the aggregation of

TABLE 3:14

EXAMPLES OF THE χ^2 AND FISHER EXACT PROBABILITY TESTS FOR THE INDEPENDENCE OF THE SUBSTRATUM AND CAGING TREATMENTS ON THE NUMBERS OF EACH SPECIES AT SITE 2.

χ^2 TEST Example chosen: Species AB1.

	Observed (O)			Expected (E)	
	$CaCO_3$	Novasteen	Totals	$CaCO_3$	Novasteen
Caged	24	25	49	21.33	27.67
Uncaged	13	23	36	15.67	20.33
Total	37	48	85	37	48

$$\chi^2 = \frac{(O - E)^2}{E} = 1.397$$

not significant at p = 0.05

FISHERS EXACT PROBABILITY TEST

Example chosen: Species AB4.

	OBSERVED		
	$CaCO_3$	Novasteen	Total
Caged	A 6	B 6	12
Uncaged	C 4	D 1	5
Total	10	7	17 N

$$\text{Fisher's exact probability } P = \frac{(A+B)!\,(C+D)!(A+C)!(B+D)!}{N!A!B!C!D!}$$

$$= 0.238$$

In both cases $P > 0.05$, and therefore there is no significant interaction of substratum and caging treatments at $p=0.05$.

TABLE 3:15

THE TOTAL NUMBER OF COLONIES OF EACH SPECIES ON EACH SUBSTRATUM, AND THE PROBABILITY OF SUCH EXTREME FREQUENCIES AS THOSE OBSERVED, IF THERE IS NO PREFERENCE FOR EITHER SUBSTRATUM.

Species	$CaCO_3$ Total	Novasteen Total	Grand Total	P Value[+]	Significance[*]
1 Ectoprocts					
AB 1	37	48	85	0.276	n.s.
AB 3	8	18	26	0.078	n.s.
AB 4	10	7	17	0.630	n.s.
EB 1	7	12	19	0.360	n.s.
EB 2	13	22	35	0.177	n.s.
EB 6	19	23	42	0.644	n.s.
EB 7	12	18	30	0.362	n.s.
EB 8	10	3	13	0.092	n.s.
EB10	12	17	29	0.46	n.s.
EB12A	19	4	23	0.002	S
EB14	7	10	17	0.630	n.s.
EB16	6	7	13	1.00	n.s.
EB18	2	8	10	0.110	n.s.
EB29	11	11	22	1.00	n.s.
EB30	14	18	32	0.596	n.s.
EB31A	7	3	10	0.344	n.s.
EB34	8	7	15	1.00	n.s.
EB40	9	5	14	0.414	n.s.
EB45	15	4	19	0.020	S
Amathea sp	9	6	15	0.608	n.s.
2. Other species					
?*Echinoclinum*	3	4	7	1.00	n.s.
Patro australis	6	12	18	0.238	n.s.
Vermetus sp	8	2	10	0.110	n.s.
Filograna implexa	0	10	10	0.002	S

[+] P value = probability of observed result if no preference exists.

[*] S = significant at p=0.05, n.s. = not significant at p=0.05.

settling larvae rather than preferential settlement on the Novasteen substratum.

Conclusions: The effects of substratum type

Substratum type appeared to have no marked effect at site 2: of 24 species (mostly ectoprocts) tested only two show clear-cut substratum preferences. However at site 1 the substratum type had more marked effects on the species (mostly algae). *Enteromorpha* sp.an abundant species on caged samples, showed a marked preference for the Novasteen surfaces. Other species were apparently indirectly affected by substratum type: as a result of interactions with *Enteromorpha*, and possibly as a result of slightly more severe grazing by fish on the calcium carbonate surfaces. '*Ectocarpus*' sp.2 in particular, and many other species, appeared to be suppressed where *Enteromorpha* was abundant. A number of species were slightly less abundant on the calcium carbonate uncaged surfaces, where grazing by fish may have been more severe.

The effects outlined above were not very important when compared with the differences in abundance between species, and the caged Novasteen surfaces on which *Enteromorpha* was abundant may in fact be similar to many natural surfaces where algae are protected from fish. However the effects of substratum type must be borne in mind when applying the results of other experiments to the natural environment. In chapter 7, where the abundances of species are compared with one another, I have used the calcium carbonate samples from site 1 described here, rather than Novasteen surfaces.

3:4 THE EFFECT OF THE AREA OF THE SETTLEMENT SURFACE.

Very few of the species I have investigated have been found to settle on top of other organisms. Thus the larvae which settle on the panels I have used presumably settle only on vacant patches of the natural coral limestone of the reef. Patches of surface may become vacant in various ways: for example fish may scrape sedentary organisms from a surface; or a piece of coral may break; or a large block of coral limestone may be overturned in a storm, exposing a fresh patch of surface. My observations indicate that most of these patches of new surface are no larger than the settlement panels I have used.

On the well lit outer surfaces of the reef the most common way in which fresh space is made available is as a result of fish (especially Scarid fishes) scraping the surface. Such scrapes are only a few square millimeters in area. However, in the darker places under overhangs fish do not scrape the surface, and the few patches of fresh surface I have observed are of about the same area as the settlement panels I have used. Rare events such as cyclones would, however, lead to extensive areas of fresh surface being exposed.

The larvae of many of the sessile marine animals which have been studied "search" a fairly large area before settling by moving over the surface (Wisely, 1958). The larvae often apparently avoid sedentary animals already present on the surface. Thus some species might avoid patches of surface which have already been colonised by another species. A possible consequence is that two adjacent areas on the same patch of surface might contain fairly similar faunas. In contrast the faunas of areas on different patches might differ more markedly.

Settling larvae may tend not to leave a patch of suitable surface once they have found it. If they space themselves as far as possible from some other species, then larger patches of surface would allow more segregation of the species than small patches. Thus a fixed area on a small patch might contain more species than the same area on a large patch.

Settlement panels can be regarded as isolated patches or islands of fresh surface (Schoener 1974), and thus the effects described above for patches of surface may apply to panels. Long (1974) measured the biomass and number of species on settlement panels of different sizes off Oaku, Hawaii. He states that the biomass per unit area increased with increasing surface area for small panels, but that the effect was not apparent for larger panels. Unfortunately it is not clear from his table how many replicates he used. Long also found that the average number of species per unit area decreased with increasing panel size, but this provides no information on the number of species which occur together in small areas of large surfaces as against equal areas of small surfaces. I have found no other published work where panels of different sizes are compared, although Levin and Paine (1974, 1975) have stressed the importance of patch size in interactions between rocky shore species.

Methods

I suspended panels measuring 220 by 240 mm alongside panels of standard size (120 by 140 mm). Two caged and two uncaged panels of each size were used. Since both sides of each panel were censused, there were four replicate surfaces of each type. To reduce edge effects I ignored organisms within

20 mm of the top and bottom edges, or within 10 mm of the side edges of all panels. Thus 0.01 m^2 areas on the small panels, and 0.04 m^2 areas on the large panels were censused. The 0.04 m^2 areas were divided into four 0.01 m^2 subareas, each censused separately. The number of colonies (or individuals) of each species in each area was recorded.

I did not compare the faunas of these samples by means of an analysis of variance of the three factors species, panel size, and caging effects, because many of the species occurred on less than half of the samples, and I wished to include these rare species in the analysis. Instead I compared the faunas of 0.01 m^2 areas using an index of similarity proposed by Schoener (1968). For two samples a and b, this index is calculated according to the formula: $S = 1-\frac{1}{2} \sum_{j=1}^{N} |P_{aj} - P_{bj}|$ where S is the index of similarity, P_{aj} is the number of colonies of species j in sample a divided by the total number of colonies in sample a, and P_{bj} is calculated in the same way for sample b. N is the total number of species in both samples.

Three sets of indices were calculated. First, the similarity indices for pairs of samples from the same surface were calculated. Second, similarity indices for randomly chosen pairs of samples from different large surfaces were calculated; and third, indices of similarity were calculated for samples from small panels paired with samples from large panels. Twenty indices of each type were calculated. These are shown in Table 3:16.

As the similarity index is a fraction ranging from zero to one, an arcsine transformation was used before analysing

TABLE 3:16

SIMILARITY INDICES FOR SAMPLES FROM THE SAME SURFACE (A); SAMPLES FROM DIFFERENT LARGE SURFACES (B); AND FOR SAMPLES FROM SMALL AND LARGE SURFACES (C).

A		B		C	
Caged Panels	Uncaged Panels	Caged Panels	Uncaged Panels	Caged Panels	Uncaged Panels
0.583	0.604	0.588	0.654	0.505	0.577
0.632	0.458	0.559	0.393	0.552	0.342
0.496	0.495	0.663	0.589	0.592	0.392
0.595	0.476	0.605	0.521	0.597	0.552
0.617	0.568	0.622	0.637	0.425	0.371
0.569	0.537	0.633	0.508	0.550	0.524
0.629	0.575	0.382	0.476	0.538	0.618
0.594	0.511	0.663	0.434	0.428	0.350
0.418	0.484	0.588	0.450	0.542	0.345
0.737	0.568	0.546	0.412	0.413	0.466
0.392	0.498	0.496	0.466	0.341	0.316
0.360	0.468	0.458	0.379	0.461	0.359
0.603	0.655	0.627	0.428	0.435	0.495
0.584	0.701	0.627	0.597	0.552	0.342
0.557	0.529	0.541	0.424	0.354	0.441
0.547	0.639	0.305	0.449	0.408	0.485
0.492	0.490	0.532	0.450	0.538	0.618
0.525	0.577	0.564	0.499	0.586	0.529
0.473	0.478	0.510	0.663	0.413	0.558
0.637	0.553	0.600	0.511	0.464	0.357

these data using an analysis of variance (Table 3:17). Two comparisons of the means were planned. First, the mean similarity between samples from the same surface was compared with the mean similarity between samples from different large surfaces. Secondly, the mean similarity between samples from different large surfaces was compared with the mean similarity between samples from small and large surfaces (Table 3:18).

Results (Part 1):

The analysis of variance (Table 3:17) shows that predation by fishes had a significant effect at $p = 0.05$ on the similarity between the faunas of different small areas. The fish reduced the numbers of species of arborescent ectoprocts, some of which were the most common species on the panels. These common species contributed greatly to the similarity between samples. Few of the encrusting species, which were not subject to predation, were common on the panels. Thus the effect of predation by fish was to reduce the numbers of the more ubiquitous species, leaving small areas with fewer species in common.

Table 3:17 also shows that the mean values for the columns A, B, and C in Table 3:16 are significantly different at $p=0.05$. The planned comparisons of these means in Table 3:18 show that the means for columns A and B are not significantly different at $p=0.05$. I conclude that the faunas of small areas on the same surface were about as similar to one another as they were to the faunas of small areas on other surfaces. The proximity of small areas did not appear to have any marked effect on their faunas.

TABLE 3:17

ANALYSIS OF VARIANCE OF SIMILARITY INDICES AFTER THE DATA HAD BEEN TRANSFORMED TO ARCSINE $\sqrt{x}$

Source of Variation	Mean Square	Degrees of Freedom	F Ratio	Significance*
Caging treatment	111.199	1	4.30	S
Surfaces (Columns A, B, C in Table 3.16)	227.512	2	8.80	S
Interaction	20.215	2	0.78	n.s.
Residual	25.849	114		

* S = significant at p=0.05, n.s. = not significant at p=0.05.

TABLE 3:18

COMPARISONS OF MEANS OF THE SIMILARITY INDICES OF COLUMNS A, B, AND C IN TABLE 3:16 USING THE LEAST SIGNIFICANT DIFFERENCE TEST AFTER THE DATA HAD BEEN TRANSFORMED TO ARCSINE $\sqrt{x}$

Comparison	Difference Between the Means	Critical Value	Significance*
Between columns A and B	1.246	2.251	n.s.
Between columns B and C	3.364	2.251	S

* S = significant at p=0.05. n.s. = not significant at p=0.05.

The means for columns B and C in Table 3:16 are significantly different at p=0.05, which shows that the faunas of 0.01 m^2 areas on the large panels were more similar to each other than to the faunas of 0.01 m^2 areas on small panels. The size of the settlement surface appeared to have an effect on the settling fauna.

To investigate this effect further I calculated the total cover of organisms, the number of colonies (or individuals) present, and the number of species present on each 0.01 m^2 area. In order to investigate whether the relative abundances of the species present varied with the panel size, I calculated indices of evenness for each 0.01 m^2 area too, using the Brillouin (1962) diversity formula as suggested by Pielou (1966).

Taking each type of data in turn, I calculated a mean for each large surface. The means for the four caged and four uncaged large surfaces were then compared with the data from the small surfaces, using an analysis of variance.

Results (Part 2):

The treatment means for each type of data are shown in Table 3:19. The analyses of variance are presented in Tables 3:20, 3:21, 3:22, and 3:23.

The total cover (Table 3:20) was significantly greater, at p=0.05, on caged than on uncaged surfaces, and was also significantly greater, at p=0.05, on small than on large surfaces. These effects appear to have been additive, as the interaction is not significant at p=0.05. There is no evidence that the higher cover of organisms was the result of an increase in the

TABLE 3:19

MEANS OF THE FOUR QUANTITIES SHOWN IN COLUMN NO. 1 FOR 0.01m^2 SAMPLES ON CAGED AND UNCAGED, SMALL AND LARGE SURFACES.

Quantity Measured	On large surfaces		On small surfaces	
	Caged	Uncaged	Caged	Uncaged
Total cover	3673	1399	4482	3449
Number of colonies or individuals	152	104	146	171
Number of species	45.1	39.3	47.8	50.5
Indices of Evenness	0.820	0.876	0.897	0.864

TABLE 3:20

ANALYSIS OF VARIANCE OF THE TOTAL COVER OF ORGANISMS ON $0.01m^2$ SAMPLES FROM SURFACES OF DIFFERENT SIZES, CAGED AND NOT CAGED.

Source of Variation	Mean Square	Degrees of Freedom	F Ratio	Significance*
Caging treatment	10,938,729	1	21.121	S
Size of surface	8,171,737	1	15.778	S
Interaction	1,537,290	1	2.968	n.s.
Residual	517,912	12		

* S = significant at p=0.05, n.s. = not significant at p=0.05.

TABLE 3:21

ANALYSIS OF V ON $0.01m^2$ SAMPLES FROM SURFACES OF DIFFERENT SIZES, CAGED AND NOT CAGED.

Source of Variation	Mean Square	Degrees of Freedom	F Ratio	Significance*
Caging treatment	561.1	1	0.386	n.s.
Size of surface	3805.3	1	2.621	n.s.
Interaction	5356.4	1	3.689	n.s.
Residual	1451.8	12		

* n.s. = not significant at p=0.05.

TABLE 3:22

ANALYSIS OF VARIANCE OF THE NUMBER OF SPECIES PRESENT ON 0.01m^2 SAMPLES FROM SURFACES OF DIFFERENT SIZES, CAGED AND NOT CAGED.

Source of Variation	Mean Square	Degrees of Freedom	F Ratio	Significance*
Caging treatment	9.379	1	0.281	n.s.
Size of surface	190.785	1	5.715	S
Interaction	73.316	1	2.196	n.s.
Residual	33.384	12		

* S = significant at p=0.05, n.s. = not significant at p=0.05.

TABLE 3:23

ANALYSIS OF VARIANCE OF INDICES OF EVENNESS FOR THE FAUNAS OF 0.01m^2 AREAS ON SURFACES OF DIFFERENT SIZES, CAGED AND UNCAGED.

Source of Variation	Mean Square	Degrees of Freedom	F Ratio	Significance*
Caging treatment	0.000532	1	0.446	n.s.
Size of surface	0.004282	1	3.594	n.s.
Interaction	0.008021	1	6.732	S
Residual	0.001192	12		

* S = significant at p=0.05, n.s. = not significant at p=0.05.

number of organisms on caged, or small surfaces, as the analysis of variance for the number of colonies or individuals present (Table 3:21) shows no significant result at p=0.05. However, Table 3:22 shows that the number of species present on 0.01 m^2 areas was significantly higher (at p=0.05) on small than on large surfaces.

For the index of evenness (Table 3:23) there was a significant interaction between the effects of caging and the size of the surface. For this reason the means for large and small surfaces were compared as shown in Table 3:24 for the caged and uncaged treatments separately. For the caged treatments the index of evenness was significantly greater on the small surfaces. For the uncaged treatment there was no significant effect of the size of the panel at p=0.05.

Discussion of Results:

The total cover of organisms was greatest on the caged small surfaces, approaching half of the space available on the surface, although the average number of organisms which had settled on these surfaces was fairly low (Table 3:19). On the uncaged small surfaces the cover of organisms was lower, but the average number of colonies or individuals was higher. I suggest that while they were immersed, the caged small surfaces may have become sufficiently crowded to discourage the settlement of further larvae.

As a greater number of species settled on the smaller surfaces, the caged small surfaces came to have approximately the same number of organisms as the larger caged surfaces, but

TABLE 3:24

COMPARISONS OF THE MEAN INDICES OF EVENNESS FOR SMALL AND LARGE SURFACES SHOWN IN TABLE 3:19, USING THE LEAST SIGNIFICANT DIFFERENCE TEST.

Comparison	Difference Between the Means	Critical Value	Significance*
Large vs small caged surfaces	0.0785	0.0532	S
Large vs small uncaged surfaces	0.0120	0.0532	n.s.

* S = significant at p=0.05, n.s. = not significant at p=0.05.

more species were represented. The numbers of the more common species appear to have been reduced, as the indices of evenness show that the species were more equally represented on the small caged surfaces.

On the uncaged surfaces the total cover was lower than on caged surfaces, presumably as a result of predation by fish. Thus the panels were not as crowded. The extra species which settled on the small uncaged panels apparently did not displace colonies of the common species: the average number of colonies on these panels was increased (Table 3:19). Thus there was no significant change in the relative numbers of the species, as measured by the index of evenness.

Conclusions:

The greater number of species on small surfaces suggests that larger patches of surface may allow the species to segregate more effectively than smaller patches. As a result the faunas of small panels were more similar to one another than to the faunas of 0.01 m^2 areas on large panels. However the other hypothesis offered at the beginning of this section was not supported by the data: the faunas of adjacent areas on one surface were no more similar to each other than to the faunas of equal areas on other surfaces.

The results presented here show that small panels provided samples of the settling fauna which are as good as samples from larger panels. Although the numbers of common species were reduced on the small caged panels, the small panels were colonised by more species per unit area than the large panels.

CHAPTER 4

THE EFFECTS OF WAVE ACTION, WATER-MOVEMENT, ILLUMINATION, DEPTH AND SEASONAL CHANGES ON SESSILE ORGANISMS.

4:1 A REVIEW OF THE EFFECTS OF VARIOUS COMPONENTS OF THE MARINE ENVIRONMENT.

The effect of wave action, water-movement, illumination, depth, and season on the abundance of organisms which settled on the panels is discussed in this chapter. These are probably among the more important components of environment which determine the distributions of the sessile species studied, but other factors may be important (see appendix 4C).

Water-movement:

A measure of the volume of water which flowed over the panels in 24 hours was obtained as described in appendix 4A. The water flow carries planktonic food and dissolved nutrients to sessile organisms, so that the average rate of water-movement determines the supply of food (Riedl, 1969, 1971). Thus barnacles and sessile hermit crabs use different modes of feeding in fast and slowly moving water (Crisp and Southwood 1961, Schuhmacher 1977): in slowly moving water they actively sweep the water towards themselves, and the barnacles trap much smaller food items, presumably to gain extra food. Bryozoans may change their pattern of growth under conditions of limited food supply in such a way that they can find nearby places on the surface where the food supply is better (Winston 1976). Bryozoans and barnacles grow more rapidly in faster currents (Crisp and Patel 1961, Doochin and Smith 1951), presumably because more food is carried to them. However, in very fast currents bryozoan growth may be reduced (Doochin and Smith 1951).

Because a velocity gradient is established when water flows over a surface projecting organisms can obtain more food as they grow taller. Riedl and Forstner (1968) and Velimirov (1976) discuss other aspects of the shape of sessile animals in relation to velocity gradients. Some organisms may even use the gradient to provide them with a feeding current (Vogel and Bretz 1972). The velocity gradient around the organism itself determines the rate of diffusion of metabolites towards and away from the organism (Doty 1971). This may explain the effect of water-movement on photosynthetic rate in algae (Gessner 1940, Schwenke 1971). Many algae require organic substances to grow (Fries 1973), and the supply of these will be controlled by the velocity gradient.

Current speeds were important in determining species' distributions in Irish lochs (Kitching and Ebling 1967). Moderate water-movement prevented the clogging of surfaces by sediment: for example a hydroid species, when transferred to quiet water, became clogged with sediment and diatoms and died (Round _et al_ 1961). Siltation was also important in determining the distribution of sessile organisms in other areas (Boaden _et al_ 1976, Moore 1973).

In the present study siltation rate could not be measured because it was correlated with the type of organism growing on the surface: algae trapped more sediment than animals.

Shear forces produced by strong currents appear to determine species' distributions in tidal rapids (Hatton 1938, Mathieson _et al_ 1976, Sloane _et al_ 1961). Strong currents may also prevent sedentary animals from settling (Walton-Smith 1949, Wood 1955).

Wave action:

To survive on a surface sessile organisms must withstand the maximum shear forces generated by water-movements. Usually these maximum forces are a result of waves, which produce short but very strong surges. Wave action determines the distribution of many algae and animals on rocky shores (Jones 1959, Lewis 1964, Harger 1970, Dayton 1971), and also in the sublittoral zone (Kitching 1941, Shepherd and Womersley 1970, 1971). Schuhmacher (1973b) has also described how turbulent water-movement resulting from wave action affects the distribution of gorgonians in the Red Sea.

The velocity of the surge produced by a wave is inversely proportional to e^D where D is the depth below the surface (Sverdrup _et al_ 1942). The distribution of organisms may reflect this exponential decay of wave action with depth: for example the distribution of the gorgonians studied by Schuhmacher was correlated with depth.

Illumination:

Illumination was measured as described in appendix 4B by means of film strips which were most sensitive to wavelengths near 450 nm. Marine algae use light energy with wavelengths between 400 and 700 nm, and especially between 400 and 550 nm (Haxo and Blinks 1950). Thus the level of illumination in the wave band measured indicates the amount of light energy available to algae. Although algal growth can, in general, be expected to increase with increasing light intensity, some shade tolerant algae may die if exposed to bright illumination (Dayton 1971).

Many sessile animals react to illumination during settlement: most species settle on the darker side of objects (Bayne 1964, Crisp and Ghobashy 1971, Ryland 1960). Furthermore Schuhmacher (1973a) has shown that many coral reef organisms are distributed according to the intensity of illumination.

Depth:

The larvae of sedentary organisms may remain within a selected depth range by reacting to changes in hydrostatic pressure (Rice 1964), so that the adults will be distributed according to depth. A narrow range of depths was investigated in the present study but some authors (e.g. Wisely 1959) have found changes in species' abundances within a few meters.

Light is absorbed and scattered in the water column, so that illumination at sites outside caves is negatively correlated with depth (Jerlov 1970). It is therefore difficult to separate the effects of illumination and depth on algae. Many authors (e.g. Gilmartin 1960) simply attribute the distribution of algae with depth to changes in illumination. This approach is supported by the fact that off Malta the same algae are abundant in caves and in deep water (Crossett and Larkum 1966).

Spectral characteristics of the illumination, as well as its intensity, change with depth (Jerlov 1970). Changes in the quality of illumination however, appear to be less important than changes in light intensity in determining algal abundances (Crossett _et al_ 1965, Larkum _et al_ 1967).

Seasonal changes:

Seasonal changes are important in controlling the composition of fouling communities in many temperate areas (Humphries 1973, Kawahara 1965, Millard 1952, Wisely 1959). In tropical areas seasonal changes might be expected to be less important, but the evidence is conflicting. Long (1974) found few seasonal changes in Hawaii, but Weiss (1948) found pronounced seasonal effects near Miami, Florida. Hawaii, Miami, and Heron Island all lie between 20° and 26° from the equator, at the edge of the tropics.

Seasonal changes in the abundance of algae have been attributed to changes in light intensity and photoperiod during the year (Hygen 1948, Feldmann 1957), and to seasonal changes in temperature (Edwards 1969). The temperature variation at Heron Island during the year is discussed in appendix 4C. Temperature appears to control the reproductive season of many sessile animals and thus the intensity of settlement during the year (Abbott 1975), but seasonal changes in food availability may also be important (Gordon 1970).

Factors acting in concert:

Environmental factors do not act in isolation. The joint effects on species' abundances of a number of factors acting together may be very different from the effects of each factor acting separately (Alderdice 1972). However, it is beyond the scope of this thesis to consider all the possible interactions between the components of environment investigated.

4:2 METHODS

As I could not manipulate the components of environment considered in this chapter I set out to determine how the abundances of species which colonised settlement panels were correlated with each component. Thirteen sample sites were chosen in order to include as wide a range of depth, illumination, water-movement, and wave action as possible.

The sites were in two general areas (Figure 4:1): on the north side of Heron reef which is exposed to wave action, especially during storms; and in the channel between Heron and Wistari reefs which is protected from wave action by the reefs on either side. Sites in the channel were assigned the value '0' as the level of wave action, and sites on the north side were assigned the value '1'. These categories of wave action do not take into account seasonal changes in wave action. Strong winds may occur at any time of the year: the southeast trade wind is usually strongest in September (Brandon 1973) but may blow strongly at any time of the year, while hurricanes may occur from January to March. Moreover there are no records kept of sea conditions around Heron Island, so that there was no basis on which to adjust the levels of wave action for different seasons.

The categories used also do not take account of the attenuation of wave action with depth, or in caves. It seems unnecessary to do so since at the deepest site on the north side and in the caves in this area there is more surge when large waves pass overhead than at any of the sites in the channel.

Water-movement and illumination were measured at each site as described in appendices 4A and 4B. There was no surveyed benchmark on Heron Island from which to measure depth. The

FIGURE 4:1

MAP OF HERON AND WISTARI REEFS

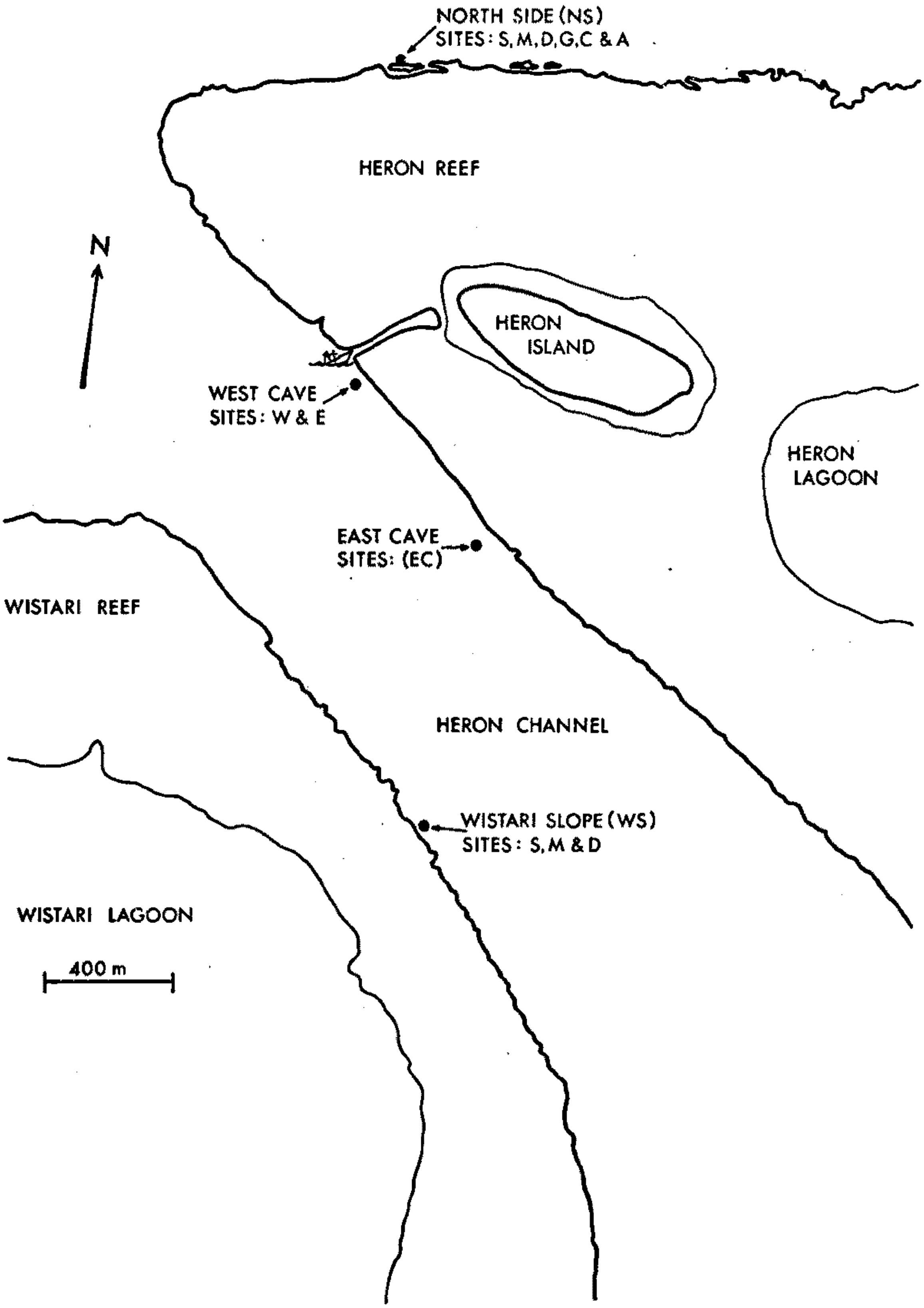
The positions of the sites where settlement panels were immersed are shown. Sites are coded according to their position as follows:

North Slope sites: NS
NSS - shallow sites, NSM - intermediate depth site. NSD - deep site,
NSG - site in 'gutter' at edge of reef,
NSC - site in cave, NSA - site in archway

Wistari Slope sites: WS
WSS - shallow site, WSM - intermediate depth site, WSD - deep site.

Western Cave sites: WC
WCW - western site in cave
WCE - eastern site in cave

Eastern Cave site: EC
(one site only)


NORTH SIDE (NS)
SITES: S, M, D, G, C & A
HERON REEF
N
HERON ISLAND
WEST CAVE
SITES: W & E
HERON LAGOON
EAST CAVE
SITES: (EC)
WISTARI REEF
HERON CHANNEL
WISTARI SLOPE (WS)
SITES: S, M & D
WISTARI LAGOON
400 m

most convenient reference height was the average height of the reef crest, which is approximately at the mean low water level (Stephenson and Searles 1960). The depth of each site was measured on a calm day using a divers depth gauge, with the tide at the average height of the reef crest. Other methods such as surveying underwater or using a measured line from a buoy, were not practical.

Settlement panels in open and closed cages were immersed at each site for five three-month periods between July 1973 and October 1974. To determine seasonal effects I compared panels immersed at different times of the year.

Data were not obtained from each site in each season because panels were sometimes lost from the frames. Alternative sites were constructed close to those on the Wistari reef slope (Figure 4:1) to cope with this problem, and on the north slope the site NSG was used as an alternative to NSM, but I could not construct suitable alternative sites in other areas. When panels were lost panels from an alternative site were examined instead where possible, and in some cases uncaged panels were used when panels in open cages were lost (Table 4:01).

Panels from the deepest sites (WSD, NSD) and from the Eastern Cave site (EC) took longer to examine than other panels, and only some of them were examined (Table 4:02). The estimation of species' abundances on each side of each panel is described in Chapter 2.

TABLE 4:01

PANELS LOST AND REPLACED AT EIGHT SAMPLE SITES.

Sampling period	Panels lost		Replacement Panels	
	Site	Caging Treatment	Site	Caging Treatment
July 1973-Oct. 1973	WSS	Open cage	WSS(2)	Open cage
July 1973-Oct. 1973	WSS	Closed cage	WSS(2)	Closed cage
July 1973-Oct. 1973	WSM	Open cage	WSM(2)	Open cage
July 1973-Oct. 1973	WSM	Closed cage	WSM(2)	Closed cage
Oct. 1973-Jan. 1974	WSM	Open cage	WSM(2)	Open cage
Oct. 1973-Jan. 1974	WSM	Closed cage	WSM(2)	Closed cage
Jan. 1974-April 1974	NSS	Open cage	NSS	Uncaged panel
July 1973-Oct. 1973	NSM	Open cage	NSG	Open cage
July 1973-Oct. 1973	NSM	Closed cage	NSG	Closed cage
Oct. 1973-Jan. 1974	NSM	Closed cage	NSG	Closed cage
July 1974-Oct. 1974	WCE	Open cage	WCE	Uncaged panel
April 1974-July 1974	WCW	Open cage	WCW	Uncaged panel
July 1974-Oct. 1974	WCW	Open cage	WCW	Uncaged panel
Jan. 1974-April 1974	NSA	Open cage	NSA	Uncaged panel
Jan. 1974-April 1974	NSA	Closed cage	Not replaced.	
July 1973-Oct. 1973	NSC	Open cage	Not replaced.	
July 1973-Oct. 1973	NSC	Closed cage	Not replaced.	
Oct. 1973-Jan. 1974	NSC	Open cage	NSC	Uncaged panel.

TABLE 4:02.

PANELS FROM SITES WSD, NSD, AND EC WHICH WERE EXAMINED.[x]

Site	Sampling Periods
WSD	July 1973 - October 1973
	October 1973 - January 1974
	April 1974 - July 1974
NSD	July 1974 - October 1974
EC	April 1973 - July 1973
	October 1973 - January 1974
	January 1974 - April 1974[+]

[x] Panels from both closed and open cages were examined for each sampling season.

[+] Two panels were immersed for this period in closed cages and both were examined.

4.3 THE EFFECT OF ILLUMINATION AS SHOWN BY THE DIFFERENCES BETWEEN CAVES AND OTHER SITES.

Introduction

Many species of algae did not occur in any samples from caves, whereas many animals which occurred in caves were absent or rare at non-cave sites. A comparison of cave and non-cave sites by means of an analysis of variance was not appropriate because very few species were common to both areas. Instead I calculated the total abundance of each species on equal numbers of samples from cave sites, and non-cave sites at 5m, 10m, and 14 to 17m depths (appendix 4D). Illumination decreased with depth at non-cave sites, but was lowest at cave sites. Because the samples were taken at various times of the year, and at a number of sites, the totals for each group of samples are probably broadly representative of caves, and of non-cave situations at each depth.

Results

1) Algae: Of seventy-five species of algae which were recorded from non-cave sites fifty were absent from cave sites. Apart from encrusting corallines, only twenty species of algae were recorded from cave sites, and all but two of these were more abundant on samples from non-cave sites (appendix 4D). One of the exceptions occurred only once and was not identified, and the second was a species of Pocockiella.

The null hypothesis that species of algae found in caves were equally abundant at cave and non-cave sites was rejected at $p = 0.01$, using a Wilcoxon matched pairs signed ranks test (Siegel

1956). Encrusting corallines, however, were excluded from this test. These were the most abundant algae on samples from caves, and although the most abundant species, Tenerea sp, was more abundant at non-cave sites, other species may have been most abundant at cave sites (see appendix 4D).

2) Animals: Sessile animals occurred frequently on the samples from non-cave sites. Many species were more common at deep than at shallow non-cave sites, and most common in caves (appendix 4D). As many of the totals for each species were based on very few samples I divided the species into taxonomic groups such as ascidians, sponges, etc. and used a Friedman analysis of variance by ranks (Siegel 1956) to test whether the abundances of species in these taxa differed between groups of samples (Table 4:03).

For most groups of animals, abundances were significantly different, at $p = 0.05$, between cave sites and non-cave sites at various depths. However, there were no significant differences for molluscs, and for a miscellaneous group of species including polychaetes, a barnacle, and crinoid juveniles.

Sessile animals might be expected to be least abundant at the shallowest non-cave sites where illumination was greatest; to increase in abundance with depth at the non-cave sites; and to be most abundant in caves. A test proposed by Page (1963) was used to examine this hypothesis (Table 4:04). The trend in abundances proposed above was significant at $p = 0.05$ for all groups of species except molluscs and soft corals. Both these groups were most abundant, in general, at the deepest non-cave sites (appendix 4D).

TABLE 4:03

RESULTS OF A FRIEDMAN ANALYSIS OF VARIANCE BY RANKS ON THE TOTAL ABUNDANCES OF ANIMAL SPECIES ON SAMPLES FROM SITES IN CAVES, AND FROM NON-CAVE SITES AT THREE DIFFERENT DEPTHS.

Taxonomic group	Chi-square value+	Significance*
Ascidians	9.93	S
Arborescent ectoprocts	37.40	S
Encrusting ectoprocts	57.80	S
Sponges	15.95	S
Molluscs	5.46	n.s.
Soft corals	11.94	S
Other, excluding corals	5.82	n.s.

\+ The chi-square value has three degrees of freedom

* S = significant at $p = 0.05$, n.s. = not significant at $p = 0.05$.

TABLE 4:04

RESULTS OF PAGE'S L TEST OF A TREND OF INCREASING ABUNDANCE OF ANIMALS FROM SHALLOW NON-CAVE SITES TO DEEP NON-CAVE SITES, AND CAVE SITES.

Taxonomic group	Observed value of L	Critical value of L	Significance*
Ascidians	250	240	S
Arborescent ectoprocts	603	547	S
Encrusting ectoprocts	760	675	S
Sponges	308	292	S
Molluscs	134.5	137	n.s.
Soft corals	110.5	137	n.s.
Other, excluding corals	137.5	137	S

* S = significant at p = 0.05, n.s. = not significant at p = 0.05.

Coral juveniles were excluded from the above tests. They were common at both the shallowest and the deepest non-cave sites, but as it was impossible to separate the juvenile corals into species, different species may have been abundant at each depth.

Discussion of Results

1) Individual species: In contrast to other algae Pocockiella was most abundant in caves. Pocockiella was found on settlement panels from non-cave sites, but always growing out of the holes used to suspend the panels. These holes were shaded, as the panels were suspended vertically, and were not included in the sample areas from which algal cover was estimated (see Chapter 2). Pocockiella also occurs on the reef flat and reef crest at Heron Island (Grassle 1973), often growing beneath large algae. It therefore appears to occur mainly in shaded places.

Encrusting corallines were the most common algae in caves. Some encrusting corallines are known to be dominant only where illumination is reduced (Adey and Vassar 1975, Crossett and Larkum 1966, Littler and Doty 1975). On Heron reef corallines are particularly abundant around the edges of caves and overhangs: they form a transition zone between the filamentous algae growing on well-lit surfaces and the animals which predominate further inside the caves. A series of panels fixed against the substratum at the edge of an overhang became completely covered by coralline algae in six months. The corallines apparently colonise vacant space more rapidly than either filamentous algae or encrusting animals at intermediate levels of illumination.

2) General discussion: Light is necessary for algae and for corals (Connell 1973) to survive and grow, and therefore filamentous algae, corals, and at least one encrusting coralline were reduced in abundance, or absent in caves. Coralline algae and Pocockiella apparently grow in reduced light better than other algae, as reported previously by Crossett and Larkum (1966), and Norton et al (1971).

How illumination affects animals other than corals is not obvious. In field studies the effects of illumination are often confounded with other factors, such as the presence of algae or sediment on the surface. As I could not prevent algae from settling on well-lit surfaces I could not separate these factors by means of experiments. However work by Barnes with barnacles suggests that the reduced abundance of sessile animals on samples from non-cave sites may have been a result of the presence of algae rather than a direct effect of illumination on animals.

In the field barnacles grow more slowly on well-lit surfaces covered with algae than on shaded surfaces (Barnes and Powell 1950, 1953). However, if algae are regularly removed from barnacles they grow more rapidly (Barnes 1955), and there is then no effect of illumination on barnacle growth (Barnes 1953). Barnes (1955) suggested that the algal filaments may become entangled in the barnacle cirri and thus interfere with the barnacles' feeding movements.

It seems likely that similar interactions occur between algae and other animals. Ryland (1960) concluded that dense algal growth and sediment on a surface led to reduced settlement of bryozoans. Since the rate of growth of algae on a surface is determined by illumination, animals which cannot survive or grow rapidly when surrounded by algae will survive best on shaded surfaces. Natural selection may therefore have favoured those variants which settled only on dimly lit surfaces. Both barnacles (Weiss 1947) and bryozoans (Ryland 1960) settled more readily on shaded than on well-lit surfaces in the laboratory, where algae were absent. The fact that the larvae of many sessile animals settle more readily on dark surfaces (Meadows and Campbell 1972) may therefore be an evolutionary consequence of lower survival of colonies which grow amongst algae.

In the present study sessile animals were more abundant at deep than at shallow non-cave sites. Algae presumably grew more slowly in the reduced light at the deeper sites and therefore may have had less effect on the sessile animals.

Molluscs and soft corals were more common at deep non-cave sites than in caves. Molluscs use ciliary currents to draw in their food, and algae may not interfere with this process as much as with the feeding of bryozoans and barnacles. Juveniles of soft corals were completely absent in caves. They may be more exposed to predation by small fish when they are not surrounded and hidden by algae.

In summary, the hard limestone surfaces of coral reefs seem to be divided between animals and plants according to the illumination reaching the surface. The animals may be most abundant in the dark because they cannot grow rapidly,or perhaps even survive, surrounded by algae. Coralline algae grow well in dim light, and dominate the transition zone between animals and filamentous algae.

4:4 THE DISTRIBUTION OF ALGAE IN RELATION TO VARIOUS COMPONENTS OF ENVIRONMENT.

Introduction

In this section I discuss the effects on algal abundances of the duration of immersion of the panels, and of season, wave action, depth, illumination, and water-movement. Data from non-cave sites were used, and the abundances of the twenty-three species of algae which were present on more than half of the samples were analysed using a multiple regression procedure.

Some limitations of multiple regression analysis are described, and the regression procedure used is discussed, in appendix 4E. A log transformation ($x = \log_e(x+1)$) of the abundances of each species was necessary, and a 'backward elimination' procedure was used where 'independent' variables were correlated. The independent variables used were the components of environment listed earlier, and 'caging treatment', since panels were suspended in open or closed cages. Seasonal changes were measured by two variables: 'season 1' describes the change from summer to winter, and 'season 2' describes the change from autumn to spring (see appendix 4E). Values of the independent variables were the same for each species because the species were all measured on the same set of samples.

The effects of caging treatment and the interactions of caging with other components of environment are discussed in the next chapter. Other interactions were not considered: only the overall effect of each component of environment was evaluated. In some instances, therefore, interactions may have obscured the effects of variables.

Results

Most of the components of environment investigated were not important in determining species' abundances. Twenty-three tests of significance at $p = 0.05$ are reported in each of the tables which follow, so that some significant results would be expected by chance.

1) Duration of immersion: This variable was included to check whether the unavoidable variation in the times for which panels were immersed was important for any of the species. Immersion time and 'season 2' were correlated, and only the independent effects of duration of immersion were tested (see appendix 4E). These effects were small: for most algal species only a small percentage of the variation in abundances was attributed to this factor (Table 4:05). However, significant effects of immersion time were detected at $p = 0.05$ for nine species.

For two species the regression slopes of abundance on duration of immersion were negative, so that these species were less abundant on older panels. Six species were more abundant on older panels, as the regression slopes were positive. All the encrusting species (the last four in the table) had significant positive regression slopes, so that 'ground cover' was much greater on older panels.

2) Seasonal changes: The variables measuring the changes from summer to winter and from autumn to spring were both important in determining species' abundances (Tables 4:06, 4:07). Each variable accounted for over five percent of the variation in abundance of about half the species.

TABLE 4:05

RESULTS OF REGRESSION ANALYSES ON ALGAL ABUNDANCES:

THE EFFECT OF DURATION OF IMMERSION (DAYS)

Species	Percentage of variation explained	Regression slope and Significance*	
Antithamnion sp 1	0.19	0.009	n.s.
Antithamnion sp 2	0.96	0.019	n.s.
Bryopsis sp	0.26	0.010	n.s.
Callithamnion sp 2	1.34	-0.023	n.s.
Champia sp	0.08	-0.002	n.s.
Cladophora sp	5.16	0.031	S
'*Ectocarpus*' sp 1	0.26	-0.013	n.s.
'*Ectocarpus*' sp 2	10.13	0.078	S
'*Ectocarpus*' sp 3	3.96	0.053	S
Enteromorpha sp	0.03	0.005	n.s.
Jania sp	0.43	0.004	n.s.
Laurencia sp 1	3.80	-0.012	S
Laurencia sp 3	0.01	0.001	n.s.
'*Lophosiphonia*' sp 1	0.01	0.001	n.s.
'*Lophosiphonia*' sp 2	0.84	0.014	n.s.
Lyngbya sp	0.31	-0.011	n.s.
Polysiphonia sp 1	4.03	-0.073	S
Pseudobryopsis sp 1	0.13	-0.011	n.s.
Sphacelaria sp	1.34	-0.009	n.s.
Ralfsia sp 2	4.30	0.054	S
Tenerea sp	6.51	0.073	S
Coralline sp 2	2.15	0.024	S
Coralline sp 3	4.79	0.023	S

* S = significantly different from zero at p = 0.05.
ns = not significantly different from zero at p = 0.05.

TABLE 4:06

RESULTS OF REGRESSION ANALYSES ON ALGAL ABUNDANCES:

THE EFFECT OF THE CHANGE FROM SUMMER TO WINTER (SEASON 1)

Species	Percentage of variation explained	Regression slope and Significance*	
Antithamnion sp 1	2.39	-0.166	n.s.
Antithamnion sp 2	1.27	-0.118	n.s.
Bryopsis sp	0.37	-0.063	n.s.
Callithamnion sp 2	4.33	-0.234	S
Champia sp	2.19	-0.059	n.s.
Cladophora sp	5.88	-0.175	S
'*Ectocarpus*' sp 1	6.82	0.379	S
'*Ectocarpus*' sp 2	3.26	0.271	S
'*Ectocarpus*' sp 3	0.02	0.019	n.s.
Enteromorpha sp	28.13	0.834	S
Jania sp	11.73	-0.109	S
Laurencia sp 1	0.39	-0.023	n.s.
Laurencia sp 3	0.41	-0.052	n.s.
'*Lophosiphonia*' sp 1	10.78	-0.448	S
'*Lophosiphonia*' sp 2	0.82	-0.073	n.s.
Lyngbya sp	18.53	-0.574	S
Polysiphonia sp 1	1.16	0.112	n.s.
Pseudobryopsis sp 1	0.01	-0.014	n.s.
Sphacelaria sp	1.84	-0.058	n.s.
Ralfsia sp 2	3.40	0.267	S
Tenerea sp	32.15	-0.850	S
Coralline sp 2	12.79	-0.315	S
Coralline sp 3	17.86	-0.230	S

* S = significantly different from zero at $p = 0.05$.
n.s. = not significantly different from zero at $p = 0.05$.

TABLE 4:07

RESULTS OF REGRESSION ANALYSES ON ALGAL ABUNDANCES: THE EFFECT OF THE CHANGE FROM AUTUMN TO SPRING.

Species	Percentage of variation explained	Regression slope and significance*	
Antithamnion sp 1	0.01	-0.002	n.s.
Antithamnion sp 2	0.24	0.055	n.s.
Bryopsis sp	15.44	-0.449	S
Callithamnion sp 2	5.73	0.290	S
Champia sp	4.03	0.089	S
Cladophora sp	1.35	0.314	S
'*Ectocarpus*' sp 1	0.39	-0.099	n.s.
'*Ectocarpus*' sp 2	13.21	-1.117	S
'*Ectocarpus*' sp 3	4.80	-0.764	S
Enteromorpha sp	14.82	-0.666	S
Jania sp	2.56	0.056	n.s.
Laurencia sp 1	6.01	0.201	S
Laurencia sp 3	5.09	0.200	S
'*Lophosiphonia*' sp 1	16.97	0.618	S
'*Lophosiphonia*' sp 2	4.86	0.194	S
Lyngbya sp	16.27	0.595	S
Polysiphonia sp 1	10.31	0.822	S
Pseudobryopsis sp 1	7.10	-0.484	S
Sphacelaria sp	4.61	0.100	S
Ralfsia sp 2	4.14	-0.680	S
Tenerea sp	0.07	-0.095	n.s.
Coralline sp 2	2.13	0.313	S
Coralline sp 3	0.95	-0.134	n.s.

* S = significantly different from zero at $p = 0.05$.
n.s. = not significantly different from zero at $p = 0.05$.

The change from summer to winter corresponds to the change from highest to lowest water temperatures (appendix 4C). The regression slope of abundance on 'season 1' (Table 4:06) was negative for most species: they were more abundant during the warmer months. Similarly the regression slope for the change from autumn to spring (Table 4:07) was positive for most species: they were most abundant in spring.

Species of '*Ectocarpus*', *Enteromorpha*, and *Ralfsia* were more abundant in winter than in summer (Table 4:06) and in autumn than in spring (Table 4:07), while *Bryopsis* sp. and *Pseudobryopsis* sp 1. showed no significant change between summer and winter, but were more abundant in autumn than in spring. Only *Antithamnion* sp 1 and sp 2 showed no significant seasonal effects.

3) Wave action: Wave action and water-movement were correlated, and only the independent effects of wave action were examined (appendix 4E). For most species wave action explained very little of the variation in abundances (Table 4:08). Wave action was apparently not an important component of environment for filamentous and encrusting algae.

Significant effects of wave action were detected for eight species. Coralline sp 3, an encrusting alga, was more abundant where wave action was greater. Seven species were less abundant where wave action was severe.

4) Depth: Depth was negatively correlated with illumination and only the independent effects of depth were examined. The percentages of variation attributed to depth were small for most species (Table 4:09). Nevertheless these effects were significant for five species: *Ralfsia* sp 2 and '*Ectocarpus*' sp 3 were more

TABLE 4:08

RESULTS OF REGRESSION ANALYSES ON ALGAL ABUNDANCES:

THE EFFECT OF WAVE ACTION.

