Spatial and Temporal Patterns of Coral Recruitment Following a Severe Bleaching Event in the Maldives

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ABSTRACT

Reef recovery processes were investigated at shallow depths (between 5 and 10 m) within two geographically distinct atolls in the Maldives archipelago from February 2000 to July 2002. Artificial settlement plates were used to determine potential availability of coral spat on settlement plates and repeat censuses of small (0.25 m^2) permanently marked quadrats were used to investigate spatial and temporal recruitment patterns over a period of two and half years. The number of spat settling on the settlement plates after approximately 8 and 12 months submergence was low, and densities ranged from 2.5 to 4.27 spat/m^2. There was no difference in spat density between cryptic and exposed surfaces however, there were significant differences between sites (Kruskal-Wallis, $p=0.02$ and $p<0.001$ for 8 months and 12 months respectively). The dominant coral settling on the plates was *Pavona* spp., which accounted for over 34% of the total. Recruit densities and size frequency distributions for one site in Malé atoll were consistent between years. Density of recruits was high ranging from 30 to 49/m^2 and did not differ between years. The survivorship of recruits between each census was high (>80%) and this combined with a consistent supply of new recruits meant that recruit turnover was low. The most common genus in the recruit and juvenile populations was *Pavona* spp., a finding consistent with the adult population. Whilst density and size frequency data confirm that reef recovery processes are well underway the population at Feydhoo fonolhu is still dominated by one genus, *Pavona* spp. indicating that the coral community structure may take several decades to recover to the pre-bleaching level.

Recovery of branching corals belonging to Acroporidae and Pocilloporidae appears to be limited by the impoverished adult population. Based on our observations to date, we conclude that longer time-scales are required to determine whether the temporal patterns demonstrated in this study are typical or whether there are occasionally years with a high or low influx of new recruits.

INTRODUCTION

Coral reefs in the Maldives were severely impacted by the 1998 coral bleaching event, with subsequent bleaching-induced mortality reducing coral cover from about 42% to 2% (Zahir, 2000). In cases where coral mortality is severe reef recovery is largely dependent upon factors that influence coral settlement and recruitment. However, the survival of fragments and asexual reproduction can be important in some systems (Pearson, 1981). Various studies have demonstrated that coral recruitment in open systems is highly variable in space and time (Smith, 1992; Connell *et al.*, 1997; Hughes *et al.*, 1999) indicating the need for studies on recovery processes at several scales. There have been several studies on patterns of coral recruitment in the Atlantic and Pacific reefs but there are few published studies on coral recruitment in the Maldives or Indian Ocean in general. A study on coral recruitment patterns on artificial reef structures at a shallow reef-flat site (<2 m) in North Malé atoll found an average of 12.6 recruits/m^2 between 1991 and 1994 (Clark & Edwards, 1999). The community was dominated by acroporids and pocilliporids with few massive corals (<2%) present. However, a survey on the same structures, conducted 11 months after the bleaching event, established that recruit densities varied from 0.6 to 2.8 recruits/m^2 and the overall ratio of branching to massive corals was 69:33, which represents a shift in the taxonomic patterns compared to the pre-bleaching coral community. It was concluded that despite the severity of the bleaching-induced mortality there were viable supplies of coral larvae from upstream or deeper reefs to recolonise the degraded reefs.