Species	Percentage of variation explained	Regression slope and significance*	
Antithamnion sp 1	0.22	-0.099	n.s.
Antithamnion sp 2	1.88	-0.267	n.s.
Bryopsis sp	9.69	-0.609	S
Callithamnion sp 2	3.13	-0.355	S
Champia sp	0.08	-0.021	n.s.
Cladophora sp	13.03	-0.489	S
'*Ectocarpus*' sp 1	1.79	-0.366	n.s.
'*Ectocarpus*' sp 2	0.08	0.079	n.s.
'*Ectocarpus*' sp 3	0.07	0.070	n.s.
Enteromorpha sp	2.17	-0.436	S
Jania sp	0.01	0.005	n.s.
Laurencia sp 1	4.07	-0.138	S
Laurencia sp 3	0.72	0.129	n.s.
'*Lophosiphonia*' sp 1	0.29	0.138	n.s.
'*Lophosiphonia*' sp 2	5.96	-0.368	S
Lyngbya sp	2.71	-0.413	S
Polysiphonia sp 1	0.99	-0.199	n.s.
Pseudobryopsis sp 1	1.77	0.417	n.s.
Sphacelaria sp	1.22	-0.088	n.s.
Ralfsia sp 2	0.01	-0.018	n.s.
Tenerea sp	1.27	0.317	n.s.
Coralline sp 2	1.17	0.180	n.s.
Coralline sp 3	3.77	0.198	S

* S = significantly different from zero at p - 0.05.
n.s = not significantly different from zero at p = 0.05.

TABLE 4:09

RESULTS OF REGRESSION ANALYSES ON ALGAL ABUNDANCES:

THE EFFECT OF DEPTH.

Species	Percentage of variation explained	Regression slope and significance*	
Antithamnion sp 1	2.24	0.063	n.s.
Antithamnion sp 2	25.98	0.203	S
Bryopsis sp	0.07	0.011	n.s.
Callithamnion sp 2	5.94	0.104	S
Champia sp	0.01	0.001	n.s.
Cladophora sp	0.29	-0.015	n.s.
'Ectocarpus' sp 1	1.84	-0.076	n.s.
'Ectocarpus' sp 2	1.67	-0.075	n.s.
'Ectocarpus' sp 3	2.06	-0.080	S
Enteromorpha sp	0.67	-0.050	n.s.
Jania sp	2.15	0.018	n.s.
Laurencia sp 1	0.24	-0.007	n.s.
Laurencia sp 3	0.06	0.008	n.s.
'Lophosiphonia' sp 1	3.20	0.094	S
'Lophosiphonia' sp 2	0.22	-0.014	n.s.
Lyngbya sp	1.64	-0.066	n.s.
Polysiphonia sp 1	7.91	0.069	S
Pseudobryopsis sp 1	0.08	0.018	n.s.
Sphacelaria sp	0.03	-0.003	n.s.
Ralfsia sp 2	3.19	-0.099	S
Tenerea sp	0.34	-0.034	n.s.
Coralline sp 2	0.73	0.029	n.s.
Coralline sp 3	0.22	-0.010	n.s.

*S = significantly different from zero at p = 0.05.
n.s. = not significantly different from zero at p = 0.05.

abundant at shallow sites, and four species were more abundant at deeper sites.

5) Illumination: Water-movement and illumination were correlated. I have calculated the regression slopes, F values, and percentages of variation explained with both variables in the regression; and also the percentage variation in abundances explained by each variable when the other was omitted.

Even when water-movement was omitted from the regression, illumination explained less than five per cent of the variation in abundance for all but five species (Table 4:10). For Antithamnion sp 1 and Lyngbya sp much of this variation could also be explained by changes in water-movement, so that the effects of illumination were significant at p = 0.05 only for three species. All three species were more abundant under brighter illumination.

6) Water-movement: Significant effects of water-movement were detected for only six species (Table 4:11). Five of these were more abundant where water-movement was greater, as the regression slopes were positive.

There was a significant negative regression of abundance on water-movement for Tenerea sp. However for this species illumination acted as a suppressor variable (see appendix 4E). When illumination was omitted, the regression slopes of abundance on water-movement was positive (0.074), and significant at p = 0.05. Since the independent effects of illumination were not significant for Tenerea (Table 4:10) the results obtained with illumination omitted should be used.

TABLE 4:10

RESULTS OF REGRESSION ANALYSES ON ALGAL ABUNDANCES: THE EFFECT OF ILLUMINATION.

Species	Percentage of variation explained		Regression slope and significance*	
	A+	B+		
Antithamnion sp 1	6.32	2.41	-0.006	n.s.
Antithamnion sp 2	8.83	7.95	0.020	S
Bryopsis sp	3.61	0.41	-0.003	n.s.
Callithamnion sp 2	0.25	0.88	0.007	n.s.
Champia sp	0.01	0.01	-0.001	n.s.
Cladophora sp	3.77	0.03	0.001	n.s.
'*Ectocarpus*' sp 1	1.71	1.63	0.007	n.s.
'*Ectocarpus*' sp 2	5.30	4.88	0.013	S
'*Ectocarpus*' sp 3	0.36	0.13	0.004	n.s.
Enteromorpha sp	0.24	1.00	0.006	n.s.
Jania sp	1.29	0.12	-0.001	n.s.
Laurencia sp 1	1.12	0.73	0.001	n.s.
Laurencia sp 3	0.49	0.32	-0.002	n.s.
'*Lophosiphonia*' sp 1	0.70	1.17	0.010	n.s.
'*Lophosiphonia*' sp 2	0.19	0.11	0.001	n.s.
Lyngbya sp	5.83	1.99	0.008	n.s.
Polysiphonia sp 1	0.33	0.30	-0.001	n.s.
Pseudobryopsis sp 1	4.89	2.50	0.010	n.s.
Sphacelaria sp	5.71	4.03	0.003	S
Ralfsia sp 2	0.06	0.04	0.004	n.s.
Tenerea sp	0.09	0.62	0.004	n.s.
Coralline sp 2	1.27	0.24	-0.002	n.s.
Coralline sp 3	0.17	0.49	0.002	n.s.

* S = significantly different from zero at p = 0.05
n.s. = not significantly different from zero at p = 0.05.

\+ A is the percentage of variation explained when water-movement was omitted from the regression. B is the percentage when water-movement was included.

TABLE 4:11

RESULTS OF REGRESSION ANALYSES ON ALGAL ABUNDANCES: THE EFFECT OF WATER-MOVEMENT.

Species	Percentage of variation explained		Regression slope and significance*	
	A+	B+		
Antithamnion sp 1	5.41	1.63	0.041	n.s.
Antithamnion sp 2	0.87	0.01	-0.002	n.s.
Bryopsis sp	5.37	2.17	0.057	S
Callithamnion sp 2	2.60	3.23	0.073	S
Champia sp	0.03	0.02	0.002	n.s.
Cladophora sp	12.09	8.36	0.077	S
'Ectocarpus' sp 1	0.23	0.09	0.011	n.s.
'Ectocarpus' sp 2	0.58	0.20	0.019	n.s.
'Ectocarpus' sp 3	0.70	0.47	-0.030	n.s.
Enteromorpha sp	0.27	1.03	0.059	n.s.
Jania sp	3.42	2.18	0.014	n.s.
Laurencia sp 1	8.44	8.04	0.038	S
Laurencia sp 3	0.39	0.11	0.007	n.s.
'Lophosiphonia' sp 1	0.44	0.92	0.040	n.s.
'Lophosiphonia' sp 2	0.07	0.01	- 0.001	n.s.
Lyngbya sp	4.58	0.74	- 0.043	n.s.
Polysiphonia sp 1	0.37	0.34	0.017	n.s.
Pseudobryopsis sp 1	2.92	0.53	-0.035	n.s.
Sphacelaria sp	1.63	0.02	-0.002	n.s.
Ralfsia sp 2	0.04	0.02	-0.006	n.s.
Tenerea sp	3.64	4.22	-0.091	S
Coralline sp 2	2.10	0.98	0.027	n.s.
Coralline sp 3	2.66	2.98	0.035	S

* S = significantly different from zero at p = 0.05.
n.s. = not significantly different from zero at p = 0.05.

\+ A and B as in Table 4:10.

For most species the variation in abundance explained by water-movement was greater when illumination was omitted (Table 4:11). The same is true for illumination when water-movement was omitted (Table 4:10). Thus Antithamnion sp 1, Jania, Lyngbya, Pseudobryopsis sp 1 and Coralline sp 2 were affected either by illumination or by water-movement, or both.

Discussion of Results

1) Species and groups of species: After three months immersion there is a dense cover of filamentous algae on the settlement panels, so that interactions between the species seem possible, but very little is known about the mechanisms of such interactions between algae. The shading effect of canopy forming algae is known to be important (Dayton 1975a, b, Sammarco et al 1974) and one might expect that encrusting species would be shaded by erect filamentous species. This shading however, does not appear to decrease the abundance of the encrusting species, since all the encrusting species were increasing in abundance after three months (Table 4:05). The encrusting corallines are known to grow well in reduced light (see section 4:3).

Two species; Laurencia sp 1 and Polysiphonia sp 1, were less abundant on older panels. It is difficult to explain this result as it seems unlikely that these species were displaced by other species.

Seasonal changes were important for many species. In contrast to other species 'Ectocarpus' spp., Enteromorpha and Ralfsia were more abundant in the colder than the warmer parts of the year. These were some of the most abundant species in the samples throughout the year. They seemed to colonise the panels more rapidly than other species and possibly during the colder months when other species were not as common these 'opportunists' were able to attain a greater abundance on the panels. They all tended to be more abundant under brighter illumination, and less abundant in deep water; although the effect of illumination was significant only for '*Ectocarpus*' sp 2, and depth was significant only for '*Ectocarpus*' sp 3 and *Ralfsia* sp 2. Only *Enteromorpha* was significantly affected by wave action.

These species therefore, constitute a group of opportunistic species which settle rapidly everywhere, but especially on shallow, brightly lit surfaces. The two less common '*Ectocarpus*' species, and *Ralfsia* sp 2, were more abundant on older panels (Table 4:05) which suggests that they may take longer to reach peak abundance on the panels than the other species.

Bryopsis and *Pseudobryopsis* sp 1 were patchily distributed. They were usually rare, but were abundant in autumn at most sites, and also at other times of the year at some sites. *Pseudobryopsis* in fact, was the most abundant species in some samples.

Most species were more abundant in the warmer than the colder parts of the year (Tables 4:06, 4:07). This group included a number of species with relatively large thalli (for example *Cladophora*, *Laurencia* spp), four species of smaller filamentous algae ('*Lophosiphonia*' sp 1 and sp 2, *Lyngbya* and *Sphacelaria*), and the jointed and encrusting corallines (*Jania*, *Tenerea*, coralline sp 2, and coralline sp 3). I will return to these groups in discussing the effects of caging in the next chapter.

Many species with relatively large thalli were significantly less common in areas of high wave action. These included *Bryopsis* and *Enteromorpha* as well as the 'warm water' species *Callithamnion* sp 2, *Cladophora* and *Laurencia* sp 1 (Table 4:08). Some of the species also appeared to be more abundant at sites with high water-movement (Table 4:11). Species with larger thalli may be more susceptible to the shear forces generated by wave action, while they may benefit from a higher average flow of water because this would result in an increased exchange of metabolites between the thalli and the water.

Water-movement and wave action were both apparently beneficial for coralline sp 3. This encrusting species may grow more rapidly in turbulent conditions where the velocity gradient is broken down so that the water close to the surface of the panel moves rapidly.

Antithamnion sp 2, *Callithamnion* sp 2, *Lophosiphonia* sp 1, and *Polysiphonia* sp 1 were more abundant in deep water (Table 4:09). These were all red algae, which are known to penetrate to deeper water than green algae (Drew 1971). *Anthithamnion* sp 1 probably belongs in this group of deep water species too: at shallow sites it was patchily distributed and was often epiphytic on other algae, whereas at the deepest site it was consistently common on the panel surfaces. Seasonal changes might be expected to be less important for deep water species, and the two *Antithamnion* species were the only algae which showed no seasonal changes in abundance.

2) General discussion: The fact that illumination was not an important component of environment for most species (Table 4:10) is surprising in view of the importance of light energy for algal growth and the virtual absence of algae from cave sites (section 4:3). The range of illumination in the data analysed here is small, and the results suggest a threshold effect: at dimly lit places the amount of light reaching the surface may be more important than in brightly lit places.

The effects of changes in illumination may have been underestimated in this analysis, because of the difficulties associated with measuring the average illumination on a settlement panel over three months (appendix 4B). In addition the algae themselves shade the surface, so that encrusting or prostrate species probably experience much lower levels of illumination than larger species, especially those which colonise new surfaces rapidly. Of the components of environment investigated, seasonal changes appeared to be most important. The species may be divided into two major groups: opportunists which were abundant throughout the year but especially in winter, and species which became common in the warmer parts of the year (October to April). Opportunistic species would be expected to be abundant on the settlement panels because the panels were immersed for only three months. If the opportunists are replaced by other species as the age of a patch of surface increases then continuous reproduction throughout the year would be necessary for these species to maintain their abundance on the reef.

The surfaces of the reef may be regarded as a mosaic of patches of various ages, with fresh patches appearing constantly as a result of grazing by fish, and other disturbances. Horn and

MacArthur (1972) have shown how fugitive species may survive in such a 'harlequin' environment.

The species which were common during the warmer part of the year seem to colonise fresh surfaces more slowly. They were more often affected by other factors, such as wave action, than the opportunistic species.

In summary, most of the components of environment investigated were important for only a few species of algae, and therefore were not important in partitioning the environment between the species. At best, opportunistic species were partly divided in time from other species, some species were rare where wave action was severe, and a few species were less abundant in deeper water or in darker places, where some species of red algae were more common.

These negative results are important. If the species composition of algae on any particular patch of surface is determined by anything other than chance, that is, if there is any structure in the algal association, then this must lie either in the effects of herbivores on the algae, or in the effects of algal species on each other.

4:5 THE DISTRIBUTION OF SESSILE ANIMALS WITH RESPECT TO VARIOUS COMPONENTS OF ENVIRONMENT.

The effects of duration of immersion, seasonal changes, depth, illumination, wave action, and water-movement on the abundances of twenty-four species of animals are discussed in this section. The species analysed included one colonial ascidian, a colonial polychaete (Filograna implexa), eight arborescent ectoprocts, thirteen encrusting ectoprocts, and the oyster Patro australis. Since arborescent bryozoans and Filograna have aggregated distributions on the settlement panels (see Chapter 3) the results for these species must be viewed with some caution.

For the oyster data from all the sites sampled were used, but for the remaining species only data from the five cave sites and the deepest non-cave sites (WSD and NSD) were used. A log transformation of the abundances of each species was necessary. The analysis was similar to that used for algae, but as the correlations between the values of the independent variables were different, the 'backwards elimination' regression procedure for animals was different from that used for algae, and the procedure for the oyster also differs slightly from that used for other species (see appendix 4E). The effects of 'caging treatment' are discussed in Chapter 5 (section 4).

Results

The components of environment investigated were more important in determining the abundances of sessile animals than of algae, although seasonal effects appeared to be less important.

1) Duration of immersion: This factor was included to check whether the unavoidable variation in immersion time (71-98 days) was important. A significant effect was detected for thirteen species (Table 4:12), and for seven of these over five per cent of the variation in abundance was explained by this factor. In each case the species were more abundant on older panels.

2) Seasonal changes: The change from summer to winter was a significant variable in the regression for fourteen species (Table 4:13), and the proportion of variation explained was high for many others. However the change from autumn to spring appeared to be less important (Table 4:14).

Some species (AB9, EB1, EB7, Patro australis) were abundant in spring and summer, and less common in autumn and winter. Five more species were more abundant in summer than in winter but were about as common in spring as in autumn. All these species were most abundant at times when the water temperatures were high. However AB1, AB3, AB13, AB14, and EB14 were common at most times of the year except spring (AB13, AB14), or summer (AB1, AB3, EB14). Inspection of the data showed that except for AB13 these seasonal changes were repeated at a number of sites, so that the results were not due to clustering effects except perhaps for AB13.

EB1A and EB2 were more abundant in winter than in summer, but also more abundant in spring than in autumn, so that they were abundant from July to January, but rare in the first half of the year. These results cannot be explained on the basis of water temperatures. Eight other species, mostly encrusting bryozoans, showed no significant seasonal changes.

TABLE 4:12

RESULTS OF REGRESSION ANALYSES ON ANIMAL, ABUNDANCES: THE EFFECT OF DURATION OF IMMERSION (DAYS).

Species	Percentage of variation explained	Regression Slope and Significance*	
Ascidian B.	4.71	0.010	S
AB 1	0.99	0.011	n.s.
AB 3	1.05	0.011	n.s.
AB 4	8.27	0.014	S
AB 5	1.79	0.015	n.s.
AB 9	2.39	-0.008	n.s.
AB13	5.20	0.032	S
AB14	6.30	0.031	S
AB17	20.40	0.030	S
EB 1	0.52	0.005	n.s.
EB 1A	0.04	-0.001	n.s.
EB 2	0.79	0.002	n.s.
EB 6	5.56	0.035	S
EB 7	5.01	0.015	S
EB 8	0.48	0.003	n.s.
EB 9	0.10	0.002	n.s.
EB10	0.33	0.001	n.s.
EB12	3.43	0.015	S
EB14	0.10	0.002	n.s.
EB16	3.43	0:013	S
EB18	8.48	0.018	S
EB29	3.51	0.005	S
Filograna implexa	4.68	0.024	S
Patro australis	2.36	0.014	S

*S = significantly different from zero at $p = 0.05$.
n.s. = not significantly different from zero at $p = 0.05$.

TABLE 4:13

RESULTS OF REGRESSION ANALYSES ON ANIMAL ABUNDANCES: THE EFFECT OF THE CHANGE FROM SUMMER TO WINTER (SEASON 1).

Species	Percentage of variation explained	Regression slope and Significance*	
Ascidian B.	16.58	-0.202	S
AB 1	16.12	0.418	S
AB 3	9.67	0.306	S
AB 4	2.90	-0.090	n.s.
AB 5	0.99	-0.108	n.s.
AB 9	3.31	-0.086	S
AB13	2.29	-0.226	n.s.
AB14	0.01	0.014	n.s.
AB17	6.02	-0.172	S
EB 1	4.07	-0.124	S
EB 1A	4.68	0.122	S
EB 2	7.41	0.061	S
EB 6	1.83	-0.215	n.s.
EB 7	12.64	-0.250	S
EB 8	0.40	0.022	n.s.
EB 9	0.82	-0.061	n.s.
EB10	0.82	-0.019	n.s.
EB12	11.17	-0.294	S
EB14	12.96	0.204	S
EB16	0.19	0.033	n.s.
EB18	9.13	-0.199	S
EB29	1.83	0.041	n.s.
Filograna implexa	4.68	-0.255	S
Patro australis	13.73	-0.291	S

*S = significantly different from zero at p = 0.05,
n.s. = not significantly different from zero at p = 0.05.

TABLE 4:14

RESULTS OF REGRESSION ANALYSES ON ANIMAL ABUNDANCES: THE EFFECT OF THE CHANGE FROM AUTUMN TO SPRING (SEASON 2).

Species	Percentage of variation explained	Regression slope and Significance*	
Ascidian B.	0.76	-0.042	n.s.
AB 1	0.74	0.097	n.s.
AB 3	0.04	0.020	n.s.
AB 4	1.15	-0.055	n.s.
AB 5	0.92	-0.103	n.s.
AB 9	5.29	0.107	S
AB13	3.56	-0.274	S
AB14	7.38	-0.344	S
AB17	0.01	-0.005	n.s.
EB 1	8.19	0.174	S
EB 1A	2.41	0.086	S
EB 2	4.58	0.047	S
EB 6	1.16	-0.167	n.s.
EB 7	2.73	0.113	S
EB 8	1.35	0.040	n.s.
EB 9	1.29	-0.076	n.s.
EB10	0.24	0.010	n.s.
EB12	1.04	-0.087	n.s.
EB14	0.59	0.043	n.s.
EB16	0.82	-0.067	n.s.
EB18	0.85	-0.059	n.s.
EB29	0.02	-0.005	n.s.
Filograna implexa	0.29	-0.061	n.s.
Patro australis	4.48	0.225	S

*S = significantly different from zero at $p = 0.05$,
n.s. = not significantly different from zero at $p = 0.05$.

3) Depth: Very little of the variation in species' abundances was attributable to depth (Table 4:15). Only Patro australis and four encrusting bryozoans showed significant changes in abundance with depth. All were more abundant at deeper sites, as the regression slopes were positive.

4) Illumination: A significant effect of illumination was detected for ten species (Table 4:16). Generally the regression slopes were negative: the animals were more abundant in darker places. Many of these results are a reflection of the virtual absence of the species concerned from the WSD and NSD sites, which were the only sites not in caves. These results are therefore in agreement with those reported in section 4:3. However, EB1A was more abundant at brightly lit sites, including the WSD and NSD sites, than in the darkest caves.

5) Wave action and water-movement: Tables 4:17 and 4:18 show the percentages of the variation in abundances explained by wave action and water-movement when both variables were included in the regressions, and also when each was omitted. The differences between columns A and B are a result of the high correlation between wave action and water-movement (correlation coefficient = 0.786).

Wave action alone explained much of the variation in abundance of a number of species (Table 4:17, column A), but in many instances some of this variation could also be explained by changes in water-movement. As a result the independent effects of wave action were not significant at $p = 0.05$ for AB13, AB14, and EB6. The independent effects of water-movement were not significant for these species either (Table 4:18), so that either

TABLE 4:15

RESULTS OF REGRESSION ANALYSES ON ANIMAL ABUNDANCES: THE EFFECT OF DEPTH.

Species	Percentage of variation explained	Regression Slope and Significance*	
Ascidian B.	1.40	-0.043	n.s.
AB 1	1.56	-0.220	n.s.
AB 3	2.14	0.119	n.s.
AB 4	0.02	0.006	n.s.
AB 5	0.11	-0.030	n.s.
AB 9	0.40	-0.025	n.s.
AB13	0.44	-0.073	n.s.
AB14	1.96	-0.135	n.s.
AB17	1.27	0.058	n.s.
EB 1	0.54	-0.037	n.s.
EB 1A	0.14	0.017	n.s.
EB 2	0.65	0.015	n.s.
EB 6	2.35	0.180	n.s.
EB 7	0.27	-0.027	n.s.
EB 8	1.54	0.036	n.s.
EB 9	5.46	0.131	S
EB10	0.11	0.006	n.s.
EB12	4.26	0.134	S
EB14	3.81	0.092	S
EB16	10.01	0.177	S
EB18	1.28	0.055	n.s.
EB29	0.21	0.010	n.s.
Filograna _implexa_	0.72	-0.074	n.s.
Patro _australis_	3.32	0.036	S

*S = significantly different from zero at p = 0.05,
n.s. = not significantly different from zero at p = 0.05.

TABLE 4:16

RESULTS OF REGRESSION ANALYSES ON ANIMAL ABUNDANCES: THE EFFECT OF ILLUMINATION.

Species	Percentage of variation explained	Regression slope and Significance*	
Ascidian B.	0.16	-0.001	n.s.
AB 1	0.60	0.008	n.s.
AB 3	0.57	-0.003	n.s.
AB 4	5.23	-0.005	S
AB 5	1.51	0.006	n.s.
AB 9	1.02	-0.002	n.s.
AB13	2.19	-0.008	n.s.
AB14	6.85	-0.013	S
AB17	0.40	-0.002	n.s.
EB 1	5.16	-0.006	S
EB 1A	3.26	0.004	S
EB 2	1.71	-0.001	n.s.
EB 6	4.87	-0.013	S
EB 7	10.24	-0.008	S
EB 8	1.50	-0.002	n.s.
EB 9	3.77	-0.019	S
EB10	3.28	-0.002	S
EB12	1.91	-0.016	n.s.
EB14	4.66	-0.018	S
EB16	7.74	-0.027	S
EB18	0.39	-0.002	n.s.
EB29	0.76	-0.001	n.s.
Filograna implexa	1.47	-0.005	n.s.
Patro australis	0.02	-0.0002	n.s.

*S = significantly different from zero at p = 0.05.
n.s. = not significantly different from zero at p = 0.05.

TABLE 4:17

RESULTS OF REGRESSION ANALYSES ON ANIMAL ABUNDANCES: THE EFFECT OF WAVE ACTION.

Species	Percentage of variation explained		Regression Slope and Significance*	
	A+	B+		
Ascidian B.	6.80	3.60	0.194	S
AB 1	0.43	0.01	-0.031	n.s.
AB 3	0.71	3.39	0.414	S
AB 4	0.01	0.64	-0.109	n.s.
AB 5	2.94	3.74	0.481	S
AB 9	12.56	4.78	-0.235	S
AB13	2.92	0.14	-0.117	n.s.
AB14	2.32	0.50	-0.235	n.s.
AB17	21.72	12.03	0.502	S
EB 1	0.24	1.16	-0.190	n.s.
EB 1A	31.83	12.37	0.569	S
EB 2	0.02	0.03	-0.008	n.s.
EB 6	6.53	0.40	0.257	n.s.
EB 7	1.87	2.18	-0.266	n.s.
EB 8	28.05	20.30	0.361	S
EB 9	0.01	4.16	-0.493	S
EB10	0.46	0.92	0.058	n.s.
EB12	0.14	1.70	-0.257	n.s.
EB14	0.38	0.20	0.090	n.s.
EB16	0.09	0.50	0.174	n.s.
EB18	5.35	7.23	0.366	S
EB29	2.64	7.04	0.167	S
Filograna implexa	0.43	4.71	0.528	S
Patro australis	0.36	1.70	-0.206	S

*S = significantly different from zero at $p = 0.05$,
n.s. = not significantly different from zero at $p = 0.05$.

+ A is the percentage of variation explained when water-movement was omitted from the regression, and B is the percentage when water-movement was included.

TABLE 4:18

RESULTS OF REGRESSION ANALYSES ON ANIMAL ABUNDANCES: THE EFFECT OF WATER-MOVEMENT.

Species	Percentage of variation explained		Regression Slope and Significance*	
	A+	B+		
Ascidian B.	3.29	0.08	-0.007	n.s.
AB 1	0.46	0.03	-0.018	n.s.
AB 3	6.35	9.03	-0.159	S
AB 4	0.34	0.97	0.033	n.s.
AB 5	0.43	1.24	-0.065	n.s.
AB 9	7.78	0.01	-0.0002	n.s.
AB13	3.67	0.89	-0.068	n.s.
AB14	1.83	0.01	-0.009	n.s.
AB17	10.07	0.37	-0.020	n.s.
EB 1	0.01	0.92	0.041	n.s.
EB 1A	20.14	0.67	-0.032	n.s.
EB 2	0.10	0.10	0.004	n.s.
EB 6	6.82	0.69	0.082	n.s.
EB 7	6.29	6.60	0.113	S
EB 8	10.19	2.44	-0.030	n.s.
EB 9	2.25	6.41	0.120	S
EB10	0.06	0.51	-0.010	n.s.
EB12	0.26	1.81	0.071	n.s.
EB14	1.26	1.08	-0.041	n.s.
EB16	0.04	0.45	-0.032	n.s.
EB18	0.58	2.46	-0.050	n.s.
EB29	0.01	4.41	-0.031	S
Filograna implexa	0.93	5.20	-0.129	S
Patro australis	0.28	1.61	0.043	S

* S = significantly different from zero at p = 0.05,
n.s. = not significantly different from zero at p = 0.05.

\+ A is the percentage of variation explained when wave action was omitted from the regression, and B is the percentage explained when wave action was included.

wave action, or water-movement, or both were important in determining the abundances of these species. AB13 and AB14 grew best in quiet conditions, whereas EB6 was more abundant in areas of high wave action and water-movement.

In many cases each variable explained more of the total variation in a species' abundance when the other variable was included in the regression. This occurred when the effects of the two variables were opposite in direction. Thus EB9 and Patro australis were apparently reduced in abundance by wave action, but were more abundant in places with high water-movement. In contrast AB3, EB29, and Filograna were more abundant in areas of high wave action, but apparently grew best where there was less water-movement.

Species for which the effects of wave action were significant were usually more abundant at the sites with high wave action.

Discussion of Results.

Many species were more abundant on panels immersed for slightly longer periods. After approximately three months immersion considerable empty space remained on the panels in caves, but the settlement of new recruits on the panels may be reduced due to crowding effects even at this stage (see section 3:4). The radius of ectoproct colonies increases at a constant rate (Vail and Wass, in preparation) so that the area covered by a colony increases as the square of the age of the colony. Therefore, the increased abundances of species on panels immersed for longer periods are probably the result of growth of established colonies rather than the addition of new colonies to the panels. Furthermore Patro australis and EB6 usually settle near the edges of panels (see section 3:2).so that the regression slopes for these species reflect growth from the edges into the central area of the panels.

Although the warmer parts of the year appeared to be favourable for many animals as well as algae, seasonal changes were not important for as many animals as algae (Tables 4:13, 4:14). Nevertheless inspection of the data revealed that seasonal changes were consistent over all the sites, so that there was considerable partitioning of the year between the species. At some times of the year some species were absent everywhere, while other species were abundant at all the sites in the same season.

Wave action and water-movement appeared to be more important for animals than for algae. The shear forces associated with wave action might be expected to reduce the abundance of projecting forms, but three arborescent bryozoans (AB3, AB5, AB17) were more abundant in areas of high wave action. AB3 and AB17 both form heavily calcified rigid colonies, and AB5 grows close to the substratum and is attached to it in many places. AB9 however, which is a delicate, jointed cyclostome, was rare at sites with high wave action; and AB13 and AB14, both similar to AB5 but more erect, were most abundant in quiet conditions.

Many encrusting species were more abundant in areas of high wave action. This is difficult to explain, especially as for AB3, EB29, and Filograna increased water-movement had a negative effect. Possibly fresh patches of natural substratum are created more frequently in areas of high wave action, as a result of pieces of coral being overturned or broken. Colonising species would be abundant where such disturbances are frequent, and more larval recruits would be available to settle on the panels in areas with large resident populations of the colonising species.

Another possibility is that turbulent water-movement past a surface is more important than the average rate of water-movement in determining the rate of supply of food to sessile organisms, and therefore their rate of growth. However the abundance of EB7 was closely related to the rate of water-movement rather than wave action (Tables 4:17, 4:18). It apparently grew best under higher water-movement.

For EB9 and the oyster Patro australis the independent effects of wave action were negative whereas the regression slopes of abundance on water-movement were positive. These results are a reflection of the abundance of both EB9 and the oyster at the WSD site, where water-movement was high but wave action was absent. EB12 and EB16 were also common at the WSD site, and these four species all show an increase in abundance with depth (Table 4:15). They are deep water species which often occur amongst algae on the lower parts of the reef slope as well as in caves and crevices.

Many species were almost entirely restricted to caves, so that illumination was an important component of environment (Table 4:16). However among the species restricted to caves only EB14 was shown to vary in abundance with depth (Table 4:15). This illustrates a problem inherent in the data: because there were no suitable caves on the lowest parts of the reef slope, the deepest sites were the most brightly illuminated sites included in the analysis. Thus depth and illumination were positively correlated in these data whereas they would not normally be so in nature, and the importance of depth as a component of environment has probably been underestimated. Species which settle most abundantly in deep, dark crevices would not have been common at any of the sample sites.

In spite of the possible underestimation of the effects of depth, the components of environment investigated, when taken together, form a basis for considerable partitioning of the environment between the species. Wave action and seasonal changes were apparently most important in this respect.

The animals do not seem to be divided into opportunistic species and 'other species' in the same way as algae. This may be because the panels were colonised more slowly by animals than by algae. Relative to other common sessile animals, most of the species considered here were opportunists. Panels immersed for more than three months usually became covered by various ascidians; or by EB6, EB7, _Filograna_, or _Patro australis_, which were all increasing rapidly in abundance after about three months (Table 4:12). Unless there are places where the other species investigated are safe from being smothered they must presumably colonise patches of fresh surface, grow, and reproduce, before they are smothered. Otherwise the numbers of new larval recruits of these species available to colonise freshly created patches should decline.

The dominant species listed above were all common in summer, and it is therefore of interest that several of the remaining species were common only in autumn or winter (Tables 4:13, 4:14).

Reef surfaces suitable for animals may be regarded as a mosaic of patches with different 'histories', and the results reported here pertain to the abundances of species on patches which are fairly 'young'. The pattern of dominance of some species over others, which determines the 'history' of each patch, is discussed in Chapter 6, and the importance of predation in altering the history of each patch, is discussed in Chapter 5. The results in this section show that wave action, seasonal changes, and other components of environment detemine, to a large extent, which species colonise, and become abundant on fresh patches. The components of environment investigated here determine the initial conditions on the patches. Predation and interactions between the species influence later developments.

CHAPTER 5

PREDATION AND GRAZING

5:1 THE EFFECTS OF PREDATORS AND HERBIVORES IN THE MARINE ENVIRONMENT.

Connell (1961a, 1972, 1975), Dayton (1971) and Paine (1966, 1969, 1971, 1974) have shown by means of field experiments that predation is often important in determining the distribution and abundance of sessile animals on rocky shores. Similar experiments have shown how algae are controlled by herbivores such as limpets (e.g. Dayton 1971, Southward 1964), snails (Castenholz 1961), sea urchins (Ebert 1977, Jones and Kain 1967, Kitching and Ebling 1961, Paine and Vadas 1969), and fish (John and Pople 1973). Many features of the distribution of prey species on rocky shores can be explained in terms of five characteristics of the predator-prey interactions.

1) The intertidal represents a gradient of 'physiological stress' and predators are often unable to reach the highest sites occupied by their prey (Connell 1970, Paine 1974) so the prey has a refuge in space. Refuges in space may also occur as a result of a gradient in wave action (see review by Connell 1972).

2) Large individuals of prey species are often relatively immune from predation (Connell 1970, Dayton 1971, Lodge 1948, Ebling <u>et al</u> 1964, Paine 1974, 1976). The prey therefore have an 'escape in growth' from predation: if individuals are not eaten when young they may attain a size which makes them invulnerable. Escape in growth apparently occurs too, in freshwater zooplankton (Brooks and Dodson 1965) and in rainforest trees (Connell 1970, 1975).

3) Herbivorous animals are often important in preventing the establishment of animals on the surfaces they graze; for example limpets prevent barnacles from becoming established (Branch 1975, Dayton 1971, Stimpson 1970).

4) Predators usually prefer some prey to others (Landenberger 1968, Paine 1969, 1974). This is important because removal of a preferred prey allows species which are lower on the predator's preference list, or which are never eaten, to colonise the areas made vacant (Paine 1966).

5) Carnivores may exert an important influence on the distribution of plants by clearing areas of herbivores, allowing algal succession to occur in these patches (Dayton 1975a).

Sublittoral areas have received less attention, but predation is apparently important in determining species distributions here too. Predation by starfish (Ebling _et al_ 1966, Forster 1975b) and fish (Forster 1975b, Sutherland 1972, 1974) is important for sessile animals such as ascidians, bryozoans, and bivalves; and herbivores such as sea urchins, various molluscs, and fish are important (Dayton 1975a, Kitching and Ebling 1961, Leighton 1971, Neill and Larkum 1966).

There are no easily defined gradients of 'physiological stress' in the sublittoral, but isolated seamounts may provide places of refuge from the starfish _Pisaster_ (Paine, personal communication) and kelp plants in New Zealand appear to have a refuge in space from sea urchins on the tops of boulders in shallow water and on rocks surrounded by sand (Choat, personal communication). Predators may release space for algae by removing sessile animals (Dayton 1975b, Forster 1975), and sea urchins may remove animals as well as algae (Leighton 1971). Furthermore escape in growth from predators by bivalves may occur (Muntz *et al* 1965) and many herbivores in kelp beds have marked food preferences (Leighton 1971).

Predation of sea urchins by starfish and crabs (Muntz *et al* 1965, Ebling *et al* 1966), by lobsters (Mann and Breen 1972), and by sea otters (Estes and Palmisano 1974, Mclean 1962) may maintain algal populations. The urchins may have a refuge in space from their predators in shallow areas or under boulders (Muntz *et al* 1965) or in deep water (Estes and Palmisano 1974); or a refuge in time (Ebling *et al* 1966) during daylight. This diurnal pattern may be set by a fourth trophic level: birds (Ebling *et al* 1966).

Predation and grazing might be expected to be important on coral reefs too, although Jackson *et al* (1971) have argued there is very little predation in some habitats. Herbivores are certainly important, particularly sea urchins (Ogden *et al* 1973, Sammarco *et al* 1974, Schuhmacher 1974) and fish (Bakus 1967, 1969, Earle 1972, Randall 1961, 1965, Stephenson and Searles 1960). Predation on corals by starfish (Porter 1972) and various other organisms (Glynn *et al* 1972) is important, and fish appear to be important predators of sessile animals such as sponges and ascidians (Bakus 1964, 1966). Kohn (1968) has shown that sessile polychaetes fall prey to some *Conus* species, and observations at Heron Island suggest that other molluscs and crabs may also be important predators and herbivores of sessile organisms.

In this study attention was focussed on the effects of predation by fish. Asteroids and echinoids were rare in the area studied, and predation by molluscs and crabs was difficult to study. Large invertebrate predators were excluded by suspending the settlement panels on nylon lines, and cages were used to exclude fish as described in Chapter 2. It should be noted, however, that predatory invertebrates were able to settle on the panels as larvae, and I occasionally found pycnogonids, small nudibranchs, nereid polychaetes, and a juvenile crab on the panels. Furthermore very small fish were able to pass through the mesh of the cages. Thus a small boxfish (Ostracion tuberculatus) was seen feeding inside one of the cages. The experiments therefore demonstrate the effect of predation by large fish rather than predation per se.

Most fish which feed on sessile organisms on coral reefs are diurnal (Hobson 1974). Invertebrate predators and grazers on Heron reef such as crabs and molluscs are usually nocturnal. Serranid and labrid fish prey on these invertebrates, and appear to limit the activities of invertebrates to areas within range of suitable cover, so that predation or grazing by invertebrates would be patchy. Fish appear to feed on almost all the limestone surfaces of the reef except for deep crevices.

A range of fish with specialised feeding mechanisms feed on sessile plants or animals (Hobson 1974). Scarids, Acanthurids, and Pomacentrids were the most common herbivores, while Pomacanthids, various Tetraodontiform fish, and some Chaetodontids (for example Chaetodon auriga) were important predators of sessile animals in caves and crevices.

5:2 THE INTENSITY OF GRAZING BY SCARID FISHES.

Parrotfish (family Scaridae) are distinctive in that their teeth are fused to form a beak, which they use to scrape algae from the limestone surfaces of the reef. They remove some of the limestone in the process, so that they have a mosaic of tiny bare patches. Some Acanthurid fish also scrape the surface (Dawson et al 1955), but Scarids appear to be the most important scraping fish on Heron Reef. Algal covered substrata are intensively grazed by these fish (Bakus 1964, 1967, Choat and Robertson 1975).

To determine the rate at which reef surfaces were cleared of algae by parrotfish an estimate of the area cleared by the average scarid scape was required. Recolonisation of scraped areas by algae around the edges would result in a progressive shrinking of the bare areas, so that I wished to measure only fresh scrapes. Two settlement panels were immersed for four months in closed cages in shallow water. The cages were then removed, and fish allowed to graze the panels for two days. A dense cover of filamentous algae had developed on the panels before the cages were removed, but very little of this remained after two days. Fish scrapes were distributed all over the panels except for areas immediately adjacent to juvenile corals which had been growing beneath the algae. Observations of the pattern of scrapes also indicated that the fish may aim at small areas of dense algal growth on the panels.

The areas of 283 scrapes which crossed a series of transects over the panels were estimated, by measuring the length and breadth of each scrape with vernier calipers. The frequency distribution of scrapes of different sizes is shown in Figure 5:1. Some estimate of the proportion of each scrape which covered, or was covered by, other scrapes appeared to be necessary, in order to determine the area which had been previously covered by algae that was cleared at each scrape. I therefore estimated the fraction of each of 266 scrapes that was overlapped by other scrapes. As I could not determine the sequence of scrapes, I attributed half of the overlap between any two scrapes to each of them. The 'effective area' of each scrape was therefore calculated by $E = A - \frac{1}{2} O$, where E is the effective area of the scrape, A is the actual area, and O is the proportion overlapped by other scrapes. The frequency distribution of the effective areas is shown in Figure 5:2.

Results

The mean actual area of the fish scrapes was 10.279 mm^2 (Standard deviation = 7.414 mm^2), and the mean effective area of the scrapes was 8.482 mm^2 (Standard deviation = 7.908 mm^2).

Assuming that parrotfish scrapes are distributed randomly over a surface, the number of times a surface is scraped before a scrape covers a chosen point will be distributed as:

$P(x) = pq^{x-1}$ where x is the number of scrapes, p is the possibility that any one scrape will cover the chosen point, and $q = 1-p$. The expected number of scrapes is $1/p$, and the number required to remove a given proportion of the algae on the surface can be calculated from the cumulative distribution:

$P(x < N) = 1-q^N$ where N is the number of scrapes required. Using the mean actual size of the scrapes on my panels, the ex-

FIGURE 5:1

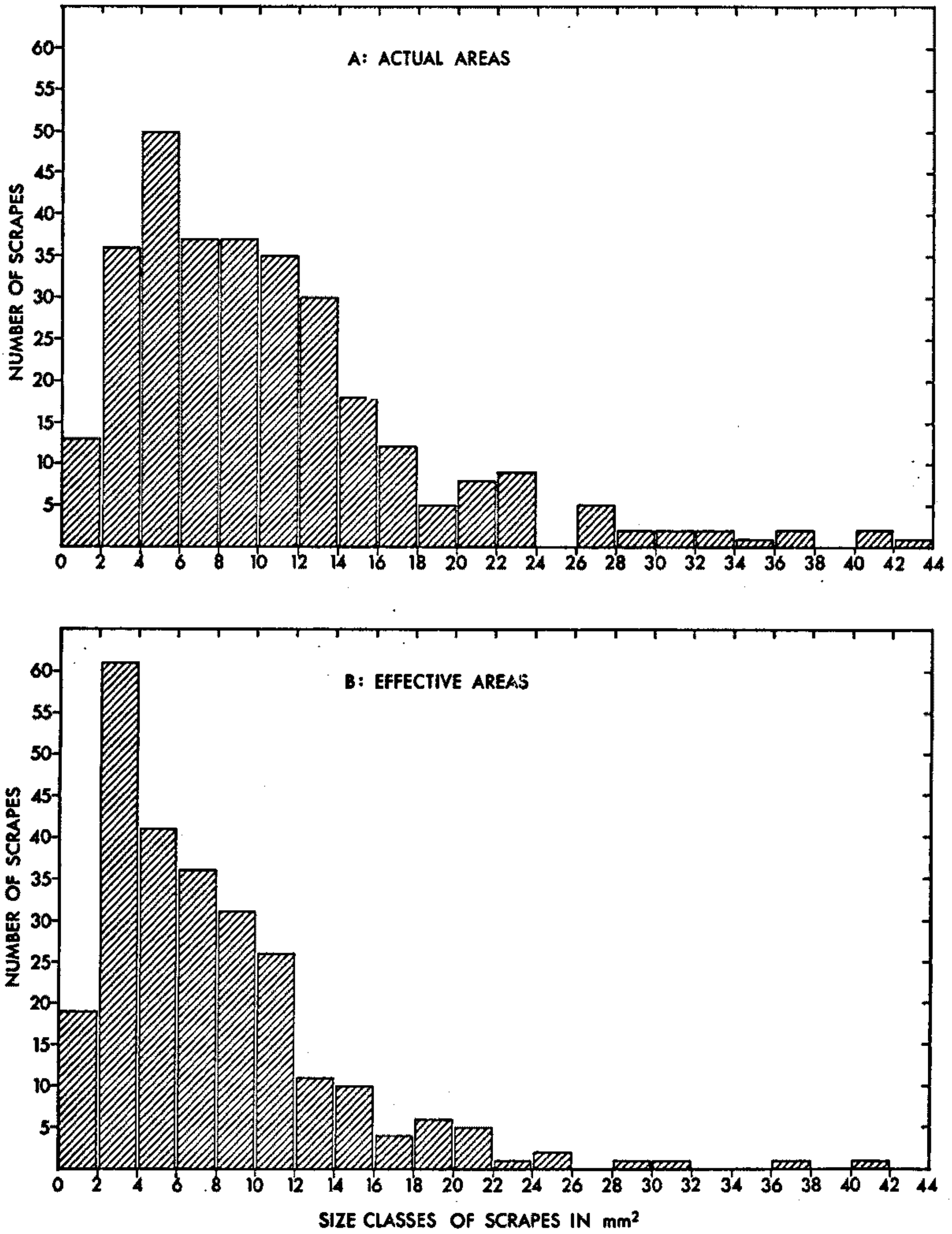
THE ACTUAL AREAS OF PARROTFISH SCRAPES.

283 scrapes were measured. The numbers of scrapes falling into size intervals of 2 mm^2 are shown.

FIGURE 5:2

THE EFFECTIVE AREAS OF PARROTFISH SCRAPES.

The area of algal covered substratum scraped by 266 scrapes was calculated as described in the text. The numbers of scrapes falling into size intervals of 2 mm^2 are shown.


A: ACTUAL AREAS
B: EFFECTIVE AREAS
NUMBER OF SCRAPES
NUMBER OF SCRAPES
5
10
15
20
25
30
35
40
45
50
55
60
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40
42
44
SIZE CLASSES OF SCRAPES IN mm²

pected number of scrapes on a $1m^2$ area before a scrape covers a chosen point is 9.729×10^4 scrapes; and the number of scrapes required to remove half of the algae on a $1\ m^2$ surface is 6.932×10^4 scrapes. If the mean effective area of the scrapes on my panels is used to calculate the number of scrapes which will cover $0.5\ m^2$, the required number is 5.895×10^4 scrapes. The first estimate is probably too high because parrotfish seem to choose tiny areas of dense algal growth rather than scrape randomly, and the second may be too low because there may have been less overlap between scrapes on the panels than would be expected on a surface which was scraped continuously. The true figure probably lies between the two values given above.

Choat has measured the rate at which scarids scrape various natural surfaces on Heron Reef (Choat and Robertson 1975). I have used Choats' estimates for four kinds of substratum together with the mean effective area of the scrapes on my panels, to calculate the rate at which algae are removed from natural substrata (Table 5:01). The expected number of scrapes to cover a fixed point has been combined with Choats' data to give the mean time between scrapes at a fixed point. I have called this the 'grazing cycle time' (Table 5:01). Similarly, the 'half life of algae' has been calculated from each of the two estimates of the number of scrapes required to clear half of a $1\ m^2$ surface (Table 5:01). These 'grazing cycle time' and 'half life' estimates are independent of area because grazing rates were measured as scrapes per square meter. They are measured in daylight hours because scarids feed only during the day.

Larkum, Borowitzka, and I have measured the dry weight of algae on caged and uncaged panels suspended for three month

TABLE 5:01

MEASURES OF GRAZING RATE FOR VARIOUS SURFACES

Substratum type	Dead *Porites* surface	Dead *Acropora* plates	*Acropora* Rubble in sand	Impacted Carbonate rock
Mean scraping rate* (scrapes.m^{-2}.hr^{-1})	301.44	505.20	74.16	84.24
Area cleared of algae (mm^2.m^{-2}.hr^{-1})	2556.8	4285.1	629.1	714.5
Dry weight organic matter removed (g.m^{-2}.hr^{-1})	0.066	0.110	0.016	0.018
Grazing cycle time (daylight hr.)	322.7	192.6	1311.9	1154.9
Half life of algae (daylight hr.)+	196-230	117-137	795-935	700-823

* Data from Choat and Robertson (1975)

\+ Two values calculated as described in the text.

periods in shallow water on the Wistari reef slope. These data showed that there were significant seasonal changes (at $p = 0.05$) in the dry weight of algae on grazed panels. The seasonal means ranged from 16.1 $g.m^{-2}$ (March to June) to 27.5 $g.m^{-2}$ (December to March). The overall mean was 21.215 $g.m^{-2}$. Using this figure, and the mean actual size of fish scrapes, the dry weight of organic matter removed per square meter per hour has been calculated (Table 5:01). The seasonal changes in dry weight suggest that the grazing may vary seasonally too, so that the figures shown should be regarded with caution.

Discussion of Results

The results presented here give an indication both of the rate at which parrotfish remove algae from reef surfaces, and the time available for individual plants to colonise a patch of surface, grow, and reproduce before that patch is scraped again. Possible sources of error in the estimates of scrape sizes lie in the following factors: 1) Each fish which visited the panels probably scraped the surface many times, so that a number of scrapes made by each fish would have been measured. This was evident from the fact that scrapes near to one another on the panels were often the same size. As a result the variation in the data is probably less than would be the case if every scrape had been made by a different fish.

2) The size range of the fish which scraped the panels may have been limited, as different areas and types of substratum tend to be used by different types of fish (Choat and Robertson 1975).

3) The estimates do not take into account browsing by fish other than parrotfish.

4) The panels are harder than most natural surfaces, and the scrapes would therefore be deeper and wider on natural surfaces.

5) The degree of overlap between scrapes on the panels may be lower than on continuously scraped surfaces, so that the effective areas of the scrapes may be greater than on natural surfaces.

6) Parrotfish probably do not scrape randomly over a surface.

The sizes and the range of sizes of scrapes are probably underestimated as a result of these errors, so that the figures in Table 5:01 for area cleared and dry weight removed may be too low, while the estimates of grazing cycle time and half life of algae are probably too high.

Choat and Robertson (1975) have shown that the intensity of grazing varies widely between different surfaces; flat uninterrrupted surfaces being preferred. The tops of Porites growths, which are the best substrata in this sense, are relatively permanent structures and are often defended by large Scarus niger (Choat and Robertson 1975). Possibly this is why grazing was most intense on the less permanent and less extensive Acropora hyacinthus plates (Table 5:01). Other, broken surfaces were grazed less intensively. Choat divided the grazing substrata into six categories, and I have used his data for the four categories which represent reasonably flat surfaces. Broken surfaces have a greater surface area, so that they would support more algae per unit area of reef.

Different species of fish tend to use different substrata (Choat and Robertson 1975). This may be because small fish are best able to use the more broken substrata (Choat, personal communication). The smaller fish appear to be more manoeuvreable so that they can align themselves with small facets of irregular surfaces in order to scrape them. The scrapes on these surfaces, then, would be smaller, and possibly more accurately placed.

The rate at which algae are removed:

As parrotfish are active for most of the day the figures for area cleared and dry weight removed should be multiplied by ten or twelve to give the rates per day. There are few data in the literature with which the present values can be compared. Bakus (1967) has estimated the grazing rates of parrotfish on the reef flat at Einewetok as about 0.3 $kcal.m^{-2}. day^{-1}$, but he did not measure this directly, deriving the value from fish counts and tenuous assumptions about the metabolism of the fish. Using Bakus' estimate of 4 k.cal per gram of organic matter for algae, this represents 0.08 $g.m^{-2}.day^{-1}$, which is about an order of magnitude below the higher estimates shown in Table 5:01. Bakus measured the standing crop of algae on grazed surfaces of the Einewetok reef flat as 51 $g.m^{-2}$, based on six 2500 mm^2 samples. This is about twice the standing crop reported here.

About one to four percent of the algae on heavily grazed surfaces is apparently removed every day by Scarid fish. The enormous impact of scraping fish on coral reefs has been noted by Bardach (1961), who calculated that fish redistribute about 2300 kg per hectare per year of calcareous material from the surfaces of a small Bermudan reef; or about 0.6 $g.m^{-2}.day^{-1}$. Stephenson (1961) noted that fish apparently removed about 0.5 mm thickness of the beachrock at Heron Island per year, and Steneck and Adey (quoted in Adey and Vassar 1975) found that nearly 3 cm per year of coralline algae were removed by fish grazing in 1.5 m of water off the U.S. Virgin Islands.

Recolonisation times for algae:

The grazing cycle time and the half life of algae indicate how quickly the algae found on grazed surfaces must colonise scraped patches, grow, and reach maturity; since reproductive material was found on panels exposed to continuous grazing. On the most intensely grazed surfaces the average time available is 20 to 30 days, while half the algae on a surface are grazed within two to three weeks.

Published figures suggest that these times may be long enough for many algae to maintain their abundance on grazed surfaces, although I could find no relevant data dealing with the time between settlement and reproduction for algae. Scraped plots on the Einewetok reef flat supported a standing crop of about 39 $g.m^{-2}$ within 17 days: a figure close to the original standing crop on grazed surfaces of 51 $g.m^{-2}$ (Bakus 1967). Caged settlement panels at 0.5 m depth in the Red Sea supported an average standing crop of about 48 $g.m^{-2}$ within 15 days (Vine 1974). Colonisation of new surfaces is very rapid: many species were present on coral skeletons within a few days after Acanthaster had killed the coral (Belk and Belk 1975).

Without an extremely rapid rate of recolonisation and growth of algae the intense grazing of reef surfaces demonstrated above could not be sustained.

5:3 THE EFFECTS OF HERBIVOROUS FISH ON SPECIES OF ALGAE.

Introduction:

The results presented in this section were obtained using the samples and regression analysis described in Chapter 4 and appendix 4E. The overall effects of excluding large fish by means of closed cages, and the importance of interactions between caging treatment and the other components of environment discussed in Chapter 4, were evaluated for twenty three species of algae.

Results

Regressions of abundance on caging treatment (Table 5:02) were significant at p = 0.05 for almost all species, and in most cases a fairly high percentage of the variation in abundance was attributable to caging. The species may be divided into two groups on the basis of the sign of the regression slope. Most species were more abundant in closed cages (positive slope), but eight species were more abundant on panels exposed to grazing (negative slope). The grazing resistant group should perhaps include '_Ectocarpus_' sp 1, for which no significant effect of caging was detected. This was the most abundant filamentous species on grazed samples, and on protected samples it was often attached to the filaments of other algae rather than to the primary substratum.

Interactions between caging treatment and the two seasonal factors were significant at p = 0.05 for fourteen species (Tables 5:03, 5:04). _Callithamnion_, _Jania_, and _Lyngbya_, were rare or absent on grazed panels throughout the year. On protected panels they were more abundant in summer than in winter.

TABLE 5:02

RESULTS OF REGRESSION ANALYSES ON ALGAL ABUNDANCES: THE EFFECTS OF CAGING TREATMENT.

Species	Percentage of variation explained	Regression Slope and Significance*	
Antithamnion sp 1	1.37	0.180	n.s.
Antithamnion sp 2	3.10	0.257	S
Bryopsis sp	17.89	0.623	S
Callithamnion sp 2	14.53	0.602	S
Champia sp	18.95	0.248	S
Cladophora sp	1.39	0.120	n.s.
'*Ectocarpus*' sp 1	0.02	0.278	n.s.
'*Ectocarpus*' sp 2	26.46	-1.101	S
'*Ectocarpus*' sp 3	39.39	-1.277	S
Enteromorpha sp	7.53	0.612	S
Jania sp	17.36	0.188	S
Laurencia sp 1	12.99	0.187	S
Laurencia sp 3	22.18	0.538	S
'*Lophosiphonia*' sp 1	19.42	-0.852	S
'*Lophosiphonia*' sp 2	12.68	-0.405	S
Lyngbya sp	2.13	0.277	S
Polysiphonia sp 1	3.34	0.272	S
Pseudobryopsis sp 1	16.84	0.962	S
Sphacelaria sp	5.44	-0.140	S
Ralfsia sp 2	20.91	-0.933	S
Tenerea sp	7.27	-0.574	S
Coralline sp 2	3.33	0.228	S
Coralline sp 3	10.98	-0.257	S

*S = significantly different from zero at $p = 0.05$.
n.s. = not significantly different from zero at $p = 0.05$.

TABLE 5:03

RESULTS OF REGRESSION ANALYSES OF CAGING INTERACTIONS: SPECIES OF ALGAE FOR WHICH THE INTERACTION OF CAGING AND SEASON 1 WAS SIGNIFICANT AT P = 0.05.

Species	Percentage of variation explained	Regression Slope
Callithamnion sp 2	2.06	-0.321
'Ectocarpus' sp 1	8.69	-0.842
Jania sp	7.79	-0.175
Lyngbya sp	3.42	-0.497
Polysiphonia sp 1	3.10	0.363
Pseudobryopsis sp 1	3.90	-0.645
Tenerea sp	5.23	0.678
Coralline sp 3	11.09	0.360

TABLE 5:04

SPECIES OF ALGAE FOR WHICH THE INTERACTION OF CAGING AND SEASON 2 WAS SIGNIFICANT AT P = 0.05.

Species	Percentage of variation explained	Regression Slope
Antithamnion sp 1	3.56	0.453
Bryopsis sp	8.16	-0.644
Callithamnion sp 2	6.55	0.614
'Ectocarpus' sp 1	7.32	0.848
Jania sp	3.80	0.134
Laurencia sp 1	3.35	0.144
Laurencia sp 3	2.85	0.297
Ralfsia sp 2	4.66	-0.670
Coralline sp 2	3.61	0.363
Coralline sp 3	1.74	-0.156

The differences between samples in open and in closed cages were therefore greater in summer than in winter for these species, and as a result the interaction between caging and 'season 1' was significant (Table 5:03). Similarly *Polysiphonia* was seldom common on grazed panels throughout the year, whereas in closed cages it became common in winter.

Callithamnion and *Jania* were also more abundant in spring than in autumn in closed cages, so that the interaction between caging and 'season 2' was significant for these species. Similarly *Bryopsis* and *Laurencia* spp 1 and 3 were always rare on grazed panels, but *Bryopsis* became abundant on protected panels in autumn, and the *Laurencia* species were common on protected panels in spring. For all these species the significant interactions are a result of the fact that grazing reduced the species' abundances to near zero on panels in open cages irrespective of their abundances in closed cages.

The remaining species in Table 5:03 and 5:04 were common on both protected and grazed panels in some seasons at least. *Tenerea* and Coralline sp 3 were rare in winter on both grazed and protected panels. They became more abundant in spring and summer, especially on grazed panels. Similarly Coralline sp 2 was more abundant in spring than in autumn, particularly on protected panels. As for other species, the effects of caging treatment were more apparent when these species were more abundant. *Antithamnion* sp 1 and '*Ectocarpus*' sp 1 apparently grew best in autumn and winter, when they were more abundant on grazed panels, whereas in spring and summer they were more abundant in closed cages. As a result the overall effects of grazing were not significant (Table 5:02) but the interactions of caging with both seasonal factors were significant (Tables 5:03, 5:04).

Pseudobryopsis grew best on protected panels throughout the year. In winter it was occasionally abundant on grazed panels too, but in summer it was rare or absent on grazed panels.

Ralfsia was more abundant on grazed than on protected panels at all times of the year. It was also more abundant in autumn and winter than spring and summer, especially on protected panels.

Interactions of caging with depth and with illumination (Tables 5:05, 5:06), are considered together because depth and illumination were negatively correlated. As a result the introduction of the caging-depth interaction term into a regression precluded the introduction of a caging-illumination interaction term, and vice-versa. A negative regression slope for the caging-depth interaction indicates that at greater depths, or at dimly-lit sites the species concerned became more common on grazed panels; or less common on protected panels; or both. A positive interaction of caging and illumination may be interpreted in the same way.

These interactions were significant at $p = 0.05$ for eight species (Tables 5:05, 5:06). On grazed panels all the species except 'Ectocarpus' sp 2 and Bryopsis became more abundant at greater depths. For most species there was no trend of abundance with depth on protected panels, but Enteromorpha and Laurencia sp 1 became less abundant at deep sites on protected panels.

'Ectocarpus' sp 2 was common only on grazed panels at shallow sites. It was rare both in open and in closed cages

TABLE 5:05

SPECIES OF ALGAE FOR WHICH THE INTERACTION OF CAGING AND DEPTH WAS SIGNIFICANT AT P = 0.05.

Species	Percentage of variation explained	Regression Slope
Antithamnion sp 1	5.73	-0.096
'Ectocarpus' sp 2	9.31	0.171
Enteromorpha sp	3.05	-0.102
Laurencia sp 1	4.49	-0.032
'Lophosiphonia' sp 1	4.31	-0.105
Polysiphonia sp 1	4.34	-0.080

TABLE 5:06

SPECIES OF ALGAE FOR WHICH THE INTERACTION OF CAGING AND ILLUMINATION WAS SIGNIFICANT AT P = 0.05.

Species	Percentage of variation explained	Regression Slope
Bryopsis sp	2.12	-0.010
Laurencia sp 3	10.07	0.017

at deeper sites, so that the effects of caging diminished with depth. Bryopsis became more abundant at deeper, darker sites, especially in closed cages.

Water-movement and wave action were correlated, so that interactions of caging with these variables are considered together (Tables 5:07, 5:08). A positive regression slope for either interaction indicates that at higher levels of water-movement or wave action the species concerned was more common on protected panels; less common on grazed panels; or both. Interactions of caging with these variables were significant at p = 0.05 for ten species, and for half of these the regression slopes were positive (Tables 5:07, 5:08). 'Lophosiphonia' sp 2 was less common on grazed panels in areas of high wave action than in other areas. The other four species with positive slopes apparently grew more rapidly under higher water-movement or wave action, especially when protected from fish.

The regression slopes were negative for five species. 'Ectocarpus' sp 3, Ralfsia, Tenerea, and Coralline sp 3 all apparently grew more rapidly in areas of high wave action on grazed panels. 'Ectocarpus' sp 3 and Ralfsia also appeared to grow more slowly in closed cages in these areas of high wave action. Bryopsis was less abundant at sites with high wave action than elsewhere, both on protected and on grazed panels, but especially on protected panels, where Bryopsis was more common overall.

TABLE 5:07

SPECIES OF ALGAE FOR WHICH THE INTERACTION OF CAGING AND WATER-MOVEMENT WAS SIGNIFICANT AT P = 0.05.

Species	Percentage of variation explained	Regression Slope
Callithamnion sp 2	3.33	0.105
Jania sp	3.00	0.029
Laurencia sp 1	3.03	0.033
Polysiphonia sp 1	5.14	0.134
Tenerea sp	1.36	-0.091
Coralline sp 3	4.16	-0.058

TABLE 5:08

SPECIES OF ALGAE FOR WHICH THE INTERACTION OF CAGING AND WAVE ACTION WAS SIGNIFICANT AT P = 0.05.

Species	Percentage of variation explained	Regression Slope
Bryopsis sp	4.92	-0.656
'*Ectocarpus*' sp 3	2.25	-0.613
'*Lophosiphonia*' sp 2	4.30	0.473
Ralfsia sp 2	3.63	-0.779

Discussion of Results

Predation by fish was an important component of environment in determining species' abundances. In these experiments there were only two levels of predation: exposed to all fish, or protected from all but the smallest fish. In the natural environment there are places with varying degrees of protection from fish, for example between projections, in confined spaces, or in Pomacentrid fish territories, as discussed in Sections 5:6 and 5:7.

Grazing pressure may also vary with other factors, as indicated by the interactions between caging and other factors reported here. However in many cases the interactions were merely a reflection of the more marked effects of grazing at the times or places where species were most common.

Many of the species which were common in closed cages were more abundant in spring or summer than in autumn or winter, whereas species which were common on grazed panels tended to be more abundant in autumn and winter. Furthermore *Antithamnion* sp 1 and '*Ectocarpus*' sp 1 were most common on closed cages in spring and summer but became more common on grazed than on protected panels in autumn and winter. *Pseudobryopsis* fits this pattern too, as it was occasionally common on grazed panels in winter, although it was normally common only on protected panels.

These results suggest that grazing was more severe in spring and summer than in autumn and winter. Perhaps this is linked with an increased metabolic rate of fishes at higher temperatures. The fact that the standing crop of algae on grazed panels varies seasonally (Larkum, Borowitzka, and Day, in preparation) also suggests a seasonal variation in grazing pressure.

Many species which were most common on protected panels became common on grazed panels at greater depths. This suggests that grazing diminished with depth. My observations and those of Gilmartin (1960) and Vine (1974) support this view: herbivorous fish appear to be concentrated in shallow water. Coral reef algae grow fastest in shallow water (Vine 1974), but algal filaments on my grazed panels from deep sites appeared to be longer than on grazed panels from shallow sites. The fish, therefore, were concentrated where algal growth was fastest, although where occasional patches of suitable surface (such as my panels) occur in deep water these may support a higher standing crop.

Interactions of caging with water-movement and wave action were detected for many species. In most cases this was because the differences between species' abundances on protected and grazed panels were most marked where the species were abundant. For example many species on protected panels grew best in areas of high water-movement, but on grazed panels they were rare even at sites with very high water-movement. Such an explanation does not apply to '<u>Ectocarpus</u>' sp 3 and <u>Ralfsia</u>. In areas with wave action both became more abundant on grazed panels and less abundant on protected panels. These results are difficult to explain. They do not seem to reflect differences in grazing pressure. Grazing by fish may, however, be reduced on the reef crest, where wave action is extreme (Adey and Vassar 1975, John and Pople 1973).

Most species were more abundant in the absence of grazing (Table 5:03). On protected panels the erect filaments of the algae were longer, so that the surfaces of the panels would have been shaded, and more sediment accumulated between the algae. Furthermore some algae, especially '*Ectocarpus*' sp 1 and *Pseudobryopsis* often grew as dense mats of tangled filaments, with diatoms and detritus trapped in the mat. Interactions between the algae, such as shading effects or chemical effects like those suggested for *Enteromorpha* (see Chapter 3), may have been important on the panels in closed cages, but I did not investigate such interactions. On grazed panels new patches of surface were constantly made available for colonisation by the scraping fish, and shading and siltation appeared to be minimal.

Amongst those species which were abundant on unprotected panels, and therefore resistant to grazing, were most of the encrusting species encountered. *Ralfsia,* an uncalcified encrusting brown alga, is easily scraped off a surface, but appeared to be able to recolonise scraped areas rapidly by growth from the edges of the scrapes. Encrusting corallines were often damaged by scrapes, but usually only the edges of the plants were affected. Thus, as might be expected, these algae were more resistant to scraping than other algae.

Coralline sp 2 was more abundant in closed cages. This species spreads out over a surface as a network of filaments which later fuse to form a continuous crust. On the fairly smooth surfaces of the panels the network was subject to scraping, but on a natural surface the filaments may extend between the 'high spots' of an irregular surface. If the surface is soft, such as the tops of *Porites* coral growths, fish scrape much of the surface away, but on hard surfaces, for example *Acropora* rubble, the fish would scrape only the high spots of the surface. The filaments of

Coralline sp 2 may be able to ramify and fuse on such surfaces so that eventually the coralline forms a hard crust resistant to grazing.

A number of studies of coralline algae (Adey and Vassar 1975, Littler and Doty 1975) have shown that coralline algae are subject to grazing on well-lit surfaces but that in most places coralline accretion occurs in spite of grazing. The corallines may even benefit from the removal of shading algae by fish (Littler 1972, 1973). The speculations above as to the kinds of surface on which Coralline sp 2 may survive suggest that the nature and hardness of the surface may be important in the initial establishment of coralline algae. Once established, they form a relatively hard surface on which grazing may be less effective.

Most encrusting species grew best on grazed panels (Table 5:02). They may be disadvantaged on protected panels because of siltation and reduced water-movement under the denser growth of filamentous algae on protected panels. This hypothesis is supported by the fact that on grazed panels encrusting species were especially abundant at sites exposed to high water-movement (Tables 5:07, 5:08). Shading beneath other algae is unlikely to be important for the corallines, but may be important for Ralfsia, which was less abundant at deeper sites (Table 4:09).

A few filamentous species were resistant to grazing. To maintain their abundance on grazed surfaces these species must rapidly recolonise scraped areas on the panels, either by growing in from the edges of scrapes, or by settlement of spores on bare areas.

The two 'Lophosiphonia' species follow the first strategy. They have a prostrate filamentous thallus with attachment points and erect filaments at intervals. Each scrape is likely to remove only a short length of the prostrate thallus, which apparently regenerates rapidly.

Sphacelaria occurs as tufts of erect filaments with encrusting filaments occasionally stretching between adjacent tufts. Regeneration probably occurs from the encrusting part of the thallus. The erect filaments bear large three-armed vegetative propagules which break off readily. Presumably when a tuft is scraped the propagules break away, and their shape ensures that they quickly lodge amongst other algae.

Both Sphacelaria and the 'Lophosiphonia" spp are apparently adapted to recolonisation at short range. They become established on the panels more slowly than 'Ectocarpus' spp, possibly because the panels were relatively isolated from other grazed surfaces.

'Ectocarpus' spp seem to colonise mainly by means of spores. In contrast to 'Lophosiphonia' spp, Sphacelaria, and the encrusting corallines, 'Ectocarpus' spp were abundant throughout the year and especially in autumn and winter when other species were less common (Tables 4:06, 4:07). Because the 'Ectocarpus' species must recolonise grazed surfaces throughout the year they must maintain reproductive activity throughout the year. Sporangia were common on these species in all seasons. Possibly 'Ectocarpus' spp may colonise grazed areas from parent populations in protected sites in the interstices of the reef, but it seems likely that these species reach maturity rapidly enough to reproduce on surfaces subject to at least moderate grazing, since sporangia were often found on grazed panels.

The algae which became common on protected panels must either have become established in the shaded, low water-movement conditions under the long filaments of algae already present, or else have colonised the panels rapidly. 'Ectocarpus' spp would have colonised the protected panels as well as the grazed panels, but only 'Ectocarpus' sp 1 was abundant on protected panels after three months.

Species which colonise rapidly but grow more slowly than 'Ectocarpus' spp would have become established along with 'Ectocarpus' on protected panels, but not on grazed panels. I suspect that Antithamnion spp, Bryopsis, Enteromorpha, and Pseudobryopsis were such rapidly colonising species. All were most common on protected panels in the colder months when other species were reduced in abundance (Section 4:4). Antithamnion sp 1 became common on grazed panels too, in deep water and in autumn. Perhaps this is related to the apparent reduction in grazing in deep water, and in the colder months (see above).

Antithamnion sp 2, Bryopsis, Entermorpha, and Pseudobryopsis were all species with relatively large thalli, and were usually restricted to closed cages. The first two were deep water species, while Entermorpha was most abundant in closed cages at shallow sites. Pseudobryopsis was patchily distributed at all depths.

The other species characteristic of protected panels were all most common in spring and summer. In chapter 4 'warm water' species were divided into encrusting and jointed corallines, smaller filamentous algae, and species with relatively large thalli. Most of the encrusting corallines and small filamentous algae were common on grazed panels, and have been discussed above. The jointed coralline Jania sp and the small filamentous blue green Lyngbya appear to be species which survive and grow well underneath the filaments of other algae. The remaining species common in closed cages were all species with larger thalli (Callithamnion sp 2, Champia, Laurencia spp, Polysiphonia sp 1). A number of rare species which were not analysed also fall into this category. These species become established under the filaments of the rapidly colonising species (e.g. Enteromorpha, 'Ectocarpus' sp 1) and later overtop them. Many, such as Callithamnion sp 2 and Polysiphonia sp 1 were most common in deep water, and some (Callithamnion sp 2, Laurencia sp 1) were rare in areas of high wave action (Tables 4:08, 4:09).

To summarise, because predation was an important component of environment for many species, the available spaces on the reef would be divided between the algae according to the degree of predation on those surfaces. It is in the interactions between predation and other factors that this partitioning becomes most apparent. The species appear to be distinguished from each other in terms of the strategies of settlement and growth used by the species to become established and maintain their abundance on a surface. Each strategy will be optimal in a particular set of circumstances. For example the 'Ectocarpus' strategy of colonising new areas by spores will be more effective than the 'vegetative growth' strategy of 'Lophosiphonia' spp when large areas are disturbed: when coral rubble is covered by sand and then exposed again, or Acropora hyacinthus plates are overturned, exposing the undersides to colonisation by algae. I have also speculated above on the advantages in certain situations of the 'network of filaments' strategy of Coralline sp 2.

In discussing these results, I have not attempted to describe the 'niche' of each species. Although the concept of the niche has been extended and modified considerably (Colwell and Fuentes 1975) it is not useful in describing the differences between the species of algae considered here. Instead I have attempted to describe a number of strategies 'adopted' by various species, which ensure the persistence of each species on reef surfaces.

5.4: THE EFFECTS OF CAGING TREATMENT ON SESSILE ANIMALS

Introduction

The effects on sessile animals of caging treatment, and the interactions of caging with other components of environment, are discussed in this section. Results obtained from the regression analyses of animal abundances which were described in Section 4:5 and appendix 4E are used for this purpose. Only the more common animals were included in the regression analyses. To supplement these results for common species, the effect of caging on the cover of ascidians and sponges on panels at cave sites was determined by non-parametric tests.

Results

There were significant differences in abundance between open and closed cages for a number of species (Table 5:09). Five of eight arborescent bryozoan species ('AB' species), and the colonial polychaete Filograna were more abundant in closed cages. In contrast only two of thirteen species of encrusting bryozoans ('EB' species) were significantly affected by caging treatment. EB2 was more common on panels from open cages, while EB10 was more common in closed cages. There was no apparent effect of caging on the oyster Patro australis, or Ascidian B.

The total cover of sponges, simple ascidians and compound ascidians on settlement panels in open and closed cages was calculated (Appendix 5), and the means are shown in Table 5:10. The area covered by each group of species was significantly greater, at $p = 0.05$, on panels from closed cages (Wilcoxon's signed ranks test for matched pairs: Siegel 1956), despite considerable variability in the data.

TABLE 5:09

RESULTS OF REGRESSION ANALYSES ON ANIMAL ABUNDANCES: THE EFFECT OF CAGING TREATMENT.

Species	Percentage of variation explained	Regression slope and Significance*	
Ascidian B.	1.47	0.071	n.s.
AB1	11.76	0.493	S
AB3	5.34	0.301	S
AB4	1.82	0.084	n.s.
AB5	16.31	0.581	S
AB9	2.12	0.091	n.s.
AB13	8.37	0.509	S
AB14	11.08	0.511	S
AB17	0.57	0.062	n.s.
EB 1	0.12	-0.028	n.s.
EB 1A	0.05	0.017	n.s.
EB 2	4.24	-0.061	S
EB 6	0.23	0.089	n.s.
EB 7	0.00	-0.001	n.s.
EB 8	1.11	0.049	n.s.
EB 9	0.88	0.084	n.s.
EB10	4.62	0.060	S
EB12	0.79	0.092	n.s.
EB14	0.00	0.004	n.s.
EB16	0.02	0.012	n.s.
EB18	0.03	0.013	n.s.
EB29	0.90	-0.034	n.s.
Filograna implexa	3.65	0.265	S
Patro australis	0.96	0.107	n.s.

*S = significantly different from zero at $p = 0.05$,
n.s. = not significantly different from zero at $p = 0.05$.

TABLE 5:10

THE MEAN AREA COVERED, IN mm^2, BY THREE GROUPS OF SPECIES ON PANELS FROM OPEN AND CLOSED CAGES.

Species group	Open cages	Closed cages
Simple ascidians	126.5	478.9
Compound ascidians	470.9	998.4
Sponges	91.0	260.9

TABLE 5:11

RESULTS OF REGRESSION ANALYSES OF CAGING INTERACTIONS FOR 23 SPECIES OF SESSILE ANIMALS.

Interaction of caging treatment with	Interaction Significant at p = 0.05 for:	Percentage of variation explained	Regression slope
'Season 1'	EB2	5.54	-0.098
'Season 2'	Filograna	4.13	0.420
Wave action	EB1A	2.93	0.272
	EB7	3.32	-0.322
	EB8	2.84	0.167
Water-movement	AB4	4.41	0.065
	EB16	2.43	0.069

Interactions between caging and the effects of wave action or water-movement were significant for five species, while interactions with seasonal variables were significant for only two species (Table 5:11). The results shown in the table are explained individually below:

1) EB2 was as common in closed as in open cages for most of the year, but it was much more numerous in open than in closed cages during winter. As a result both the interaction of caging and 'season 1', and the overall effect of caging were significant (Tables 5:09, 5:11).

2) Colonies of Filograna were well developed in spring and summer, and Filograna was more abundant on protected panels in these seasons. There were no obvious differences in abundance between open and closed cages in other seasons.

3) EB7 was more abundant in open than in closed cages at sites with high wave action, but slightly more common in closed cages at other sites.

4) EB1A and EB8 were rare at the cave sites with low wave action, so that the effects of caging treatment were apparent only at sites where the waves were more powerful. At these sites both species were more abundant, on average, in closed cages. EB1A was also common at the non-cave WSD site, where wave action was absent, and at this site it was more common in open cages.

5) AB4 was more abundant in closed than in open cages at most sites, but at one site with low water-movement it was more abundant in open cages.

6) EB16 settled most frequently at the two deepest cave sites: EC and NSC. At the EC site, where wave action and water-movement

were low, the colonies were larger, on average, on the panels in open cages. At almost all other sites EB16 was more abundant in closed than in open cages, but the differences were marked only at the two non-cave sites WSD and NSD, where water-movement was high.

Discussion of Results

The effects of caging treatment suggest that predation by fish was less important for animals than for algae. Cave walls are, in fact, visited by predatory fish rather infrequently (personal observations) while algal substrata are heavily grazed (Section 5:2). Seasonal changes were also less important for animals than for algae (Section 4:5), and as a result very few interactions between the effects of caging and seasonal variables were detected. In contrast, wave action and water-movement were apparently important for animals, and interactions between caging and these variables were detected for a number of species.

In general projecting and soft-bodied organisms were subject to predation, while hard encrusting forms were not. Projecting organisms included the arborescent ectoprocts (both cyclostomes and cheilostomes), simple ascidians, a few sponges, and Filograna implexa. These were bitten off, often leaving the base of the animal behind. Fish appeared to suck soft-bodied encrusting sponges and compound ascidians off the surface as they snapped at them. Calcareous encrusting forms included encrusting ectoprocts, and tubicolous polychaetes such as Spirobranchus, which occurred too infrequently to be included in the analysis.

Although most of the results conformed to this general pattern, there were some exceptions, and these are discussed below. In five instances the expected effects of predation by fish were not always apparent:

1) AB4. There was no significant effect of caging on AB4, AB9, or AB17 (Table 5:09). The result for AB4 was due to the interaction between caging and water-movement (Table 5:11) which is a reflection of the abundance of AB4 in open cages at one site only. As AB4 was not a common species, and probably had an aggregated distribution (Section 3:1), the interaction may not be a real effect. At most sites, AB4 was more common in closed than in open cages.

2) AB9: This arborescent bryozoan was much smaller than other species, and it may escape predation as a result of its small size.

3) AB17: This retiporate species may be attacked less often than other species because it is heavily calcified. AB17 can also regenerate after parts have been bitten off. On panels exposed to predation stumps of AB17 were found which appeared to be regenerating, whereas stumps of other rigid arborescent species (AB1, AB3) showed no regeneration. Flexible arborescent species (AB5, AB13, AB14) were usually removed entirely by fish.

4) Filograna: This species was less subject to predation in autumn and winter than in spring and summer because the tubes of the polychaetes projected upwards only in well-developed colonies, and the colonies were best developed in spring and summer.

5) Ascidian B: Whereas the total abundance of ascidians was reduced on unprotected panels, the abundance of Ascidian B was not. Very small colonies of this encrusting ascidian had densely

packed white spicules in the test, and possibly they may be mistaken for encrusting ectoprocts by predatory fish, which are diurnal (Hobson 1974) and appear to hunt mainly by sight. Larger colonies of Ascidian B are bright orange, and may be found in exposed places on the reef as well as on panels. It seems possible that Ascidian B may be distasteful or toxic to fish. The orange colour may serve as a warning colouration.

In three other instances the effects of caging do not seem to be directly attributable to predation by fish:

1) EB2: Most encrusting ectoprocts were not affected by caging, yet EB2 was more abundant in open than in closed cages in winter. EB2 settled predominantly at the edges of panels (Section 3:2), forming small colonies which were often smothered by compound ascidians, oysters (Patro australis), and EB6. The oysters and EB6 were common both in open and in closed cages, at the edges of panels (Section 3:2). In winter they did not extend as far into the central areas of the panels, but arborescent ectoprocts, sponges, and ascidians were common in the central areas of panels in closed cages. Therefore, in open cages only, there was more unoccupied space available in the central areas of the panels in winter than in summer; and as a result larve of EB2 may have settled closer to the centre of unprotected panels in winter, within the sampling area.

2) EB7: This species had large zooids and formed very large colonies. It was more abundant in open than in closed cages at sites with high wave action. Species with large zooids can capture larger food particles (Dudley 1970). Large particles would occur less frequently than small particles in the water,

so that species adapted to feed on large particles may require rapid water-movement. On protected panels arborescent ectoprocts and other projecting organisms may cut down the water flow close to the panel surface.

3) <u>EB8, EB10, EB1A, and EB16</u>: All these species form small encrusting colonies with small zooids, and all were more abundant in closed than in open cages, at least at sites exposed to high wave action or water-movement. I found no fragments or broken colonies which would indicate that these species had been attacked by fish. Possibly the effect on water flow of the higher cover of projecting organisms in closed cages was important for species with small zooids, in areas of high water-movement. This suggestion is speculative, but no other explanation seems reasonable. EB1A and EB16 were also common among algae at the WSD and NSD sites, where the algae would have reduced the water flow close to the surface. Ryland (1975) discusses a situation where zooid size appeared to influence species' abundances.

The results discussed in the latter three paragraphs above show that caging treatment may have effects other than those directly related to predation by fish. In particular the effects of subtle changes in the way water moves over a surface require further investigation.

The exceptional results discussed earlier show that although as a rule projecting and soft bodied organisms were subject to predation, some species are selected less often by fish than others. The factors which may reduce predation or the effects of predation include regeneration and heavy calcification (AB17), small size (AB9), camouflage (young Ascidian B colonies) and toxicity or distastefulness (larger Ascidian B colonies).

Bakus (1969, 1971) and Green (1977) have proposed that toxicity has evolved in many sedentary organisms, particularly sponges, on coral reefs as a defense against predation by fish. I have suggested that Ascidian B may be toxic or distasteful to fish, and also that it may have a 'warning' colour.

Randall and Hartman (1968) found no correlation between the colour of sponges and their abundance in fish stomachs, and Green (1977) found no correlation colour and toxicity in sponges. Nevertheless I have observed that *Pomacanthus semicirculatus* feeds mainly on inconspicuous organisms when boulders are turned over for it on Heron Reef; and Ascidian B was the only conspicuous ascidian on the panels, the others being dull red, grey to black, or transparent. All the teleosts investigated have been found to have colour vision (Walls 1963). Possibly fish discriminate between colours which are similar to the human eye.

Simple ascidians were not analysed as separate species, but observations indicate that some may escape detection because they are transparent (*Ascidia* spp), or covered with sand grains (*Molgula* spp). Others, for example *Polycarpa aurata*, develop thick leathery tests, and may become immune to predation when they are large enough: I have observed very large *P. aurata* growing in exposed places. Most ascidians however, are found only in crevices or under boulders on the reef.

Arborescent ectoprocts apparently all had aggregated distributions (Section 3:1). Aggregation probably facilitates cross-fertilisation between colonies, but it may also act as a strategy to decrease predation. If the aggregated distributions are the result of the settlement of larvae close to established colonies, then colonies which survive and grow act as indicators to settling larvae, of places which are probably safe from predation.

Obviously the most successful strategy against predation by fish is the encrusting, calcified habit adopted by many ectoprocts. Encrusting ectoprocts, however, are almost certainly subject to predation by molluscs, particularly nudibranchs; and they are also liable to be smothered, eventually, by large sponges or ascidians or oysters (see Chapter 6). Thus, although one might expect encrusting ectoprocts to be dominant on cave walls exposed to predation, such surfaces are usually dominated by large sponges, ascidians, oysters, or ahermatypic corals.

In summary, predation by fish apparently determines which groups of species will be successful in the early stages (the first three to six months) of colonisation of newly created patches on reef surfaces. The species are divided according to life form: projecting organisms (simple ascidians, arborescent ectoprocts), and soft bodied encrusting forms (compound ascidians, sponges) are subject to predation, while calcareous encrusting forms are not. Species in each group use various strategies in the face of predation, such as aggregated distributions, toxicity, inconspicuous appearance, escape in growth from predation, or small size.

I believe that the differences between these strategies are important. If the reef surfaces are viewed as a multitude of patches with different histories, then each strategy may be successful in a different set of patches. Perhaps, with so many patches, there are always places on the reef which suit the strategy of each species.

5.5 THE EFFECTS OF GRAZING FISH ON ANIMALS AMONGST ALGAE

Introduction

It has been shown (Section 4:3) that animals were less common at shallow sites outside caves than in caves. The data used in Section 4:3 were the total abundances of species on samples from both open and closed cages. In this section the relative abundances of animals in open and in closed cages at the sites WSS, WSM, NSS, and NSM are considered, in order to determine whether grazing fish had any effect on animal abundances. The deep sites, WSD and NSD, are not considered here because too few panels from these sites were examined to analyse by means of the non-parametric tests employed in this section.

Because almost all species of animals were rare at the WSS, WSM, NSS and NSM sites, similar species were grouped together, and the total area covered by each group on both sides of each settlement panel were calculated. Paired panels from open and closed cages were then compared. Where the distribution of some species in a group appeared to differ from that of others, I have presented data for individual species.

Results

Sites at 6 m and 10 m below the reef crest were considered separately. At both depths each group of species covered a smaller area, on average, on panels from open cages than on panels from closed cages; except that at the 10 m sites spirorbids were more abundant in open than in closed cages (Table 5:12). The totals for pairs of panels were compared using a Wilcoxon matched pairs rank sum test (Siegel 1956). The differences

TABLE 5:12

THE MEAN AREA (IN $mm^2.m^{-2}$) COVERED BY GROUPS OF SPECIES ON PANELS AT NON-CAVE SITES.

Depth below reef crest	6m		10m	
Cages:	Closed	Open	Closed	Open
Species Groups:				
Sponges	895	45	4160	15
Simple ascidians	6475	20	12990	5
Compound ascidians	9900	10	25330	0
Arborescent ectoprocts	3235	10	43630	55
Encrusting ectoprocts	8465	40	36260	4175
Oysters	4000	180	10035	9500
Spirorbids	1220	250	1390	5145
Coral juveniles	750	50	225	80
'Other tubicolous worms'	420	290	1925	830

between caging treatments were significant at p = 0.05 at both depths for sponges, simple and compound ascidians, and arborescent and encrusting ectoprocts; but only at the shallower sites for oysters, spirorbids, and coral juveniles. No significant differences were detected for 'other tubicolous worms', a group comprising Hydroides spp, Spirobranchus sp, and Filograna; all serpulid polychaetes, as well as vermetid molluscs.

Species of sponges, ascidians, and arborescent ectoprocts all were apparently affected to the same degree by grazing fish, but some species of encrusting ectoprocts were more common on grazed panels than others, and the same is true of the 'other tubicolous worms' group. The nine species of encrusting ectoprocts most common on grazed panels at the 10 m sites have been included in Table 5:13, which shows the area covered by each species on grazed panels at 10 m depth. Fifteen other species were absent from these grazed panels but present on protected panels at the same sites. Only one colony of each of the four species marked was present on grazed panels at 6 m depth.

The mean abundance of miscellaneous species, including those in the 'spirorbids' and 'other tubicolous worms' groups, are shown in Table 5:14. As there appeared to be a connection between the ease with which these organisms might be scraped off a surface and their abundances on grazed panels, I arranged the molluscs, polychaetes, corals, and other organisms in order of increasing 'scrape resistance'; and presented their abundances on grazed panels as a percentage of their abundance on protected panels (Table 5:15).

The percentages shown in the 10 m depth column were ranked, and this ranking was compared with the order of species

TABLE 5:13

THE MEAN AREA COVERED, IN $mm^2.m^{-2}$ BY NINE ENCRUSTING ECTOPROCTS ON GRAZED PANELS AT THE WSM AND NSM SITES.

Species	Area covered on grazed panels	Percentage of area on protected panels
*EB6	2465	18
*EB1A	465	15
EB9	355	15
EB11	320	30
*EB16	110	31
EB40	100	40
EB15A	95	25
*EB2	90	58
EB12	20	2

*These species were present on grazed panels at the WSS and NSS sites too.

TABLE 5:14

THE MEAN ABUNDANCE (IN $mm^2.m^{-2}$) OF MISCELLANEOUS SESSILE ANIMALS ON PANELS AT NON-CAVE SITES.

Depth below reef crest	6m		10m	
Cages:	Closed	Open	Closed	Open
Species				
Crinoid juveniles	0	0	25*	0
Barnacle	0	0	15*	30*
Pteriid bivalves	425*	0	280	0
Chama	0	0	515*	0
Vermetids	0	15*	50*	25*
Filograna	10*	0	1255*	0
Hydroides	190	0	600	705
Spirobranchus	375	275	20*	100*
Spirorbid 1	750	40*	195	50*
Spirorbid 2	470	210	1195	5095

*Based on data from three samples or less.

TABLE 5:15

THE ABUNDANCE OF MISCELLANEOUS SESSILE ANIMALS ON GRAZED PANELS, AS A PERCENTAGE OF THEIR ABUNDANCE ON PROTECTED PANELS.

Species	6m Depth	10m Depth
Crinoid juveniles	*	0
Pteriid bivalves	0	0
Filograna	0	0
Spirorbid 1	5	26
Spirorbid 2	45	426
Vermetid	**	50
Barnacle	*	200
Hydroides	0	118
Oysters	5	95
Chama	*	0
Spirobranchus	73	500
Coral juveniles	7	35

*Not present on grazed or protected panels.

**Present on grazed panels but not on protected panels.

in the table, using the Spearman rank correlation coefficient (Siegel 1956). There was no significant concordance between the two rankings at $p = 0.05$. This result is due to the positions of Spirorbid 1, and Chama in the table.

To investigate whether animals which grew beneath the algal mats on protected panels could survive when the panels were scraped by fish, I used data from the panels described in Section 5:2. These panels were protected in cages for four months, then exposed to fish for two days. The sizes of sessile animals which remained on the panels were recorded, and the number of damaged individuals was noted. Larger coral juveniles, oysters, and possibly Hydroides appeared to be less liable to damage by grazing fish than smaller individuals (Table 5:16). Vermetids and spirorbids did not attain sizes larger than 3 mm^2 on these panels.

Discussion of Results

Sponges, ascidians, and arborescent ectoprocts are removed by predatory fish in caves, and their absence from unprotected panels outside caves may be due to the activities of the same predators. However, the results for other groups of animals cannot be explained in the same way. Herbivorous fish which scrape algal substrata appear to remove many animals in the process. This may be compared to the effects of grazing by limpets on rocky shores (see Section 5:1): the herbivores keep the algal 'lawns' free of animal 'weeds'. The result is that more space is occupied by algae than would be the case if the herbivores were absent.

TABLE 5:16

THE NUMBER OF ORGANISMS OF VARIOUS SIZES REMAINING ON PANELS PROTECTED FROM FISH FOR THREE MONTHS, THEN GRAZED FOR TWO DAYS.

Species	Size range (mm^2)	Total No.	No. Damaged
Coral juveniles	1-2	5	2
	3-4	7	5
	5-8	11	4
	9-16	8	0
	17-32	3	0
Oysters	5-8	1	1
	17-32	2	2
	32-64	1	0
	64-128	1	0
Hydroides	1-2	2	2
	3-4	6	3
	5-8	3	3
	9-16	3	2
	17-32	1	0
Vermetids	1-2	2	0
	3-4	1	1
Spirorbids 2	1-2	5	3

The fact that animals were more abundant on grazed surfaces at 10m than at 6m depth supports the conclusion reached in Section 5:3 that grazing decreases with depth. The data for the WSD and NSD sites shows a continuation of the trend demonstrated here: there are many animals on unprotected panels at these sites.

Some animals were more common on grazed panels than others (Tables 5:13, 5:14). For encrusting ectoproct species growth rate and degree of calcification appeared to be important in this respect. EB6 (Table 5:13) grows rapidly, but is lightly calcified. EB1A, EB9, EB12, and EB15A are moderately well calcified, and do not grow as rapidly as EB6, but have well developed giant buds, which extend around the colonies like a frill and increase the area occupied by the colonies.

Observations of large (15mm diameter) encrusting ectoprocts and thick crusts of coralline algae growing among filamentous algae on natural surfaces indicate that scraping fish avoid these objects: the scrapes are directed around the ectoprocts or corallines rather than across the interface between animal or coralline and algae. Birkeland (1977) has noted too, that grazing fish avoid coral recruits as small as 3 mm in diameter (7 mm^2 in area), and the results presented in Table 5:16 support these observations.

Calcareous animals may, therefore, escape in growth from grazing fishes, and species which grow rapidly would be more likely to attain a 'safe' size before they are smashed by a rasping fish. The development of large giant buds around young colonies may be important, because the colonies may be able to attain a 'safe' size more rapidly by expanding the giant buds rather than adding new zooids to the colony. Giant buds, however, may have other advantages too, as discussed in Chapter 6.

EB11, EB16, EB40, and EB2 (Table 5:14) do not grow rapidly or have well developed giant buds, but they are heavily calcified and presumably resistant to damage. EB2 forms a small hard mound with small rounded zooids; a shape which would presumably be more resistant to damage than a flat encrusting shape. Other animals with strong calcification such as corals, oysters, *Hydroides*, and *Spirobranchus* also became established on grazed panels, whereas species which would be more easily dislodged, such as crinoid juveniles, Pteriid bivalves, and *Filograna*, were absent from grazed panels (Table 5:15).

No significant correlation between calcification and abundance on grazed relative to protected panels was established, because *Chama* sp, a small heavily calcified bivalve, was completely absent from grazed panels, and *Spirorbid* 1, a small but numerous serpulid polychaete with moderate calcification, was abundant on grazed panels.

Spirorbids were more abundant on grazed than on protected settlement plates in the Red Sea too (Vine 1974). Vine postulated that because grazing removed algae, the surfaces were freed for settlement by invertebrates. In fact, surfaces are freed for colonisation by both invertebrates and algae; and the results presented here suggest that animals do not colonise as rapidly as algae, nor grow as rapidly as the algae, so that they seldom become established before they are smashed by fish grazing the algae around them.

However, spirorbids may colonise surfaces very rapidly. Vine (1974) found densities of up to 14 x 10^3 per square meter (figure calculated from graph) on panels immersed for thirty days. I suggest that these polychaetes, which never attain a large size, may grow rapidly on grazed panels where the algae do not restrict water-movement close to the surface.

In contrast to spirorbids, Chama appears to grow slowly, and may attain a large size. Furthermore Chama was present on only two protected samples so that its absence from grazed samples may well be due to chance. Although the data for other species is also based on a few samples in many cases it seems reasonable to conclude that heavily calcified and rapidly growing species are more likely to become established on grazed surfaces than other animals.

The data in Table 5:16 support the conclusions reached above. Very small animals, even of heavily calcified species such as corals, were subject to damage by fish, whereas larger animals were apparently avoided. Further, if for some reason a surface is subject to reduced grazing then corals, oysters, and Hydroides, and perhaps other species such as Spirobranchus are able to grow underneath the algae on the surface and attain a size at which they begin to overtop the algae, and they are then immune to grazing.

Bakus (1969), Dart (1972), and Birkeland (1977) have suggested that the growth of invertebrates and corals may be inhibited by sedimentation and dense algal growth where grazing is absent, and that grazing enhances the settlement and growth of these organisms. Birkeland (1977) showed that coral settlement and survival was greater on vertical or deep surfaces where algal growth was reduced, than on horizontal upper surfaces in shallow water, where algal growth was greatest. He also showed that there was a more rapid accumulation of fouling on protected than on grazed panels but he apparently did not count the numbers of coral recruits on grazed and protected panels.

The settlement panels used in this study were all suspended vertically, so that sedimentation under algae was probably much less important than it would have been on horizontal surfaces. Perhaps on horizontal surfaces some grazing is beneficial to coral recruits; certainly the relation between corals, fishes, and fouling organisms is more complex than that suggested by Birkeland (1977) and others.

5:6 REDUCTION OF PREDATION BY PROJECTIONS AND CONFINED SPACES.

Introduction

Flat settlement panels were used to obtain the data discussed in preceeding sections because replicate surfaces were required. However, natural surfaces are seldom flat. Two kinds of complex surfaces were investigated: surfaces with projections, and surfaces in confined spaces such as the side walls of crevices; in order to test the hypothesis that predation by fish is reduced on such surfaces. Water-movement and illumination are normally reduced on the kinds of surfaces considered, but the experiments were designed to exclude the effects of these factors.

Methods

Square projections of 3.2, 6.4, 12.7, and 25.4 mm height were attached on either side of standard settlement panels as shown in Figure 5:3. Three controls were used. Control panel 1 had no projections, Control panel 2 had no projections but was enclosed in a closed cage, and Control panel 3 had 12.7 mm high projections and was caged.

Sets of panels were suspended for three months at a non-cave site in shallow water, and in a cave at about the same depth. When examining the panels, areas within 12 mm of a projection were considered. Corresponding areas were examined on control panels.

Confined spaces were investigated by means of narrow cages, open at one end (Figure 5:4). These cages were fixed against the substratum by means of wire strands rather than sus-

FIGURE 5:3

ARRANGEMENT OF PROJECTIONS ON PANELS.

20mm by 20mm Novasteen blocks of various heights were arranged 20mm apart on settlement panels as shown in the figure. The arrangement was designed so as to interfere as little as possible with water-movement over the panels. The blocks were fixed to the panels using contact adhesive.

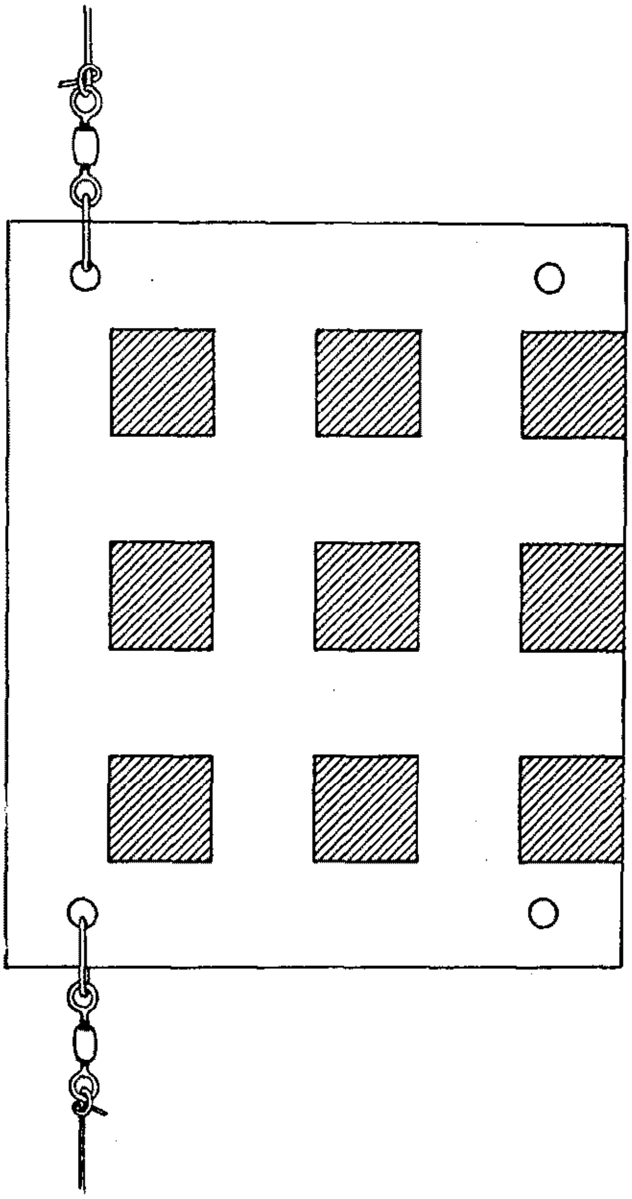
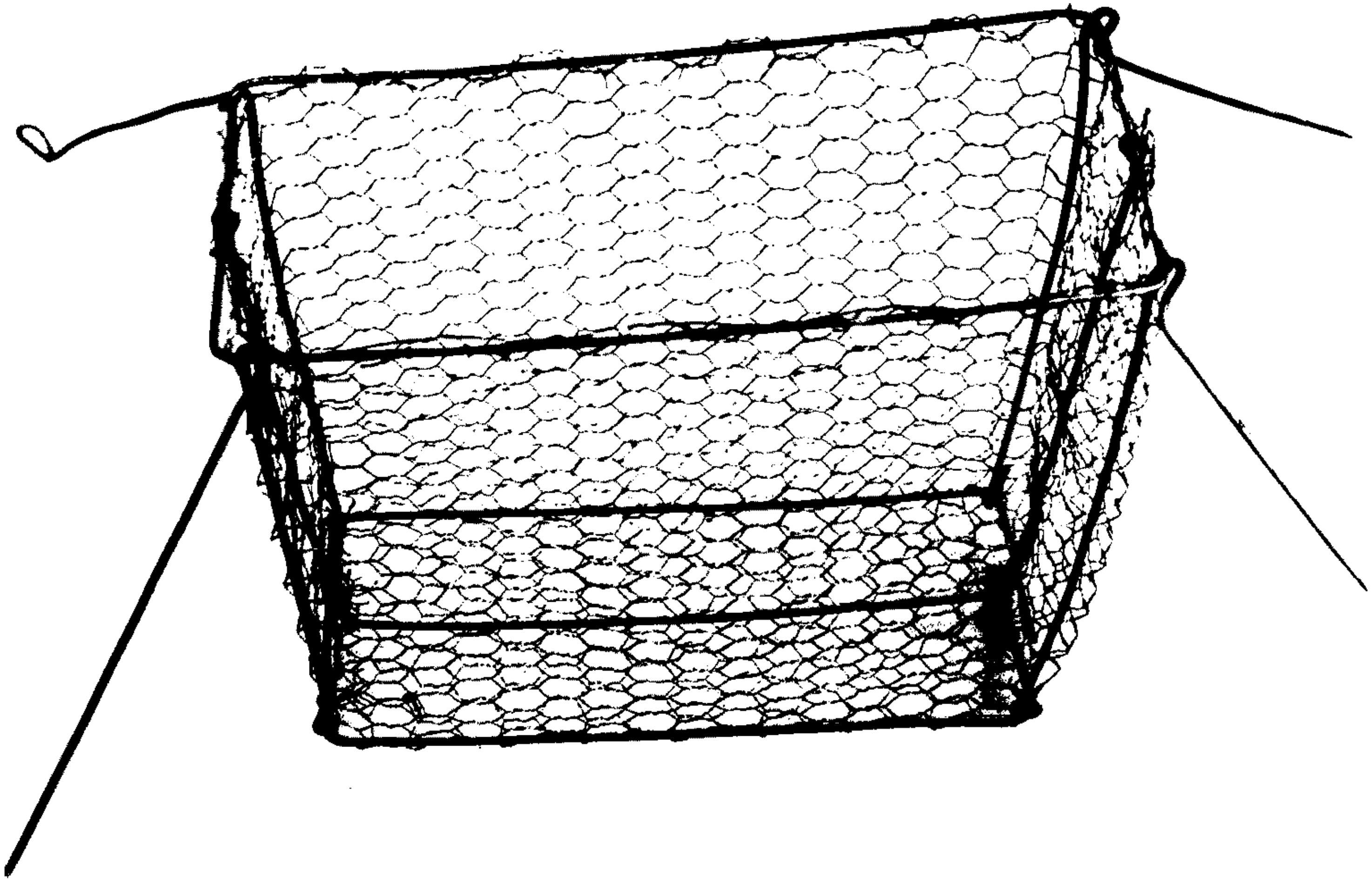


FIGURE 5:4

CONFINED SPACE CAGE

Panels were mounted in the center of the cage shown, and the cage was fixed against the substratum using the wire struts shown so that the panels were vertical. Cages 160mm and 320mm wide were constructed. The figure shows a narrow cage.



pending the panels in the normal way in case movement of the cages discouraged fish from entering narrow spaces. The narrow cages were 160 mm wide, and the panels were fixed vertically in the center of the cages so that distance from the panel to the mesh was 80 mm. These panels were compared with panels in similar cages 320 mm wide, fixed alongside the narrow cages.