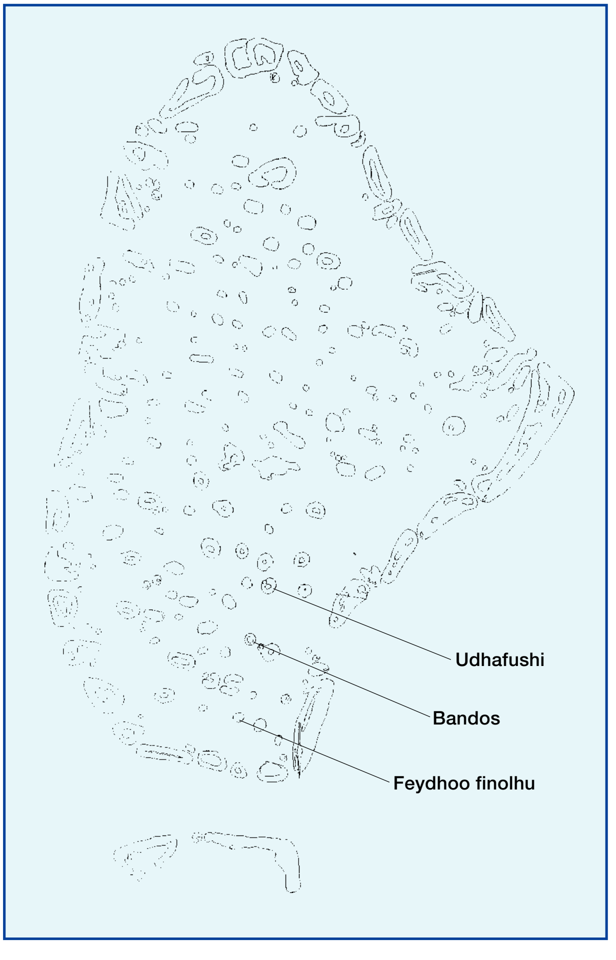

Figure 1. The three sites in North Male Atoll: Bandos island reef, Udhafushi reef and Feydhoo finolhu reef.

In 1999, an investigation funded by the CORDIO programme was initiated to determine the spatial and temporal patterns of coral settlement and recruitment at six reefs within two central atolls, North Malé atoll and Vaavu atoll. Integrated studies combined the use of ceramic tiles to investigate the potential availability of coral spat on settlement plates with in-situ studies of recruitment to the natural reef. In February 2000 a preliminary assessment on coral recruitment (approximately 21 months after the bleaching event) at Feydhoo finolhu in Malé atoll found that recruit density ranged between 19–26 individuals/m^2 at 10 and 5 m respectively (Clark, 2000) suggesting that recovery is not recruitment limited. This report presents the results of the research and monitoring that has been continued from the preliminary studies. The aims of this study were to:

- determine the spatial and temporal patterns of coral spat settlement and recruitment;
- investigate the relationship between availability of larvae and in-situ recruitment;
- determine sucessional processes of sessile communities to natural and artificial substrates.

MATERIALS AND METHODS

Sites

A hierarchical sampling design was adopted with 3 random sites (reefs) within each location (atoll) nested within two geographically distant atolls (70–80 Kms). Three sites were selected in North Male Atoll (Fig. 1): Bandos island reef, Udhafushi reef and Feydhoo finolhu reef. An additional three sites were selected in Vaavu atoll (Fig. 2): Wattaru reef, Kuda Ambaraa reef and Foththeyo reef. These sites are also part of a long-term reef monitoring study using line intercept transects to document spatial and temporal changes in benthic communities since the bleaching in 1998.

Figure 2. The three sites in Vaavu atoll: Wattaru reef, Kuda Ambaraa reef and Foththeyo reef.

Coral Spat Settlement

To investigate potential larval availability artificial settlement tiles were deployed directly onto the reef and exposed for periods between 160 and 395 days. An overlapping design was adopted so that tiles with suitably conditioned surfaces were always available. Deployment and retrieval dates for both atolls are shown in Table 1 (next page). Ceramic bathroom tiles were selected because they are locally available and cheap and have been shown to be a suitable surface for coral spat settlement (Harriot & Fisk, 1987). The tiles were 20 cm x 20 cm and 5 mm thick and had a central hole drilled to facilitate attachment to the reef. For each pair of tiles a cryptic push-mount plug was fixed into a solid section of the reef framework, and each tile pair was attached directly to the mount using two plastic cable ties. This method of attachment allowed tiles to be fixed in various orientations, facilitated the removal of tiles and has been shown to be very robust (Mundy, 2000). Twenty pairs of tiles (with the unglazed surfaces facing out) were deployed at each site, within the upper reef-slope between 5–10 m depth. After retrieval from the field, a point count method was used to determine the benthic sessile community on the tiles. Tiles were then bleached and examined microscopically for the presence of coral spat.