Four cages of each type were placed in a cave, and four on the side of a large coral growth at the same depth. As both sides of each panel were used there were eight replicates per treatment. Algae were scraped off the panels at the non-cave site and dried at 80°C after calcium carbonate debris had been dissolved in dilute hydrochloric acid. The cover of various groups of organisms on the panels from the cave was estimated as described in Chapter 2.

Results

Unfortunately projections shaded the surfaces of the panels at the non-cave site. As a result panels with projections were colonised by animals rather than algae: the caged panel without projections (Control 2) supported a luxuriant growth of algae, whereas the caged panel with projections (Control 3) was almost entirely covered by ascidians. The results from the non-cave site are therefore not considered further.

At the cave site, there was a trend towards greater abundance of each group of species on panels with higher projections (Table 5:17), except for encrusting ectoprocts and perhaps compound ascidians. Page's (1963) test for trend showed that there was a progressive increase, from Control panel 1 to the panel with 25.4 mm projections, in the abundances of sponges,

TABLE 5:17

THE AREA COVERED BY GROUPS OF SPECIES, AND THE MEAN SIZES OF ARBORESCENT ECTOPROCTS ON PANELS WITH PROJECTIONS.

Height in mm of Projections	0 (Control 1)	3.2	6.35	12.7	25.4	0,Caged (Control 2)	12.7,Caged (Control 3)
Area covered in mm^2 by:							
Sponges	88	213	77	196	180	196	436
Simple ascidians	1	2	11	94	20	12	45
Compound ascidians	138	269	81	9	1066	353	35
Arborescent ectoprocts	145	1516	1586	2936	2615	5357	6464
Encrusting ectoprocts	649	452	383	738	221	569	200
Mean size in mm^2 of arborescent ectoprocts	6.3	4.6	13.4	19.7	24.9	127.5	53.0

TABLE 5:18

THE MEAN DRY WEIGHT OF ALGAE AND THE MEAN AREA COVERED BY GROUPS OF SESSILE ANIMALS ON PANELS IN NARROW AND WIDE CAGES.

Measure of Abundance	Distance from panel to cage	
	80mm	160mm
Dry weight of algae (mg).	246	199
Area covered, in mm^2 by:		
Sponges	58	68
Simple ascidians	2	5
Compound ascidians	12	9
Arborescent ectoprocts	1167	73
Encrusting ectoprocts	280	345

simple and compound ascidians, and arborescent ectoprocts; which was significant at $p = 0.05$. Thus predation by fish appears to be reduced by projections and tall projections are more effective in this respect than short ones.

The area covered by a group of species is determined both by the sizes of organisms and by the number which have settled on the panel. A large number of arborescent ectoprocts settled on some panels, and less settled on others. I have therefore calculated the mean size of arborescent ectoproct colonies on each panel (Table 5:17). There is an obvious trend towards increased colony size on panels with higher projections.

The mean dry weights of algae on each side of panels from wide and narrow cages at the non-cave site (Table 5:18) show that there was a greater growth of algae on the panels from narrow cages. This difference was significant at $p = 0.05$ (Mann-Whitney U test).

The mean areas covered by sponges, ascidians, and arborescent and encrusting ectoprocts on the panels in wide and narrow cages in the cave are also shown in Table 5:18. Only the cover of arborescent ectoprocts was significantly greater on panels from narrow cages. The areas covered by sponges and ascidians on these panels were low relative to the average cover on panels suspended on nylon lines at cave sites (see Section 5:4, Table 5:10).

Discussion of Results

Sessile organisms may be at least partially protected from fish predators by projections from the surface or in confined spaces. Although the effect of projections on grazing by herbivorous fish was not shown, I observed that the filaments of algae growing between projections on the panels were longer than the filaments of algae on panels without projections. Thus projections probably protect algae from fish too. Further experiments with transparent projections might be used to demonstrate this effect, and the spacing of projections might also have an effect on predation, which could be revealed by other experiments.

The experiments using narrow cages were suggested by the results from preliminary experiments in which panels were suspended in closed and in narrow open cages. There appeared to be a gradient in predation across the panels in narrow open cages, and the open cages used to obtain the data presented in earlier sections were therefore made very wide (Chapter 2).

The narrow and wide cages described in this section were fixed against the substratum rather than suspended on nylon lines, and therefore invertebrates such as crabs could gain access to these panels. Observations of these panels at night revealed that small spider crabs (Menaethius monoceros) were present in the corners of the cages at the non-cave site, and larger crabs (Schizophrys ?asper) were seen foraging near the cages in the cave. Predation by invertebrates may be responsible for the low cover of sponges and ascidians on these panels, and the lack of any differences between wide and narrow cages for these organisms.

It is surprising that crevices 80 mm wide and perhaps wider can afford protection from fish. The explanation appears to lie in the mechanics of feeding by fish. The fish must swim towards a surface in order to bite an object on it. The space available above the surface must therefore be greater than the length of the fish. This can be seen when watching parrotfish or angelfish feeding. However, Aluterid fishes appear to have been adapted to exploit confined spaces. I have watched balistid fish using undulations of the anal, dorsal and pectoral fins to position the mouth so that it could bite off ascidians.

The natural surfaces of a reef are very complex, and the results shown here can be used to explain many features of the distribution of animals and plants on the reef. For example dead Acropora corals are often seen with a cover of filamentous algae, and the algal filaments are much longer between the coral 'fingers' than on top of them. Also, large Halimeda opuntia and H. discoidea are fairly common in the network of staghorn coral thickets on the reef slope, but are seldom seen in more exposed places. In caves arborescent ectoprocts are often seen near the bases of the projections formed by the ahermatypic coral Tubastrea, and ascidians are occasionally seen to be growing behind the oultline of a projecting rock or in confined spaces. The relation between predation and the configuration of the surface is probably one of the most important factors controlling the local distribution of sessile species on the reef.

5:7 THE PROTECTION OF ALGAE BY POMACENTRIDS

Introduction

Pomacentrid fishes defend territories against other species of herbivorous fish (Low 1971, Robertson *et al* 1976), and thus reduce grazing by other fish within their territories (Vine 1974). On Heron Reef Pomacentrids are particularly abundant on the reef flat and on patches of coral rubble on the upper reef slope (Sale 1974). The reef flat and rubble banks provide an abundance of both grazing substratum and cover for Pomacentrids. This section presents further evidence for Vine's (1974) conclusion that there is an increased standing crop of algae on surfaces inside Pomacentrid territories. It is further suggested, on the basis of somewhat incomplete evidence, that Pomacentrids are important in determining the distribution of many species of large algae on Heron Reef.

Influence of Pomacentrids on standing crop of algae:

To test the hypothesis that there is an increased standing crop of algae in Pomacentrid territories, three dead *Montipora* coral plates were collected, one from within the territory of a *Eupomacentrus apicalis* and the other two outside Pomacentrid territories. All the dead coral plates had a fairly flat surface and were collected from 1.5m below the low water level in One Tree Island lagoon (11 km from Heron Island). After preserving the plates in formalin-seawater, 1200mm^2 plots on each plate were scraped, and the coral fragments in the scrapings dissolved in dilute hydrochloric acid, leaving the algae. After filtration the algae were dried to constant weight at 80^{o}C.

The dry weights of algae from the two unprotected coral plates were lumped together and compared with those from the protected plate (Table 5:19). The mean dry weight of algae on samples from the protected plate was significantly greater than the mean for unprotected plates (Mann-Whitney U test, $p = 0.05$).

Evidence from settlement panels supports this result. Larkum, Borowitzka, and I have suspended panels in One Tree Island lagoon for three month periods. One of these panels was protected by an aggressive *Eupomacentrus apicalis*. The dry weight of algae on this panel is compared with that on five unprotected panels suspended in the same area for the same period (June to September 1974) in Table 5:20. The dry weight of algae on the protected panel was more than three times the highest dry weight recorded for unprotected panels. Clearly the territorial behaviour of *Eupomacentrus apicalis* leads to an increased standing crop of algae within the protected territory.

Rate of browsing by a Pomacentrid.

A large (120mm) *Eupomacentrus apicalis* became established adjacent to a frame on which settlement panels were suspended, 5 m below the reef crest in the Heron Channel, and all the panels at this site were defended. To determine the rate of browsing by the Pomacentrid I filmed the area with a camera attached to a stake, using a slow frame speed. In a period of sixty-five minutes at midday, the *E. apicalis* defended the area 28 times, and took 12 bites from the panel on the frame. The surface area of the panel was 33600 mm^{2}, so that the rate of browsing by the *Eupomacentrus apicalis* was about 330 bites.m^{2}.hr^{-1}. This is comparable with the grazing rates of Scarid fishes on some surfaces (Section 5:2),

TABLE 5:19

DRY WEIGHTS OF ALGAE FROM 1200 mm^2 PLOTS ON DEAD CORAL PLATES (mg).

Protected by Pomacentrid	Not Protected
145.6	54.5
188.6	74.4
173.2	56.1
157.5	137.1
195.3	91.4
150.6	98.1
	61.3
	63.8

TABLE 5:20

DRY WEIGHTS OF ALGAE (in mg) ON SIX SETTLEMENT PANELS SUSPENDED FOR THREE MONTHS IN ONE TREE LAGOON.

Protected by Pomacentrid	Not Protected
194.0	41.5
	35.7
	33.8
	47.3
	43.2

but the bite size of Pomacentrids is very much smaller than the average scrape size of Scarid fish.

Grazing by fish on macroalgae

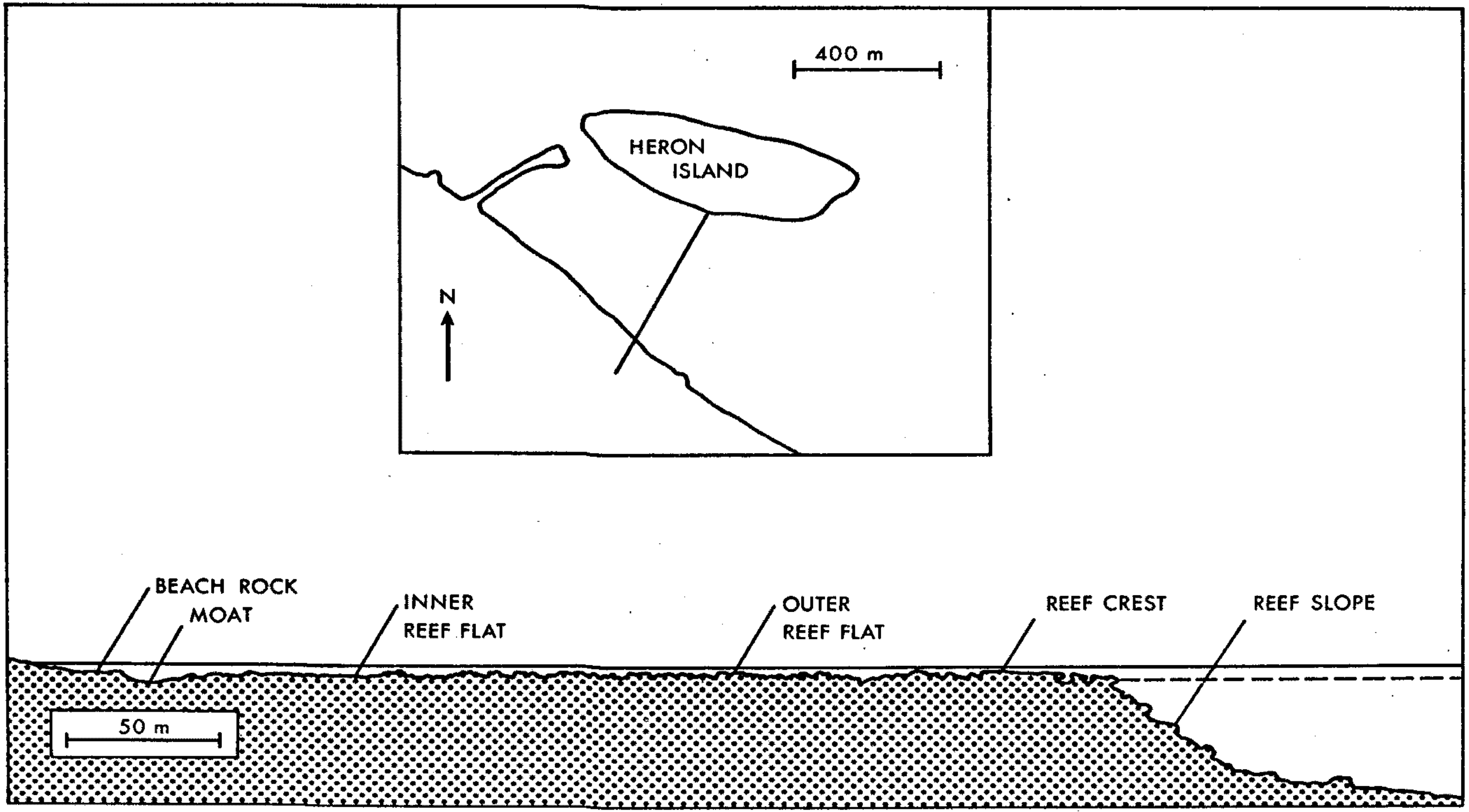
Algae with relatively large thalli (for example Sargassum spp., Caulerpa spp.) are abundant on the wide stretch of reef flat around the cay on Heron reef (Figure 5:5), yet they are rare or absent on the reef slope. Grassle (1973) lists the algae on the reef flat, reef crest, and reef slope in order of abundance. Sargassum spp, Chnoospora, Hydroclathrus and Padina were the most abundant species on the reef flat, but on the reef slope only Gymnosorus (an encrusting brown alga) and Chlorodermis were common.

A number of species were found occasionally on settlement panels suspended in closed cages at shallow sites in the Heron Channel. They were not found on equal numbers of panels exposed to grazing fish. Large algae would not be expected to become established on grazed surfaces because of the frequent scraping of these surfaces by Scarids (Section 5:2), but I have observed that the scraping fish seldom feed on large algae once they are established. A different set of fishes appears to feed on large algae. These include Naso unicornis, Siganids; and Scarus lunula which Choat (personal communication), was observed to consistently feed on large algae.

To test whether large algae were subject to intensive grazing by large fish, pairs of boulders about 20 cm across, covered with large algae, were moved from the inner reef flat to the reef slope and to the outer reef flat near the reef crest

TRANSECT ACROSS HERON REEF FLAT.

The transect is modified from Choat (1969), and runs in the direction shown in the inset from the island into the Heron Channel.


400 m
HERON ISLAND
N
BEACH ROCK
MOAT
INNER REEF FLAT
OUTER REEF FLAT
REEF CREST
REEF SLOPE
50 m

(see Figure 5:5). Controls were moved approximately one meter. One boulder in each pair was caged with 40 mm mesh wire netting, and the boulders were observed at intervals thereafter (Table 5:21). On the reef slope unprotected boulders were cleared of algae within one, or at most two days.

A gradient in grazing might be expected over the Heron Reef flat, with grazing being most intense near the reef crest, and least intense on the inner reef flat. The fronds, and not the stipes of Sargassum are eaten, so that if grazing was most intense near the reef crest Sargassum plants near the reef crest should have a lower proportion of fronds to stipes than Sargassum plants on the inner reef flat. Whole plants of Sargassum cf crassifolium were collected from the inner reef flat and from just behind the reef crest; and preserved. The fronds were detached and the stipes broken into pieces which would lie flat. The area covered by fronds and stipes was then estimated using a photographic technique (Marshall 1968). Finally, the plants were dried at 65°C to a constant weight. The ratio of area covered to weight was used as a measure of the proportion of fronds and stipes (Table 5:22). The ratio was significantly greater for samples from the inner reef flat (Mann-Whitney U test, $p = 0.05$).

Discussion of Results.

Algae grew more luxuriantly when protected by Pomacentrids. This effect is most pronounced near the holes into which the Pomacentrids retreat when threatened. Inside the holes compound ascidians and encrusting ectoprocts are common. Pomacentrids therefore create patches in which species normally subject to

TABLE 5:21

FATE OF ALGAE ON BOULDERS TRANSPLANTED FROM THE INNER REEF FLAT ON 17-7-1974.

Position of Boulders, and Algae Initially Present	Caging Treatment	Boulders Observed on: 18-7-1974	23-7-1974	18-8-1974
Reef Slope (Pair 1) *Sargassum* cf *crassifolium* *S. polycystum*	caged	No change	No change	*Colpomenia* abundant
Padina *Colpomenia* *Chlorodesmis*	not caged	Only *Chlorodesmis*, stipes of *S.* cf. *crassifolium* remain	No further change	No further change
Reef Slope (Pair 2) *S.* cf *crassifolium* *Padina*	caged	No change	No change	*Colpomenia* fairly common
Turbinaria *Halimeda*	not caged	Only *Halimeda* and stipes of *Sargassum* and *Turbinaria* remain.	*Halimeda* absent	No further change
Reef Crest (Pair 1)				
S. cf *crassifolium* *Padina*	caged	No change	No change	*Colpomenia* present, new fronds of *Sargassum*
Halimeda *Chlorodesmis*	not caged	No change	No change	No change
Reef Crest (Pair 2) *S.* cf *crassifolium* *S. polycystum*	caged	No change	No change	*Colpomenia* abundant.
Padina	not caged	No change	No change	Algal cover reduced ± 30%.

TABLE 5:21 (Continued)

Position of Boulders and Algae Initially Present	Caging Treatment	Boulders Observed on: 18-7-1974	23-7-1974	18-8-1974
Inner Reef Flat (Control Pair 1) *S.* cf *crassifolium*	caged	No change	No change	New *Sargassum* fronds, filamentous epiphytes abundant
S. polycystum *Padina* *Colpomenia*	not caged	No change	No change	*Colpomenia* absent
Inner Reef Flat (Control Pair 2) *S.* cf *crassifolium* *Padina*	caged	No change	No change	*Colpomenia* abundant, *Sargassum* growing through cage
Colpomenia *Halimeda* *Chlorodesmis*	not caged	No change	No change	No change

TABLE 5:22

THE SURFACE AREA AND DRY WEIGHT OF SAMPLES OF *SARGASSUM* CF. *CRASSIFOLIUM.*

Origin of Samples	Surface Area (cm^2)	Dry Weight (g)	Ratio
Near the reef crest	174	238	0.731
	307	467	0.657
	332	491	0.676
	263	359	0.733
	236	360	0.656
Inner reef flat	488	491	0.994
	365	362	1.009
	435	500	0.870
	331	332	0.997

grazing or predation can survive.

With exception of *Chlorodesmis* all large algae are decimated by fish on the reef slope within one, or at most two days unless they are protected in some way. I put further unprotected boulders in various places on the reef slope and in every case algae other than *Chlorodesmis* were removed within 48 hours. Littler and Doty (1975) have also reported that fish grazing was more intense on reef slopes in Hawaii than on reef flats.

Suitable cover for large fish is available on the reef slope but not on the reef flat, and large fish can only feed on the flat during diurnal high tides. Yet the rapidity with which exposed boulders were stripped of algae on the slope suggests that the algae on the reef flat could be consumed within a few weeks at most.

Chlorodesmis, which is a conspicuous yellow-green colour, appeared to be immune to grazing (Table 5:21). *Scarus lunula* and some Acanthurids have been observed cropping *Chlorodesmis*, but only infrequently. Further work is necessary to determine whether this species is distasteful or toxic to fish.

Halimeda spp may be less appealing to fish than other algae because the fronds are composed very largely of calcium carbonate, and it would therefore be a 'low calorie' food item. Emlen (1966) and Paine and Vadas (1969b) have proposed that animals should select food categories on the basis of calorific value per mouthful. *Halimeda* spp. grow abundantly in the interstices of staghorn coral thickets on the reef slope, where they are presumably partly protected in the confined spaces of the coral. Furthermore Dahl (1972) reported that off Puerto Rico *Halimeda* is one of the algae which occurs closest to the reefs, where grazing by fish was most intense.

If there is a gradient in grazing across the Heron reef flat, then a progressive elimination towards the reef crest of the species most favoured by grazing fish would be expected. Grassle (1973) lists *Turbinaria* and *Halimeda* spp as the dominant species on the reef crest, whereas other species are more abundant on the flat. Grassle's data together with the results presented in Table 5:22 show that grazing was more intense near the reef crest than on the inner reef flat.

Surprisingly, Stephenson and Searles (1960) have shown that the beachrock at Heron Island was intensively grazed by fish. Since the beachrock lies inshore of the reef flat (Figure 5:5), grazing intensity was not correlated to distance from the reef slope. Nor can reduced grazing be ascribed to high wave action (John and Pople 1973, Littler and Doty 1975), since this part of Heron Reef is protected from wave action by the nearby Wistari Reef, and what wave action there is is most severe at the reef crest.

The boulders on the reef flat provide ample cover for Pomacentrids, whereas such cover is scarce on the beachrock and near the reef crest. The hypothesis that the abundance of Pomacentrids on the reef flat contributes to the persistence of macroalgae therefore seems reasonable. The hypothesis was tested further by J.H. Choat, who found that macroalgae such as *Padina* were present beneath *Halimeda* spp on the reef slope, and tended to be more abundant within Pomacentrid territories. Furthermore pieces of large algae placed on the reef slope survived for longer periods when placed in Pomacentrid territories (Choat, personal communication). Further support for the hypothesis is provided by Brawley and Adey (1976), who found that the abundance of brown algae on reef terraces off Jamaica was decreased when resident Pomacentrids were removed.

The abundant growth of macroalgae on the reef flat at Heron Island probably results from a combination of factors, the most obvious ones being the rapid growth of algae in shallow water, and the fact that large herbivores are present only during diurnal high tides. A less obvious, but possibly crucial factor, is the presence of large numbers of Pomacentrid fish on the reef flat.

CHAPTER 6

THE EFFECTS OF SESSILE ORGANISMS ON EACH OTHER

6:1 THE TYPES OF INTERACTIONS RECORDED.

As a large number of species may be found in a small area of reef surface, I expected that interactions between sessile species might be important in determining their distribution and abundance. Interactions between sessile species have been shown to be important among the epibionts of algae and bryozoans by Stebbing (1971, 1973a, 1973b), Ryland (1973) and Hayward (1973); on rocky shores by Connell (1961b), Dayton (1971) and others, and on coral reefs by Jackson and Buss (1975). The interactions recorded may be divided into categories according to the mechanism by which species affect each other. These categories are described in this section. I attempted to find evidence for interactions of each type, as described in other sections of this chapter.

1) Reduction of resources: Barnacles may reduce the rate at which food reaches their neighbours, Crisp (1964). Canopy forming algae reduce the available light, so that other species growing beneath them are reduced in abundance (Dayton 1975b). Sessile species also occupy space and thus may reduce the space other species may occupy: Dayton (1971) has shown that in quiet areas on rocky shores barnacles occupy space which would otherwise be invaded by anenomes.

2) Provision of suitable habitat: Dayton (1971) found that the anenomes which colonised areas from which barnacles had been removed were prone to dessication in summer, whereas anenomes in areas with barnacles were not, so that the barnacles provide 'safe sites' for anenomes in unfavourable periods. Many algae grow best in the shade of canopy forming plants (Dayton 1975a,

Hatton 1938). The surfaces of sessile organisms can also act as areas of substratum for other species: for example barnacles often occur on the plates of other barnacles (Knight Jones and Moyse 1961), and algae often grow attached to other species of algae (e.g. Dayton 1975b), or on animals such as barnacles (Dayton 1973).

Complex interactions presumably involving both of the above occur. Burrows (quoted by Chapman 1974) has shown that stands of *Fucus* species are more suitable places for sporelings of the alga *Ascophyllum nodosum* to develop than are mature stands of *A. nodosum* itself. However, growth of the sporelings under the *Fucus* canopy is retarded until the *Fucus* plants die, after which the *Ascophyllum* plants grow to form a canopy.

3) Effect of one species on the predators of another: Landenberger (1967, quoted by Connell 1974) found that anenomes on pilings formed a barrier to starfish so that barnacles higher on the pilings were protected. In contrast anenomes on a rocky shore provided shelter for *Thais* which preyed on neighbouring barnacles (Dayton 1971).

4) Siltation between projecting organisms: *Mytilus californianus* may be eliminated from clumps of *M. californianus* and *Mytilus edulis* because *M. edulis* crawls to the outside of the clumps, and silt accumulates inside the clumps (Harger 1968). Sediment also accumulates between the basal stolons of hydroids (Osman 1977) and between filamentous algae (personal observations) and may smother silt-intolerant species.

5) Interference with feeding: Barnacles grow more slowly when surrounded by algae, possibly because the algal filaments inter-

fere with the barnacles' feeding movements (Barnes 1955).

6) Undercutting or shoving: Barnacles may be undercut or shoved off the surface by other barnacles, Connell (1961b). Large algae may be pushed off the surface by barnacles too (Dayton 1971).

7) Overgrowth: When two encrusting species come into contact one colony may grow over the other, so that the species beneath is denied access to food. Usually, but not always (Gordon 1972) animals which are completely covered are killed. Projecting species such as arborescent bryozoans are almost immune from such overgrowth (Stebbing 1973a, Osman 1977) and tubicolous species are often able to keep the open ends of their tubes beyond or above encrusting species which grow over the remainder of the tube (Osman 1977). However spirorbids are usually overgrown eventually (Gordon 1972, Stebbing 1973a).

8) Chemical interactions: Complex chemical interactions are known to occur between both terrestrial and aquatic organisms (Whittaker and Feeney 1971). Many marine organisms produce antibacterial agents, and many produce toxins which prevent other organisms from growing on them (Al-Ogily and Knight-Jones 1977, Burkholder 1973). Chiba and Kato (1966) have shown that a hydroid releases chemicals which inhibit the growth of other hydroid species, and encrusting sponges inhibit growth or kill other species by chemical means (Buss 1976, Jackson and Buss 1975). Goodbody (1961) describes results which suggest that chemicals released by sponges may even reduce the settlement of other organisms on surrounding surfaces. A special case of chemical interactions involves corals, which may digest the tissue of neighbouring corals by means of extramesenterial filaments (Lang 1973).

9) Cooperation: Various forms of cooperation between animals of the same species have been reviewed by Knight-Jones and Moyse (1961). These include spacing out among species which reach a maximum size, and fusion of colonies in corals, sponges, and ascidians. Neighbouring encrusting ectoproct colonies of the same species often cease or reorient growth at the point of contact between them (Gordon 1972, Stebbing 1973b). Fusion between conspecific bryozoan colonies, and other relationships between bryozoans are discussed by Ryland (1977).

6:2 INTERACTIONS BETWEEN ALGAE AND SESSILE ANIMALS.

Introduction

Animals were less common amongst algae on settlement panels at non-cave sites than on panels in caves, where algae were absent (Section 4:3). This was partly due to the removal of animals from unprotected panels by herbivorous fish (Section 5:5). It was also argued in Section 4:3 that filamentous algae might interfere with the feeding of some animals. This hypothesis is investigated further in this section.

Filamentous algae may affect animals in three ways: 1) sediment collects between the filaments and this may clog the feeding apparatus of some animals, 2) water-movement between the algae is reduced, so that less food would reach animals growing beneath the algae, and 3) the algal filaments may become entangled in feeding structures such as barnacle cirri.

The first two effects should be important to encrusting organisms but not erect ones. To test this hypothesis the mean abundances of sponges and ascidians on protected panels at the non-cave sites WSS, WSM, NSS, and NSM; and at cave sites, were calculated. Encrusting and projecting ascidians and sponges were compared using the ratio of their abundance at non-cave sites to their abundance at cave sites. Species present in only one or two samples from the non-cave sites were not considered.

Whereas sponges and ascidians use ciliary currents for feeding, ectoprocts use movements of a lophophore to gather food. Algal filaments might interfere with the lophophore movements, and encrusting and projecting ectoprocts were therefore not compared. It might be expected that rigid arborescent ectoprocts would be more affected by algae than flexible ones, since algal filaments would be swept across the arms of rigid colonies, whereas flexible arms would move with the water in the same way as the algae. Secondly, some arborescent ectoprocts (mostly Scrupulocellariidae) have long virbacular which arise from the back of the arms and would be able to sweep algae away from the feeding zooids. Arborescent ectoprocts were therefore divided into three groups: rigid colonies without vibraculae, very flexible colonies, and partly flexible colonies with vibraculae. These groups were compared in the same way as the groups of sponges and ascidians described earlier. Examples of rigid and flexible colonies are shown in Figure 6:1.

Results

The ratios of abundance at non-cave sites to abundance at cave sites for compound and simple ascidians (Table 6:1) were compared using a Mann-Whitney U test. The probability that the two groups do not differ was 0.083 (Table J, Siegel 1956). Thus the two groups were not significantly different at $p = 0.05$, but further data might show a significant difference. However, there was no difference in the ratios for erect and encrusting sponges (Table 6:2).

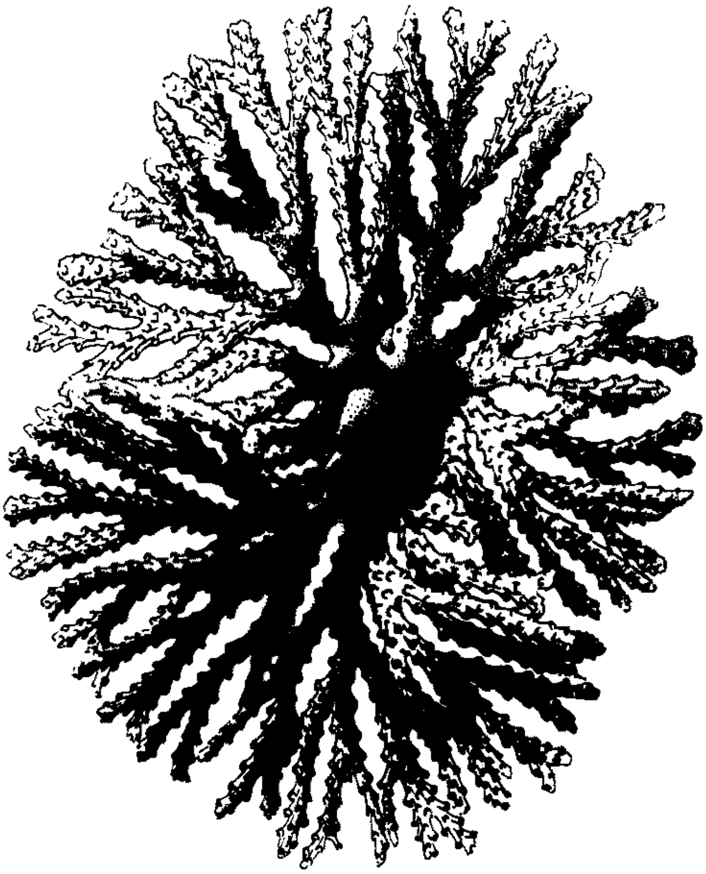
The data for the groups of arborescent ectoprocts described above is shown in Table 6:3. Group I differed significantly, at $p = 0.05$ from both groups 2 and 3, but there was no significant difference between the second and third groups.

Thus although I have not been able to demonstrate that encrusting species are at a disadvantage as against projecting

FIGURE 6:1

RIGID AND FLEXIBLE ARBORESCENT ECTOPROCTS.

Two arborescent ectoprocts are shown to contrast the rigid and flexible types. The top species is AB29 and the lower is AB7 (*Bugula dentata*).



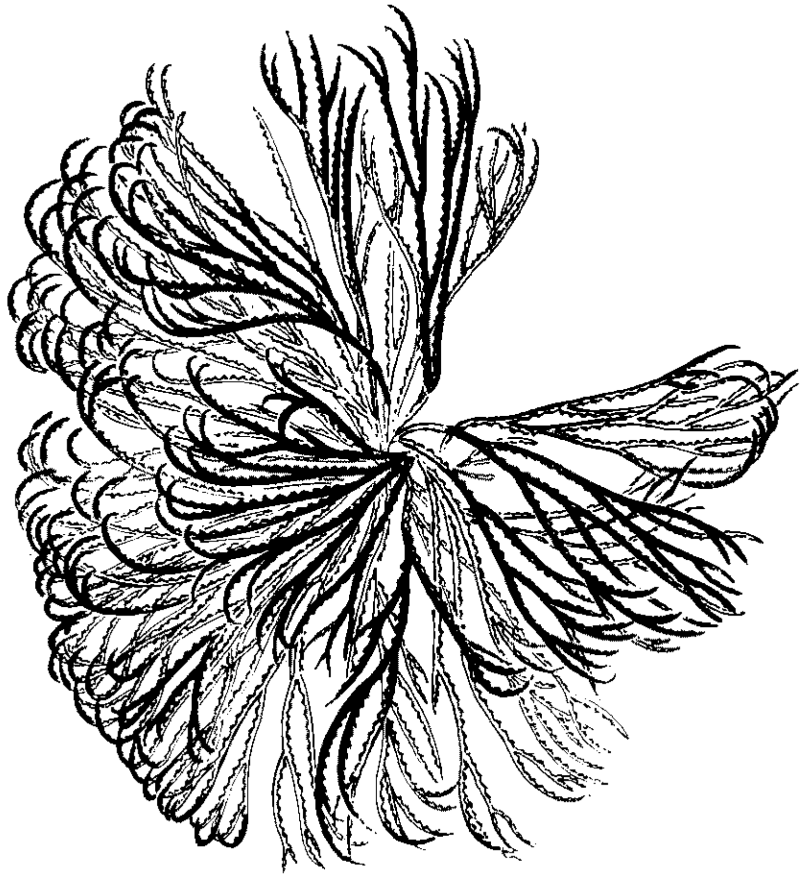


TABLE 6:1

THE MEAN ABUNDANCE (IN $mm^2.m^{-2}$) OF ASCIDIANS ON PROTECTED PANELS AT CAVE AND NON-CAVE SITES.

Species	Non-cave Sites	Cave Sites	Ratio
Compound ascidians:			
Ascidian B	405	3725	0.11
?*Botryllus*.	505	14083	0.04
?*Diplosoma*	9310	10450	0.89
Simple ascidians:			
Ascidia spp.	1798	9478	0.19
?*Herdmania* A	2953	9080	0.33
?*Herdmania* B	233	2028	0.11
molgulid	1580	466	3.39
?*Polycarpa*	1223	1120	1.09
Rhopalia	808	163	4.97

TABLE 6:2

THE MEAN ABUNDANCE (IN $mm^2.m^{-2}$) OF SPONGES ON PROTECTED PANELS AT CAVE AND NON-CAVE SITES.

Species	Non-cave Sites	Cave Sites	Ratio
Group 1: encrusting			
Sponge C	85	1694	0.05
Sponge J	223	518	0.43
Sponge K	210	350	0.60
Sponge L	3	100	0.03
Sponge M	60	258	0.23
Sponge N	93	189	0.49
Group 2: erect			
Sponge A	875	2281	0.38
Sponge B	320	1611	0.20
Sponge D	150	616	0.24
Sponge G	113	1274	0.09

TABLE 6:3

THE MEAN ABUNDANCE (IN $mm^2.m^{-2}$) OF ARBORESCENT ECTOPROCTS ON PROTECTED PANELS AT CAVE AND NON-CAVE SITES.

Species	Non-cave Sites	Cave Sites	Ratio
Group 1: rigid			
AB 1	0	25423	0
AB 3	65	18453	0.003
AB17	18	5028	0.001
AB32	55	1718	0.032
Group 2: flexible			
AB 6	805	7613	0.106
AB 6A	515	3663	0.141
AB 7	8910	24488	0.364
AB 7A	675	23	30
AB 8	178	3078	0.058
AB 9	223	4053	0.055
Group 3: with vibraculae.			
AB 5	2523	22280	0.113
AB10	618	2175	0.284
AB11	658	3113	0.212
AB13	1853	38268	0.048
AB14	593	33645	0.018
AB34	600	50	12

species when growing amongst algae, arborescent ectoprocts with rigid arms are apparently less able to survive and grow amongst algae than flexible species, or species with well developed vibraculae.

Discussion of Results

These results suggest that some e

perhaps ascidians, may survive and grow fa

Some encrusting ectoprocts are common amongst algae too, but it is difficult to formulate hypotheses as to why some might do better than others. Many of the encrusting ectoprocts common amongst algae have small zooids. These may feed on small food particles (see Section 5:4). It is difficult, however,to divide the species into groups on this basis, as zooid size varies with colony size. Furthermore, some species with fairly large zooids and large giant buds at the growing edges of the colonies are common amongst algae. Giant buds may serve to keep algal filaments away from the feeding zooids.

Two species of Bugula with no vibraculae but otherwise similar to the arborescent ectoprocts in group 3 (Table 6:3), have abundances at the non-cave sites similar to those of species in group 3. These two species both have large numbers of stalked avicularia which may act in the same way as vibraculae.

The results for the arborescent ectoprocts suggest that morphological differences between species may be important in determining the outcome of inter-specific interactions. As a result, on each particular patch of substratum the abundance of different bryozoan species will depend, to some extent, on the amount of algae present, and different bryozoan species will be abundant on different patches. The environment is, in effect, partitioned between the species according to their flexibility, and the presence of vibraculae.

6:3 REDUCTION OF PREDATION DUE TO 'STINGING' HYDROIDS

Introduction

Panels without cages were suspended at each sample site as 'emergency' panels in case panels in open cages were lost (Section 4:2). On two occasions panels without cages at a cave site were colonised by hydroids of the genus Lytocarpus. The hydroids have conspicuous white zooids and are known as 'fireweed' or stinging hydroids, because the nematocysts can puncture a diver's skin.

The hydroids on the panels were about 80mm high and covered both sides of each panel. I noticed that ascidians were abundant beneath the hydroids, and I therefore recorded the abundances of species on these panels to test the hypothesis that the hydroids protected the surfaces of the panels from predatory fish.

Results

Data from the panels covered with hydroids were compared with data from panels in open cages which were suspended at the same site for the same period. Table 6:4 shows the abundances of groups of species on these panels. The abundance of each group except encrusting ectoprocts was considered to be a separate measure of the degree of predation by fish. Wilcoxon's signed ranks test (Siegel 1956) of the eight matched pairs of data showed that predation by fish was significantly lower on the panels with stinging hydroids than on the panels in open cages.

TABLE 6:4

THE ABUNDANCE (IN mm^2) OF GROUPS OF SPECIES ON PANELS WITH AND WITHOUT THE HYDROID LYTOCARPUS SP.

Immersion Times	July 1973-October 1973		April 1974-July 1974	
Hydroid cover	60%	-	90%	-
Caging Treatment	No cage	Open cage	No cage	Open cage
Compound ascidians	1599	276	684	2
Simple ascidians	270	52	29	0
Sponges	28	2	66	3
Arborescent ectoprocts	1391	1225	613	97
Encrusting ectoprocts	3149	4837	1308	1186

Discussion

Presumably the hydroid nematocysts can puncture the skin of fishes and the fishes avoid them; so that both the hydroids and the animals beneath them are not eaten. This effect is similar to that described by Harper and Sagar (1953): in grasslands distasteful plants protected immediately adjacent plants from grazing animals. The colonisation of a patch of surface by stinging hydroids will substantially alter the subsequent 'history' of that patch because species normally removed by fish will become established and grow there.

6:4 INTERACTIONS AMONG SESSILE ANIMALS ON SETTLEMENT PANELS.

Introduction

As settlement panels were not examined while they were immersed, interactions between settling species could not be demonstrated experimentally by removing species. Instead, evidence for the interactions (described in Section 6:1) was sought from the preserved panels to determine whether any interactions between sessile animals might be important in determining distribution and abundance.

Three types of interaction were easily quantified. These were 1) instances in which one species settled on top of another, 2) Instances where neighbouring colonies of the same species ceased growth along the line of contact between them, and 3) overgrowth, where one animal grew partly or completely over another.

Because many different species settled on the panels, few pairs of species came into contact frequently. Therefore, similar species, for example compound ascidians, were sometimes grouped together in order to analyse the data.

Results

1) Settling of one species on top of another: Arborescent ectoprocts were often used as a substratum for settlement by ascidians, sponges, and other arborescent ectoprocts, especially AB1 and AB3 (Table 6:4). Most of the epizoic sponges were erect species. Hydroids were placed next to arborescent ectoprocts in the table because both form erect colonies. Hydroids were also

TABLE 6:4

THE NUMBER OF OCCASIONS ON WHICH SPECIES SETTLED ON OTHER ANIMALS.

Epizoic species	Species used as a substratum					
	Oysters	Encrusting Ectoprocts	Sponges	Ascidians	Arborescent Ectoprocts	Hydroids
Compound ascidians	1	4	1	1*	2	
Simple ascidians		3			10	
Sponges	1	5	1		5	1
EB 7		3				
EB 6						3
EB 2					5	2
Other encrusting ectoprocts	11	1		1	1	
AB1	1				29	
AB3	3				58	
AB6					2	3
Other encrusting ectoprocts	2	2			14	2
Vermetid juvs.		17				
Spirorbids		10				
Hydroides	1	1			1	
Spirbranchus		1				
Bivalve juvs.			1	1	1	
Coral juvs.		2				

*Compound ascidian used as a substratum. In other cases animals settled on simple ascidians.

used as a substratum by arborescent ectoprocts and sponges.

Only one compound ascidian, one sponge, and a mytalid bivalve settled on top of sponges. Ascidians were also usually free of epizoic animals. Only a few animals were found on simple ascidians, and compound ascidians were entirely free of epizoic animals, except that one compound ascidian settled on top of another.

Encrusting ectoprocts were used as a substratum by a variety of species, but seldom by encrusting ectoprocts except for EB7, or by arborescent ectoprocts, which were the most common animals on the panels. In contrast ectoprocts settled on oysters fairly frequently. The species which settled on encrusting ectoprocts included ascidians, sponges, corals, and species in calcareous tubes. In particular, vermetid gasteropods were rare on the panel surfaces, but often found on encrusting ectoprocts and occasionally on coralline algae.

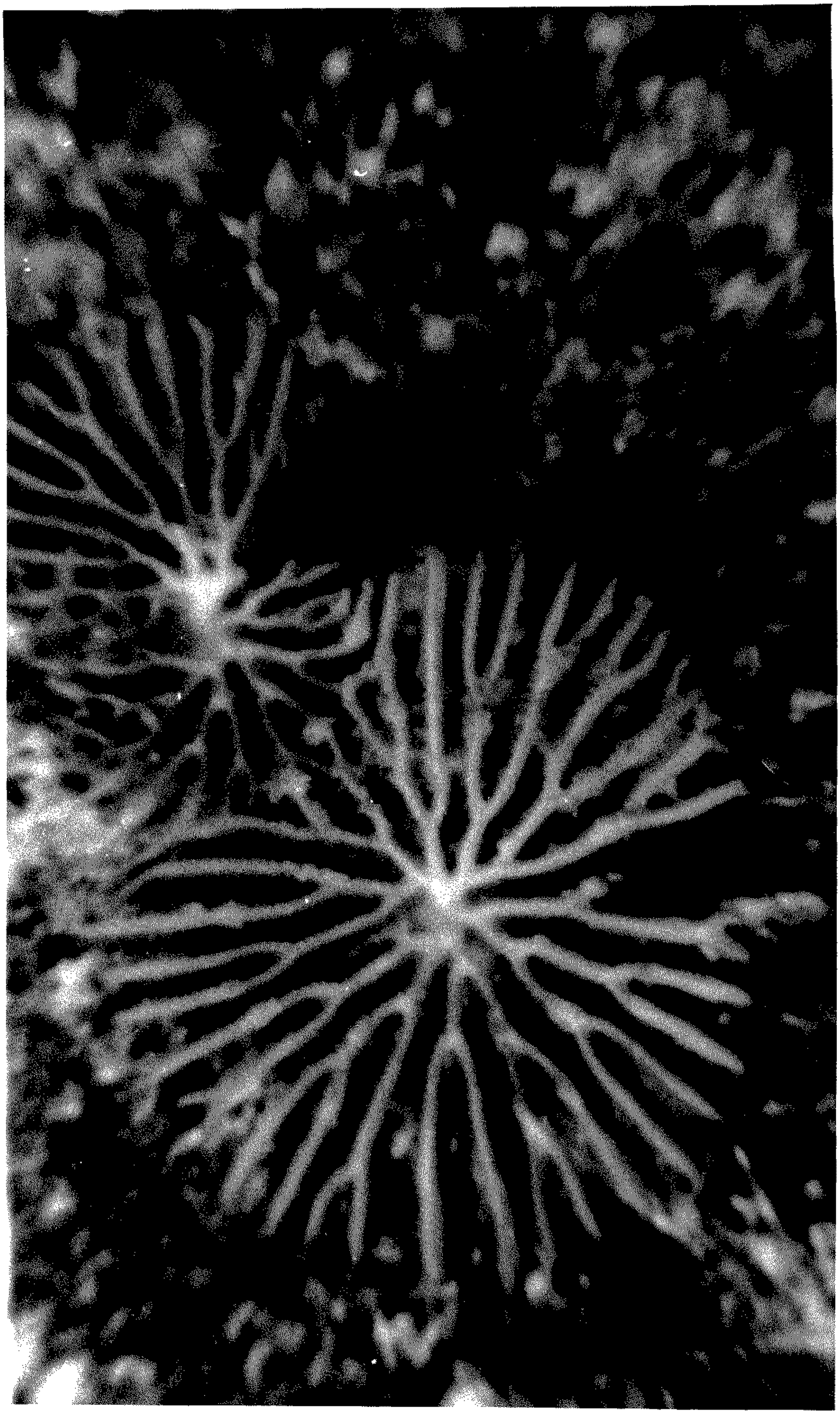
Encrusting ectoprocts rarely settled on erect organisms, but EB6 was found on hydroids, and EB2 on hydroids and arborescent ectoprocts.

2) Cessation of growth between colonies of the same species. Examples of this phenomenon were found in three species of arborescent ectoprocts. On four occasions two colonies of AB1 had grown close together. The branches of each colony nearest the other were stunted or absent (Figure 6:2), so that the branches of the two colonies together formed an approximate circle. On one occasion the colonies were the same size, but on three occasions one colony was larger than the other, so that branches of the larger colony which would have stretched

FIGURE 6:2

COOPERATION BETWEEN TWO AB1 COLONIES.

The arms of both the larger and the smaller colony are stunted on the sides facing the other colony, so that the large colony does not cover the smaller.



over the smaller one were stunted. A similar stunting of branches of two neighbouring colonies of AB3 was observed.

Colonies of AB17 were found which had apparently merged together. In one instance three colonies of different sizes were joined together, and in two instances two colonies were joined. The observed relationshipsbetween adjacent arborescent ectoprocts of the same species should be contrasted with the interactions between different species described in 3) below.

Among encrusting ectoprocts cessation of growth at the line of contact between colonies of the same species was observed on fourteen occasions involving nine species. Raised ridges between the colonies but no overgrowth was observed on six occasions, and growth of the larger colony over the smaller occurred in eleven species. In two species (EB1A, EB11), mutual cessation of growth occurred in some instances, but when the colonies were very different in size the larger grew over the smaller.

3) Growth of one animal over another: This was the most common interaction observed. Arborescent ectoprocts were observed growing over their neighbours. Where two colonies grew close together the branches of the smaller colony were stunted under the larger. If the two colonies were the same size the branches of each were bent upwards to rise above the other colony. Overgrowth of this sort would result in a reduction in the amount of food reaching the shorter colony.

Arborescent ectoprocts, particularly flexible ones, were also frequently overgrown by encrusting species, particularly ascidians, EB6, and Filograna; but growth of one encrusting species over another was more common. The pattern of overgrowth among common species of encrusting ectoprocts is shown in Figure 6:3. Larger colonies usually grew over smaller colonies, as indicated by the fact that most of the arrows point upwards. There were three exceptions: 1) Small EB7 colonies often grew over larger colonies of other species (Figure 6:3). Small colonies of EB10 (Figure 6:3) and EB8 frequently escaped being overgrown even when they were partly surrounded by a larger colony of another species. 3) Smaller colonies of many species sometimes grew over larger colonies of EB6 (Figure 6:3).

Ascidians were able to grow over both larger, and smaller (Figure 6:4), encrusting ectoproct colonies. There were only three exceptions to this rule, and the relative sizes of the ectoproct and ascidian colonies are shown below the figure. In all three instances the ectoprocts were very much larger than the ascidians.

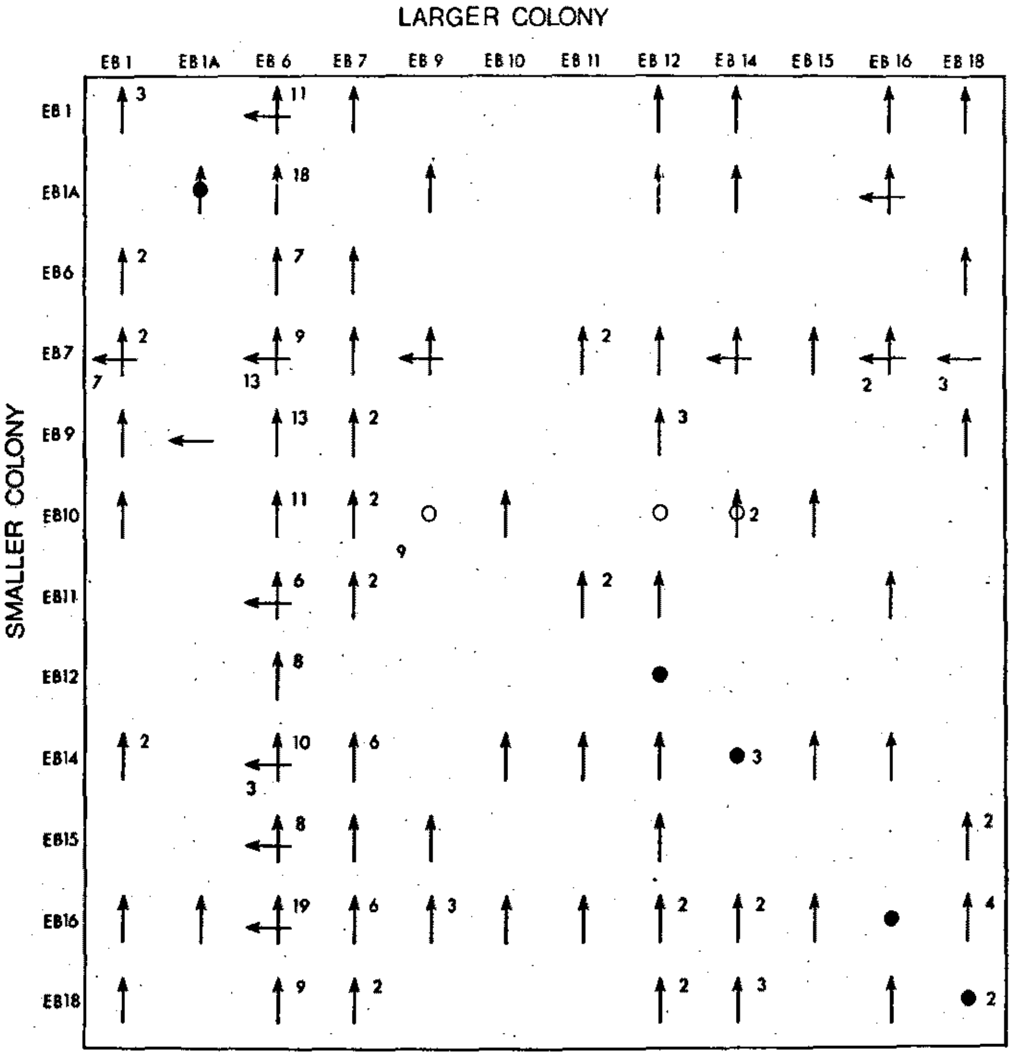
Although contacts between ascidians occurred infrequently the data is consistent with the hypothesis that the relative size of the colonies determines which one will grow over the other (Figure 6:5). In one case a smaller compound ascidian grew onto the test of a simple ascidian, but otherwise the larger ascidian always grew over the smaller one.

There was an overall hierarchy of overgrowth among different kinds of organisms (Table 6:5). Compound and simple ascidians usually grew over all other animals. Encrusting ectoprocts other than EB7 and EB6 were usually overgrown by any of the other animals. Spirorbids (not shown in the table)

FIGURE 6:3

OVERGROWTH IN ENCRUSTING ECTOPROCTS.

Interactions between neighbouring colonies of encrusting ectoprocts are indicated by arrows or circles. The species to which the larger colony belonged is listed across the top, and the species of the smaller colony along the side of the figure. The arrows indicate that one colony had begun to grow over the other, or had smothered it completely. A vertical arrow indicates that the larger colony grew over the smaller. Open circles indicate that although one colony was partly encircled by the other, no overgrowth had occurred. Closed circles indicate that cessation of growth had occurred at the line of contact between the colonies. Numbers next to the symbols show the number of occasions on which the interaction was observed, where this was greater than one.



	EB 1	EB 1A	EB 6	EB 7	EB 9	EB 10	EB 11	EB 12	EB 14	EB 15	EB 16	EB 18
EB 1	↑ 3		↑← 11	↑				↑	↑		↑	↑
EB1A		●↑	↑ 18		↑			↑	↑		↑←	
EB6	↑ 2		↑ 7	↑								↑
EB7	↑ 2 ← 7		↑ 9 ← 13	↑	↑←		↑ 2	↑	↑←	↑	↑← 2	← 3
EB 9	↑	←	↑ 13	↑ 2				↑ 3				↑
EB10	↑		↑ 11	↑ 2	○ 9	↑		○	↑○ 2	↑		
EB11			↑← 6	↑ 2			↑ 2	↑			↑	
EB12			↑ 8					●				
EB14	↑ 2		↑← 10 3	↑ 6		↑	↑	↑	● 3	↑	↑	
EB15			↑← 8	↑	↑			↑				↑ 2
EB16	↑	↑	↑← 19	↑ 6	↑ 3	↑	↑	↑ 2	↑ 2	↑	●	↑ 4
EB18	↑		↑ 9	↑ 2				↑ 2	↑ 3		↑	● 2

FIGURE 6:4

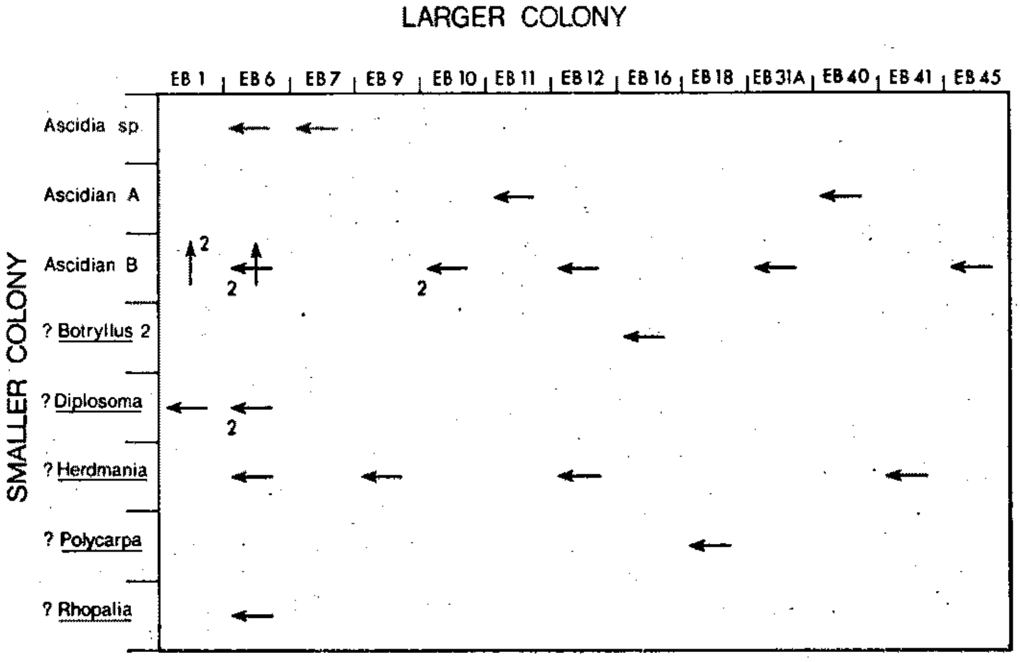
OVERGROWTH OF ENCRUSTING ECTOPROCTS BY SMALLER ASCIDIANS.

The symbols are explained for Figure 6:2. In two cases the arrows are vertical: the sizes in mm^2 of the ectoproct and ascidian colonies are shown beneath the figure.

FIGURE 6:5

OVERGROWTH IN ASCIDIANS.

The symbols are explained in Figure 6:2. ?*Herdmania* and ?*Polycarpa* are simple ascidians. The remaining species are compound ascidians.



EB1/Cascid B = 155/8 + 150/3 EB6/Cascid B = 2000/4

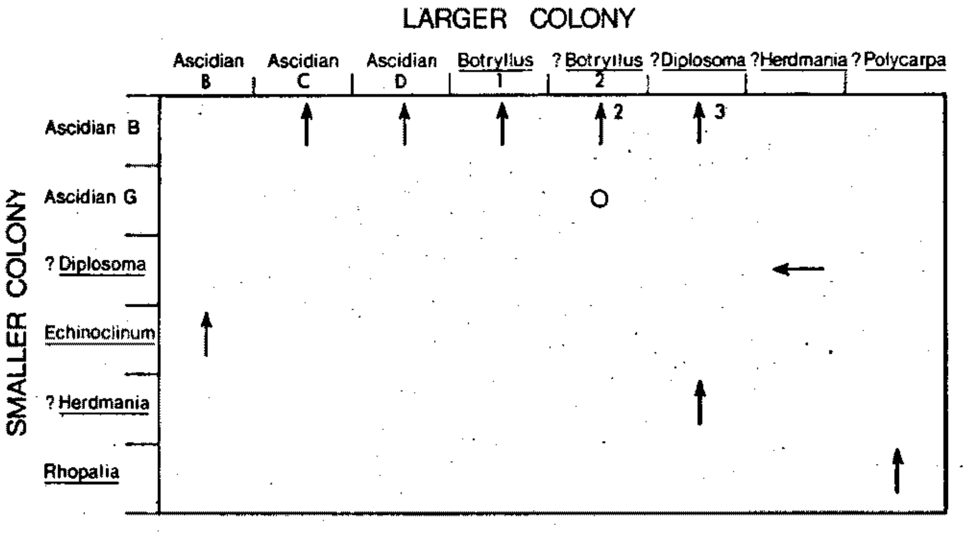


TABLE 6:5

CONTACTS BETWEEN SESSILE ANIMALS: THE PERCENTAGE OF CONTACTS IN WHICH ONE TYPE OF ANIMAL GROWS OVER ANOTHER*

Animal which grows over the other	Animal which is Overgrown					
	Simple ascidians	EB6	Oysters	EB7	Sponges	Encrusting Ectoprocts
Compound ascidians	100 (2)	83 (12)	93 (14)	75 (8)	82 (11)	80
Simple ascidians		100 (3)	67 (3)	100 (3)	? (0)	97
EB6			75 (20)	39 (23)	89 (9)	93
Oysters				75 (8)	100 (2)	76
EB7					20 (5)	81
Sponges						58

---

*Number of contacts shown in brackets if less than 30.

were always overgrown by other animals although some had extended the aperture of the tube above surrounding ectoproct colonies.

However, there was no simple hierarchy of dominance between oysters, EB7, EB6, and sponges. EB6 usually grew over oysters and sponges, and oysters usually grew over sponges and EB7, but EB7 usually grew over EB6, and was overgrown by sponges. Very few contacts were observed between sponges and other animals, because the sponge colonies were always small. More data would probably reveal differences among different species of sponges.

Encrusting ectoprocts were overgrown by some animals more often than others, and they were more likely to be overgrown if they were smaller than the other animal (Table 6:6). In Table 6:6 the numbers in brackets show the relative frequency of contacts between ectoprocts and other sessile animals on the panels. Compound ascidians frequently grew over ectoprocts, and EB6, EB7, oysters, and <u>Filograna</u> were also important in this respect. Vermetid gasteropods and the polychaete <u>Hydroides</u> were seldom larger than the ectoprocts they came into contact with, yet they were often able to grow over the ectoprocts.

Because the size of ectoproct colonies was important in determining whether other animals would grow over them or not, the relative rate of growth of different ectoproct species would be important. The maximum colony size of each species on three-month panels was assumed to be a measure of growth rate. As the panels used were suspended at four cave sites in different seasons it was assumed that some of the colonies of each of the common species would have been growing under favourable

TABLE 6:6

CONTACTS BETWEEN ENCRUSTING ECTOPROCTS AND OTHER SESSILE ANIMALS: THE PERCENTAGE OF CONTACTS IN WHICH THE ECTOPROCT IS OVERGROWN.*

Animal in contact with Ectoproct	Relative size of Ectoproct			
	Smaller		Larger	
Compound ascidian	86.7	(150)	90.4	(21)
Simple ascidian	96.6	(29)	100	(8)
Filograna	96.9	(32)	63.6	(11)
Vermetid gasteropod	?	(0)	55.6	(9)
EB7	100	(31)	38.2	(34)
Oysters	100	(36)	30.6	(49)
Hydroides	?	(1)	22.2	(9)
EB6	95.1	(267)	12.5	(8)
Other encrusting ectoprocts	84.1	(196)	9.7	(196)

---

*Number of contacts shown in brackets.

conditions for about three months. The number of colonies on panels at cave sites was taken as a measure of the rate of settlement of the common species on these panels. The faster-growing species seemed to occur less frequently than the species which grew slowly.

To determine whether there was any correspondence between the growth rate of colonies and the frequency of settlement given the assumptions stated above, the twelve most common encrusting and arborescent ectoprocts were ranked according to the number of colonies on 75 samples from panels suspended in caves (Table 6:7). The mean size of the largest ten colonies of each species was calculated, and these means were ranked as shown in the table. EB2 was not considered among the encrusting ectoprocts because this species settles predominantly at the edges of panels (Section 3:2), so the estimate of settlement frequency from the samples would be biased. The numbers for EB6, however, could be adjusted for the edge effect because the EB6 colonies always extended from the edges into the central sampling area on the panels.

For both encrusting and arborescent ectoprocts there was a significant correlation between the rankings at $p = 0.05$ (Spearman's correlation coefficient, Siegel 1956). Thus if the assumptions stated earlier are correct, then among common species slower-growing species settled more frequently than fast-growing ones. It should be noted that this result has been restricted to species which were common on panels at the sites considered. Other species may have occurred only occasionally on the panels because the conditions at these sites were not favourable for them, and these species would not be expected

TABLE 6:7

THE RELATION BETWEEN FREQUENCY AND MAXIMUM SIZE OF ECTOPROCTS.

Species in order of Frequencies	No. of Colonies on 75 samples	Mean size of Largest ten Colonies	Ranking of Sizes
Encrusting Ectoprocts:			
EB16	317	87	9
EB 8	282	31	3
EB14	238	71	7
EB29	219	24	2
EB1A	195	58	5
EB 7	164	49	4
EB10	163	18	1
EB18	150	64	6
EB 9	127	73	8
EB 1	123	134	10
EB 6	85	934	12
EB12	58	175	11
Arborescent Ectoprocts:			
AB 5	698	113	4
AB 9	616	11	1
AB 3	353	260	6
AB17	245	40	2
AB14	242	319	7
AB 1	196	229	5
AB 7	98	324	8
AB13	87	848	12
AB 4	78	83	3
AB 6	64	543	11
AB21	53	362	9
AB22	32	467	10

to grow rapidly when they did occur.

Discussion of Results

1) Epizoic animals: Encrusting animals were seldom used as a substratum for settlement despite the fact that they occupied a relatively high proportion of the panel surfaces. In general, therefore, the resource 'settlement space' was reduced by established colonies. However, dominant animals such as ascidians, EB7, sponges, and perhaps corals, occasionally settled on top of encrusting ectoprocts.

Animals with calcereous tubes were able to settle on encrusting ectoprocts. Spirorbids were abundant, but never grew very large. They were usually overgrown by other animals on my panels, and elsewhere (Osman 1977, Stebbing 1973a). Hence their ability to settle on other species may be important in maintaining their abundance (Osman 1977). Vernetids were rare, but they must be considered as dominant species because they were able to grow over larger ectoprocts as well as settle on them.

EB6 and EB2 both settled on hydroids. Both species were more common near the edges of panels than at the centres (Section 3:2). Perhaps the hydroid stems acted as 'edges' with turbulent water-movement around them. Colonies of EB6 grew predominantly in one direction, and on hydroids they were all growing downwards, towards the panel surface.

EB2 formed small mound-shaped colonies. On hydroids and arborescent ectoprocts where colonies of EB2 were found, encrusting colonies would not have much space to spread out, except along the branches of the arborescent ectoprocts or the stems of the hydroids. Encrusting species may have been selected so as not to settle in places where the colonies would be less likely to grow to reproductive size. Erect animals do not require much attachment space. This may be why erect sponges, simple ascidians, and arborescent ectoprocts were more common on arborescent ectoprocts than encrusting species.

2) Cessation of growth between colonies of the same species: Redirected growth of two neighbouring colonies of the same species will increase the area covered by that species, so that fewer animals of other species are able to settle. There may be other advantages which accrue to an ectoproct colony if it does not grow over a neighbour of the same species, such as the possibility of cross-fertilisation. If overgrowth occurs more slowly than growth over a bare surface, then the colony may grow faster if it does not grow over its conspecific neighbour.

3) Overgrowth: Three exceptions to the general rule that larger ectoprocts grew over smaller ones were noted (see Figure 6:3).

a) EB8 and EB10, two small lichenoporid cyclostomes, were overgrown less often than might be expected. As noted previously by Stebbing (1973b), discoid cyclostomes secrete a raised basal lamina between themselves and other animals.

b) EB6 was often overgrown by smaller ectoprocts. EB6 colonies grew predominantly in one direction rather than in a circular fashion, and the colonies were usually overgrown from the sides, or from behind, but not head on. Oysters grew predominantly in one direction too, and were occasionally overgrown from behind. Both oysters and EB6 settled at the edges of panels where they were less likely to be approached from behind. On natural surfaces 'edges' would also be exposed to predation by fish, so that the oysters and EB6 colonies would not be smothered by ascidians in these places.

c) Small colonies of EB7 often grew over larger ectoproct colonies of many species (Figure 6:3). EB7 even grows over EB6, which grows rapidly and smothers oysters and sponges. Yet EB7 is overgrown by oysters and sponges. Possibly EB7 produces a substance which suppresses growth in ectoprocts, but not oysters and sponges.

Jackson and Buss (1975) suggested that in a situation where species A grows over species B, and species B grows over species C, diversity will be greater if C grows over A than if A grows over C, because in the former situation no one species can monopolise the space available. I shall call the situation where A grows over B, B grows over C, and C grows over A a circular path of dominance. EB6 grows over oysters, and oysters grow over EB7, but EB7 grows over EB6. These three species all grow over other ectoprocts (Table 6:5), so that they are likely to come into contact in the later stages of the colonisation of a patch of surface. Hence the circular path of dominance between these species may be important in maintaining the abundance of each species.

An overall hierarchy of dominance between categories of species was evident (Table 6:5). Ascidians were dominant.

A second category consisted of EB6, EB7, oysters and sponges. Encrusting ectoprocts other than EB6 and EB7 formed a third category, and spirorbids a fourth. Within each of these categories no clearly defined hierarchy of dominance existed. Arborescent ectoprocts usually escaped overgrowth, as noted by Osman (1977), but not completely: they were sometimes smothered by compound ascidians and EB6, especially when small.

Fishes selectively remove ascidians and sponges (Section 5:4). Hence predation by fish increases the chance of survival of animals low in the dominance hierarchy relative to those higher in the hierarchy, and therefore the relative abundance of the former is presumably increased. Presumably, this increases the diversity of animals on the reef. The effects of predation on the diversity of sessile organisms on panels is examined in more detail in the next chapter.

Among encrusting ectoprocts other than EB6 and EB7 there was no clearly defined hierarchy of dominance, because larger colonies generally grew over smaller ones, irrespective of which species were concerned (Figure 6:3). Larger colonies were also less often overgrown by other animals than smaller ones (Table 6:6) as noted previously by Osman (1977). Hence encrusting ectoproct species which grew rapidly would be at an advantage over those which grew slowly, as colonies of fast-growing species would be expected to survive on a patch of surface for longer than colonies of slow-growing species. However, common species which grew slowly apparently settled more frequently than common fast growing species. If this is so then the slow growing species may be regarded as fugitive species with respect to the species which grow rapidly: the former would colonise new patches of surface more often, but would be overgrown more often. Probably however, some of the species encountered grow best in other places than the ones where the panels were suspended.

Conclusions

The available data supports the following hypotheses:

1) Among similar species, for example different species of encrusting ectoprocts, there is no clearly defined hierarchy of dominance. Rather, large colonies grow over small ones, so that species which grow rapidly, or species which become established first, will be at an advantage.

2) Space covered by established species is, in general, less suitable for other species to settle on, so that animals which cover the substratum first will be at an advantage over those which settle later.

3) There may be a negative correlation between settlement rate and growth rate of colonies among the species which commonly settle on the same surfaces. Such a correlation may increase the diversity of animals on the reef.

4) Among animals of different kinds, for example ascidians and ectoprocts, there is a hierarchy of dominance, but predators selectively remove the dominant species, and this favours species lower in the dominance hierarchy.

5) Oysters and EB6 may settle preferentially on edges as a result of the fact that in these places they are less likely to be overgrown.

6) A 'circular path of dominance' between EB6, oysters, and EB7 may be important in maintaining the abundances of these species.

6:5 INTERACTION BETWEEN CORALS AND A SPONGE

Introduction

Two of the most obvious groups of large sessile animals on the reefs are corals and sponges; yet these animals settled infrequently on settlement panels. To the casual observer the abundances of these large organisms do not change from year to year, whereas the abundances of animals on the panels changed rapidly due to interactions between the species. The observations described in this section were made to determine whether an unidentified brown sponge species affected the abundances of corals growing adjacent to it.

The sponge was observed growing on one side, and around the base, of a colony of the coral Goniastrea sp. Between the coral and the sponge was a 5-10mm wide band of white coral skeleton with filamentous algae growing on it. In January 1973 a metal stake was hammered into the coral, and one into the sponge. The position of the edge of the coral colony between the stakes was then measured at intervals. Similar pairs of stakes were hammered into three Hydnophora sp. coral growths and adjacent colonies of the sponge, in September 1973.

Results

The sponge apparently killed the Goniastrea coral and covered the limestone skeleton at the rate of 134mm per year (Figure 6:5). For the three Hydnophora colonies, the initial distances from the edge of the sponge to the stake in the coral were 49mm, 68mm, and 98mm. When these corals were observed

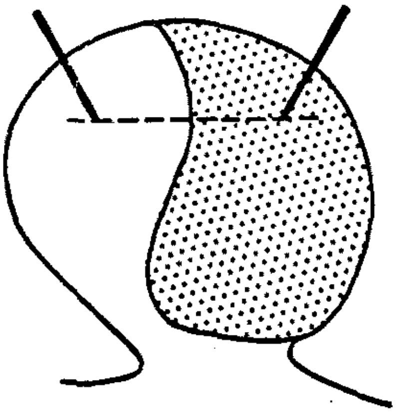
FIGURE 6:6

INTERACTION BETWEEN A SPONGE AND A CORAL

The coral skeleton is shown diagrammatically on four dates. The area occupied by the coral colony (*Goniastrea* sp) is stippled, the remaining area being occupied by the sponge. The position of two stakes and the line between them is shown. The position of the edge of the coral colony was measured along this line.

A

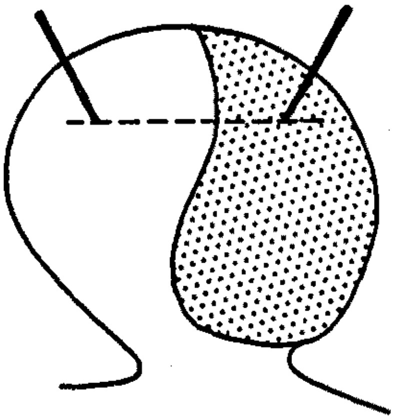
12 Jan. 1973



Contact at 161 mm
from left hand stake

B

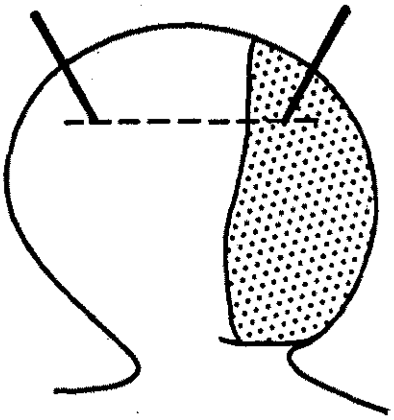
20 April 1973



Contact at 204 mm
from left hand stake

C

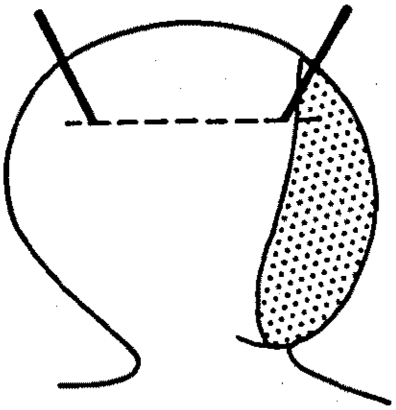
20 Oct. 1973



Contact at 257 mm
from left hand stake

D

13 April 1974



Contact at 328 mm
from left hand stake

again on the 13th April 1974, each coral growth had been entirely covered by the sponge.

Discussion

The sponge discussed here kills at least two species of corals. The sponge probably secretes a chemical which kills the coral, because there was always a 5-10mm space of white coral skeleton between the sponge and the coral polyps. Coral species are known to interact with other corals too (Lang 1973). Hence interactions between large, relatively permanent animals on the reef are probably important in determining the abundances of these organisms. There is, however, a much longer time scale involved than is the case with the animals on the settlement panels.

I suggest that for both the small animals which settled on the panels, and the large, more obvious sessile animals on the reef; both interactions between the species, and predation and physical disturbances are important in determining species' abundances. For large animals occasional aggregations of the starfish *Acanthaster planci* and cyclones will be important disturbances. These disturbances are on a larger scale, and less frequent, than disturbances such as the breaking of small coral slabs, or sand abrasion of a surface, which will be important for small sessile animals. When an ascidian colony, for example, is eaten by a fish this will also act as a disturbance for small sessile animals because a small patch of fresh surface will be made available for colonisation.

Fish graze surfaces covered by algae very frequently (Section 5:2) and the patches produced are extremely small. Hence, the associations of sessile organisms on the reef may be placed along a spectrum according to the size and frequency of the disturbances which are important, from the algal association at one end of the spectrum, to the coral and sponge association at the other.

CHAPTER 7

THE DISTRIBUTION OF SPECIES ABUNDANCES

In preceeding chapters I have described the effects of predation and other components of environment on the abundances of individual species. In this chapter attention is focussed on the relative abundances of species, and the number of species living together, in order to answer the following questions:

1. How many species may settle and grow at the same time and in the same place on the reef?
2. How is abundance distributed between species which grow together on the same surfaces?
3. How does predation by fish affect the number of species which may live together, and the relative abundance of these species?
4. Are the number and relative abundances of species, or the effects of predation, different in different reef habitats?
5. How different are the distributionsof abundance obtained when the abundances of species are measured by the number of individuals of each species, and by the area covered by each species?

Methods

I chose two sites on the reef which appeared each to be typical of a large number of places on Heron and neighbouring reefs. Site 1 was well illuminated, and the natural coral limestone surfaces were dominated by algae. It was on the side of a large head of Porites coral, 6 m below the reef crest. Site 2 was inside a cave under the same coral head, 1 m below site 1. The levels of illumination and water-movement were lower at site 2 than at site 1, and algae were absent at site 2. Different species of fish were present at each site.

Settlement panels immersed for three months were used to obtain samples of the assemblage of species which settled on hard surfaces at each site. I shall call the assemblage of species which may settle at a site an "association of species", and the assemblage of species found in a sample a "collection". It is often difficult to estimate parameters of an association of species from a collection. A number of methods are discussed in Appendix 7A.

For samples from site 1 I used samples from calcium carbonate surfaces which were described in section 3:3. There were eight 2500 mm^2 samples from caged panels and eight from uncaged panels. As it was impossible to count numbers of organisms for algae, the area covered by each species in each sample was measured instead.

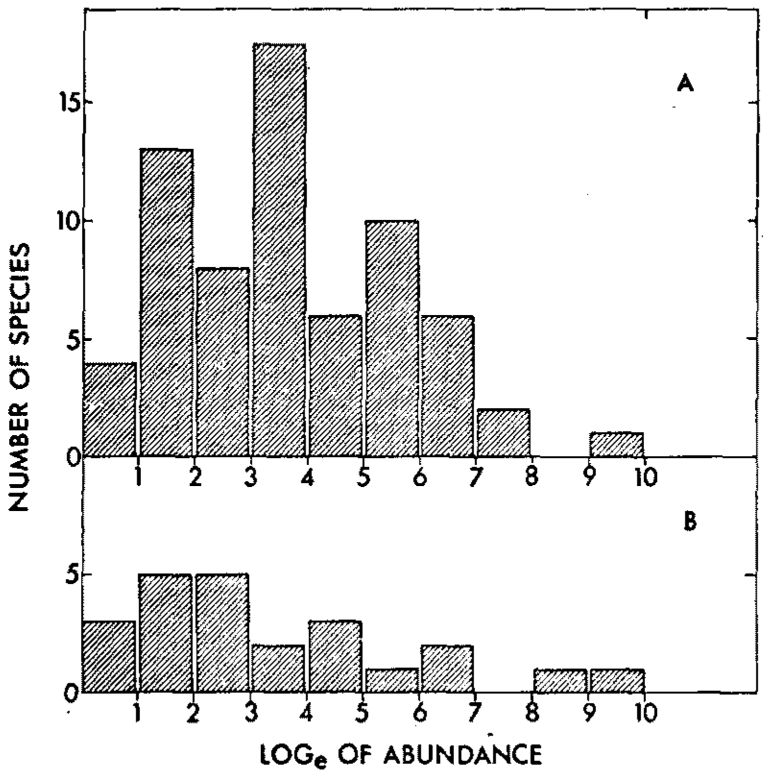
The samples from site 2 were obtained from both the large and small settlement panels described in section 3:4. There were forty caged and forty uncaged samples, each sample being 5000 mm^2 in area. I used Novasteen settlement surfaces as opposed to the calcium carbonate surfaces used at site 1. However I have shown in section 3:3 that there is very little difference in the abundances of species on Novasteen and calcium carbonate surfaces at site 2. The samples from site 2 were colonised mainly by ectoprocts and ascidians. Both the area covered by each species and the number of individuals or colonies of each species were measured.

Results

The observed distribution of species' abundances (as measured by area covered) for the collections from caged and uncaged samples from site 1 are shown in Figure 7:01A and B. The equivalent histograms for site 2 are shown in Figure 7:02A and B. Using numbers of individuals to measure abundance leads to a different pair of histograms for site 2 (Figure 7:03A and B).

Lognormal distributions cannot be used to describe the observed distributions of abundance (see Appendix 7:B). I therefore used two other procedures to provide descriptions of the distribution of abundances in the associations. I investigated the relationship between the number of species in the sample and the area of the sample, and I estimated the Shannon-Weiner diversity index H', (Shannon and Weaver 1949) using the method described by Pielou (1966). These methods are discussed in Appendices 7:, 7C, and 7D.

The first method leads to an index of "species richness" which is in fact a type of species diversity index (see Appendix 7A). The index of species richness is sensitive to changes in the relative abundance of common species, whereas the Shannon-Weiner index of diversity, H', is most sensitive to changes in the relative abundance of moderately rare species (Whittaker 1972).


A
B
NUMBER OF SPECIES
0
5
10
15
0
5
1
2
3
4
5
6
7
8
9
10
LOG$_e$ OF ABUNDANCE

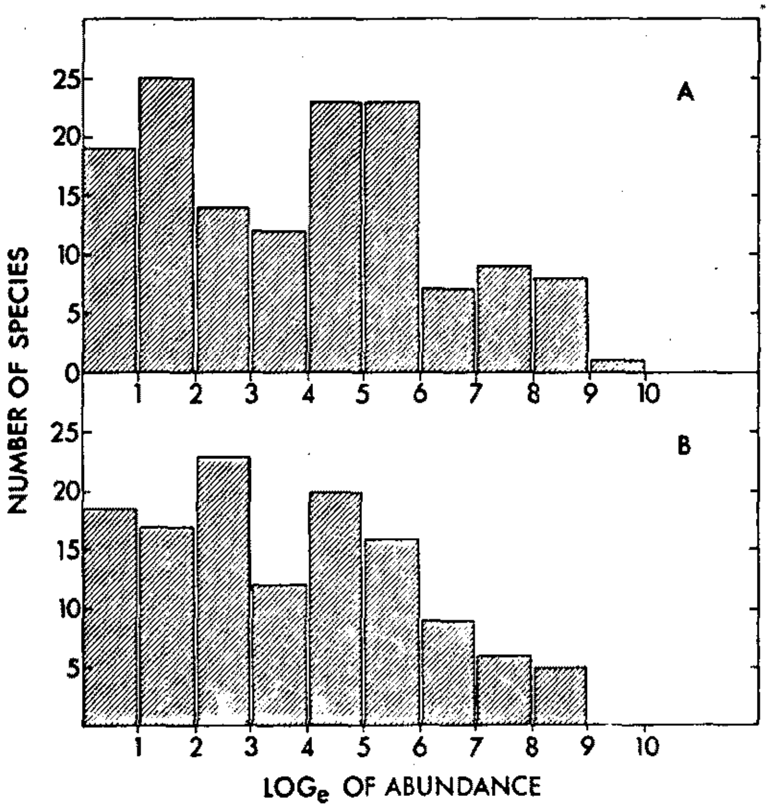

A
B
NUMBER OF SPECIES
0
5
10
15
20
25
5
10
15
20
25
1
2
3
4
5
6
7
8
9
10
LOG$_e$ OF ABUNDANCE

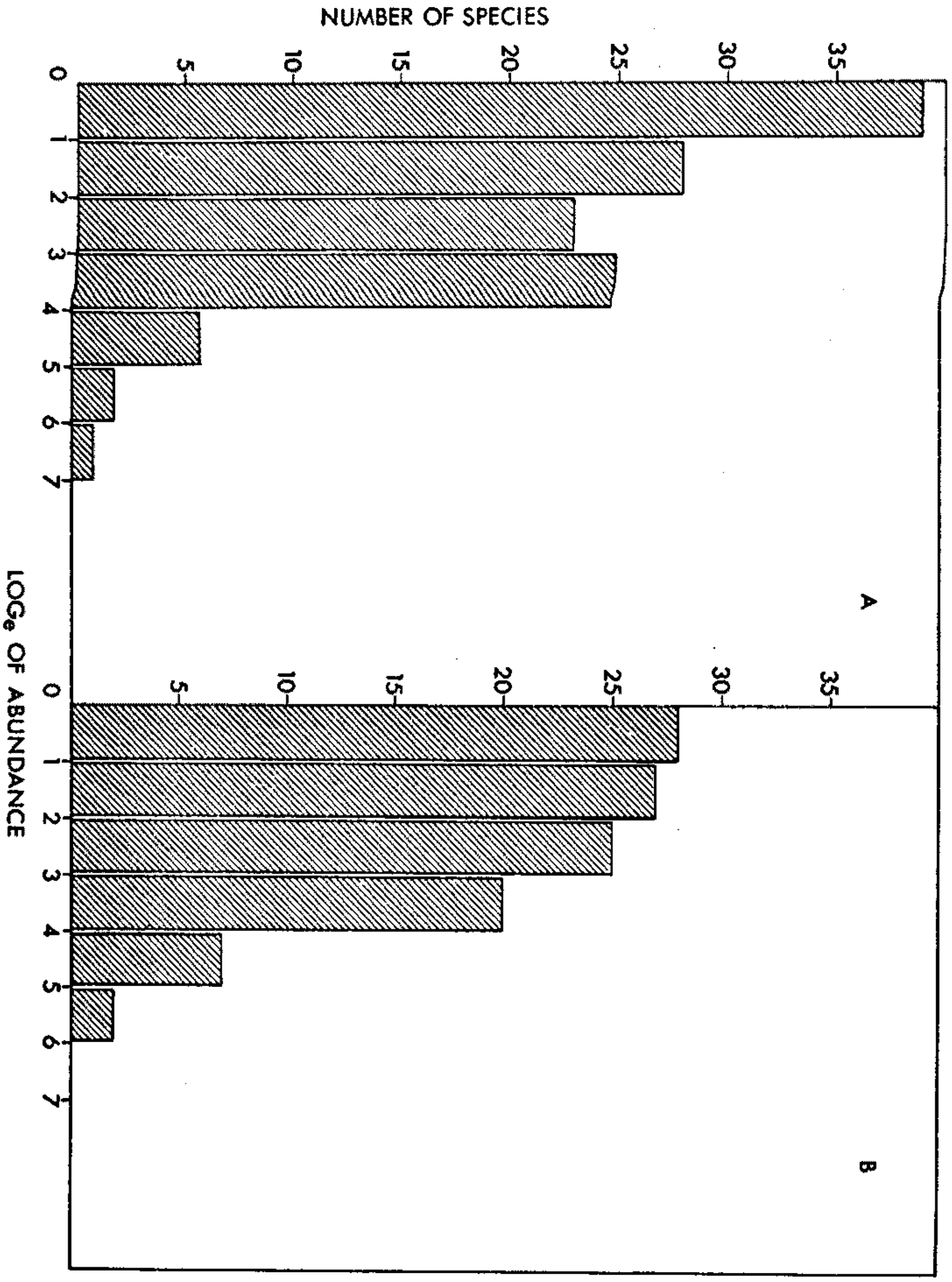
FIGURE 7:03

HISTOGRAMS OF SPECIES' NUMBERS AT SITE 2.

The number of species whose abundances fall into logarithmic intervals of abundance is shown by the height of each bar. Abundances were measured as the number of individuals of each species.

A Collection from caged samples.

B Collection from uncaged samples.


NUMBER OF SPECIES
5
10
15
20
25
30
35
LOGe OF ABUNDANCE
0
1
2
3
4
5
6
7
A
B

The species-area relationship:

Figures 7:04 and 7:06 show the number of species plotted against the area of the sample for site 1 and site 2. The data from both caged and uncaged samples is shown in each figure. Regressions of the logarithm of the number of species against the logarithm of the sample area were used to estimate the constants of the equation $S = CA^k$ as described in Appendix 7C. The constant C measures the expected number of species in a sample of unit area, and is thus an index of "species density". k is an index of species richness. The estimated values of the constants are shown in Table 7:01. Analyses of variance showed that all the regressions were significant at $p = 0.01$ (Tables 7:02, 7:03). The fit of the data to the calculated lines is shown in Figure 7:05 for site 1 and Figure 7:07 for site 2.

To compare the species-area relationships between sets of samples I used a multiple regression technique with dummy variables, as discussed in Appendix 7C. The results are shown in Table 7:04. The value of C, the index of species density, was not significantly different between sites at $p = 0.05$. The index of species richness, k, varied significantly between sites ($p = 0.05$). However the interaction between the effects of site and caging treatment was significant. This indicates that the effects of predation on species richness were significantly different at the two sites, and each site was therefore examined separately.

I used the multiple regression technique to compare the results from caged and uncaged samples at each site.
Table 7:05 shows that the index of species richness, k, was

FIGURE 7:04

The mean number of species on samples of various sizes from calcium carbonate surfaces at site 1 is plotted against the area of the sample considered, in cm^2. Successive sample areas were obtained by fusing 25 cm^2 samples in three random orders.

● : Caged samples

○ : Uncaged samples.

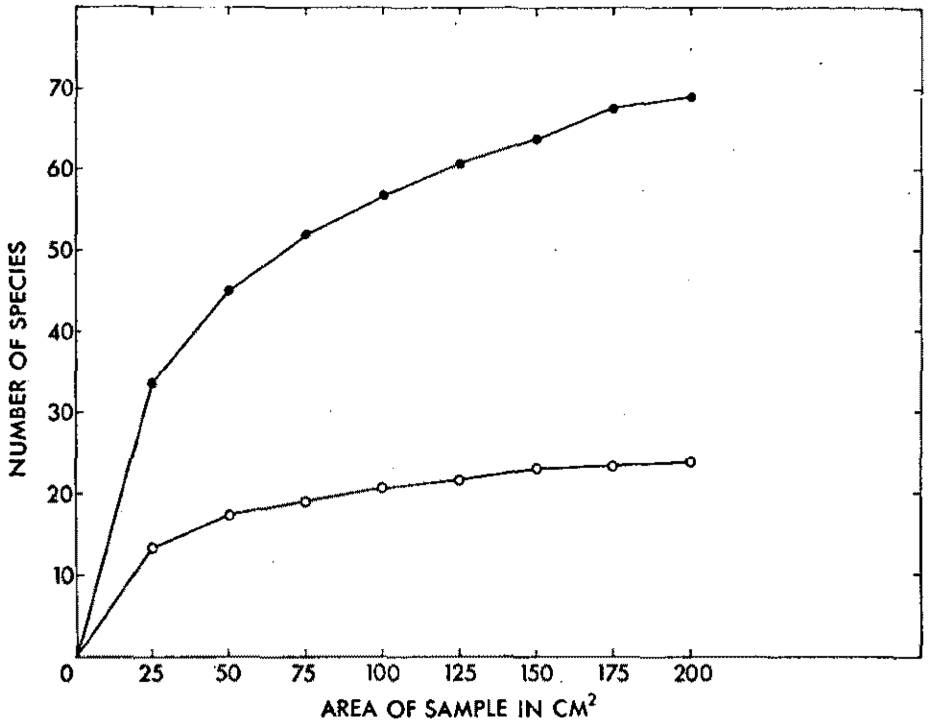
FIGURE 7:05

The number of species on samples from site 1 is plotted against the logarithm of the area of the sample, together with the theoretical curves fitted to the data.

● : Caged samples; fitted line is $S = 11.508\ A^{.343}$

○ : Uncaged samples; fitted line is $S = 5.641\ A^{.278}$

(where S = number of species, A = sample area)


NUMBER OF SPECIES
70
60
50
40
30
20
10
0
25
50
75
100
125
150
175
200
AREA OF SAMPLE IN CM²

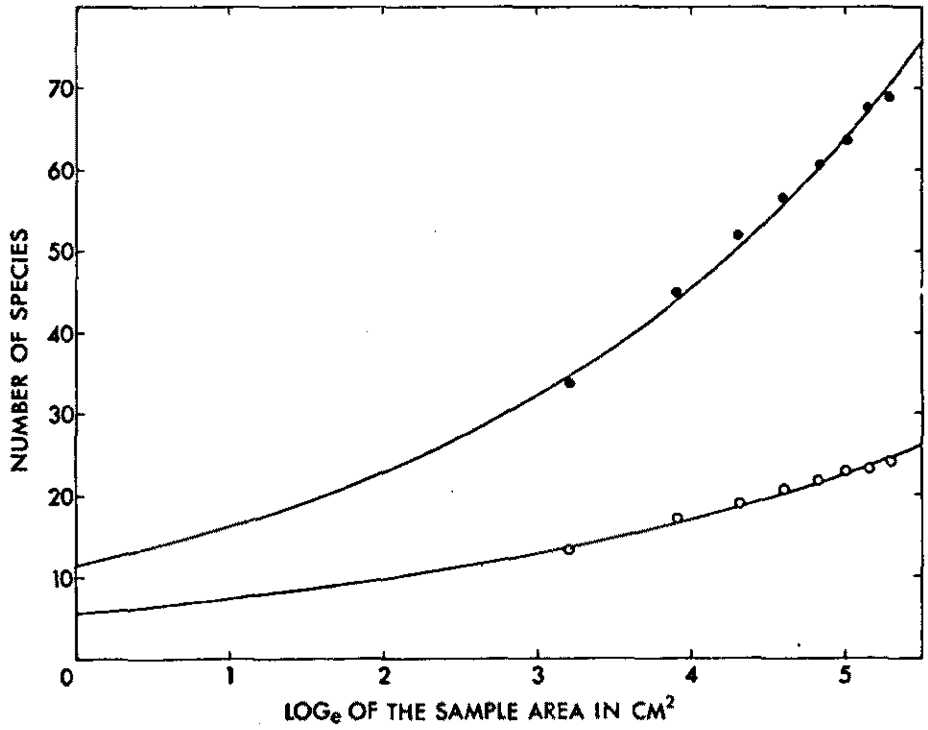

NUMBER OF SPECIES
70
60
50
40
30
20
10
0
1
2
3
4
5
LOGₑ OF THE SAMPLE AREA IN CM²

FIGURE 7:06

The mean number of species on samples of various sizes from site 2 is plotted against the area of the sample considered, in cm^2. Successive sample areas were obtained by fusing 50 cm^2 samples in three random orders.

● : Caged samples

○ : Uncaged samples.

FIGURE 7:07

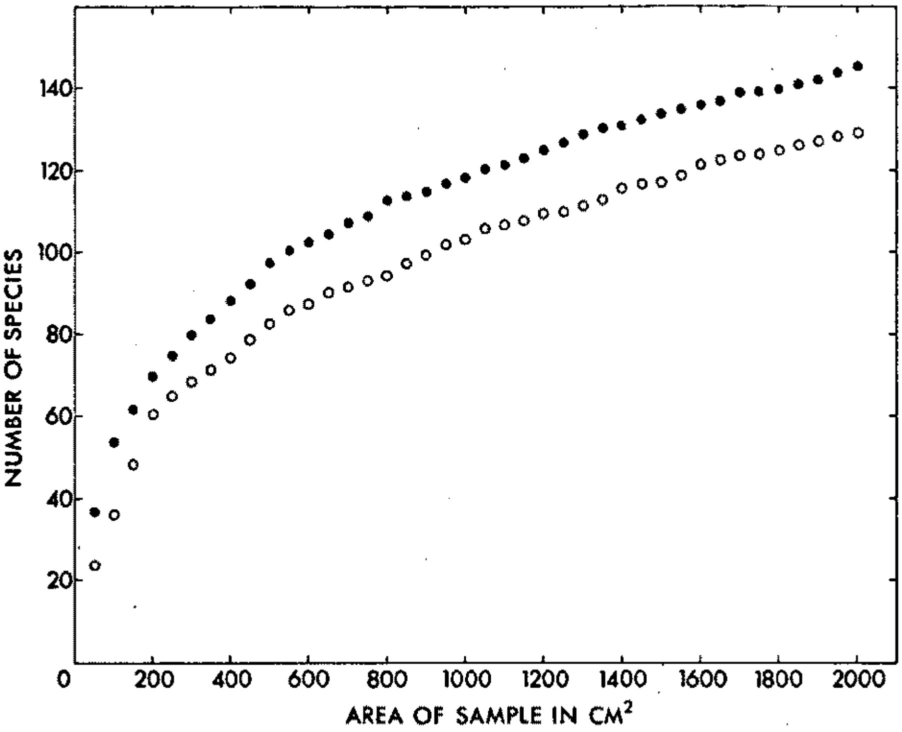
The number of species on samples from site 2 is plotted against the logarithm of the area of the sample, together with the theoretical curves fitted to the data.

● : Caged samples; fitted line is $S = 10.070\, A^{.343}$

○ : Uncaged samples; fitted line is $S = 6.013\, A^{.410}$

(where S = number of species, A = sample area)

For clarity every second data point has been omitted beyond the value 6 on the abcissa.


NUMBER OF SPECIES
20
40
60
80
100
120
140
0
200
400
600
800
1000
1200
1400
1600
1800
2000
AREA OF SAMPLE IN CM²

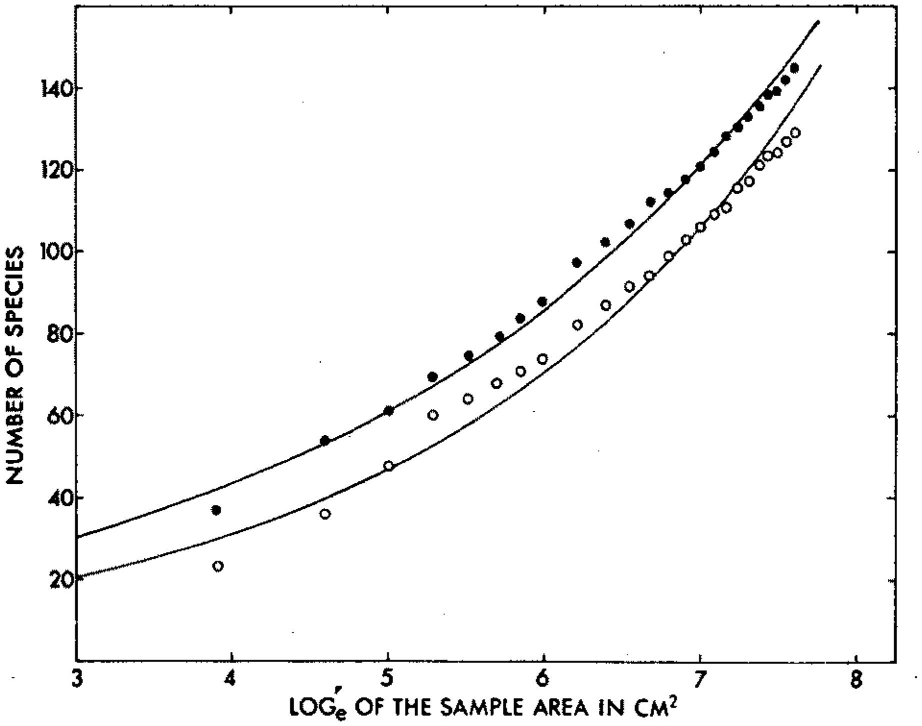

NUMBER OF SPECIES
20
40
60
80
100
120
140
3
4
5
6
7
8
LOGₑ OF THE SAMPLE AREA IN CM²

TABLE 7:01

REGRESSION CONSTANTS CALCULATED FOR THE ASSOCIATIONS OF SPECIES AT SITE 1 AND SITE 2 ON CAGED AND UNCAGED SETTLEMENT PANELS.