Coral Recruitment

Coral recruitment was assessed using small permanently marked quadrats 50 x 50 cm (0.25 m^2) on hard substrates at 2 depths (5 m and 10 m) on the upper reef slope. The quadrats were divided into twenty-five grid squares, each 5 x 5 cm, to enable observers to closely scrutinise the reef surface for recruits and small juveniles. Care was taken to distinguish between recently settled recruits (with intact

Table 1. The sampling protocol for the investigation of coral spat settlement using an overlapping design. Settlement tiles were deployed and retrieved between December 1999 and April 2001 at three sites within two atolls (Male and Vaavu atoll)

	Deployment date	Retrieval date	No. days	No. months
Male atoll				
Feydhoo finolhu				
Sample 1	07-Dec-99	Apr-00	137	5
Sample 2	07-Dec-99	Aug-00	245	8
Sample 3	Apr-00	Mar-01	331	11
Bandos				
Sample 1	13-Dec-99	12-Apr-00	121	4
Sample 2	13-Dec-99	11-Sep-00	273	9
Sample 3	21-Mar-01	Mar-01	343	11
Udhafushi				
Sample 1	12-Dec-99	10-Apr-00	120	4
Sample 2	12-Dec-99	13-Sep-00	276	9
Sample 3	Apr-00	Mar-01	349	12
Vaavu atoll				
Ambaraa				
Sample 1	09-Mar-00	16-Aug-00	160	5
Sample 2	09-Mar-00	Apr-01	392	13
Wattaru				
Sample 1	10-Mar-00	Aug-00	160	5
Sample 2	10-Mar-00	04-Apr-01	390	13

margins) and small colonies as a result of partial mortality or fragmentation. Here we define a recruit as an individual coral colony that can be detected by visual inspection and which has a maximum colony diameter of 50 mm. Each individual colony was given a unique identification code and its' position within the quadrat grid noted to determine recruit turnover in terms of survivorship, mortality, losses and new stock. Quadrats were resurveyed as part of a repeated measures design after 6, 13, 19, 24, 27 and 30 months. Detailed information on the status of individual colonies (i.e. partial mortality, fragmentation, overgrowth by algae) was recorded. Individual colony sizes (maximum and minimum colony diameter) were measured to nearest millimetre using vernier callipers.

RESULTS

Coral spat settlement on artificial settlement plates

Overall densities of coral spat on settlement plates were very low (ranging from 0.1 to 1.71 spat/0.04 m^2) at all sites after approximately 8 and 12 months deployment (Fig. 3). There was no significant difference in spat density between the two sampling periods (Kruskall-Wallis test H=0.66, p=0.417) but there was however, a significant difference in spat densities between sites after eight months (Kruskall-Wallis test H=11.34, p=0.023) and 12 months (Kruskall-Wallis test H=21.6, p=<0.001). This suggests that larval settlement is patchy between reefs. Overall there was no significant difference in spat settlement on cryptic or exposed surfaces after eight months

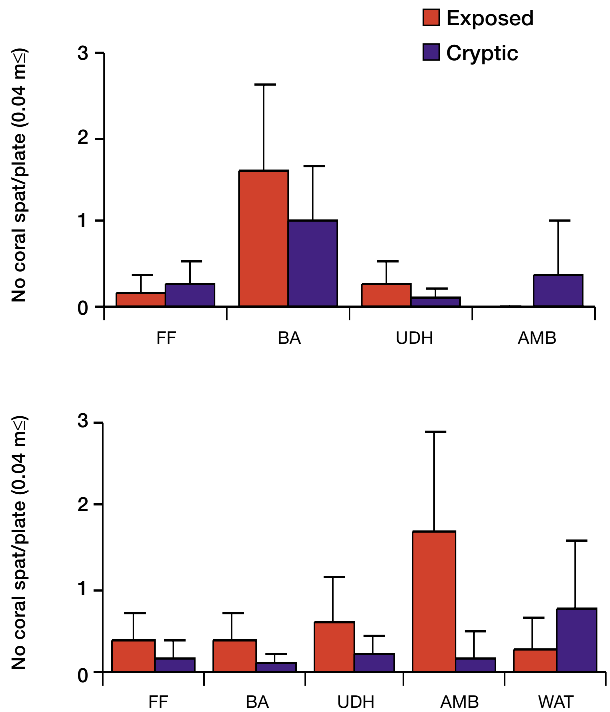

Figure 3. Mean density of coral spat on the settlement plates for plates collected after a) approx. 8 months and b) approx.12 months. Site codes: FF = Feydhoo finolhu; BA = Bandos; UDH = Udhafushi; AMB = Ambaraa and WAT = Wattaru. (Error bars are 95% CI).

(Kruskal-Wallis test H=1.63, p=0.202) or twelve months (Kruskal-Wallis test H=0.34, p=561). Taxonomic patterns were consistent on all plates. Dominant corals identified to generic level belonged to Agariciidae which accounted for over 34% of the total, however approximately 60% of the spat were too small to group taxonomically with certainty, thus a mixture of species may be represented.

Patterns of Succession and Community Structure on Artificial Surfaces

An initial pilot study demonstrated that a 60 random point sampling method was sufficient to represent all major benthic categories present on the artificial settlement tiles. The benthic communities on the tiles were classified according to nine major benthic categories and the percent cover of each group was determined. The data presented below is for one site – Feydhoo fonolhu. However, similar patterns were observed at all sites in Malé atoll.

The benthic communities that colonised the settlement plate surfaces after 126, 245 and 341 days of submergence are shown in Fig. 4 (next page) for two depths. After 126 days submergence the exposed surfaces were dominated by filamentous and turf algal groups (72% and 86% at 5 m and 10 m respectively). Algae was also the dominant group on the cryptic surfaces at both depths however, the percent cover was lower (46% at 5 m and 52% at 10 m) than that observed on the exposed surfaces. The second major benthic group on the cryptic surfaces was bryozoans but this group was virtually absent from exposed surfaces. Competition for space was so intense that there was virtually no bare space on either cryptic or exposed surfaces after 4 months of exposure for both depths.

After 265 days the percent cover of algae declined on all surfaces and at both depths, although it was still the dominant group on exposed surfaces (47% at 5 m and 49% at 10 m). Conversely, the cryptic surfaces were dominated by bryozoans (52% at 5 m and 35% at 10 m). Bryozoan diversity appeared to be high but taxonomic identification was not carried out for the purpose of the study. There was high variability in the percent cover of crustose coralline algae on both surfaces and at both depths. However, there was an overall increase in cover with increased submergence. Other invertebrates such as molluscs and polychaetes also increased in abundance on both surfaces with increased submergence. However, colonisation by colonial ascidians was more variable over all exposure periods and *Diademnum molle* was the dominant species present.

Data was pooled for sites and orientation to investigate temporal trends in community structure at the atoll level (Fig. 5). Overall similar trends in algal colonisation were observed in both atolls; the percent cover of algae was high initially but declined with increased exposure and at the same time the diversity of assemblages on the tiles increased. The major difference in the benthic com-