Regression Constants	SITE 1		SITE 2	
	Caged	Uncaged	Caged	Uncaged
k	0.343	0.278	0.343	0.410
C	11.508	5.641	10.979	6.013

TABLE 7:02.

ANALYSES OF VARIANCE OF THE REGRESSIONS FOR SITE 1 OF LOG (NUMBER OF SPECIES) AGAINST LOG (AREA OF SAMPLE)

A. CAGED SAMPLES

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Ratio	Significance*
Total	0.4107	7			
Regression	0.4075	1	0.4075	760.04	S
Residual	0.0032	6	0.0005		

REGRESSION EQUATION: $\text{Log}_e(S) = 2.443 + 0.343\ \text{Log}_e\ (A)$

FRACTION OF VARIATION ACCOUNTED FOR BY REGRESSION: 0.992

B. UNCAGED SAMPLES

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Ratio	Significance*
Total	0.2718	7			
Regression	0.2679	1	0.2679	410.01	S
Residual	0.0039	6	0.0007		

REGRESSION EQUATION: $\text{Log}_e\ (S) = 1.730 + 0.278\ \text{Log}_e\ (A)$

FRACTION OF VARIATION ACCOUNTED FOR BY REGRESSION: 0.985

*S = significant at p = 0.01.

TABLE 7:03

ANALYSES OF VARIANCE OF THE REGRESSIONS FOR SITE 2 OF LOG (NUMBER OF SPECIES) AGAINST LOG (AREA OF SAMPLE).

A. CAGED SAMPLES

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Ratio	Significance*
Total	3.5436	39			
Regression	3.5015	1	3.5015	3162.6	S
Residual	0.0421	38	0.0011		

REGRESSION EQUATION: $\text{Log}_e(S) = 2.396 + 0.343\ \text{Log}_e(A)$

FRACTION OF VARIATION ACCOUNTED FOR BY REGRESSION: 0.988

B. UNCAGED SAMPLES

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Ratio	Significance*
Total	5.1688	39			
Regression	4.9986	1	4.9986	1116.1	S
Residual	0.1702	38	0.0045		

REGRESSION EQUATION: $\text{Log}_e(S) = 1.795 + 0.510\ \text{Log}_e(A)$

FRACTION OF VARIATION ACCOUNTED FOR BY REGRESSION: 0.967

*S = significant at p = 0.01.

TABLE 7:04

RESULTS OF A MULTIPLE REGRESSION ANALYSIS OF THE SPECIES - AREA RELATIONSHIP.

Source of Variation	Mean Square	Degrees of Freedom	F Ratio	Significance*
Changes in the value of C due to:				
1) Site x caging interaction	0.00080	1	0.32	n.s.
2) Site effect	0.00003	1	0.01	n.s.
3) Caging treatment	0.16046	1	64.18	S
Changes in the value of k due to:				
1) Site x caging interaction	0.0270	1	10.78	S
2) Site effect	0.0268	1	10.72	S
3) Caging treatment	0.0470	1	18.81	S
RESIDUAL	0.0025	88		

*S = significant at p = 0.05, n.s. = not significant at p = 0.05.

TABLE 7:05

MULTIPLE REGRESSION ANALYSIS OF THE EFFECT OF CAGING ON SPECIES RICHNESS AT EACH SITE SEPARATELY.

Source of Variation	Mean Square	Degrees of Freedom	F Ratio	Significance*
Effect of caging on species richness index at Site 1	0.04178	1	70.8136	S
Residual	0.00059	12		
Effect of caging on species richness index at Site 2	0.06669	1	23.8179	S
Residual	0.00280	76		

* S = significant at p = 0.05.

significantly decreased (at $p = 0.05$) on uncaged samples at site 1, but was significantly increased on uncaged samples at site 2.

The Shannon-Weiner diversity index, H':

The methods used to calculate H' are described in Appendix 7D. Each set of samples yielded a number of estimates of H', and the mean and standard error of these were calculated.

At site 2 the abundances of species were measured in two ways, and therefore two types of diversity index were calculated. The first type is based on the area covered by each species and I shall call this a "cover diversity" index. The second type is based on the number of individuals of each species. To distinguish this more commonly used type of index I shall call it a "numbers diversity" index. At site 1 the algae could not be enumerated and only cover diversity indices were calculated. The results for each type of index at site 2 are shown in Table 7:06, and Table 7:08 shows the values of the cover diversity index for caged and uncaged samples from both sites.

To compare the values of H' at site 2 for cover diversity and numbers diversity on caged and uncaged surfaces, I used an analysis of variance. As discussed in Appendix 7C an analysis of weighted means was required as the analysis was inescapably based on unequal numbers of replicates. Bartlett's test showed no significant heterogeneity of variance at $p = 0.05$.

The results (Table 7:07) show that the only significant difference, at $p = 0.05$, in the values of H' was due to the way in which species' abundances were measured. The numbers diversity

TABLE 7:06

VALUES OF THE SHANNON-WEINER DIVERSITY INDEX H' AND ITS STANDARD ERROR FOR COVER DIVERSITY AND NUMBERS DIVERSITY[+] AT SITE 2.

Type of Diversity	Caged Surfaces	Uncaged Surfaces
Cover diversity	4.900 (S.E. = 0.153)	4.425 (S.E. = 0.200)
Numbers diversity	5.236 (S.E. = 0.352)	5.346 (S.E. = 0.179)

TABLE 7:07

ANALYSIS OF VARIANCE ON ESTIMATES OF COVER DIVERSITY AND NUMBERS DIVERSITY[+] OF ASSOCIATIONS OF SPECIES AT SITE 2 ON CAGED AND UNCAGED SURFACES.

Source of Variation	Adjusted Mean Square	Degrees of Freedom	F Ratio	Significance[*]
Caging treatment	0.282	1	0.584	n.s.
Cover vs Numbers Diversity	2.740	1	5.674	S.
Interaction	0.483	1	1.054	n.s.
Residual	0.458	23		

[*] S = significant at p = 0.05, n.s. = not significant at p = 0.05.

[+] The terms 'numbers diversity' and 'cover diversity' are explained in the text.

index was greater than the cover diversity index. This result is explained in the discussion of results, part 5.

To compare the values of the cover diversity index between sites and caging treatments I again used an analysis of variance with unequal numbers of replicates. The data were transformed to $\log_e H'$ to stabilise the variance, and Bartlett's test on the transformed data showed no significant heterogeneity of variance at $p = 0.05$. The results (Table 7:09) show that the interaction between the effects of site and caging treatment was significant at $p = 0.05$. This shows that the effects of predation on cover diversity were different at the two sites. I therefore examined each site separately. Comparisons of the mean values of H' from caged and uncaged surfaces at each site are shown in Table 7:10. The effects of predation on H' were significant only at site 1, where predation reduced cover diversity.

Discussion of Results

1) The number of species which may settle and grow together:

An estimate of the total number of species in an association can be obtained from a sample collection if the observed abundances of species in the collection fit a distribution such as the lognormal. Lognormal distributions did not provide good fits to the observed abundances in the collections described here, although a lognormal distribution of abundance is expected where there are a large number of species in the association (May 1975). Estimates of the number of species in each association are therefore not available.

TABLE 7:08

VALUES OF THE COVER DIVERSITY INDEX AND ITS STANDARD ERROR FOR CAGED AND UNCAGED SURFACES AT SITE 1 AND SITE 2.

Site	Caged Surfaces	Uncaged Surfaces
Site 1	3.376 (S.E. = 0.097)	1.652 (S.E. = 0.030)
Site 2	4.900 (S.E. = 0.153)	4.425 (S.E. = 0.200)

TABLE 7:09

ANALYSIS OF VARIANCE ON THE LOGARITHM OF ESTIMATES OF COVER DIVERSITY FOR ASSOCIATIONS OF SPECIES AT SITE 1 AND SITE 2 ON CAGED AND UNCAGED SURFACES.

Source of Variation	Adjusted Mean Square	Degrees of Freedom	F Ratio	Significance*
Caging treatment	0.8606	1	116.20	S.
Between sites	2.3879	1	322.42	S.
Interaction	0.5321	1	71.84	S.
Residual	0.0074	18		

* S = significant at $p = 0.05$.

TABLE 7:10

COMPARISONS OF THE MEAN COVER DIVERSITY OF ASSOCIATIONS OF SPECIES ON CAGED AND UNCAGED SURFACES AT EACH SITE, USING DATA TRANSFORMED TO LOG (H′).

Caged and Uncaged Associations Compared at:	Difference Between Means	Critical Value	Significance*
Site 1	0.714	0.114	S.
Site 2	0.085	0.106	n.s.

*S = significant at p = 0.05, n.s. = not significant at p = 0.05.

2) Differences between the sites:

The sessile animals at the cave site occur as discrete colonies which may each occupy a fairly large area. The algae at site 1 occur as much smaller, diffuse plants, although the species are, on average, more abundant than at site 2 (Table 7:11). One might therefore expect that the species would be more finely mingled at site 1, so that more species would be expected in a sample of unit area. However the index of species density is not significantly different between the sites (Table 7:04).

Species richness varies significantly between sites (Table 7:04) but as the interaction between the effects of sites and caging treatments is significant it is best to compare the caged and uncaged surfaces separately. Table 7:11 shows that there is no marked difference in the species richness of caged surfaces between the sites. The overall difference between the sites is therefore due to the opposite effects of predators on species richness at each site.

The Shannon-Weiner diversity index, H', was also significantly different between sites, and the interaction between the effects of sites and caging treatment was significant (Table 7:09). However H' was greater at site 2 for both caged and uncaged surfaces. This difference between the sites may be a result of the uneven distribution of abundance for the less common species at site 1. At site 2 there was a more even distribution of abundance between the less common species, and H' is sensitive to the relative abundances of moderately rare species (Whittaker 1972).

TABLE 7:11

SUMMARY OF RESULTS OF ANALYSES OF THE SPECIES ASSOCIATIONS ON CAGED AND UNCAGED SURFACES AT SITES 1 AND 2.

Calculated Measure	SITE 1		SITE 2	
	Caged Surfaces	Uncaged Surfaces	Caged Surfaces	Uncaged Surfaces
Mean abundance of species per 1000 mm^2 of settlement surface	15.02	39.58	2.64	1.41
Index of species density (C)	11.508	5.641	10.979	6.013
Index of species richness (k)	0.343	0.278	0.343	0.410
Index of cover diversity (H')	3.376	1.652	4.900	4.425

3) The effects of predation by fish:

Predation leads to an increase in species diversity in associations of sessile intertidal organisms (Paine 1966, 1971), tropical forests (Janzen 1970) and grasslands (Hope-Simpson 1940). The results presented here show that the effects of predation were different at the two sites investigated.

Predation led to a significant decrease in species density at both sites (Tables 7:04, 7:11), so that the number of species to be found together on small areas of surface was reduced. However there was a significant interaction between the effects of sites and caging treatment for both the index of species richness and the Shannon-Weiner diversity index (Tables 7:04, 7:09). Both indices therefore showed that predation had different effects on diversity at each site.

At site 1 predation led to a decrease in species diversity. Both indices were significantly lower on uncaged surfaces than on caged surfaces at site 1 (Tables 7:05, 7:10, 7:11). At site 2 the index of species richness was significantly greater on uncaged surfaces (Tables 7:05) but the Shannon-Weiner indices of cover diversity and of numbers diversity showed no significant change between caged and uncaged surfaces (Tables 7:07, 7:10). The results suggest that the index of species richness was more sensitive to the changes in the distribution of species' abundances which took place as a result of predation at site 2.

Figure 7:02 shows that there were fewer abundant species on uncaged samples at site 2 than on caged samples, but the number of relatively rare species was similar in the collections from caged and uncaged samples. In small samples one might expect to find most of the abundant species, but only one or two of the species which are rare. Thus the number of species in small samples would depend on the number of abundant species. Large samples, however would be expected to contain many rare species as well as all the common species. One might expect therefore that small uncaged samples would contain far fewer species than small caged samples from site 2, but that there would be comparable numbers of species on large caged and uncaged samples. The fitted lines in Figure 7:08 show that this was the case: the line for uncaged surfaces has a lower intercept than that for caged surfaces, but it rises more steeply.

Because the index of species richness measured the rate at which species were added as the sample area was increased, it was greater for uncaged surfaces. The difference was however, a result of the lower number of abundant species on uncaged samples, rather than an increase in the total number of species encountered on uncaged surfaces. This illustrates that indices of species richness are sensitive to the relative abundances of species as well as the number of species in an association. Because the Shannon-Weiner diversity index is not very sensitive to the abundances of common species (Whittaker 1972, Peet 1974) it did not vary significantly between caging treatments at site 2.

Thus at site 1 predation led to a decrease in species diversity, with fewer species in the samples, and a less even distribution of abundance between species (Figure 7:01) but at site 2 although there were fewer species in uncaged samples there was a more even distribution of abundance between species because the numbersof abundant species were reduced.

Why were the effects of predation different at the two sites? The prey organisms are similar in many respects: at both sites they are sessile, and appear to form an interactive association of species, as discussed in Chapter 6, so that if an abundant species is absent another species may occupy the space left vacant. Addicott (1974) suggests that predation can only result in an increase in prey diversity if interactions between prey species are important. At both sites too, some species are reduced in abundance to a greater extent by predation than others.

Differences in the foraging behaviour of the fish at each site are probably responsible for the contrasting effects of predation at the two sites.

The most important predators of algae were herbivorous scarid and acanthurid fishes. As discussed in Chapter 5 the grazing is intense. The scarids scrape the surface and do not appear to select particular species, but rather aim for small areas of dense algal growth, so that every part of a surface would eventually be scraped.

On the other hand the pomacanthid and balistid fish in caves search for and remove individual colonies of ascidians and arborescent ectoprocts, and the predation is less intense.

The difference in the intensity of predation at the two sites may partly explain the contrasting effects of predation on species richness at each site. Emlen (1973) and Addicott (1974) have argued that intense grazing will result in a reduction of the diversity of prey organisms whereas mild predation may lead to an increase in prey diversity. Paine and Vadas (1969) found that after sea-urchins were removed from rocks and pools a large number of new algal species colonised these areas, but that after periods of two or three years one or two species predominated where the urchins were removed. They suggested that algal diversity would be increased by intermittent grazing by urchins, whereas severe grazing led to low algal diversity.

The effect of predation on prey diversity may depend on whether the predators select particular species of prey, and which species they select. Paine (1966) proposed that prey diversity is determined by the extent to which predators prevent the monopolisation of resources by one species. This implies that a predator which attacks a dominant species of prey in preference to other species will be most effective in increasing prey diversity. The starfish studied by Paine (1966, 1971, 1974) attacked dominant prey species. Similarly, host specific seed eating insects prevented species of tropical trees from becoming abundant, so that the forest consisted of a large number of tree species, each in low numbers (Janzen 1970, 1973).

At site 1 the herbivorous fish were not selective predators. In the face of the intense non-selective grazing at this site only species of algae such as Ectocarpus spp and Lophosiphonia sp 1, which appear to recolonise scraped surfaces rapidly, were abundant. Most algal species were much less abundant on uncaged than on caged surfaces, as described in Chapter 5.

In cages the more selective fish predators appear to prevent the eventual monopolisation of space to settle and grow by ascidian species, as discussed in Chapter 5. Thus the fish allow a larger number of species to coexist on cave walls by removing the dominant species. This effect is important, but since the settlement panels from site 2 discussed here were immersed for only three months, ascidians had not yet excluded other species from the panels. If these panels had been immersed for a longer period the effect of predation by fish at site 2 would probably have been more striking.

The fish at site 2 also removed arborescent ectoprocts from the panels. Since the species which covered the largest area on the caged panels were arborescent ectoprocts and ascidians, the effect of predation was to reduce the numbers of the most abundant species, as shown previously. The total number of species was not markedly reduced on large samples because the fish did not entirely eliminate ascidians and arborescent ectoprocts from the uncaged samples: many of these species occurred occasionally, especially as juveniles.

Why were the arborescent ectoprocts and ascidians not completely eliminated from the uncaged panels? Because the fish fed on some species and not others, the cave walls or settlement panels covered with sessile organisms would have been spatially heterogeneous areas to the fish. As a result the fish would have to search far longer for some prey items than others (Smith 1972). If a man were searching for coloured stones lying on a mosaic he would have to search much longer for some stones than others. Therefore a few of the selected prey items would survive for long periods on unprotected surfaces, and the species subject to predation would never be entirely eliminated.

At site 1 the herbivorous fish attacked all the organisms on the panels. The fish treated the surfaces of the panels as homogenous areas.

The contrasting effects of predation on species diversity at the two sites investigated appear to be a result of the more selective foraging behaviour of the fish at site 2.

4) A comparison of the results based on the area covered by each species with those based on numbers of individuals at site 2.

This section of the discussion is concerned with the last question posed at the beginning of the chapter: how different are the distributions of abundance obtained when abundance is measured by area covered, or by numbers of individuals?

The histograms based on numbers of individuals at site 2 (Figure 7:03) are highest near the origin: many species are represented by one or two individuals in the collections. The modes of the histograms based on area covered (Figure 7:02) are greater. This is because many of the species which occur only occasionally grow to form very large colonies. This is an important feature of the associations at site 2, since the fish select species which are abundant in terms of cover, but not necessarily in terms of numbers.

The fish removed arborescent ectoprocts and ascidians. Arborescent ectoprocts occurred in large numbers, and often covered large areas, whereas ascidians occurred in low numbers, but usually covered large areas. Figure 7:03 shows that on uncaged surfaces the number of species with very few individuals was reduced as well as the number of species occurring in large numbers. In Figure 7:02 the number of species which covered small areas was similar on caged and uncaged samples. The major difference between the collections on caged and uncaged surfaces in terms of area covered is that there were fewer species which covered large areas on the uncaged samples.

The Shannon-Weiner index of diversity is normally calculated on the basis of numbers of individuals, but I used it to measure 'cover diversity' to compare the associations at sites 1 and 2. The numbers diversity index for the species association at site 2 was significantly greater than the cover diversity index (Results: Table 7:07). The Shannon-Weiner index is normally a measure of "diversity per individual" (Pielou 1975). Thus the cover diversity index is a measure of diversity per unit area: the square millimeter in this case. If I had used a larger unit of area the cover diversity index would have had larger values. The numbers diversity index was larger than the cover diversity index because the average area covered by an individual was greater than one mm^2.

CHAPTER 8

DISCUSSION

This study is concerned with the way in which the distribution and abundance of sessile species on the reef is determined, and the way in which the diversity of associations of sessile organisms is determined. The species that settle on panels can be considered as two separate associations of species: algae and corals that grow on brightly lit surfaces; and ectoprocts, ascidians, and other animals that live in dark places. The scarcity of animals on brightly lit surfaces is probably due to interactions between algae and animals, and the scraping activities of herbivorous fish.

Within each association the major differences between species were associated with the rate at which they cover bare surfaces. Species of algae were divided into two main groups: opportunists which colonised rapidly, and species which colonised more slowly. The opportunists were abundant throughout the year, especially on grazed panels. Other algae tended to be common in summer, and were confined to protected panels with three exceptions. These were _Lophosiphonia_ spp., _Sphacelaria_, and encrusting algae, which maintained their abundances on grazed surfaces by vegetative growth, rather than colonisation by spores.

Animals which covered bare surfaces most rapidly were not necessariily those which settled most frequently. Ascidians settled infrequently but grew very rapidly, so they often occupied large areas on the panels. Arborescent ectoprocts settled frequently and grew fairly rapidly, so they too, covered a large area on the panels.

Both predatory and herbivorous fish fed mainly on the most abundant species in terms of cover. The predatory fish selected particular animals (ascidians and arborescent ectoprocts), whereas the herbivorous fish did not. As a result, predation increased the diversity of sessile animals on panels whereas grazing reduced the diversity of algae on panels.

Another consequence of the difference in foraging strategy of herbivorous and predaceous fish was that algae and animals common on exposed surfaces used a different set of strategies to maintain their abundances on reef surfaces. Algae subject to grazing recolonised cleared patches rapidly by various means, whereas animals which escaped predation were small, inconspicuous, toxic or distasteful, or hard and encrusting.

The animals and algae which were eliminated or reduced in abundance by fish are protected in many places on the reef, such as areas between projections, in confined spaces, in pomacentrid territories, or under stinging hydroids.

Ascidians are eaten by fish, but predominate on dark protected surfaces because they grow over other species. Algae with large thalli such as <u>Enteromorpha</u> and <u>Laurencia</u> spp. are eliminated from grazed surfaces, presumably because they do not grow as rapidly as other algae. They become abundant on protected well-lit surfaces because they colonise rapidly and grow large, or else because they can become established under the other algae and later overtop them. Hence, both in dark places and on brightly lit surfaces species which are rapidly removed by fish predominate in the absence of predation. Places which are protected from fish and places exposed to fish will therefore eventually be occupied by different sets of species. This also occurs on rocky shores (Paine 1966, 1971, 1974). Mussels on rocky shores may exclude other sessile species, but are subject to intense predation by starfish and other predators. This situation leads to an increase in local diversity (Paine 1966), as the predators are selective. However, even if the predators are not selective predation may lead to a difference in the species composition of protected places and places exposed to predation.

The diversity of the species which may settle on the reef should be distinguished from local diversity, which is the diversity of animals or plants which may live together in the same area. The effect of predation on local diversity was discussed in Chapter 7. The diversity of the species on the reef will depend both on local diversity, and on the faunistic or floristic differences between different patches of surface (β diversity in the terminology of Whittaker 1972).

Many factors contribute to the faunistic differences between different places on the reef. Some of these are 1) Species which predominate in the absence of predation are rapidly removed by predatory fish, 2) The fauna of small patches of surface may be different from the fauna of large patches. 3) Some species settle more abundantly in places with fast-flowing water than elsewhere, while other species are more abundant in darker places, deep water, and so forth. 4) Some species settle more abundantly near edges.

Other factors may also contribute to the differences between patches. Larger ectoproct colonies grow over smaller ones, and areas occupied by established colonies are, in general, less suitable for settlement of other species. This means that to some extent, space is occupied on a first come, first served basis: once a species has occupied most of the available surface on a patch of surface other species are unlikely to be able to exclude it. As a result different patches may be occupied by different species. Sutherland (1974) calls this situation one with 'multiple stable points'. The first come, first served rule may apply among ascidians as well as among encrusting ectoprocts, and will contribute to the differences between places on the reef, and thus to the diversity of species on the reef (Levin 1974, Russell et al. 1974, Sale 1974).

If one species both colonised and grew rapidly then it would exclude other species from most newly created patches of surface very quickly. The abundances of the excluded species would decline rapidly, and therefore the diversity of species colonising new patches would be low. However, this does not happen. Instead, there may be a negative correlation between settlement rate and growth rate among common species. If so, then the diversity of ectoproct species on the reef must be increased thereby.

The situation where species A grows over B, B grows over C, and C grows over A must also lead to an overall increase in diversity (Jackson and Buss 1975, Buss 1976). Only one example of such a situation was found among the animals which settled on the panels, but other such circular paths of dominance may occur among sponge species, especially where these kill their neighbours by means of chemicals (Buss 1976).

There are thus many factors which tend to increase the diversity of settling animals on the reef. Ultimately however, the continued survival of species low in the overall hierarchy of dominance, such as ectoprocts, must depend on the continuous creation of new patches of surface by disturbances of various kinds. Algae which are common only on grazed surfaces are in the same position: their abundance must depend on the grazing activities of fish, which continuously create tiny patches of free surface.

Porter (1972) and Glynn *et al* (1972) have suggested that the abundances of many coral species on the Pacific coast of Panama may depend on various disturbances, and Osman (1977) has suggested that the fauna of rocks may be controlled by the frequency of disturbance, which in turn is related to the size of the rocks. I have suggested that various associations of sessile species on Heron Reef may be placed along a spectrum according to the size and frequency of disturbances which they are subject to. The most important disturbances for algae are the scrapes made by parrotfish, which are small and frequent. For large corals and sponges large infrequent disturbances are caused by cyclones, and perhaps also outbreaks of the coral predator *Acanthaster planci*.

The differences between species in each association can be understood in terms of strategies which serve to maintain species' abundances in the face of the pattern of disturbance which applies to that association. This is the model proposed for species on rocky shores by Levin and Paine (1974, 1975), and elaborated by Levin (1974, 1976a,b).

The spatial heterogeneity of the environment, the local nature of disturbances, and the fact that the sessile species are constantly dispersing from one patch to another, are all important characteristics of Levin's model. In the model these characteristics are important in maintaining the diversity and the stability of the community.

The dispersal of some species on the reef appears to be cued to environmental indicators. For example, the presence of a species of arborescent ectoproct may act as an indication of a safe site for settling larvae of the same species; and the presence of edges may act as an indication of the absence of ascidians for oysters and EB6. Thus species may follow complex strategies for survival on the mosaic of patches which are constantly created on the reef (Levin 1976b).

Spatial heterogeneity and dispersal have been ignored in traditional Lotka-Volterra models of population dynamics, but its importance is becoming more widely appreciated (Levin 1974, Taylor and Taylor 1977).

My conclusion is that a number of characteristics of the reef communities are important in maintaining the diversity of species which colonise patches of surface on the reef. These characteristics may be important in other communities where dispersal and local disturbances interact. They are:

1) Various local features of the environment provide refuges for species subject to predation.

2) Species which are reduced or eliminated by predators become dominant in the absence of predation.

3) 'Circular patches of dominance' (defined earlier) among species high in the dominance hierarchy may be important in maintaining diversity.

4) Dispersal may be cued to various indicators of favourable habitat.

5) Among similar species, space is occupied to some extent on a 'first come, first served' basis.

6) Among common species of the same type there may be a negative correlation between the rate of dispersal of species to new patches of surface, and their rate of growth, or competitive dominance.

CHAPTER 9

SUMMARY

1. Most arborescent ectoprocts had aggregated distributions, but very few encrusting ectoprocts were aggregated.

2. The oyster *Patro australis*, *Amathea* sp and a few encrusting ectoprocts settled preferentially near the edges of panels but most animals were randomly distributed between the centres and edges of panels.

3. The colour, or chemical nature of the substratum appeared to be important for algae, possibly because of the influence of *Enteromorpha* on other algae.

4. The size of the settlement surface influenced both species composition and number of species present.

5. Panels in caves were occupied almost exclusively by animals, whereas algae dominated brightly lit surfaces. Coralline algae may form a transition zone between the associations of animals and filamentous algae.

6. The effect of illumination on algae appears to be a threshold effect, since illumination had very little effect on algal abundances at non-cave sites.

7. Season of the year was an important component of environment in determining algal abundances. Some algae were abundant throughout the year, but most were more common in the warmer part of the year. Seasonal changes were not as important for animals, but many species showed pronounced seasonal changes in abundance.

8. Wave action and water-movement were important components of environment for animals, many of which were more abundant in areas with wave action. Algae with relatively large thalli were often less abundant in areas with wave action.

9. The effects of depth were not important in determining species' abundances but two algae occurred mainly at shallow sites and some red algae were more abundant at deeper sites. Some animals were also more abundant in deep water.

10. Predation or grazing by fish was an important component of environment both for algae and animals. Grazing by herbivorous fish was intense. It varied with substratum type and resulted in the elimination of many algae from grazed surfaces. However, other species of algae were abundant only on grazed surfaces.

11. Grazing by herbivorous fish eliminated most animals from well-lit surfaces, although the fish avoided heavily calcified animals once these had reached a minimum size.

12. Grazing was apparently reduced in winter, and in deep water.

13. Predatory fish removed soft-bodied and projecting animals from panels. These included ascidians, sponges, and arborescent ectoprocts, but some species were less affected by predation than others. Various characteristics of the animals, such as an inconspicuous appearance, or heavy calcification, were important in this respect.

14. Both predatory and herbivorous fish fed mainly on the most abundant species, but the predatory fish selected particular organisms, whereas the herbivorous fish did not.

15. Predatory fish increased the diversity of animals on panels in caves, whereas grazing fish reduced species diversity on well-lit panels.

16. Animals and algae subject to predation were protected among projections and in confined spaces, in the territories of pomacentrid fish, and beneath stinging hydroids.

17. Algae appeared to interfere with the feeding of animals, but some animals were affected more than others. In particular flexible arborescent ectoprocts were more abundant among algae than rigid ones.

18. Space already occupied by encrusting animals was made less suitable for settlement by other animals, although erect species often settled on top of other erect species.

19. While two colonies of ectoprocts of the same species usually ceased growing at the line of contact between them, where two colonies of different species met, one usually grew over the other. This applied to arborescent as well as encrusting ectoprocts.

20. Larger ectoproct colonies usually grew over smaller colonies, irrespective of which species were involved. Hence there was no strict hierarchy of dominance among species of encrusting ectoprocts. There was a negative correlation between settling and growth rate among common ectoproct species, which may be important in maintaining the abundances of species which grow slowly.

21. There was an overall hierarchy of dominance among sessile animals of different kinds, but the dominant organisms, ascidians, were subject to predation by fish, so they

could become abundant only in places protected from fish.

22. Chemical substances may have been produced by one species of ectoproct to affect other ectoprocts. Similarly, a species of sponge was observed to kill and grow over corals, probably because it produced a chemical which killed the corals.

23. The surfaces of the reef can be regarded as a mosaic of patches which are continuously created by disturbances, and then occupied by settling species. Species have various strategies to maintain their abundance over this mosaic. For each association of species there was a characteristic size and frequency of disturbances.

APPENDICES

APPENDIX 2

Identification of species

A list of generic and in some cases specific names given to the species found in this study is shown in Tables A2:1, A2:2. Many of the identifications are tentative, but they are included to assist those who may undertake future work on settling organisms on the Barrier Reef.

Only the species which are mentioned in the thesis have been included in the tables. Many other species were found, but these were rare, so that their abundances were not analysed. No taxonomic identifications were obtained for animals other than ectoprocts, except where these names are used in the thesis.

TABLE A2:1

TAXONOMIC NAMES FOR ALGAE

Name used in the Thesis	Taxonomic Name
Antithamnion sp. 1	*Antithamnion* sp.
sp. 2	*Antithamnion* sp.
Bryopsis sp.	*Bryopsis* sp
Callithamnion sp. 1	*Dasya* sp
sp. 2	*Dasya* sp + *Veleroa*?
sp. 5	Probably *Polysiphonia* sp
Ceramium sp. 1	*Ceramium* sp.
sp. 3	*Ceramium* sp.
sp. 5	*Ceramium* sp.
Champia sp.	?*Champia* sp.
Cladophora sp.	*Cladophora* (2 species)
?*Colpomenia* sp.	Probably *Colpomenia*
cf. *Colpomenia*	?sp.
Coralline sp. 2	?sp.
sp. 3	*Tenerea* sp.
?*Distromium*	?sp.
'*Ectocarpus*' sp. 1	*Ectocarpus* sp.
sp. 2	*Giffordia* sp.
sp. 3	*Giffordia* sp.
Enteromorpha sp.	*Enteromorpha*
Gelidella sp. 1	*Polysiphonia* sp.
Hypoglossum sp. 1	*Hypoglossum* sp.
sp. 2	*Hypoglossum* sp.
Jania sp.	*Jania capillacea*

TABLE A2:1 (Continued)

Name used in the Thesis	Taxonomic Name
Laurencia sp. 1	*Laurencia* sp.
sp. 3	*Laurencia* sp.
'*Lophosiphonia*' sp. 1	*Lophosiphonia* sp.
sp. 2	*Lophosiphonia* spp. (2 species)
Lyngbya sp.	*Lyngbya* sp. + another blue green species.
Peyssonelia sp. 2	Probably *Peyssonelia*
Pocockiella	*Gymnosorus* sp.
Polysiphonia sp. 1	*Polysiphonia* sp.
sp. 2	*Polysiphonia* sp.
sp. 3	?sp.
Pseudobryopsis sp. 1	*Pseudobryopsis* sp.
Ralfsia sp. 2	Includes *Ralfsia* and undentified algal crusts.
Sphacelaria sp.	*Sphacelaria* sp.
Tenerea sp.	*Tenerea* sp.
Zanardinia sp.	*Padina* sp.

TABLE A2:2

TAXONOMIC NAMES FOR ECTOPROCTS

Designation of species in Thesis	Taxonomic Name
Arborescent ectoprocts:	
AB 1	Idmidronea sp.
AB 3	Tubilipora pulcherrima
AB 3A	Steganoporella magnilabus
AB 4	cf. Tubilipora
AB 5	Scrupocellaria sp. near spatulata
AB 6	Catenicellid near Vittaticella
AB 6A	Catenicellid near Vittaticella
AB 7	Bugula dentata
AB 7A	Bugula sp.
AB 8	Nellia simplex
AB 9	?sp. (small jointed cyclostome)
AB10	? Scrupocellariid
AB11	? Scrupocellariid
AB12	Bicellariella sp.
AB13	Scrupocellaria sp.
AB14	Scrupocellaria sp.
AB17	Sertellid cf. Retepora
AB21	Bugula robusta ?var. rubra
AB22	Bugula robusta
AB29	Reteporellina denticulata
AB32	Buskia ?nitens
AB33	?sp.
AB34	?sp.
Amathea sp.	Amathea sp.

TABLE A2:2 (Continued)

Designation of species in Thesis	Taxonomic Name
Encrusting ectoprocts:	
EB 1	*Rhynchozoon bispinosa*
EB 1A	cf. *Celleporaria*
EB 2	*Celleporaria fusca*
EB 6	*Thalamoporella granulata*
EB 7	*Celleporaria columnaris*
EB 8	?*Lichenopora* sp.
EB 9	*Smittina levis*
EB10	?*Lichenopora*
EB11	*Smittina* sp.
EB12	*Parasmittina* cf. *parsevaliformis*
EB12A	*Smittia reticulata* var *spathulata*
EB12B	?sp.
EB12C	*Smittia signata*
EB14	?sp.
EB15	*Rhynchozoon incrassatum*
EB15A	?sp.
EB15B	*Rhynchozoon ?detectum*
EB16	*Microporella ciliata*
EB18	*Smittina* cf *raigii*
EB18A	?sp.
EB20	*Cribrilina radiata*
EB26	*Schizoporella cecilii*
EB29	cf. *Tubilipora*
EB30	*Setosellina ?coronata*
EB31	*Membranipora calpensis*

TABLE A2:2 (Continued)

Designation of species in Thesis	Taxonomic Name
EB31A	*Membranipora* sp.
EB32	?sp.
EB34	*Schizoporella insignis*
EB39	*Fenestrulina* ?*malusii*
EB40	?*Porella abyssicola*
EB41	*Evochella lobata*
EB43	*Schizoporella nitens*
EB45	?sp.
EB46A	*Beania* cf *conferta*
EB53	*Crepidacantha poissoni*
EB60	?sp.

APPENDIX 4A.

The measurement of water-movement at the sites where panels were suspended.

Muus (1968) and Doty (1971) have suggested the use of calcium sulphate blocks to measure the rate of water movement over a surface. Doty pointed out that water movement around and over benthic organisms produces a steepening of diffusion gradients, so that materials may diffuse towards and away from the organisms more rapidly. The loss in weight from calcium sulphate blocks during immersion on a fixed surface provides a measure of the steepening of diffusion gradients due to water-movement. The technique therefore measures an aspect of water-movement which is important to benthic organisms.

However other aspects of water-movement are not included. These include the shear forces which are produced by strong currents and wave action, and the impact forces due to breaking waves. I have assessed the effects of wave-action separately in. Chapter 4 by dividing the sites into two groups with respect to their exposure to wave action. Another possible aspect of water-movement is abrasion by sediment carried in the water. The loss in weight from calcium sulphate blocks is not greatly affected by sand abrasion (Doty and Doty 1973).

As the calcium sulphate blocks may be immersed for periods of 24 hours or longer, they may be used to measure the average water-movement at a site over a tidal or diurnal cycle. Furthermore replicated measurements of a large number of sites may be made simultaneously and cheaply.

I modified the method described by Doty (1971) as follows: I used hemispherical blocks rather than cuboid blocks so as to reduce the amount of turbulence in the water moving over the blocks. It seemed reasonable that this might make the relation between loss in weight and the rate of water-movement a more linear one. Secondly, I mounted the blocks on each side of freely rotating settlement panels. Thus the water always flowed over the blocks from the same direction, and the blocks were in the same position as sessile organisms on the settlement panels.

Methods:

Calcium sulphate powder and fresh water were mixed in the ratio 10:8 by weight. The mixture was stirred to remove lumps, but care was taken not to introduce air bubbles. Then the mixture was poured into polyethylene 'egg tray' moulds so as to fill the hemispherical pits. All the blocks used for one experiment were made at the same time.

The blocks were dried in the sun for a day, then removed from the moulds and the bottom surfaces scraped flat. Sufficient material was removed so that all the blocks fell within 1.0g of a selected weight. Blocks with very low weights were discarded as possibly containing air bubbles. Then the blocks were glued to numbered squares of 0.2 mm thick white plastic sheet (Figure A4:1A), and the glue allowed to dry overnight.

The mounted blocks were weighed and then attached on either side of novasteen settlement panels (Figure A4:1B). A cardboard jig was used to ensure that the blocks on each panel

FIGURE A4:1

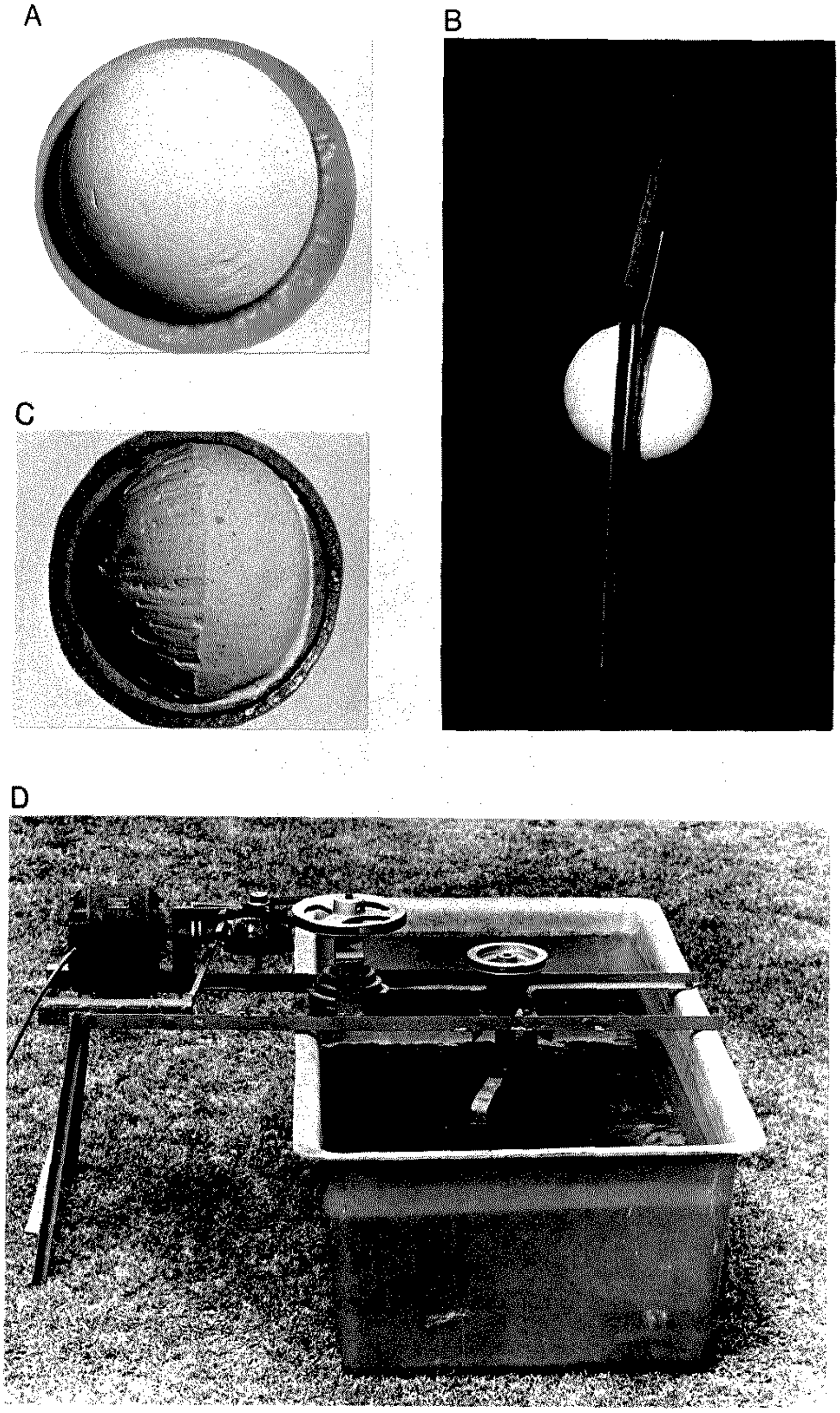
Illustrations of the method used to measure water-movement.

A Calcium sulphate block mounted on plastic sheet prior to immersion

B Two blocks attached on either side of a settlement panel. The panel was suspended vertically during immersion.

C Eroded calcium sulphate block after immersion. Water-movement was from left to right.

D Apparatus used to determine the relation between the weight lost from the blocks, and the rate of water-movement past them.


A
B
C
D

were exactly opposite each other, and that they were in the same position on each panel. I shall refer to such panels as "water-movement panels".

The water-movement panels were enclosed in plastic bags for transport on the boat and through the water to the sites, where they were suspended on the frames described in Chapter 2. The plastic bags were then removed, and the time was noted. After about 24 hours the panels were again enclosed in plastic bags, then taken off the frames and brought back to land. There they were sun-dried for a day before being weighed.

Figure A4:1C shows a mounted calcium sulphate block which has been partly dissolved while immersed.

Calibration:

To determine the relationship between the rate of water-movement over the blocks and the loss in weight from the blocks, I attached water-movement panels at either end of a metal rod which was rotated in a large tank of water. An electric motor and a set of variable pulley gears was used to rotate the rod, drawing the panels through the water at various speeds (Figure A4:1D).

The five speeds used were measured by counting the number of revolutions of the panels in five minute intervals. The losses in weight from calcium sulphate blocks stirred for eight hours at each speed are shown in Table A4:01. Cochran's test showed no significant heterogeneity of variance at $p = 0.05$ for these data. A regression of loss in weight against speed through the water (Table A4:02) was significant at $p = 0.05$, and deviations from

TABLE A4:01

THE LOSS IN WEIGHT IN GRAMS FROM CALCIUM SULPHATE BLOCKS DRAWN THROUGH THE WATER AT FIVE SPEEDS.

	SPEED IN METERS PER MINUTE				
Replicates	6.141	11.116	18.586	30.642	52.339
A	1.59	2.37	2.85	5.00	8.20
B	1.30	1.96	2.30	4.32	7.32
C	1.38	2.42	2.83	4.99	8.40
D	1.38	2.04	2.24	4.16	7.26

TABLE A4:02

ANALYSIS OF VARIANCE OF A REGRESSION OF WEIGHT LOSS AGAINST SPEED FOR CALCIUM SULPHATE BLOCKS, USING THE DATA IN TABLE A4:01.

REGRESSION EQUATION: $L = 0.423 + 0.139\ S$

where: L is the weight lost from the blocks in grams after eight hours.

S is the speed of the blocks in meters per minute.

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Ratio	Significance*
Total	107.802	19			
Regression	104.493	1	104.493	568.45	S
Residual	3.308	18	0.184		
Deviations from linearity	1.150	3	0.383	2.66	n.s.
Residual Within Groups	2.158	15	0.144		

*S = significant at $p = 0.05$, n.s. = not significant at $p = 0.05$.

linearity were not significant at $p = 0.05$. There is thus a linear relationship between the weight lost from the blocks and the rate of water-movement past the blocks. The mean and standard deviation of weight lost from blocks at each speed is shown in Figure A4:2 together with the fitted regression line. In field experiments I have simply used the weight lost from the blocks in gm. to measure water-movement.

At all speeds replicates A and C lost more weight than replicates B and D in the calibration experiment. (Table A4:01). Replicates A and C were on the outside of the circle of rotation as the water-movement panels moved through the water.

Variation in water-movement between sides of panels in the field:

To determine whether both sides of the panels received the same degree of water-movement in the field, and to test the sensitivity of the method, I mounted two calcium sulphate blocks on each side of six panels, and immersed them about 0.5 m apart on a long metal frame on the slope below Wistari reef. The losses in weight from these blocks are shown in Table A4:03. There is no reason why water-movement over side A of one panel should correspond to water-movement over side A of another panel, so that if sides A and B of the panels are regarded as treatments, then the treatments are "nested" within panels, and a nested analysis of variance was used (Table A4:04). Cochran's test for heterogeneity of variances gave a non significant result at $p = 0.05$.

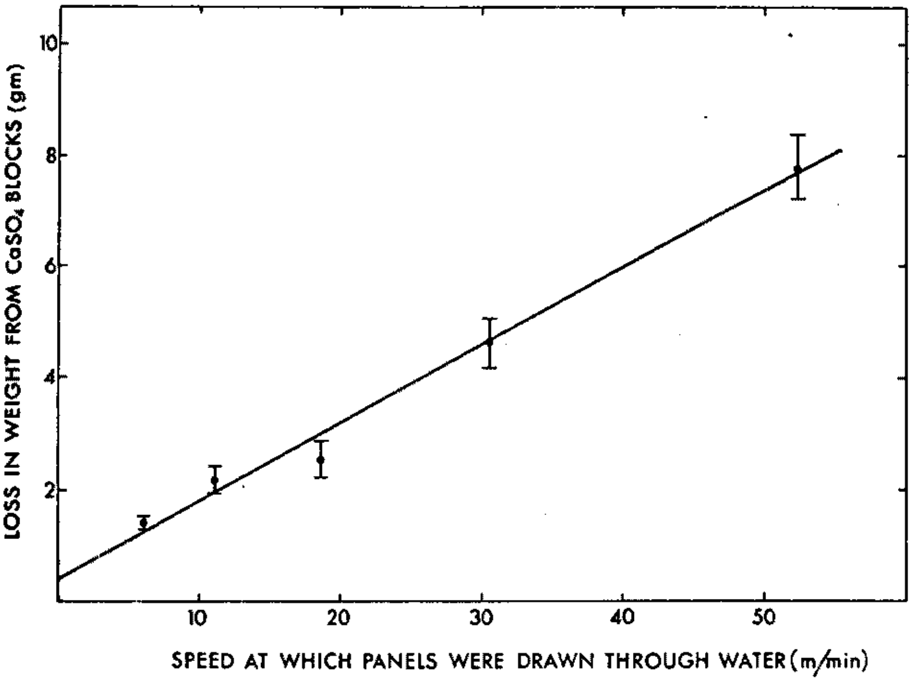
The sensitivity of the method is shown by the small proportion of the total sum of squares which is attributable

FIGURE A4:2

Calcium sulphate blocks were drawn through the water at various speeds. The weight lost from the blocks, in grams, is plotted against the speed at which the panels moved through the water, in meters per minute.

FIGURE A4:3

The twelve sites used in experiments described in Chapter 4 are shown along the abcissa, ranked in order of increasing water-movement. The measure of water-movement used was the weight lost from calcium sulphate blocks immersed at each site in two experiments. This measure is plotted on the ordinate. The mean and standard deviation of weight loss at each site is shown.


LOSS IN WEIGHT FROM $CaSO_4$ BLOCKS (gm)
10
8
6
4
2
10
20
30
40
50
SPEED AT WHICH PANELS WERE DRAWN THROUGH WATER (m/min)

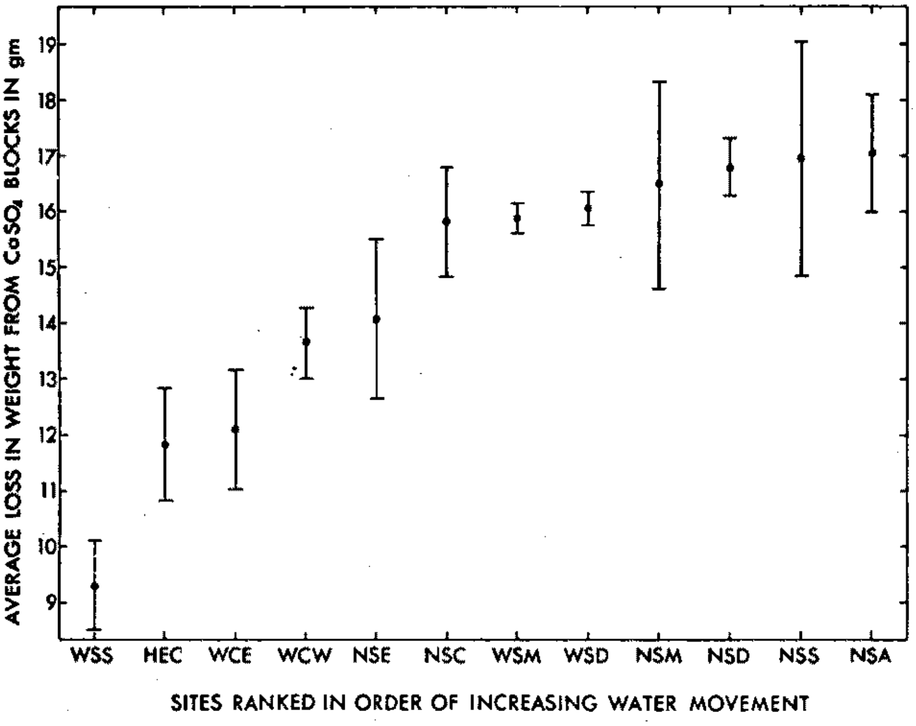

AVERAGE LOSS IN WEIGHT FROM $CaSO_4$ BLOCKS IN gm
19
18
17
16
15
14
13
12
11
10
9
WSS
HEC
WCE
WCW
NSE
NSC
WSM
WSD
NSM
NSD
NSS
NSA
SITES RANKED IN ORDER OF INCREASING WATER MOVEMENT

TABLE A4:03

THE LOSS IN WEIGHT, IN GRAMS, FROM CALCIUM SULPHATE BLOCKS MOUNTED IN PAIRS ON EITHER SIDE OF SETTLEMENT PANELS, AND IMMERSED FOR 24 HOURS.

Panel No.	Side A	Side B
1	10.1	9.9
	10.1	10.6
2	8.8	10.2
	8.8	10.2
3	10.7	11.1
	9.7	10.4
4	9.1	8.9
	8.3	10.2
5	8.3	9.0
	8.7	8.8
6	8.6	8.9
	8.1	8.0

TABLE A4:04

RESULTS OF A NESTED ANALYSIS OF VARIANCE OF THE LOSS IN WEIGHT FROM CALCIUM SULPHATE BLOCKS, USING THE DATA IN TABLE A4:03.

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Value and Significance*
Total	19.290	23		
Panels	13.327	5	2.665	5.028 S
Sides of Panels	3.178	6	0.530	2.282 n.s.
Between replicates (Residual)	2.785	12	0.232	

*S = significant at p = 0.05, n.s. = net significant at p = 0.05.

to the variation between replicates. However the variation between the sides of panels is not significant at $p = 0.05$. Most of the variation in the data occurs between panels.

Since the variation between sides of panels was not significant, I felt justified in using blocks from each side of a panel as replicates in further experiments.

Water-movement in different parts of a large cave.

For some experiments on settling organisms I needed to obtain as many replicates as possible from the same site. However the fact that the panels were caged and suspended individually meant that they could not be suspended close together. It became important to discover how large an area could be considered as one site in the cave where such experiments were carried out. I therefore determined how water-movement (and light - see appendix 4B) varied between parts of the cave.

Five water movement panels were suspended approximately 0.25 m apart on three 1 m frames in the cave, and another outside the cave for comparison. The losses in weight from the calcium sulphate blocks over 24 hours (Table A4:05) were analysed by means of a nested analysis of variance (Table A4:06) since the panels were 'nested' within the frames. Cochran's test for heterogeneity of variance yielded a non-significant result at $p = 0.05$. Not only the differences between frames but also the differences between panels are significant at $p = 0.05$. This shows that the technique is sensitive enough to detect differences in the degree of water-movement in places less than 1 m apart. I used a Student-Newman-Keuls procedure (Snedecor and Cochran

TABLE A4:05

THE LOSS IN WEIGHT, IN GRAMS, FROM CALCIUM SULPHATE BLOCKS ON PANELS IMMERSED ON FOUR FRAMES FOR 24 HOURS.

Panels	FRAMES			
	Outside Cave	Cave Frame 1	Cave Frame 2	Cave Frame 3
A	14.1	10.1	9.4	11.5
	14.7	10.5	9.3	11.9
B	14.4	10.0	8.9	11.4
	14.7	10.1	9.3	11.4
C	14.5	9.3	9.3	10.8
	14.2	9.6	9.0	11.8
D	14.1	9.8	8.8	11.8
	13.9	9.6	9.5	11.9
E	14.1	8.8	9.0	11.0
	13.9	9.1	9.3	11.0

TABLE A4:06

RESULTS OF A NESTED ANALYSIS OF VARIANCE OF THE LOSS IN WEIGHT FROM CALCIUM SULPHATE BLOCKS ON FOUR FRAMES USING THE DATA IN TABLE A4:05.

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Value and Significance*
Total	162.500	39		
Between frames	157.355	3	52.452	204.891 S
Between panels	4.090	16	0.256	4.845 S
Between replicates (Residual)	1.055	20	0.053	

* S = significant at p = 0.05.

1967) to determine which differences between the frames were significant at $p = 0.05$ (Table A4:07). Water-movement at each frame was significantly different from that at each other frame. Thus frames in different parts of the same cave could not be considered as replicate sites in terms of water-movement, and were considered as separate sites. Two of the frames investigated here were used in the experiments described in Chapter 4 (cave frame 1 = WCE in Table A4:10, Cave frame 3 = WCW).

Water-movement inside cages overgrown by algae.

When settlement panels enclosed in cages were suspended at well lit sites, algae grew on the cages, so that in three months the cages were gradually overgrown by algae, even though fish browsed extensively on the cages. In caves the cages were colonised only by small hydroids. To determine the effect of algal growth on the cages on water-movement through the cages, I suspended water-movement panels in pairs along two long steel frames; one panel of each pair being enclosed in a cage which had been immersed for three months.

The losses in weight from the calcium sulphate blocks over 24 hours (Table A4:08) were analysed by a two-way analysis of variance, with the position of the pairs of panels on the frame as random factor, and the caging treatment as a fixed factor (Table A4:09). Cochran's test showed no significant heterogeneity of variance in these data at $p = 0.05$.

Most of the variation in the data was between positions, but the variation between caging treatments was significant at $p = 0.05$, as was the interaction between positions and caging

TABLE A4:07

COMPARISONS OF THE MEAN LOSS IN WEIGHT FROM CALCIUM SULPHATE BLOCKS AT EACH OF FOUR FRAMES, USING A STUDENT-NEWMAN-KEULS PROCEDURE, AND DATA FROM TABLE A4:05.

Comparison	Difference Between Means	Critical Value	Significance*
Outside Cave versus:			
Cave frame 1	4.57	0.584	S
Cave frame 2	5.18	0.648	S
Cave frame 3	2.88	0.480	S
Cave frame 3 versus:			
Cave frame 1	1.69	0.480	S
Cave frame 2	2.20	0.584	S
Cave frame 2 versus:			
Cave frame 1	0.51	0.480	S

*S = significant at $p = 0.05$

TABLE A4:08

THE LOSSES IN WEIGHT, IN GRAMS, FROM CALCIUM SULPHATE BLOCKS IMMERSED WITH AND WITHOUT CAGES FOR 24 HOURS, AT TWELVE POSITIONS.

Position Number	Caged	Not Caged
1	9.1	10.0
	10.3	9.9
2	10.3	10.2
	10.0	10.8
3	10.0	10.2
	10.1	11.2
4	10.5	10.8
	9.9	10.2
5	11.4	12.7
	10.0	13.0
6	9.2	11.5
	9.5	11.8
7	8.7	9.1
	8.7	8.9
8	9.1	10.4
	10.1	10.9
9	9.1	10.6
	9.6	11.1
10	11.3	12.7
	11.4	12.9
11	11.5	11.8
	11.9	11.7
12	8.0	8.6
	8.1	8.4

TABLE A4:09

RESULTS OF AN ANALYSIS OF VARIANCE OF THE LOSSES IN WEIGHT FROM BLOCKS IMMERSED WITH AND WITHOUT CAGES, USING THE DATA IN TABLE A4:08.

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Value and Significance*
Total	75.777	47		
Between positions	55.457	11	5.042	30.555 S
Caging treatment	9.720	1	9.720	16.102 S
Interaction	6.640	11	0.604	3.658 S
Residual	3.960	24	0.165	

*S = significant at p = 0.05.

treatment. The results show that cages overgrown by algae did affect the rate of water-movement over the settlement panels, and this effect varies from place (or from cage to cage). To avoid this difficulty I mounted panels in open cages, which were designed so that water flowed through the mesh before flowing over the panels. These are described in Chapter 2. Panels from open cages were used as controls for the effect of caging in Chapter 4, except that on four occasions the open cage panels were lost, and uncaged panels were substituted.

Water-movement at the sites discussed in Chapter 4:

Since the sites discussed in Chapter 4 were widely separated it was not possible to suspend or retrieve water-movement panels at all these sites simultaneously. Instead the sites were visited in the same order to suspend and to retrieve the water-movement panels, and the time each site was visited was noted.

The losses in weight from calcium sulphate blocks immersed at each site in January 1974 are shown in Table A4:10. These data were corrected as shown in the table for the time each water-movement panel was immersed.

The rates of water-movement at each site may vary with the time of year, or the prevalent weather conditions. I attempted to measure water movement at the sites again in April 1974 but fell ill, and the experiment was not repeated until December 1974. In this case the water movement panels at each site were all retrieved approximately 24 hours after immersion (± 10 minutes) and no correction for time of immersion was made. The data are

TABLE A4:10

THE LOSS IN WEIGHT, IN GRAMS, FROM CALCIUM SULPHATE BLOCKS IMMERSED AT ELEVEN SITES IN JANUARY 1974.

Site[*]	Actual Loss in Weight	No. of Hours Immersed	Calculated Weight Loss in 24 Hr.
WSS	9.8	23.08	10.2
	9.3		9.7
WSM	15.0	23.17	15.5
	15.5		16.1
WSD	15.7	23.25	16.2
	15.1		15.6
NSS	16.8	21.83	18.5
	17.3		19.0
NSM	16.0	22.05	17.4
	17.1		18.6
NSD	15.4	22.22	16.6
	16.1		17.4
NSG	14.3	22.08	15.5
	13.9		15.1
WCE	11.5	24.25	11.4
	11.1		11.0
WCW - not sampled.			
NSA	16.3	22.08	17.7
	16.7		18.2
NSC	15.1	21.83	16.6
	15.0		16.5
EC	11.0	23.58	11.2
	-		11.2[+]

[*] Symbols for sites are explained in Chapter 4, Figure 4:1.

[+] This value was inserted for purposes of analysis, as one block became detached and was lost at this site.

shown in Table A4:11. Four extra sites at which frames were constructed for extra experiments were included in December.

The data from the eleven sites included in both experiments were analysed by a two way analysis of variance (Table A4:12). Since the blocks for the two experiments were made from different batches of calcium sulphate at different times any overall differences between the data for January and for December may be due to differences between the batches of blocks. However a change in the relative rates of water-movement at the various sites should result in a significant interaction between the effects of sites and times.

Cochran's test showed no significant heterogeneity of variance at $p = 0.05$. The results of the analysis of variance (Table A4:12) show that there is a significant interaction between sites and times at $p = 0.05$, as well as a significant overall difference between sites.

The significant interaction suggests that relative rates of water-movement at the various sites are different at different times. In January 1974 the water-movement panels were immersed during a period of heavy wave action, whereas in December 1974 the panels were immersed during a calm period. Wave action would be expected to affect the sites on the exposed north side of Heron reef (sites beginning with NS) more than the sites on the Wistari reef slope (beginning with WS) or the remaining sites in the Heron channel (WCE, WCW and HEC). This is borne out by a comparison of the mean loss in weight from blocks at each site for each experiment (Table A4:13). One might also expect that shallow sites (WSS and NSS: 5.5 m below the reef crest) would

TABLE A4:11

THE LOSS IN WEIGHT, IN GRAMS, FROM CALCIUM SULPHATE BLOCKS IMMERSED AT SIXTEEN SITES IN DECEMBER 1974 FOR 24 HOURS.

Site[*]	Loss in Weight	
	Replicate 1	Replicate 2
WSS	8.9	8.4
WSM	16.0	15.9
WSD	16.2	16.2
NSS	15.5	14.8
NSM	15.3	14.6
NSD	16.2	17.0
WCE	13.2	12.8
WCW	13.2	14.1
NSA	16.2	16.1
NSC	15.7	14.5
EC	11.3	13.0
NSG	12.9	12.8
WSS(2)	11.2	12.2
WSM(2)	16.2	16.8
WSD(2)	16.0	17.0
Outside Cave[+]	16.9	16.3

[*] Symbols for sites are explained in Chapter 4, Figure 4:1. The last five sites were used as alternative sites as described in Chapter 4, or for extra experiments.

[+] See Table A4:05.

TABLE A4:12

RESULTS OF AN ANALYSIS OF VARIANCE OF THE WEIGHT LOST FROM CALCIUM SULPHATE BLOCKS AT ELEVEN SITES SAMPLED IN JANUARY 1974 AND DECEMBER 1974.

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Value and Significance*	
Total	317.068	43			
Sites	272.221	10	27.222	111.327	S
Sampling times	10.702	1	10.702	43.767	S
Interaction	29.011	10	2.901	11.864	S
Residual	5.135	21+	0.245		

*S = significant at $p = 0.05$

+Degrees of freedom adjusted for one missing replicate.

TABLE A4:13

THE MEAN LOSS IN WEIGHT AT ELEVEN SITES FOR CALCIUM SULPHATE BLOCKS IMMERSED IN JANUARY AND IN DECEMBER 1974, AND THE DIFFERENCES BETWEEN THESE MEANS.

Sites	Mean Weight Lost from Blocks (gm)		Difference Between Jan. and Dec.	Overall Mean
	January 1974	December 1974		
Heron Channel:				
WSS	9.95	8.65	+ 1.3	9.30
WSM	15.8	15.95	- 0.15	15.88
WSD	15.9	16.2	- 0.3	16.05
WCW	-	13.65	-	13.65*
WCE	11.2	13.0	- 1.8	12.10
EC	11.2*	12.15	- 0.95	11.83*
North Slope:				
NSS	18.75	15.15	+ 3.6	16.95
NSM	18.0	14.95	+ 3.05	16.48
NSD	17.0	16.6	+ 0.4	16.80
NSA	17.95	16.15	+ 1.8	17.05
NSC	16.55	15.1	+ 1.45	15.83
NSG	15.3	12.85	+ 2.45	14.08

*These values based on a reduced number of replicates.

be more affected by wave action than the remaining deeper sites (9.5 - 17.5 m below the reef crest). This is also borne out by the data.

A comparison of the mean loss in weight for the north side sites with the mean for the Wistari slope and Heron channel sites in each experiment (Table A4:14), shows that there is a significant difference at p = 0.05 between the two groups of sites in both the January and December experiments. However there is a significantly larger difference between the groups of sites in January 1974 when wave action was more intense (Table A4:14). Wave action, therefore, appears to be responsible for the difference in the relative amounts of water-movement at the various sites between the January and December experiments.

Weather conditions vary seasonally at Heron Island, with the most severe storms occurring in January or February as a rule, but extremely calm conditions may occur too, during these months. Strong wave action may, in fact, be encountered at any time of year, and there is no source of data on wave height through the year, or the frequency and severity of storms at Heron Island, so that I cannot estimate the degree of wave action in different seasons.

The best estimate therefore, of the degree of water-movement at each site through the year is an average of the data from the January and December experiments. The site 'WCW' was not included in the January experiment, but the data from the incomplete experiment carried out in April 1974 (when wave action was moderately severe) indicates that the value obtained in December 1974 (Table A4:13) is a reasonable one. This is one

TABLE A4:14

COMPARISONS OF THE AVERAGE WEIGHT LOST FROM CALCIUM SULPHATE BLOCKS AT SITES ON THE NORTH SLOPE WITH THE AVERAGE AT SITES IN THE HERON CHANNEL.

Comparison Tested	Difference Between Means	Critical Value	Significance*
North Slope sites versus others in December 1974	1.943	0.441	S
North Slope sites versus others in January 1974	4.448	0.441	S
Comparison of the above differences	2.505	0.623	S

*S = significant at $p = 0.05$.

of the sites where water movement is not expected to vary much with wave action.

Since there is a significant interaction between sites and the times of the experiments it is not meaningful to compare the sites statistically. Instead I have calculated the mean and standard deviation for each site using the data from both experiments, and these are presented in Figure A4:3, where the sites are ranked in order of increasing water movement.

APPENDIX 4B

THE MEASUREMENT OF ILLUMINATION

Friend (1961) described a method to measure illumination which depends on the bleaching of diazo compounds by light. A stack of sheets of translucent plastic sheets coated with diazo compounds is exposed to light. The light bleaches the sheets in successive order through the stack. I adapted Friend's method for underwater use because I wished to measure illumination at a number of sites simultaneously. If photo-electric light meters had been used a large number would have been needed.

I used 'Ammo' black line, ammonia developed diazofilm, No. BAF 3, with a 0.18 mm thick plastic backing. The film was cut into small square sheets, and piles of ten sheets, each with the coated side uppermost, were put into aluminium foil packets. Each foil packet had a 22 mm diameter hole in one side (Figure A4:4 A). The film packets were put into small plastic bags which were sealed with contact cement. To prevent condensation of moisture on the film under pressure I included small wads of toilet tissue in the bags.

The bags were taped onto each side of standard settlement panels, and covered with sheets of clear celluloid to prevent fish from pecking open the plastic bags. The fish were annoyed by their reflections in the plastic.

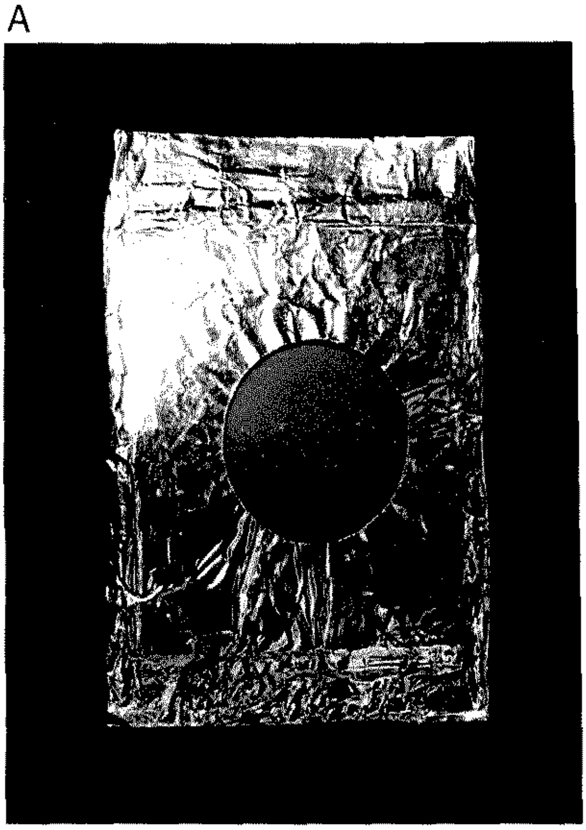
Aluminium foil envelopes were used to exclude light from the film packets until the panels had been suspended in position. The foil envelopes were replaced when the panels were retrieved two or three days later. I chose

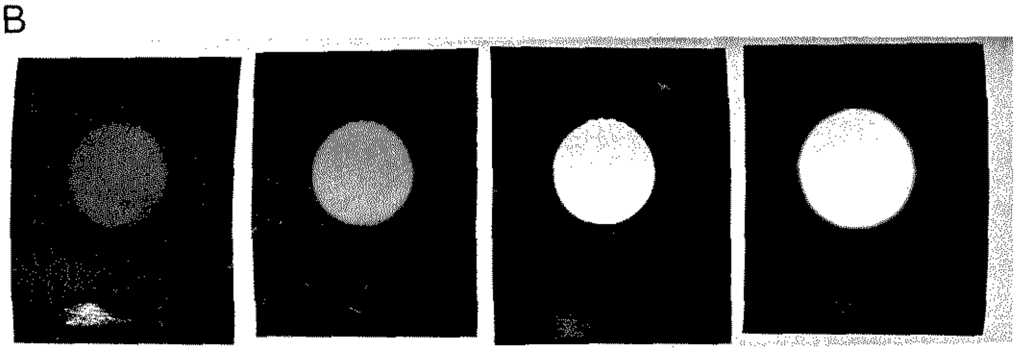
FIGURE A4:4

ILLUSTRATIONS OF THE METHOD OF MEASURING ILLUMINATION.

A An aluminium foil film packet containing sheets of diazofilm.

B A series of developed diazofilm sheets, showing the areas bleached by light. The sheet on the left was uppermost in the film packet.


A


B

periods of fine weather to conduct all the experiments.

The film sheets were developed in ammonia fumes for fifteen minutes. The unexposed parts of the film turn black on development, while the exposed parts remain clear. A series of sheets is shown in Figure A4:4 B. The number of fully exposed sheets was counted, and the degree to which the last few sheets were bleached was estimated.

Spectral sensitivity:

It is important to determine which parts of the light spectrum affect a light measuring device most; especially when illumination in the sea is being measured. Seawater transmits only a part of the spectrum.

The transmission spectrum of seawater varies from place to place (Jerlov 1970), but the transmission spectrum of 'Railway glass' (Figure A4:5) mimics that of oceanic water fairly well (Jitts 1963). Wavelengths outside the range from 350nm to 650nm are rapidly absorbed by the water, so that only wavelengths inside this range are likely to be important for sublittoral marine organisms.

Darker places may provide refuges from predators which hunt by sight, but the most important aspect of light in this study is as a source of energy for algae. Algal use light in the range of wavelengths which are best transmitted by the water (Rabinowitch 1951).

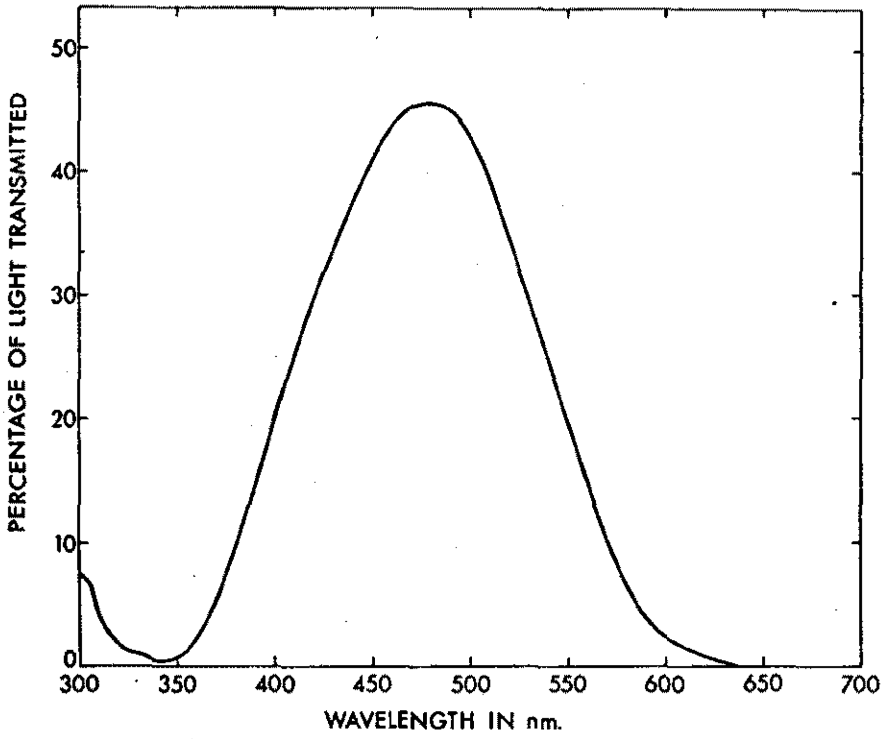
Friend (1961) shows that the diazo compounds on the Ozalid film he used were most sensitive to wavelengths of about 410nm. when light was passed through layers of bleached film. He does not specify how many bleached layers he used. This is important

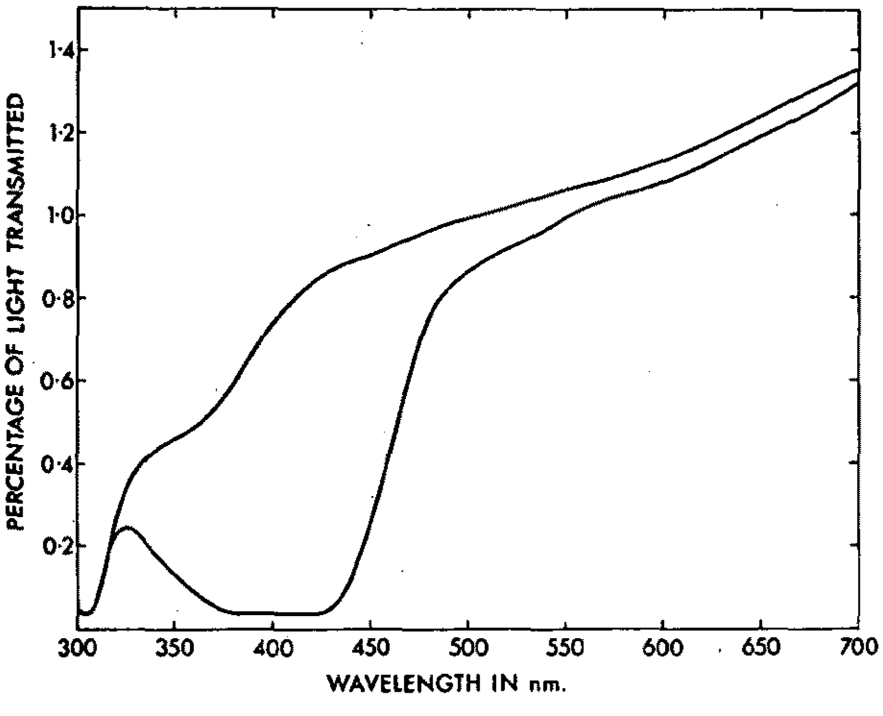
FIGURE A4:5

The percentage of incident light transmitted by blue 'Railway glass' plotted against the wavelength of the incident light.

FIGURE A4:6

The percentage of incident light transmitted by sheets of exposed (top line) and unexposed (bottom line) 'Ammo' BAF 3 diazofilm, plotted against the wavelength of the incident light. The percentages shown do not include light scattered by the film sheets.


PERCENTAGE OF LIGHT TRANSMITTED
50
40
30
20
10
0
300
350
400
450
500
550
600
650
700
WAVELENGTH IN nm.


PERCENTAGE OF LIGHT TRANSMITTED
1·4
1·2
1·0
0·8
0·6
0·4
0·2
300
350
400
450
500
550
600
650
700
WAVELENGTH IN nm.

because a bleached film strip absorbs light more strongly at shorter than at longer wavelengths, as shown by the transmission spectrum of bleached film (Figure A4:6). Therefore, the fraction of the total energy in each part of the incident light spectrum will depend on how many bleached film sheets the light has passed through.

Since I enclosed the film packets in polythene bags, and protected these with sheets of celluloid, the effect of these as light filters must be considered too. The transmission spectrum of the polythene and celluloid sheets together (Figure A4:7) shows that they absorb the shorter wavelengths more strongly just as the bleached film sheets do. Thus the effect of the celluloid, polythene, and bleached film sheets will be to shift the peak sensitivity of the method towards longer wavelengths than those absorbed most strongly by the diazo compounds.

Unexposed film absorbs light strongly in the range from 350nm to 450nm (Figure A4:6). The difference between the transmission spectra for bleached and unbleached film represents the absorbtion spectrum of the light sensitive compounds, and perhaps also the action spectrum of these compounds.

I measured the spectral response of the film packets by exposing them to equal amounts of light energy of different wavelengths. Monochrome filters with a bandwidth of approximately 11nm were used in front of a projector lamp. The light energy transmitted through each filter was measured in microeinsteins $m^{-2}sec^{-1}$, and appropriate exposure times calculated so that 3000 microeinsteins m^{-2} were transmitted through each filter. Film packets were exposed for these times after allowing the lamp to warm up for one minute.

Maximum bleaching of the first film sheet in the packets occurred at 416, 430, and 454nm. The readings obtained with each filter, using the first two strips to measure film response, are shown in Table A4:15 and in Figure A4:7. The maximum response was at 454nm, on the red side of the absorbtion peak for the diazo compounds (Figure A4:6).

Calibration Scale:

Friend (1961) showed that the number of sheets of Ozalid paper bleached was proportional to the logarithm of the light energy striking the top sheet. I checked that this was true of the diazofilm I used; both for varying light intensities and for varying times of exposure at the same light intensity. Film packets were exposed to sunlight shining through six different neutral density filters for six minutes. The relationship between the readings and the logarithm of percentage transmission of the filters was linear (Tables A4:16, A4:17). Film packets were also exposed to sunlight shining through six layers of grey plastic for various times between 11 am and 1 pm. The relationship between the readings obtained and the logarithm of exposure time was linear (Tables A4:18 and A4:19).

The logarithmic calibration scale of the film packets means that the method is less sensitive to differences in intense illumination than to differences in weak illumination. However, the time for which film packets are exposed does not affect the sensitivity of the method. Consider a site A, where the illumination is twice that at another site, B. A constant number of extra film sheets will be bleached at A however long the diazofilm packets are exposed.

TABLE A4:15

READINGS OBTAINED FROM DIAZOFILM PACKETS EXPOSED TO 3000 MICRO-EINSTEINS m^{-2} THROUGH FILTERS WITH PEAK TRANSMITTANCE AT DIFFERENT WAVELENGTHS.

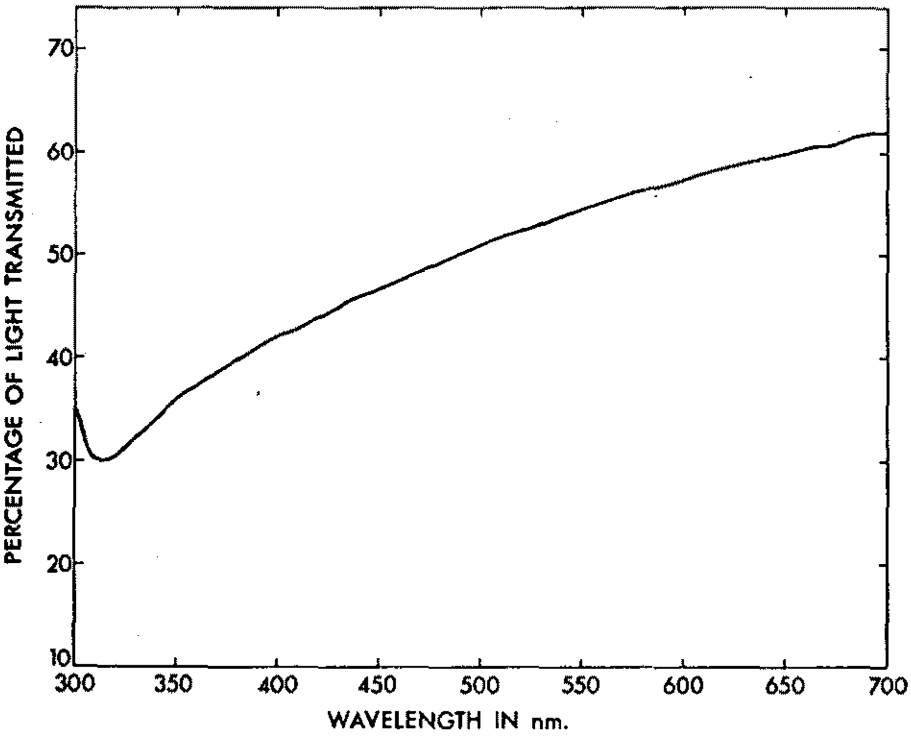
Wavelength of Filter (nm)	Readings from Diazofilm Packets			Mean Readings
416	1.6	1.25	1.4	1.42
430	1.4	1.4	1.6	1.47
454	1.7	1.8	1.7	1.73
469	1.3	1.25	1.3	1.28
487	0.75	0.55	0.95	0.75
505	0.4	0.25	0.1	0.25
545	0.1	0.05	0.1	0.08
596	0.15	0.05	0.25	0.15
650	0.05	0.05	0.05	0.05

FIGURE A4:7

The percentage of incident light transmitted by a two-layered filter made from strips of the polythene and the celluloid in which the film packets were enclosed for use underwater. The percentages shown do not include light scattered by the filter.

FIGURE A4:8

Readings obtained from diazofilm packets exposed to 3000 microeinsteins m^{-2} of light plotted against the wavelength of the light used (Bandwidth of filters: 11 nm).
The mean readings from three experiments are shown by the solid circles. The horizontal lines show extreme values.


PERCENTAGE OF LIGHT TRANSMITTED
70
60
50
40
30
20
10
300
350
400
450
500
550
600
650
700
WAVELENGTH IN nm.

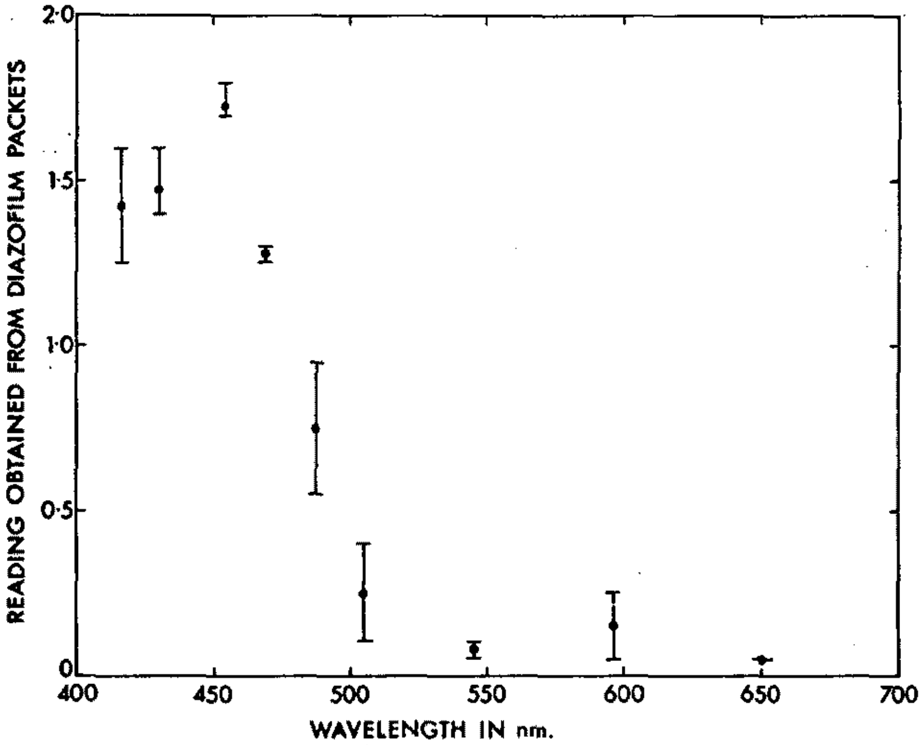

READING OBTAINED FROM DIAZOFILM PACKETS
2·0
1·5
1·0
0·5
0
400
450
500
550
600
650
700
WAVELENGTH IN nm.

TABLE A4:16

READINGS OBTAINED FROM DIAZOFILM PACKETS EXPOSED TO SUNLIGHT UNDER NEUTRAL DENSITY FILTERS WITH DIFFERENT PERCENTAGES OF TRANSMITTANCE

Percentage Transmittance of Filter	Readings from Diazofilm Packets
5.4	1.85
9.5	2.70
24.2	3.45
51.8	4.45
65.0	4.45
86.3	4.70

TABLE A4:17

RESULTS OF A REGRESSION OF READINGS FROM DIAZOFILM PACKETS AGAINST THE LOGARITHM (BASE e) OF THE PERCENTAGE OF FULL SUNLIGHT STRIKING THE FILM PACKETS

Regression equation: $R = 0.257 + 1.018 \text{ Log}_e (P)$

where: R is the reading from a diazofilm packet

P is the percentage of full sunlight striking the packet.

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Value and Significance*
Total	6.550	5		
Regression	6.446	1	6.446	306.95 S
Residual	0.084	4	0.021	

*S = significant at p = 0.05.

TABLE A4:18

READINGS OBTAINED FROM DIAZOFILM PACKETS EXPOSED FOR VARIOUS TIMES.

Exposure Time (Minutes)	Readings from Film Packets	
10	2.5	2.5
15	3.45	2.7
20	3.45	-
22	3.65	-
30	4.25	3.45
45	3.85	-
50	4.65	-
60	5.30	5.50
90	5.65	-
107	5.5	-
120	5.85	5.70

TABLE A4:19

RESULTS OF A REGRESSION OF READINGS FROM DIAZOFILM PACKETS AGAINST LOG_e OF EXPOSURE TIME (IN MINUTES).

Regression equation: $R = 0.623 + 1.354 (Log_e (T)$

where: R is the reading obtained from a diazofilm packet
T is the exposure time in minutes.

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Value and Significance*	
Total	21.977	15			
Regression	20.286	1	20.286	167.96	S
Residual	1.691	14	0.121		
Deviations from linearity	1.058	9	0.118	0.93	n.s.
Within groups	0.633	5	0.127		

*S = significant at $p = 0.05$, n.s. = not significant at $p = 0.05$.

Variation in illumination in a cave between sides of panels, caged and uncaged panels, and positions:

To determine to what extent illumination varied from place to place in the cave in which many of my experiments were carried out, I suspended panels with film packets in four positions about 1.5m apart in the cave. To check whether caging had any effect on illumination a pair of panels were suspended about 0.3m apart at each position; one panel of each pair being enclosed in a cage which had been immersed in a cave for three months.

Tidal currents were responsible for most of the water-movement through the cave, so that the swinging panels were all aligned in the same way for long periods. Since illumination in the cave was from one side only I expected that one side of each panel would receive more illumination than the other. I therefore mounted two film packets on either side of each panel.

The film packets were exposed for 73 hours. The readings obtained (Table A4:20) were analysed by a three way analysis of variance (Table A4:21). Cochran's test showed that there was no significant heterogeneity of variance at $p = 0.05$.

Table A4:21 shows that the three factor interaction was significant at $p = 0.05$. This is a result of the fact that at position 3 illumination on the uncaged panel was lower than on the caged panel, whereas the reverse was true at the other positions (Table A4:20). I suggest that the differences in illumination on caged and uncaged panels were probably due to the small differences in position of the panels rather than the caging treatment. Position was an important factor in determining illumination; it accounted for a high proportion of the variance in the data

TABLE A4:20

READINGS OBTAINED FROM DIAZOFILM PACKETS EXPOSED FOR 73 HOURS ON TWO SIDES OF PANELS, IN AND OUT OF CAGES, AT FOUR POSITIONS IN A CAVE.

	POSITION			
Treatment	1	2	3	4
Caged Panels: Left side	1.4	3.1	3.45	3.45
	1.4	3.25	3.65	3.85
Right side	2.7	3.7	4.25	4.3
	2.65	3.7	4.25	4.4
Uncaged Panels: Left side	2.1	3.7	2.75	3.85
	2.25	3.5	2.75	3.85
Right side	3.1	4.45	4.15	4.7
	3.4	4.1	4.15	4.45

TABLE A4:21

RESULTS OF A THREE-WAY ANALYSIS OF VARIANCE ON READINGS FROM FILM PACKETS EXPOSED AT FOUR POSITIONS IN A CAVE (DATA IN TABLE A4:20)

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Value and Significance*	
Total	22.714	31			
Main effects:					
Sides	6.257	1	6.257	349.73	S
Caging treatment	0.439	1	0.439	24.56	S
Position	13.543	3	4.514	252.32	S
Interactions:					
Sides x Positions	0.445	3	0.148	8.28	S
Sides x Caging	0.057	1	0.057	3.18	n.s.
Caging x Positions	1.467	3	0.489	27.33	S
Three factor	0.220	3	0.073	4.09	S
Residual	0.286	16	0.0179		

*S = significant at p = 0.05, n.s. = not significant at p = 0.05.

(Table A4:21). For this reason the true effect of caging treatment cannot be determined because the caged and uncaged panels were not true replicates with respect to position.

Illumination on either side of the uncaged panel at position 3 was markedly different: more so than for any other panel, and this contributed too, to the three factor interaction. The interaction between the effects of sides and position is probably a result of differences in the direction of illumination in various parts of the cave.

I conclude that there were marked differences in illumination from place to place in the cave. There were also differences in illumination between sides of panels, and this effect varies from place to place in the cave. The effect of caging was not well tested in this experiment: caging may reduce illumination on panels but the data showed a reversal of this trend at one position.

The differences in illumination between sides of panels may result in differences between the flora and fauna on either side of the panels. However, the film packet readings were taken over three days only, and as the diurnal and tidal cycles change phase in the course of weeks, the currents in the middle of the day will change in direction. Furthermore the instantaneous illumination on either side of a panel will vary widely as the panels swing from side to side. Thus the differences between sides of panels as experienced by the organisms which settle and grow on them for three months are probably not as marked as suggested by the data in Table A4:20.

The effect of depth and caging on illumination at well-lit sites:

To determine the effect of depth on illumination at well-lit sites, and whether cages overgrown by algae affected illumination on the panels, I exposed light packets on caged and uncaged panels suspended on long steel frames 2 m and 7 m below the reef crest. The caged and uncaged panels were suspended in pairs, about 0.3m apart, at four positions on each frame, the positions being about 2 m apart. The cages used had been immersed on the same frames for three months, so that they were overgrown with algae.

As illumination on either side of the panels was not expected to vary markedly only one film packet was mounted on each side of the panels. The film packets were immersed for 66 hours. The readings obtained (Table A4:22) were analysed by a three-way analysis of variance (Table A4:23). Cochran's test showed no significant heterogeneity of variance in the data at $p = 0.05$.

The differences between sides of panels (between replicates in Table A4:22) are less marked than in the cave (Table A4:20), but they result in a fairly large residual mean square (Table A4:23). Only the main effects of position and depth were significant at $p = 0.05$. The effect of depth was probably mainly due to light scattering and absorbtion by particles in the water. The position effect may be a result of differences in the light reflected by sand and corals near each pair of panels. The position effect may also have obscured the caging effect to some extent as the caged and uncaged panels were not in exactly the same places. The variation in illumination due to caging treatment was not significantly greater than the variation between sides of panels.

TABLE A4:22

READINGS OBTAINED FROM DIAZOFILM PACKETS EXPOSED FOR 66 HOURS ON CAGED AND UNCAGED PANELS AT TWO DEPTHS.

	POSITIONS			
Treatment	1	2	3	4
Shallow depth (2 m):				
Caged Panels	4.4	4.45	4.8	-*
	4.6	4.4	5.6	4.4
Uncaged Panels	4.85	4.4	4.6	4.65
	4.6	4.65	4.6	4.6
Deeper Depth (7 m):				
Caged Panels	4.65	3.9	4.4	4.1
	4.4	4.4	4.4	4.0
Uncaged Panels	4.65	4.85	4.85	4.25
	4.7	4.25	4.25	4.25

*This replicate missing as the plastic bag leaked.

TABLE A4:23

RESULTS OF A THREE-WAY ANALYSIS OF VARIANCE ON READINGS FROM FILM PACKETS EXPOSED ON CAGED AND UNCAGED PANELS AT TWO DEPTHS

(DATA IN TABLE A4:22)

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Value and Significance*	
Total	2.9572	30+			
Main effects:					
Depth	0.4278	1	0.4278	6.919	S
Caging treatment	0.0903	1	0.0903	1.461	n.s.
Positions	0.6578	3	0.2193	3.546	S
Interactions:					
Depth x Positions	0.2278	3	0.0759	1.228	n.s.
Depth x Caging	0.1128	1	0.1128	1.825	n.s.
Caging x Positions	0.2966	3	0.0989	1.599	n.s.
Three factor	0.2166	3	0.0722	1.228	n.s.
Residual	0.9275	15+	0.0618		

*S = significant at p = 0.05, n.s. = not significant at p = 0.05.

+Degrees of freedom adjusted for one missing data point.

As illumination at the sites used for this experiment was more intense than in the cave, the film packets were less sensitive to differences in illumination than in the previous experiment.

Illumination at the sites discussed in Chapter 4:

As discussed in the appendix on water-movement, the sites described in Chapter 4 had to be compared by visiting the sites in the same order at the beginning and end of the experiment to ensure that light packets at each site were suspended for the same length of time (70 hours). The relative levels of illumination at each site were not expected to change at different times of the year as the levels of water-movement did, so I did not repeat the experiment in different months.

As illumination varied between positions 2 m or less apart, and between sides of panels (Tables A4:21 and A4:23) two panels were suspended at each site and the readings from the four film packets on these panels were treated as replicates (Table A4:24). In this way the variation within sites included the variation between sides of panels and positions at each site. The sites were compared using a one-way analysis of variance (Table A4:25). Cochran's test showed that there was no significant heterogeneity of variance at $p = 0.05$.

The analysis showed that there were significant differences in illumination between the sites at $p = 0.05$. These differences were examined by means of a Student-Newman-Keuls procedure (Zar, 1974) as shown in Table A4:26. In the first series of tests the site NSA, with the lowest mean reading, was compared with the other sites, beginning with the site with the greatest mean reading. The cave site NSA differs significantly at $p = 0.05$ from all the non-cave

TABLE A:24

READINGS FROM DIAZOFILM PACKETS EXPOSED FOR 70 HOURS AT 17 SITES AROUND HERON REEF.

Site[x]	Readings				Mean Readings
WSS	4.25	5.1	5.4	4.7	4.86
WSM	4.6	4.4	4.1	4.25	4.34
WSD	3.85	4.85	4.4	4.25	4.34
NSS	4.4	4.6	5.85	4.4	4.81
NSM	4.4	4.6	4.4	4.4	4.45
NSD	4.0	4.25	4.25	-[+]	4.17
WCE	2.6	2.4	2.6	2.6	2.55
WCW	2.25	3.25	3.4	2.25	2.79
EC	3.85	3.6	3.6	3.4	3.61
NSA	2.25	2.4	2.25	3.25	2.54
NSC	2.6	3.0	3.4	-[+]	3.00
WSS(2)	5.1	4.1	5.25	4.25	4.68
WSM(2)	5.1	4.25	4.4	4.85	4.65
WSD(2)	3.6	4.25	4.25	4.4	4.13
NSG	3.85	5.1	4.25	5.0	4.55
Exp. Site 1	5.4	4.4	4.85	5.25	4.98
Outside Cave	4.85	5.1	5.1	4.6	4.91

[x] Symbols for sites are explained in Chapter 4. The last six sites are alternative or experimental sites.

[+] Readings not available as film packets leaked. The mean of the remaining three readings was used in the analysis.

TABLE A4:25

RESULTS OF AN ANALYSIS OF VARIANCE ON READINGS FROM FILM PACKETS EXPOSED AT 17 SITES (DATA IN TABLE A4:24)

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Value and Significance*	
Total	55.360	65+			
Between sites	46.391	16	2.899	15.840	S
Residual	8.969	49+	0.1830		

*S = significant at $p = 0.05$.

+Two degrees of freedom subtracted as two readings missing.

sites, and also from EC, a site in a shallow cave; but not from the remaining cave sites WCE, WCW, and NSC. In the next series of tests in the table WCE, WCW and NSC are all shown to be significantly different at $p = 0.05$ from all the non-cave sites and EC. Thus the cave sites NSA, NSC, WCE and WCW can be regarded as a distinct, homogenous group of sites with respect to illumination.

All the non-cave form a similar homogenous group with respect to illumination, since none of these sites is significantly different at $p = 0.05$ from any of the others. EC, the shallow cave site, occupies an intermediate position. Illumination at this site does not differ significantly from the deeper non-cave sites WSD, WSD(2), NSD, WSM, and NSM; but is significantly different at $p = 0.05$ from the remaining well-lit sites.

In Chapter 4 the antilog (to base e) of the mean reading for each site was used, as the readings from the film packets were proportional to the logarithm of the intensity of illumination.

TABLE A4:26

COMPARISONS OF THE MEANS FOR 17 SITES OF READINGS FROM DIAZOFILM PACKETS EXPOSED AT EACH SITE.

Sites Compared	Difference Between Means	Critical Value and Significance*	
NSR with Exp Site 1	2.438	1.105	S
with Outside Cave	2.375	1.099	S
with WSS	2.325	1.081	S
with NSS	2.275	1.062	S
with WSS (2)	2.138	1.054	S
with WSM (2)	2.113	1.039	S
with NSG	2.013	1.022	S
with NSM	1.913	1.001	S
with WSM, WSD	1.800	0.982	S
with NSD	1.630	0.931	S
with WSD (2)	1.588	0.898	S
with NSC	0.463	0.805	n.s.

thus NSA, WCE,WCW, and NSC are not significantly different at $p \doteq 0.05$.

Sites Compared	Difference Between Means	Critical Value and Significance*	
WCE with Exp Site 1	2.425	1.099	S
with Outside Cave	2.363	1.081	S
with WSS	2.313	1.062	S
with NSS	2.263	1.054	S
with WSS (2)	2.125	1.039	S
with WSM (2)	2.100	1.022	S
with NSG	2.000	1.001	S
with NSM	1.900	0.982	S
with WSM, WSD	1.788	0.958	S
with NSD	1.618	0.931	S
with WSD (2)	1.575	0.898	S
with EC	1.063	0.857	S

TABLE A4:26 - Continued (2)

Sites Compared	Difference Between Means	Critical Value and Significance*	
WCW with Exp Site 1	2.188	1.081	S
with Outside Cave	2.125	1.062	S
with WSS	2.075	1.054	S
with NSS	2.025	1.039	S
with WSS (2)	1.888	1.022	S
with WSM (2)	1.863	1.001	S
with NSG	1.763	0.982	S
with NSM	1.663	0.958	S
with WSM, WSD	1.550	0.931	S
with NSD	1.380	0.857	S
with WSD (2)	1.338	0.805	S
with EC	0.825	0.732	S
NSC with Exp Site 1	1.975	1.062	S
with Outside Cave	1.913	1.054	S
with WSS	1.863	1.039	S
with NSS	1.813	1.022	S
with WSS (2)	1.675	1.001	S
with WSM (2)	1.650	0.982	S
with NSG	1.550	0.958	S
with NSM	1.450	0.931	S
with WSM, WSD	1.338	0.898	S
with NSD	1.168	0.805	S
with WSD (2)	1.125	0.732	S
with EC	0.613	0.608	S
EC with Exp Site 1	1.363	1.054	S
with Outside Cave	1.300	1.039	S
with WSS	1.250	1.022	S
with NSS	1.200	1.001	S
with WSS (2)	1.063	0.982	S
with WSM (2)	1.038	0.958	S
with NSG	0.938	0.931	S
with NSM	0.838	0.898	n.s.

Thus EC, WSD(2), NSD, WSD, WSM, and NSM do not differ significantly at p = 0.05.

TABLE A4:26 - Continued (3)

Sites Compared	Difference Between Means	Critical Value and Significance*
WSD (2) with Exp Site 1	0.850	1.039 n.s.

Thus WSD (2), NSD, WSD, WSM, NSM, NSG, WSM (2), WSS (2), NSS, WSS, Outside,Cave and Exp Site 1 do not differ significantly at $p = 0.05$.

APPENDIX 4C

FACTORS NOT CONSIDERED IN CHAPTER 4.

A large number of components of environment may play a part in determining the abundances of the species studied. Apart from the factors discussed in Chapter 4, temperature, salinity, and the chemical composition of seawater are important components of the marine environment. Larvae of benthic organisms are known to respond to these factors during settlement (Meadows and Campbell 1972) and these factors also affect the metabolism of attached animals and plants (Gessner 1970, Gessner and Schramm 1971, Kinne 1970, 1971).

Salinity and composition of seawater:

Heron Island is 64 km from the mainland. The salinity and chemical constituents of the seawater around the reef, therefore, will not be affected by runoff from the mainland. The predominant current over the southern half of the Great Barrier Reef is southerly, and there is an eddy around the Swain reefs to the north of Heron Island (Woodhead 1970), so that the residual flow past Heron Island is toward the mainland.

Brandon (1973) describes the pattern of rainfall and salinity over the Barrier Reef area during 1967-1968. Salinities fluctuate much less at the southern end of the Barrier Reef than farther north. South of 20°S salinities greater than 36°/oo, or less than 35°/oo occur very rarely, and usually only near the mainland. The concentration of nutrients in the water in this area is apparently fairly constant through the year too, as local upwelling of nutrient-rich water is probable only for reefs at the outer barrier (Brandon 1973).