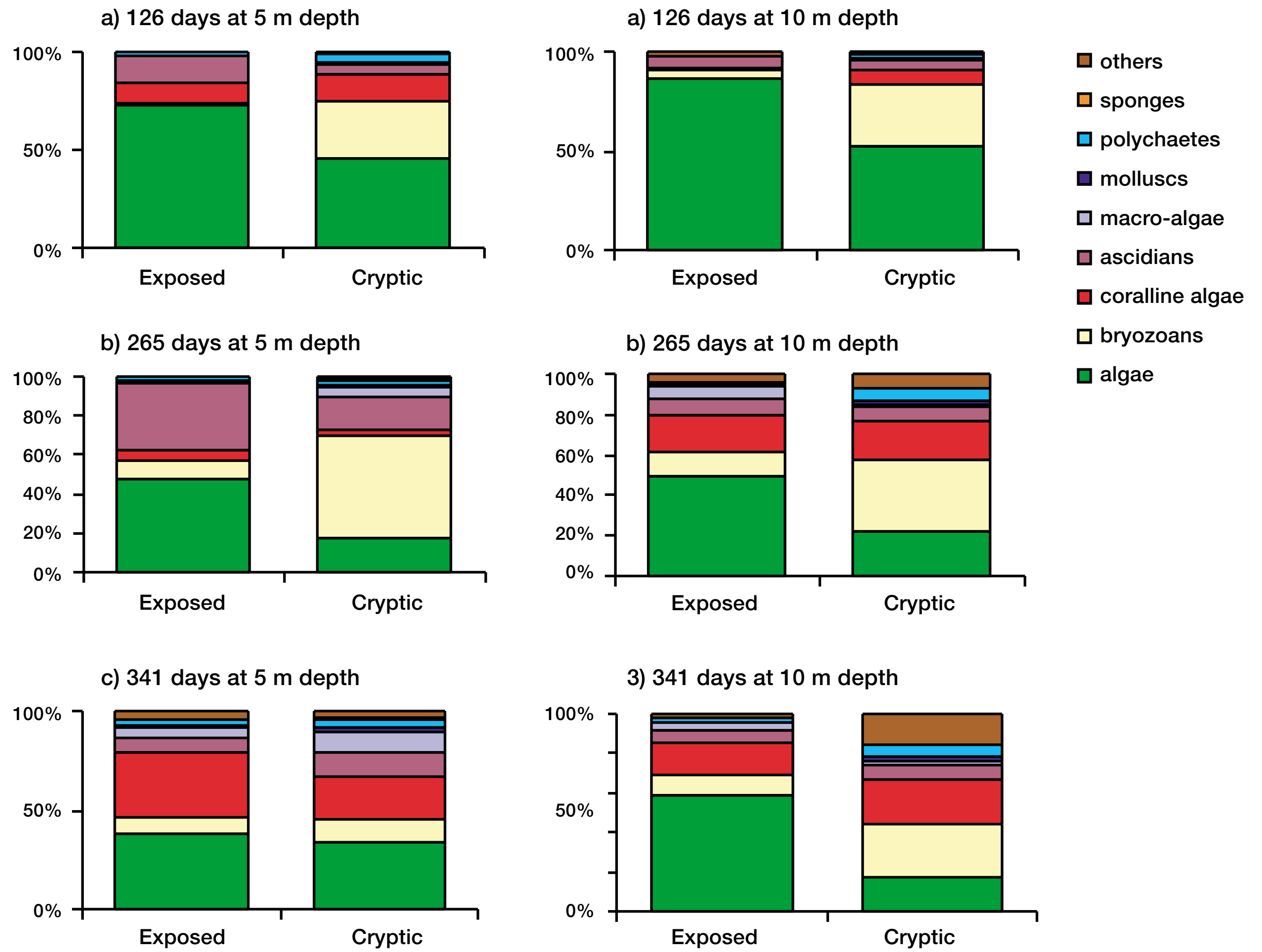

Figure 4. Benthic sessile communities developing on cryptic and exposed surfaces of settlement plates deployed at Feydhoo finolhu after 3 periods of submergence at 5 m and 10 m depth.

munities between the two atolls was the low colonisation of bryozoans in Vaavu atoll compared to Malé atoll. Further analysis will investigate the relationship between the benthic community structure on tile and spat settlement preferences.

Coral Recruitment

Data on coral recruitment has been collected for 6 sites over 7 sampling periods between February 2000 and July 2002. A database has been designed to facilitate the storage, manipulation and analysis of the data-set on coral recruitment. At this time a detailed analysis of temporal patterns in coral recruitment processes is only available for one site – Feydhoo finolhu. The remaining sites will be analysed in the next 3 months.

Overall densities of coral recruits (<50 mm) on the natural substrate within permanently marked quadrats were high for all sampling periods (Fig. 6a). Generally the highest densities of recruits within both reef zones were observed during the initial census in February