Only minor local variations in salinity are to be expected, because rainfall in the southern section of the Barrier Reef is much lower than farther north. The average annual rainfall at Heron Island is 996.2 mm, and the monthly averages vary from 142.2 mm in January to 17.5 mm in September (Brandon 1973). Very little surface runoff is to be expected from the small island, but the Heron and Wistari lagoons may act as traps for rainwater during low tides, and the lagoon water may become diluted. Kinsey and Kinsey (1967) showed that the oxygen content of this water may also vary widely.

As the tide rises sea-water flows into Heron lagoon from the southeast, pushed by the southeast trade wind, and waves. Some lagoon water is pushed over the reef edge at the northern end of the reef, near the island. Water continues to flow over the northern edge of the reef as the tide falls, until the lagoon level drops below that of the reef edge. The lagoon water, which may become diluted, might therefore affect organisms on the outer reef slope in the areas where I worked. However, the lagoon water is probably drawn away rapidly, and dispersed, by the strong tidal currents which flow past the reef. The influence of lagoon water therefore, is probably only important on the reef flat and in shallow water near the reef edge. Tsuda (1974) describes a similar situation in Guam: intertidal algae were affected by rainfall at some times of the year, and were therefore absent, while the algae found in deeper water were present throughout the year.

Temperature:

Changes in temperature affect photosynthesis in algae (Gessner 1970), and the metabolism and growth of animals (Kinne 1970). Tropical organisms may be particularly sensitive to low temperatures: for example many corals do not grow at temperatures below about 18°C (Kinsman 1964). Brandon (1973) presents a graph of monthly average surface-water temperatures plotted against latitude for the Barrier Reef area. At the latitude of Heron Island the maximum is 27.6°C (during February) and the minimum is 20.4°C (during August). Brandon notes that there is never a steep gradient of temperature with depth in the southern part of the Barrier Reef area, as the year-round trade wind ensures good vertical mixing of the water. The average vertical variation in temperature in the Capricorn channel between Heron Island and the mainland was 1-2°C (Brandon 1973).

Local variations in temperature may occur in the same way as variations in salinity. The water impounded in the lagoon and on the reef flat at low tide will cool overnight, and will be heated on calm sunny days. Endean, Stephenson, and Kenny (1956) found that water temperatures on the Heron reef flat varied from 14°C to 33°C. However, this lagoon water probably only affects shallow depths near the reef edge when it flows over the northern parts of the reef crest, so that wide temperature fluctuations are unlikely except near the reef crest.

I suspended maximum-minimum thermometers at a number of sites to determine the extent of fluctuations in temperature at the sites I used, but the thermometers were frequently destroyed by wave action. The incomplete records obtained are set out in

Tables A4:27 and A4:28. The tables show that temperatures ranged from 18°C to 27°C at sites 2 m or more below the reef crest, but at the site 1.5 m below the reef crest the temperature reached a maximum in February of 28.5°C. The temperature range is wider than that of the oceanic water around the reef, but the seasonal variation in temperatures is not very great.

TABLE A4:27

MAXIMUM TEMPERATURES (^{o}C) AT VARIOUS DEPTHS BELOW THE CREST OF HERON REEF IN 1973-1974.

Depth of Site Below Reef Crest	MONTH OF THE YEAR										
	Dec. 1973	Jan. 1974	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.
1.5 m	26	28.5									
2 m							23	23	22.5	23.5	
6 m		26.5			26						
7 m (Site 1)							25	21.5	21	22	
7 m (Site 2)	27	27			26			21.5	23		
7 m (Site 3)		26			26						
10 m							23				
11 m	26	25.5			25.5						

TABLE A4:28

MINIMUM TEMPERATURES (^{o}C) AT VARIOUS DEPTHS BELOW THE CREST OF HERON REEF IN 1973-1974.

Depth of Site Below Reef Crest	MONTH OF THE YEAR										
	Dec. 1973	Jan. 1974	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.
1.5 m	22	23									
2 m							21	18	20	22	
6 m		22			19						
7 m (Site 1)							21	18	20	20	
7 m (Site 2)	23	23			21			18	21		
7 m (Site 3)		24			21						
10 m							19				
11 m	22	18			18						

APPENDIX 4D

THE TOTAL ABUNDANCES OF PLANTS AND ANIMALS AT CAVE AND NON-CAVE SITES.

The abundances of algal species in caves and at non-cave sites were compared by calculating the total abundance of each species on sixty samples from the cave sites: WCE, WCW, NSA, and NSC; and on sixty samples from the non-cave sites: WSS, WSM, NSS, and NSM (Table A4:29). As encrusting corallines were not separated into different species on samples from cave sites, only the total abundance of all corallines is shown in the table. Tenerea sp was the most abundant species both in caves and elsewhere, and the total abundance of all the corallines on samples from caves was less than that of Tenerea at non-cave sites (Table A4:29). Tenerea was therefore most abundant at non-cave sites, although the distribution of other encrusting coralline species is not known.

I compared the abundances of sessile animals at four groups of sites: non-cave sites at 6m depth (WSS and NSS); at 10m depth (WSM and NSM); and at 14 to 17m depth (WSD and NSD); and cave sites (WCE, WCW, NSA, NSC). Only sixteen samples from the WSD and NSD sites were examined, whereas forty or more samples from each of the other site groups were examined. The total abundance of each species on the sixteen samples from WSD and NSD was therefore multiplied by 2.5 so that these totals could be compared with the totals based on forty samples. Species which were present on only one or two samples from non-cave sites were omitted.

The results (Table A4:30) are discussed in Chapter 4.

TABLE A4:29

THE TOTAL AREA COVERED, IN mm^2, BY SPECIES OF ALGAE ON SIXTY SAMPLES FROM FOUR CAVE SITES AND ON SIXTY SAMPLES FROM FOUR NON-CAVE SITES.

Species	Cave sites	Non-cave sites
Antithamnion sp 1	35	8172
Antithamnion sp 2	2	1178
Bryopsis	15	7857
Ceramium sp 1	10	265
Ceramium sp 3	3	187
?*Distromium*	24	48
'*Ectocarpus*' sp 1	410	37940
Enteromorpha	11	63003
Gelidella	7	120
Hypoglossum sp 1	5	54
Hypoglossum sp 2	15	197
Jania	9	397
Laurencia sp 3	4	3467
'*Lophosiphonia*' sp 1	162	15786
Peyssonelia sp 2	2	5
Pocockiella	10	0
Polysiphonia	1	8378
?*Pseudobryopsis*	23	38326
Ralfsia sp 2	160	99350
?sp.	1	0
Encrusting coralline algae (all spp)	5459	29664
Tenerea sp	?	23226
Other encrusting corallines	?	6438

TABLE A4:30

TOTAL ABUNDANCES, AS AREA COVERED IN mm^2, OF SESSILE ANIMALS AT FOUR GROUPS OF SITES.

Species	Non-cave sites at 5m depth	Non-cave sites at 10m depth	Non-cave sites at 14-17m depth	Sites in caves
Ascidians:				
Ascidia spp	347	375	628	2116
Ascidian B	88	74	203	1203
?*Botryllus*	111	91	935	4436
?*Diplosoma*	1511	2214	150	2656
?*Herdmania* A	87	1094	1038	2801
?*Herdmania* B	21	72	418	527
molgulid	178	456	110	166
?*Polycarpa*	234	255	113	354
Rhopalia	4	319	1163	15
Arborescent ectoprocts:				
AB1	0	0	45	4961
AB3	2	27	160	5373
AB4	14	30	315	1311
AB5	155	857	2803	6696
AB6	54	268	465	4765
AB6A	6	200	4263	1550
AB7	42	3524	1913	4933
AB7A	39	231	150	9
AB8	26	46	75	408
AB9	4	85	673	1202
AB10	9	238	138	297
AB11	15	248	1213	185
AB13	27	715	1610	6572
AB14	0	237	220	5065
AB17	1	7	80	2330
AB21	47	751	575	3118
AB22	54	821	995	1231
AB32	2	20	18	272
AB33	0	1	48	0
AB34	46	194	1500	4
Amathea sp	0	310	8	1625

TABLE A4:30 (continued)

Species	Non-cave sites at 5m depth	Non-cave sites at 10m depth	Non-cave sites at 14-17m depth	Sites in caves
Encrusting ectoprocts				
EB1	1	20	166	2156
EB1A	37	718	876	1600
EB2	40	52	158	554
EB6	1091	3165	60	14619
EB7	15	163	64	2033
EB8	31	68	22	1141
EB9	14	545	2598	1583
EB11	207	277	418	776
EB12	36	203	2384	2325
EB12A	26	146	555	1448
EB12B	12	25	453	502
EB12C	0	458	340	505
EB14	3	44	51	2323
EB15	34	99	209	1109
EB15A	12	96	47	370
EB15B	0	14	5	58
EB16	68	93	572	3340
EB18	0	35	101	1584
EB18A	0	0	26	787
EB29	8	37	30	771
EB32	12	338	15	34
EB39	2	168	227	1730
EB40	51	70	938	713
EB46A	0	24	13	146
EB53	0	0	19	12
EB60	0	2	8	45

TABLE A4:30 (continued)

Species	Non-cave sites at 6m depth	Non-cave sites at 10m depth	Non-cave sites at 14-17m depth	Sites in caves
Sponges:				
Sponge A	61	289	103	581
Sponge B	36	92	8	663
Sponge C	4	30	35	588
Sponge D	17	52	68	277
Sponge G	22	27	5	499
Sponge J	14	79	255	189
Sponge K	13	71	0	69
Sponge L	0	1	138	35
Sponge M	0	24	0	97
Sponge N	10	27	30	20
Sponge W	9	25	10	13
Molluscs:				
?*Chama* sp	0	103	73	16
Patro australis	845	3868	6915	2088
Pteriid	85	56	63	278
Spiny oyster	0	40	333	0
Vermetid	3	15	85	40
Soft Corals:				
Soft coral 1	0	6	38	0
Soft coral 2	2	0	25	0
Soft coral 3	4	8	25	0
Soft coral 5	1	6	48	0
Soft coral 7	3	1	5	0
Polychaetes and others:				
Filograna	2	251	0	9574
Hydroides	37	261	1068	372
Spirobranchus	103	24	290	126
Barnacle	0	9	15	6
Crinoid juvs.	0	5	5	3
Coral juvs.	175	61	248	19

APPENDIX 4E

Assumptions and methods of regression analysis.

Regression, particularly multiple regression, is best regarded as a procedure to describe the variation in a set of data, rather than a procedure which can be used to test hypotheses. The results obtained from the multiple regression analysis used are therefore not a series of statistical tests of the effects of various components of environment, but rather a description of how the variation in species' abundances is related to various components of environment.

Tests of significance at the p = 0.05 level were used in this thesis to determine whether the components were useful in predicting, or explaining, the variation in abundance of each species. Conclusions were usually based on the number of species which appeared to be affected by each component of environment, rather than the results of individual tests of significance. However, more reliance has been placed on the results for caging treatment (Chapter 5). Caging treatment was an experimental manipulation rather than an environmental variable, and was not correlated with any other component of environment.

Assumptions:

For assumptions of multiple regression analysis are germane to the analysis in Chapter 4. These are:

1) The regression procedure requires that the variance of the dependent variable is homogenous (Mead 1971). Transformations of the data may be required if, for example, the mean and variance are correlated.

2) The form of the relation between the dependent and independent variables is important. For example, if the abundance of a species varies as the logarithm of illumination, then a linear regression of abundance on illumination may provide a poor fit to the data. Various transformations of the independent variables such as log x, x^2, exp(x) etc. can be tried on a pilot set of data, but when there are many independent variables this method is lugubrious.

If an independent variable can take only one of two values (for example zero or one) then transformations will affect the slope of the regression, but not whether the slope is significantly different from zero.

3) If independent variables are correlated then only one may be required. The other may contribute nothing significant. Where two correlated variables are included in a regression model, part of the variation in the data may be attributed to either variable. The standard regression procedure attributes to each variable only the variation not explained by other variables (Nie _et_ _al_ 1975).

With correlated variables the estimated regression slopes for each variable are unbiased, but the regression is less efficient: it is less likely that the regression slopes will be significantly different from zero (Mead 1971).

4) Interactions between the effects of independent variables may be important. For example the effects of water-movement on a species' abundance may be different in shallow and in deep water. This will not be evident from a linear regression analysis. Unless the interaction is included as a separate variable the analysis will provide only an estimate of the average effects of

water-movement. With many independent variables the analysis becomes very complex if all the interactions are included. Furthermore the interaction variables may be correlated with other variables so that the analysis becomes less efficient.

Procedures:

Three sets of data were analysed: 1) The abundances of algae on samples from non-cave sites. 2) The abundances of animals on samples from cave sites and the deepest non-cave sites. 3) The abundance of *Patro australis* on all the samples. The values of the independent variables were the same for each species of alga because each species was measured over the same set of samples. Similarly the independent variables were the same for each animal species except *Patro australis*.

The values of wave action, water-movement, and illumination at each site are shown in Table A4:31. The values of caging treatment were zero for samples from open cages and one for samples from closed cages.

1) Homogeneity of variance: This was examined using Cochran's test. A log transformation of the data ($x' = \log_e (+1)$ where x is the area covered by the species in mm^2 and x' is the transformed abundance) was required for all species.

2) Transformations of independent variables: Except for seasonal changes, the linear form of each component of environment was used. There were only two levels of caging treatment and wave action, but transformations might have been useful for the other variables.

Seasonal changes are cyclical, so the appropriate trans-

TABLE A4:31

VALUES OF WAVE ACTION, WATER-MOVEMENT, ILLUMINATION, AND DEPTH AT THE SAMPLE SITES USED.*

Site	Wave action	Water-Movement	Illumination	Depth
Non-cave sites:				
WSS	0	9.3	129.3	5.5
WSS (2)	0	11.7	107.2	5.5
WSM	0	15.8	76.5	10.0
WSM (2)	0	16.5	104.6	9.5
WSD	0	16.1	76.5	17.0
NSS	1	17.0	123.0	5.5
NSM	1	16.5	85.6	11.0
NSG	1	14.1	94.6	9.5
NSD	1	16.8	64.7	14.0
Cave sites:				
EC	0	12.1	12.8	6.0
WCE	0	13.7	16.3	6.5
WCW	0	11.8	37.0	12.0
NSA	1	17.1	12.7	9.0
NSC	1	15.8	20.1	10.0

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*The methods and units of measurement are described in appendices 4A, 4B and Section 4:2.

formation is to use two variables 'season 1' and 'season 2' as outlined by Crome (1976). The four quarters of the year during which panels were immersed were numbered from 1 (for panels immersed in July and taken out in October) to 4 (panels immersed from April to July). The two seasonal variables were then calculated by: 'season 1' = sine $(0.5 \pi x)$

'season 2' = cosine $(0.5 \pi x)$

where x is the number given to the quarter of the year.

Table A4:32 shows the values taken by the two variables. 'Season 1' may be taken to measure the change from summer to winter, as the warmest water temperatures occur from January to March, while the coldest period is from July to September (Appendix 4C). 'Season 2' then measures the change from autumn to spring.

3) Correlated variables: Where two components of environment were correlated one of them was selected on biological grounds. The variation in species' abundances which could be attributed to either component was attributed to the chosen component. For example illumination and depth were correlated for the algal data. Illumination was chosen as an important component of environment for algae. The effects of depth were evaluated with all the other components of environment included in the regression model. Depth was then omitted, and the effects of illumination were evaluated using the simplified regression model. This type of 'backwards elimination' procedure (Draper and Smith 1966) was used to determine 1) the effects of illumination on algal abundances, and 2) whether depth explained any extra variation in the data not explained by illumination or other components of environment.

TABLE A4:32

THE VALUES ASSIGNED TO THE TWO SEASONAL VARIABLES USED IN THE REGRESSION ANALYSES.

Period of Immersion of settlement panels	Values Assigned to Variables	
	'Season 1'	'Season 2'
July to October	1	0
October to January	0	1
January to April	-1	0
April to July	0	-1

When one of a pair of correlated variables is omitted the other usually explains a larger proportion of the variation in the data. However the reverse may sometimes be true. Consider the case where a species of algae is more abundant at shallow sites, but less abundant under brighter illumination. Because illumination and depth are negatively correlated neither depth alone, nor illumination alone would be very useful in explaining the variation in abundance of the alga. However, both variables together might explain a large proportion of the variation. A variable which increases the amount of variation explained by another is called a suppressor variable because it suppresses the noise in the data around the values predicted by the second variable. Several examples of such suppressor variables were found.

The choices made between correlated variables for algae are described below:

a) 'Season 2' was significantly correlated with immersion time. Immersion time was included as a variable only to check whether the unavoidable variation in the time the panels were immersed affected species' abundances. Therefore the variation which could be attributed to either variable was attributed to 'season 2'.

b) Wave action and water-movement were correlated. The variation explained by either variable was attributed to water-movement, as the shear forces generated by wave action were not expected to be important for small filamentous algae.

c) Water-movement, illumination, and depth were all intercorrelated. Depth was omitted from the regression in favour of water-movement and illumination.

d) For the latter variables the proportion of variation explained by each variable alone as well as in conjunction with the other were calculated (see Tables 4:10, 4:11 in Chapter 4).

The correlations between the components of environment were different for animals, and a different set of components were considered to be important.

a) Immersion time was correlated with wave action, water-movement, 'season 1' and 'season 2', and was omitted in favour of these variables.

b) Depth was positively correlated with water-movement and illumination, and was omitted in favour of these variables.

c) Variation in the data which could be attributed to illumination or water-movement was attributed to water-movement.

d) Wave action and water-movement were highly correlated. The proportion of variation explained by each variable alone, and with the other included in the regression, was calculated.

The abundances of <u>Patro australis</u> were analysed over all the samples. For these data illumination was not significantly correlated with depth or water-movement, and the regression procedure was changed accordingly. Otherwise the procedure was the same as for other animals.

4) Interactions: No interaction terms were included in the regressions used to evaluate the various components of environment. However interactions between caging treatment and other components of environment were considered (Chapter 5). The interaction variables were formed by multiplying together the values for caging treatment and other components. Interaction terms were added 'stepwise' (Draper and Smith 1966) to a regres-

sion model which included the various components of environment, provided that the interaction terms together contributed significantly to the variation explained by the regression.

Interaction terms which explained most additional variation were added first, provided their contribution was significant at $p = 0.05$. Therefore, interaction terms which were correlated with variables or other interaction terms already in the regression were not likely to be added. Their additional contribution to the regression would be small.

APPENDIX 5

THE AREA COVERED BY SPONGES AND ASCIDIANS ON SETTLEMENT PANELS.

Because individual species occurred too infrequently for analysis the total areas covered by sponges, simple ascidians, and compound ascidians on settlement panels were calculated. The totals for both sides of each panel from cave sites were summed, and the data for twenty-two pairs of panels in open and closed cages is shown in Table A5:1.

TABLE A5:1

TOTAL AREAS, IN mm^2, COVERED BY GROUPS OF SPECIES ON PANELS.

Sponges		Simple Ascidians		Compound Ascidians	
Open cages	Closed cages	Open cages	Closed cages	Open cages	Closed cages
2	5	56	1	272	554
3	5	0	280	2	1
5	102	6	1071	112	1233
42	75	6	163	7	97
7	147	283	791	58	215
62	14	237	11	544	.0066
23	454	0	64	6240	744
52	68	0	0	8	6
88	144	189	83	103	339
178	263	18	299	152	488
125	231	215	570	131	247
88	196	1	10	138	358
0	75	0	450	10	575
199	289	1448	494	15	268
500	1729	8	235	305	23
0	0	10	363	4	28
0	0	2	2175	0	0
222	234	75	0	5	2
93	429	0	733	0	246
50	144	0	6	83	22
80	386	45	1852	35	218
0	228	58	405	1665	5237

APPENDIX 7A

Ways of measuring the distribution of abundances of species in an association from a sample collection.

The most complete way to describe the distribution of abundance between species in an association or community is to determine a probability distribution function which specifies the number of species which have a given relative abundance. However very often neither the relative abundances of species, nor even the number of species in the association can be measured directly. In such cases one can estimate the optimum parameters of a chosen probability distribution function from a sample collection, and test the fit of the theoretical distribution to the sample data, as discussed by Pielou (1975). If a truncated lognormal or negative binomial distribution provides a good fit, then the total number of species in the association can be estimated by an extrapolation of the graph of the distribution (Pielou 1975).

If the abundances of the species in an association are a result of the combined effect of a large number of independent random variables then the observed distribution of species' abundances would be expected to fit a lognormal distribution (May 1975). For a large number of species in the association one might expect that many variables would act to control their abundances. Therefore the lognormal distribution is the obvious first choice to fit to sample data.

If the abundances of species in an association are not independent of one another, and are controlled by a few variables only, then the lognormal will not provide a good fit to the data.

The observed species' abundances may be less evenly or more evenly distributed than predicted by the lognormal distribution. In the first case the observed distribution will be close to a log-series distribution, and in the second case the observed distribution will approximate a broken-stick distribution.

The models of resource partitioning from which these distributions were derived are not testable (Boswell and Patil 1971; Pielou 1975) so that no conclusions about the sharing of resources between the species can be drawn from the fit of sample data to one of these distributions. Nevertheless the broken-stick or log series distributions may provide good descriptions of the data. The fit of a log series distribution to sample data may be assessed visually. If the species are ranked in order of decreasing abundance, then a plot of the logarithm of species' abundance against the rank of the species will be nearly linear for a log series distribution (Whittaker 1972).

A partial description of the distribution of species' abundances in an association can be provided by calculating an index of species diversity. These indices depend on both "species richness" - the number of species in the association, and "evenness" - how evenly abundance is distributed between the species. However these two aspects of diversity cannot be estimated separately when the total number of species in an association is not known (Pielou 1975).

The number of species in a sample of an association of species will depend on the size of the sample. In many vegetation studies a particular relationship between the area of the sample and the number of species in it is assumed. Using the assumed relationship an index may be calculated which describes the rate at which species are added as the sample area is increased. Such indices are called indices of species richness (Peet 1974) although they depend on both the number of species in the association and their relative abundances, and are thus in fact species diversity indices.

For many studies of vegetation the relation $S = CA^k$, where S is the number of species in the sample, A is the area of the sample, and C and k are constants to be estimated, provides a good empirical fit to the data (Kilburn 1966). May (1975) has derived a theoretical basis for this relationship assuming a lognormal distribution of actual abundances in the association (as opposed to the sample collection). To derive the relationship May also assumes that $J \propto A$ where A is the area of the sample, and J is the ratio of the total abundance of all species to that of the rarest species. This assumption is valid for my samples. May comments that the assumption is likely to hold only if the samples can be considered as islands in some sense. This seems reasonable for my samples of sessile organisms on settlement panels.

The assumed relationship may be expressed as $\log(S) = k \log(A) + \log C$, so that a regression of log (S) against log (A) will give estimates of k (the slope) and log C (the intercept). Kilburn (1966) discusses the interpretation of the constants. C is the predicted number of species in a unit area, and is thus a measure of "species density". The constant k is a measure of how rapidly species are added as the sample area is increased, and thus is called an index of species richness.

A different relationship between the number of species in the sample and the area of the sample should be assumed if the samples must be regarded as random samples from a homogeneous mixture of species (May 1975). In this case the relationship $S = k' \log (A)$, where the symbols have the same meanings as before, should provide a better fit to the data. In the present study this relationship would be appropriate if the number of species were compared with the total area covered by all the species. It does, in fact, provide a good description of such data, and the results obtained are similar to those described in Chapter 7 where the relationship $S = CA^k$ is used.

Animal ecologists frequently use the Shannon-Weiner index of diversity (Shannon and Weaver 1949), $H' = - \sum pi \log pi$, where pi is the proportion of the ith species in the association. This index is usually based on the numbers of individuals of each species sampled, but as Pielou (1975) has pointed out, for encrusting organisms the area covered by a species is appropriate as a measure of abundance. Pielou (1966) has provided a method which yields an unbiased estimate of H' from a series of samples, and also the standard error of this estimate.

The Shannon-Weiner index H' and the index of species richness measure somewhat different aspects of the distribution of species' abundances in an association, and I have therefore calculated both. The methods used to calculate the indices are described in appendices 7C and 7D.

APPENDIX 7B

Fitting lognormal distributions to collections obtained from samples.

I attempted to fit lognormal distributions to the data from the samples using the method described by Pielou (1975). The choice of the lognormal distribution is discussed in appendix 7A. A lognormal distribution was not fitted where the mode of the observed distribution was at the origin. In these cases the fitted curve may provide a poor estimate of the true distribution (Edden 1971). Thus lognormal distributions were not fitted to the observed distribution of numbers of individuals between species at site 2 (Figure 7:03A and B).

Table A7:1 shows the parameters of the lognornal distributions fitted to the sample data shown in Figures 7:01A, 7:02A, and 7:02B. A chi-squared test was used to judge the fit of the theoretical distributions to the data. For a good fit the chi-squared statistic will be associated with a high probability. I chose $p = 0.25$ as a criterion for a good fit.

The results of the chi-squared tests are shown in Tables A7:2, A7:3, and A7:4. In no case did a lognormal distribution provide a good fit to the data.

There are too few species in the sample collection from uncaged surfaces at site 1 to allow a test of the fit of the lognormal distribution. Instead the observed distribution of abundances was assessed graphically. The species were first ranked from the most abundant to the least abundant species. The logarithm of the abundance of each species was then plotted against its rank, as shown in Figure A7:1. If the species' abundances conformed with a lognormal distribution then the graph should resemble an S on one side (). A logseries distribution of species' abundances would be represented by a straight line, as discussed in appendix 7A.

Figure A7:1 also shows the abundances of species on caged samples at site 1 for comparison. The line for the uncaged sample collection is much less strongly curved than the line for the collection from caged samples. This shows that the distribution of species' abundances on uncaged samples is very uneven, so that the distribution is close to a log-series distribution.

TABLE A7:1

THE MEAN AND VARIANCE OF THE NORMAL DISTRIBUTIONS FITTED TO THE LOGARITHM OF THE ABUNDANCES OF SPECIES IN THE SAMPLES.*

Samples	Mean	Variance
Site 1: Caged samples	1.433	1.042
Site 1: Uncaged samples	0.714	2.497
Site 2: Caged samples	1.416	1.530
Site 2: Uncaged samples	1.180	1.339

*Species' abundances were measured by the area covered by each species, in mm^2; and logs to base 10 were used.

TABLE A7:2

CHI-SQUARED TEST OF THE FIT OF A LOGNORMAL DISTRIBUTION TO THE OBSERVED ABUNDANCES OF SPECIES ON CAGED SAMPLES AT SITE 1.

Range of Abundances as Logarithms to the Base e	Observed Frequency	Expected Frequency
1 *	4	8.5446
1 - 2	13	9.1585
2 - 3	8	11.5348
3 - 4	17	12.1054
4 - 5	6	10.7114
5 - 6	10	7.8945
6	9	9.0508

*The smallest abundance detected was 0.5 mm^2. The expected frequency was therefore calculated from this point.

χ^2 with 4 degrees of freedom = 9.7248; $p < 0.05$

TABLE A7:3

CHI-SQUARED TEST OF THE FIT OF A LOGNORMAL DISTRIBUTION TO THE OBSERVED ABUNDANCES OF SPECIES ON CAGED SAMPLES AT SITE 2.

Range of Abundances as Logarithms to the Base e	Observed Frequency	Expected Frequency
1 *	19	20.705
1 - 2	25	18.255
2 - 3	14	21.274
3 - 4	12	21.954
4 - 5	23	20.041
5 - 6	23	16.217
6 - 7	7	11.601
7 - 8	9	7.365
8	9	7.587

*The smallest abundance detected was 0.5 mm^2. The expected frequency was therefore calculated from this point.

χ^2 with 6 degrees of freedom = 15.358; $p < 0.05$.

TABLE A7:4

CHI-SQUARED TEST OF THE FIT OF A LOGNORMAL DISTRIBUTION TO THE OBSERVED ABUNDANCES OF SPECIES ON UNCAGED SAMPLES AT SITE 2.

Range of Abundances as Logarithms to Base e	Observed Frequency	Expected Frequency
1[*]	18.5	22.869
1 - 2	17	19.242
2 - 3	23	20.589
3 - 4	12	21.149
4 - 5	20	17.091
5 - 6	16	12.446
6 - 7	9	7.886
7	11	7.728

[*] The smallest abundance detected was 0.5 mm^2. The expected frequency was therefore calculated from this point.

χ^2 with 5 degrees of freedom = 8.389; $0.25 > p > 0.10$

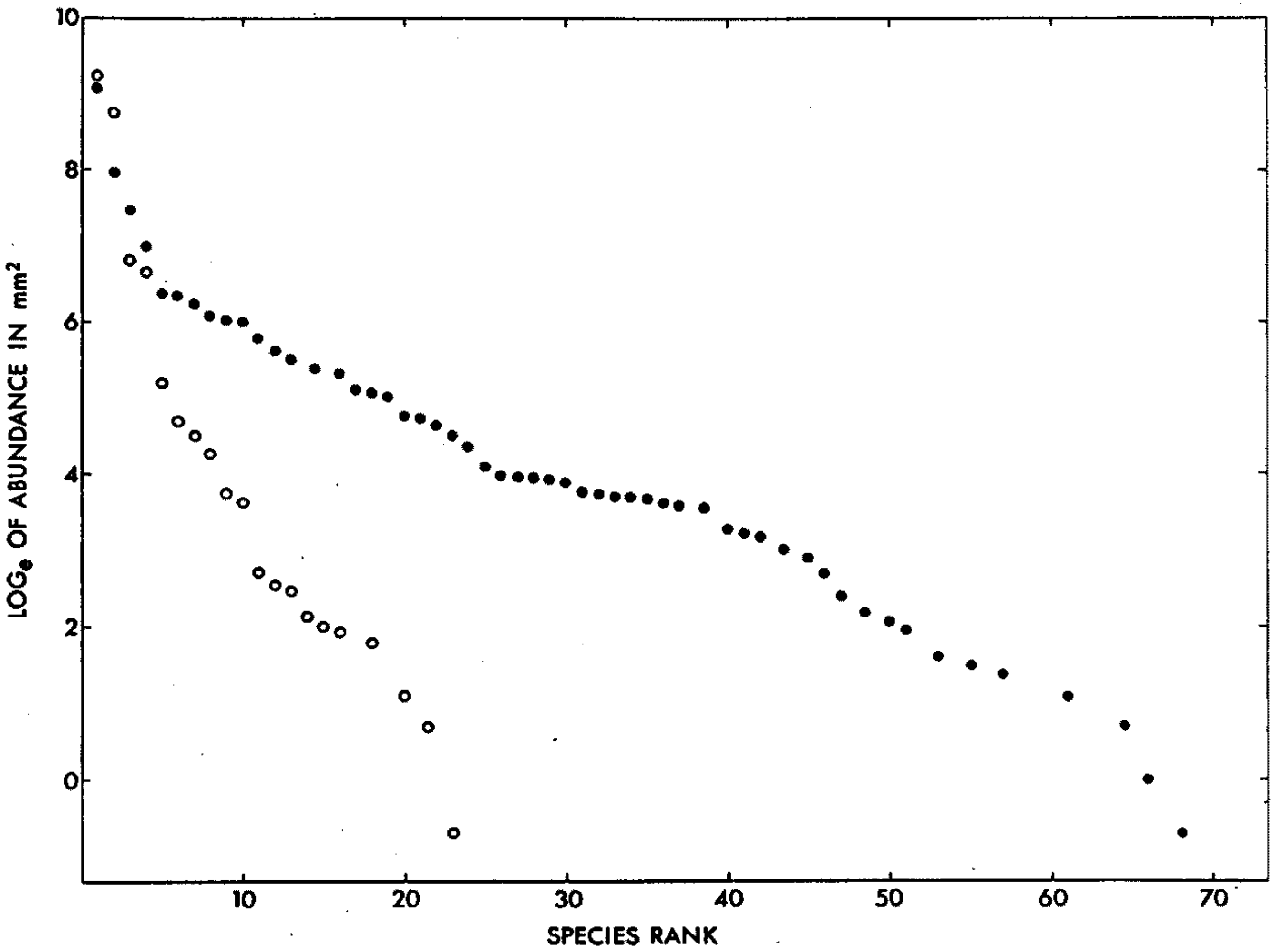
FIGURE A7:1

PLOTS OF ABUNDANCE AGAINST SPECIES' RANK FOR SITE 1

The logarithm of the abundance of each species is plotted against the rank of that species where the species are ranked in order of decreasing abundance.

● : Caged samples

o : Uncaged samples.


10
8
6
4
2
0
LOG$_e$ OF ABUNDANCE IN mm^2
10
20
30
40
50
60
70
SPECIES RANK

APPENDIX 7C.

The methods used to calculate the constants of the assumed relationship $S = CA^k$ between S, the number of species in a sample, and A, the area of the sample.

There were four sets of samples as two sites and two caging treatments were investigated. Each set of samples was considered separately. The samples were first arranged in a random order, and the number of species in the first sample counted. The second sample was then added to the first, and the number of species in the pooled sample counted. Further samples were added until all the samples had been added together.

Three random orderings were used for each set of samples, so that three estimates were obtained of the number of species in each size of sample. Figures 7:04 and 7:06 (Chapter 7) show the average number of species in each size of sample.

Regressions of the logarithm of the number of species in a sample against the logarithm of the sample area were used to estimate the constants C and k in the assumed relationship $S = CA^k$, where S is the number of species in a sample, and A is the sample area. The regression equation has the form:
$\mathrm{Log}_e S = \mathrm{Log}_e C + k \log_e A$.

To compare the constants C and k between sites and caging treatments I used a multiple regression technique. Dummy variables were used as shown in Draper and Smith (1966) to represent the effects of sites, caging treatments, and the interaction of these effects. The regression model and the values and interpretation of the dummy variables are shown in Table A7:5.

TABLE A7:5

THE REGRESSION MODEL FOR A MULTIPLE REGRESSION ANALYSIS OF THE RELATIONSHIP BETWEEN NUMBER OF SPECIES AND AREA OF SAMPLE; AND THE INTERPRETATION AND VALUES OF THE DUMMY VARIABLES USED.

Regression model

$$\text{Log}_e (S) = a+\beta_0 \text{Log}_e (A) + \beta_1 D1+\beta_2+D2+\beta_3 D3+\beta_4+D_4+\beta_5 D_5+\beta_6 D_6$$

where: S is the number of species in a sample

A is the area of the sample in mm^2

a is the intercept constant of the regression

β_i are regression constants for each of the variables

D1 etc are dummy variables.

Interpretation of dummy variables.

β_1D1 is the change in the regression intercept between sites.

β_2D2 is the change in the regression intercept between caging treatments.

β_3D3 is the change in intercept as a result of the interaction of the effects of site and caging treatment.

β_4D4, β_5D5, β_6D6 are corresponding changes in the slope of the regression.

Values of dummy variables

Dummy variables:	D1	D2	D3	D4	D5	D6
Samples from:						
Site 1, Caged surfaces	0	0	0	0	0	0
Site 2, Caged surfaces	1	0	0	Log_e(A)	0	0
Site 1, Uncaged surfaces	0	1	0	0	Log_e(A)	0
Site 2, Uncaged surfaces	1	1	1	Log_e(A)	Log_e(A)	Log_e(A)

The samples which were added together as described above were drawn from a number of settlement panels. I assumed in carrying out the procedure described that there were no differences between the faunas of different settlement surfaces other than those due to sampling variation. There are two lines of support for this assumption: (1) I have shown in section 3:4 that the faunas of samples from different large surfaces are as similar to one another as the faunas of samples from the same surface. (2) I have used the large surfaces at site 2 to determine how many species there are in successively larger samples from the same surface. The relationship between number of species and area of sample obtained for single surfaces was compared with the relationship based on a number of surfaces, and the differences are small. The analysis is described below.

Four regressions of the logarithm of the number of species against the logarithm of the sample area were carried out, using data from site 2. For the first regression adjacent $50cm^2$ samples on the same caged surface were added together to form larger and larger samples, and the number of species in each size of sample was recorded. As there were four caged large surfaces there were four replicates for this regression. For the second regression eight $50cm^2$ samples selected at random from all the caged surfaces were added together one by one. Four such sets of eight samples were used so as to obtain four replicates for this regression. For the third and fourth regressions samples from the uncaged settlement surfaces were used rather than the caged surfaces.

The constants of the equation $S = CA^k$ as estimated by the four regressions are shown in Table A7:6. The two regres-

TABLE A7:6

THE CONSTANTS ESTIMATED BY FOUR REGRESSIONS OF LOG (NUMBER OF SPECIES) AGAINST LOG (AREA OF SAMPLE).

Regression*	k	Log_e C
Caged Samples:		
Regression 1	0.397	2.038
Regression 2	0.415	2.017
Uncaged Samples:		
Regression 3	0.529	1.133
Regression 4	0.580	0.911

*The type of data used for each regression is explained in the text.

sions for caged samples are not based on independent sets of data, nor are the regressions for uncaged samples. Therefore no formal test of the differences between the constants for regressions 1 and 2, or 3 and 4 can be made. However the estimated constants for regression 1 are not very different from those for regression 2, and the constants for regressions 3 and 4 are also very similar to one another.

APPENDIX 7D

The calculation of the Shannon-Weiner diversity index.

The Shannon-Weiner diversity index H' (Shannon and Weaver 1949) is defined by $H' = -\sum p_i \log p_i$ where p_i is the proportion of the ith species in an association of species, and the sum is taken over all the species in the association. The units of H' depend on the base of the logarithms used. I have used natural logarithms throughout.

Unfortunately in most cases the number of species, and the proportions of each species in the association are not known. Using the proportions of species in a sample to estimate their proportions in the association produces a biased estimate of H' (Pielou 1966). Pielou has proposed a method to circumvent this problem, whereby a set of independent small samples are used to estimate H' and its standard error. This is the method used here.

The samples were arranged and added together one by one as described for the species-area relationship (Appendix 7C). In this case the Brillouin index of diversity (Brillouin 1962) and the combined abundance of all species were calculated for the pooled sample after each new sample had been added. This procedure was repeated five times for each set of samples, using different random orders of the samples. In each case the values of the Brillouin index were plotted against the number of samples added together, and the point where the plotted line became effectively horizontal was estimated by eye. Figures A7:2, A7:3, and A7:4 show examples with the estimated points indicated by arrows.

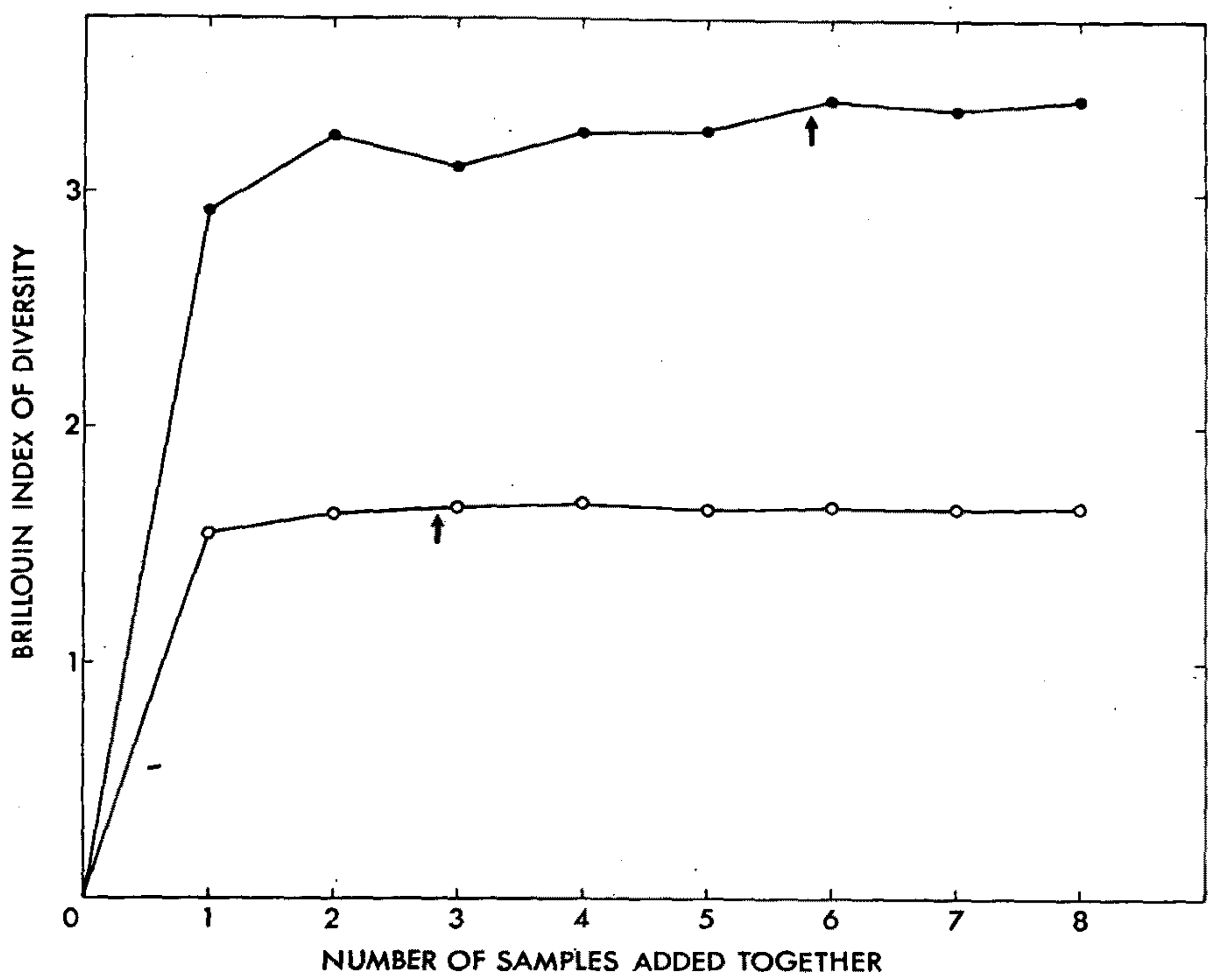
FIGURE A7:2

Brillouin indices of diversity for pooled samples from site 1, plotted against the number of small samples added together. Samples from 25 cm^2 areas on settlement panels were added together in five random orders. Typical results are shown.

● Caged samples

o Uncaged samples

↑ Points, estimated by eye, where the series of data points becomes effectively horizontal.


BRILLOUIN INDEX OF DIVERSITY
0
1
2
3
0
1
2
3
4
5
6
7
8
NUMBER OF SAMPLES ADDED TOGETHER

FIGURES A7:3 AND A7:4

Brillouin indices of diversity for pooled samples from site 2, plotted against the number of small samples added together. Samples from 50 cm^2 areas on settlement panels were added together in five random orders. Typical results are shown.

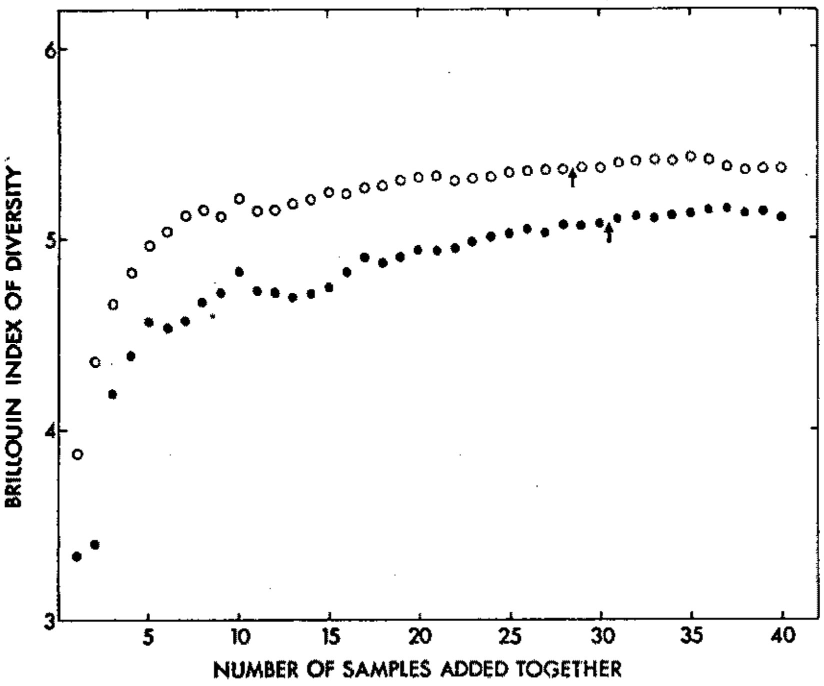
Figure A7:3: The abundance of each species was measured by the number of individuals of each species, and the Brillouin indices were calculated from these data.

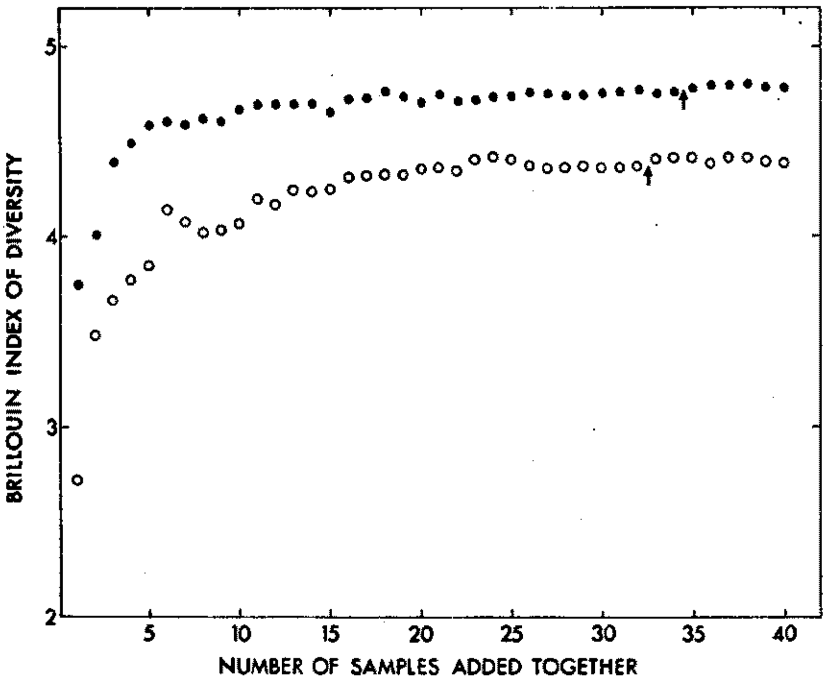
Figure A7:4: The abundance of each species was measured by the area covered by that species.

● Caged samples

○ Uncaged samples

↑ Points, estimated by eye, where the series of data points becomes effectively horizontal.


BRILLOUIN INDEX OF DIVERSITY
3
4
5
6
5
10
15
20
25
30
35
40
NUMBER OF SAMPLES ADDED TOGETHER


BRILLOUIN INDEX OF DIVERSITY
2
3
4
5
5
10
15
20
25
30
35
40
NUMBER OF SAMPLES ADDED TOGETHER

The values of the Brillouin index beyond the estimated points on each graph were used, together with the corresponding abundances of all species combined, to calculate a number of estimates of H' as shown in Table A7:7. As the plotted values of the Brillouin index may become horizontal at a different point on each graph, each random order of the samples may lead to a different number of estimates of H'. The mean and standard error of the estimates from each random order were calculated, and following Lloyd, Inger and King (1968), I used the median value of the means as the definitive estimate of H' for a set of samples.

Pielou (1966) recommends that a test of serial correlation be used on the estimates of H' obtained from each ordering of the samples. I did not obtain a sufficient number of estimates from most random orders for such tests, but where possible, I used 'one sample runs tests' (Siegel 1956). An example of the calculations used in these tests is shown in Table A7:8.

An analysis of variance was used to compare the values of H' between sites and caging treatments. I chose at random one particular ordering of each set of samples, and I used the estimates of H' obtained from this ordering in the analysis. An analysis of weighted means (Snedecor and Cochran 1967) was necessary because a different number of estimates of H' was obtained from each ordering used.

TABLE A7:7

ESTIMATING THE SHANNON-WEINER INDEX OF DIVERSITY FOR THE FAUNA OF CAGED SURFACES AT SITE 2.

Formula: $H'_k = \dfrac{(B_k \cdot T_k)-(B_{k-1} \cdot T_{k-1})}{T_k - T_{k-1}}$

where: H'_k = Shannon-Weiner diversity index for k pooled samples.

B_k = Brillouin index for k pooled samples.

T_k = Total abundance of all species in k pooled samples.

and $k > k^*$, the number of pooled samples beyond which there is no upward trend in the values of B_k.

Sequence of Brillouin Indices (B_k)	Total Abundance of. Species (T_k)*	Calculated Shannon-Weiner Index (H'_k)
5.1009	1482	-
5.1418	1547	6.0743
5.1558	1579	5.8326
5.1202	1682	4.5744
5.0870	1800	4.6138
5.0917	1874	5.2060
5.1033	1889	6.5525
5.0854	1970	4.6680
5.0950	2042	5.3577
5.1129	2098	5.7656
5.1223	2162	5.4304
5.1373	2204	5.9094
5.1651	2280	5.9713
5.1317	2380	4.3702
5.0926	2458	3.8995
5.0824	2503	4.5252
5.0976	2562	5.7424
5.1305	2652	6.0671
5.1408	2698	5.7346
5.1095	2822	4.4285
5.1160	2915	5.3132
5.1007	3016	4.6591

Mean Value of H'_k = 5.271 Standard Error: 0.158

* Abundances were measured by the number of individuals of each species.

TABLE A7:8

EXAMPLE OF ONE SAMPLE RUNS TESTS ON A SERIES OF ESTIMATES OF THE SHANNON-WEINER DIVERSITY INDEX, USING THE ESTIMATES SHOWN IN TABLE A7:7.

1. Runs above and below the median estimate

Median estimate (see Table A7:7) = 5.3577

Estimates greater than the median are assigned a +, and estimates less than the median are assigned a -

The series of estimates of H'_k is therefore denoted:

$+ +, ---,+,-,++++,---,+++,---$

Number of estimates above median = 10

Number of estimates below median = 10

Number of runs = 8 (Runs are separated by commas in the sequence above).

Tables F_I and F_{II} in Siegel (1956) show that the number of runs is not significant at $p = 0.05$.

2. Runs up or down

Estimates larger than the previous estimate are assigned a +, and estimates smaller than the previous one a -,

The series of estimates of H'_k is therefore denoted:

$--,+++,-,++,-,++,--,+++,--,+,-$

Number of + : 10

Number of - : 9

Number of runs: 11

This result is not significant at $p = 0.05$ (Tables F_I,F_{II}, Siegel 1956).

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