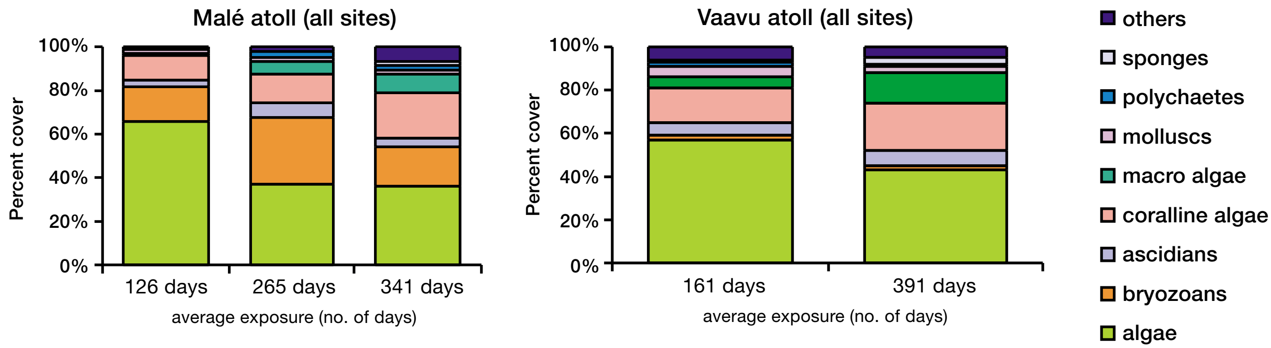

Figure 5. Temporal patterns in benthic communities developing on settlement plates in Malé and Vaavu atolls.

2000 (49.2 per m^2 at 10 m) with the lowest densities being recorded in September 2001 (30 per m^2 at 10 m). There was however, no significant difference in recruit densities with sampling periods within both reef zones (Kruskal-Wallis test; H=2.35, p=0.885 for 5 m and H=8.76, p=0.188 for 10 m). Similarly, pairwise comparisons indicated no differences in recruit density with depth at each census. Densities of juveniles colonies (>50 and <100 mm mean colony diameter) within the same quadrats were generally lower than recruit densities (Fig. 6b). There were no significant differences in juvenile densities with sampling periods for both reef zones however, pairwise comparisons (Mann Whitney – p<0.001) revealed that there were significantly more juveniles at 5 m than 10 m for February 2000 and August 2000.

Coral recruitment at all sites was dominated by colonies belonging to Agariciidae followed by Poritidae and Siderastreidae. The branching corals Acroporidae and Pocilloporidae were found in low densities at all sites suggesting that recovery will be slow, presumably due to the limited source of larvae.

Recruit Turnover

Survivorship of recruits and small juvenile corals within the permanent quadrats was high (>80%) and did not differ significantly over the six survey periods, between February 2000 and July 2002. The number of colonies missing (e.g. no evidence of skeletal remains) from the

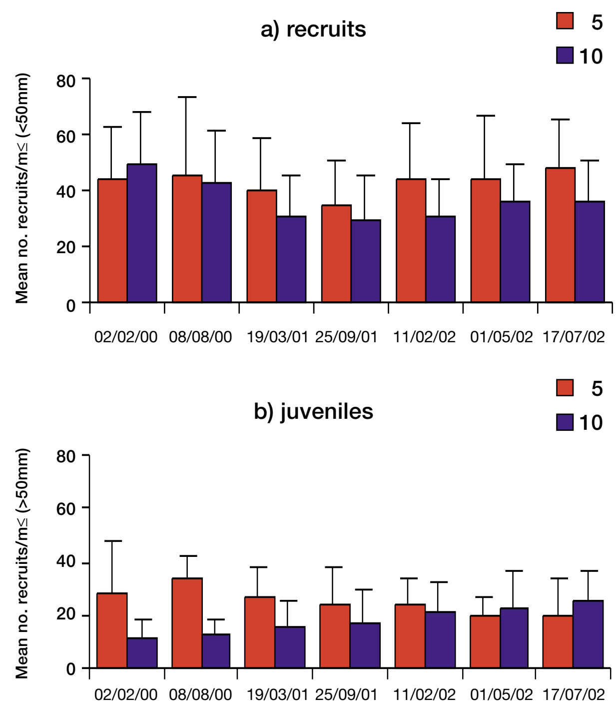

Figure 6. a) Densities of the mean number of coral recruits/m^2 (colonies < 50 mm mean diameter) at Feydhoo Finolhu. b) Densities of the mean number of coral juveniles/m^2 (colonies > 50 mm mean diameter) at Feydhoo Finolhu. (Error bars are 1 S.D.)

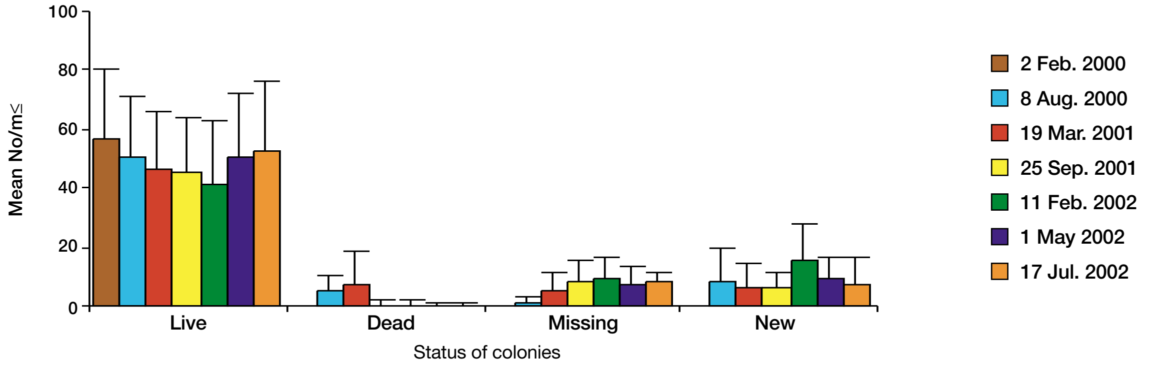

Figure 7. The status of coral recruits measured within small permanent quadrats between six census periods from February 2000 to July 2002 at Feydhoo finolhu. (Error bars are 1 S.D.)

Table 2. The abundance of coral colonies within 3 size classes measured in permanent quadrats between February 2000 and September 2001.

Date	Colony size (mm) <40	40–80	>80
Feb-00	40.4	8.4	0.9
Aug-00	46.2	8.7	1.6
Mar-01	48.4	10.4	1.1
Sep-01	52.0	13.3	1.8

sampling area was less that the numbers found dead (e.g. skeletal remains present) in the first two surveys, but this trend was reversed in the subsequent surveys (see Fig. 7). Overall losses (dead and missing) were low in all survey periods, and this low turnover combined with a high influx of new recruits meant that the final stock densities were equal or greater than the initial standing stock, indicating that the current potential for reef recovery in the Maldives is favourable.

Colony Size Frequency Distributions

The results of the colony size frequency distributions presented in Fig. 8 demonstrate that the coral population at Feydhoo finolhu had a truncated size distribution at the initial census (approx. 2 years after the 1998 bleaching event) with very few large colonies present. Although a similar pattern in size frequency distribution was observed in subsequent census periods there was a slight increase in the frequency of larger colonies over time (see Table 2).

Conclusions

The preliminary results have shown that there was high spatial variation in coral spat settlement on the artificial surfaces at the level of regional atolls. Such variation may have profound effects on the long-term recovery from the 1998 bleaching event, with some reefs displaying slower rates of recovery than others. There was however little taxonomic variability. The dominant taxonomic group of coral spat settlement belonged to the genus *Pavona*, which is consistent with the existing adult population on the reefs (see Zahir, this volume). The survey design (i.e. frequency of tile deployment and retrieval) was not sufficiently sensitive to detect any seasonal patterns in coral settlement thus a more intensive sampling programme has been initiated to collect data at bi-monthly intervals for three sites in Male atoll between 2001 and 2002.

Rapid colonisation of settlement plates by various algal groups (mainly turf and filamentous algae) and bryozoans may pre-empt space and limit the settlement of coral spat. The lack of bare space on tile surfaces after 4 months suggests that competition for space may have been a limiting factor in this study. As coral spat were observed on both cryptic and exposed surfaces there was

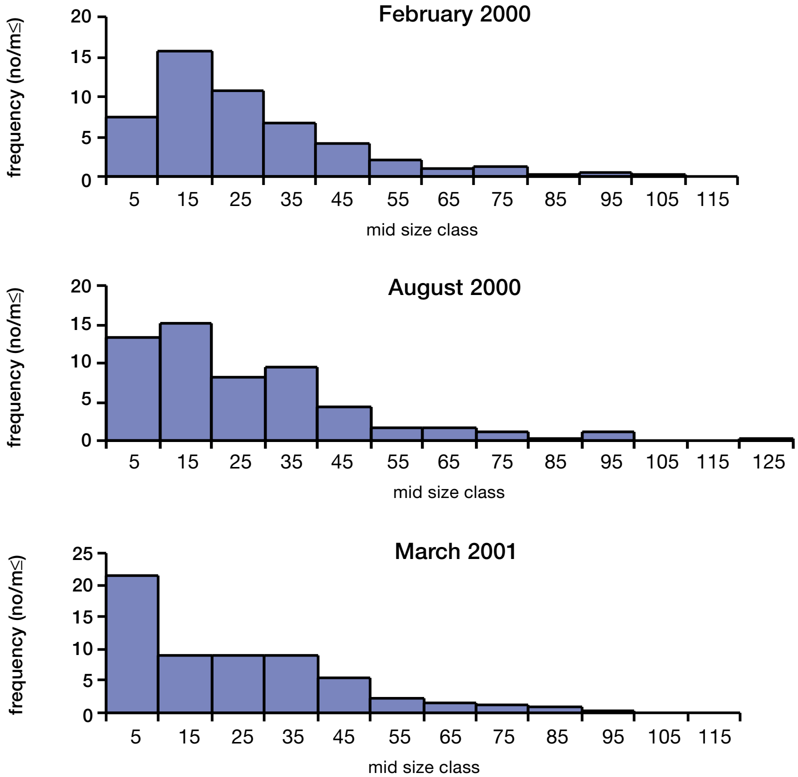

Figure 8. Size frequency distributions for all coral colonies recorded in the permanent quadrats at Feydhoo finolhu between February 2000 and March 2001.

no apparent relationship between the sessile benthic community developing on the settlement plates and spat settlement preferences.

The study of coral recruitment patterns at Feydhoo finolhu between April 2000 and July 2002 indicated that recruit densities were high overall (up to 49 individuals/m^2) and that there was very low variation in the densities of new recruits and small juveniles over the two and half year period. Further analysis of data collected for five additional sites will investigate spatial patterns in coral recruitment processes. Small individuals representing the new influx of recruits dominated the size frequency distribution of colony sizes. Such results are expected in a population that has suffered a major mortality event. Whilst density and size frequency data confirm that reef recovery processes are well underway the population at Feydhoo fonolhu is still dominated by one genus *Pavona* spp. indicating that diversity is low and that the coral community structure may take several decades to recover to the pre-bleaching level or may never recovery to its' former state.

Turnover of recruits in terms of mortality and loss versus new influx was consistently low at all sites and sampling periods The low level of turnover together with the high influx of new recruits meant that the recorded densities of recruits were equal or greater than initial standing stock indicating that the potential for reef recovery is high. However, longer time scales (e.g. a minimum of five years) would be required to determine whether the temporal patterns demonstrated in this study are typical or whether there are occasionally years with a high or low influx of new recruits. Provided post-recruitment mortalities are low (as indicated in this study) it is likely that coral populations will develop with a multitude of cohorts over the next 5–10 years and this in turn may result in higher recruitment.

Taxonomic patterns of spat settlement on artificial surfaces and natural recruitment are consistent with *Pavona* being the dominant genus in both studies. This also correlates with results of the long-term coral monitoring study (see Zahir, this volume), which show the most abundant adult colonies in reefs across several atolls are *Pavona spp*. Branching corals belonging to Acroporidae and Pocilloporidae, which were severely affected by the bleaching-induced mortality, were relatively low in abundance at all survey periods suggesting that the source and supply of larvae for these species are limited.

In the Chagos archipelago where bleaching-induced mortality was less severe than that observed in the Maldives (Sheppard, 1999) a recent study of new coral recruitment found average densities of juveniles was approximately 78 individuals/m^2 with twenty five coral genera observed and *Acropora* being the most dominant (Sheppard *et al.*, 2002). This included larger colony sizes than those typically measured in recruit studies however, after adjustment to represent smaller colonies (i.e. 20 mm) the levels of recruitment were still greater than those reported here for the Maldives. In the Seychelles a broad-scale assessment of 15 reefs found that recruitment was patchy and low, particularly for *Acropora* and *Pocillopora* (Turner *et al.*, 2000). Densities of small corals (2–15 cm) varied between 0.25 and 8 individuals/m^2 (converted from densities per 24 m^2 area for comparative purposes). Although the densities of recruits recorded in the Maldives were higher than those reported for the Seychelles the taxonomic patterns were very similar. These results indicate that recruitment processes throughout the Indian Ocean are very patchy and that a range of studies at several spatial and temporal scales are required to understand the mechanisms underlying the observed patterns.

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