Coral Reefs (1995) 14:201–213

Coral Reefs

Coral transplantation as an aid to reef rehabilitation: evaluation of a case study in the Maldive Islands

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Accepted: 27 June 1995

Abstract. As part of a study of reef rehabilitation, whole coral colonies (primarily *Acropora, Pocillopora, Porites, Favia* and *Favites*) were transplanted and cemented in place onto three approximately 20 m^2 areas of Armorflex concrete mats on a 0.8–1.5 m deep reef-flat in the Maldives which had been severely degraded by coral mining. Growth, in situ mortality, and losses from mats due to wave action of a total of 530 transplants were monitored over 28 months. Natural recruitment of corals to both the transplanted Armorflex areas and concrete mats without transplants was also studied. Overall survivorship of corals 28 months after transplantation was 51%. Most losses of transplants due to wave action occurred during the first 7 months when 25% were lost, with only a further 5% of colonies being lost subsequently. Within 16 months most colonies had accreted naturally to the concrete mats. Thirty-two percent of transplants which remained attached died with *Acropora hyacinthus* and *Pocillopora verrucosa* having the highest mortality rates (approx. 50% mortality over two years) and *Porites lobata* and *P. lutea* the lowest (2.8 and 8.1% mortality respectively over two years). Growth rates were very variable with a quarter to a third of transplants showing negative growth during each inter-survey period. *Acropora hyacinthus, A. cytherea* and *A. divaricata* transplants had the highest growth rates (colony mean linear radial extension 4.15–5.81 cm y^{-1}), followed by *Pocillopora verrucosa* (mean 2.51 cm y^{-1}). Faviids and poritids had lowest growth rates. *Favia* and *Favites* showed the poorest response to transplantation whilst *Acropora divaricata,* which combined a high growth rate with relatively low mortality, appeared particularly amenable to transplantation. Natural recruitment did not differ significantly between concrete mats with and without transplanted corals. 'Visible' recruits were first recorded 10 months after emplacement of the mats and were predominantly *Acropora* and *Pocillopora*. On near vertical surfaces their density was almost 18 m^{-2}. Recruits grew fast producing many 20–30 cm diameter colonies on the mats within 3.5 years. Growth and survival of transplants are compared with results of transplantation studies in other locations. We conclude: (1) species transplanted should be selected with care as certain species are significantly more amenable than others to transplantation, (2) the choice of whether fragments or whole colonies are transplanted may profoundly influence survival, (3) considerable loss of transplants is likely from higher energy sites whatever method of attachment, (4) transplantation should, in general, be undertaken only if recovery following natural recruitment is unlikely.

Introduction

Over the last three decades there has been a change worldwide from traditional, usually sustainable, exploitation of coral reef resources to a heavy increase in demands largely as a result of demographic changes. At the same time coral reefs in a wide range of geographic locations have suffered degradation as a result of both natural (e.g. tropical cyclones, volcanic activity, catastrophic low tides, El Niño-Southern Oscillation events) and anthropogenic disturbances (e.g. coral mining, dredging, sewage, dynamite fishing, chemical pollution, oil spills, ship groundings, and sediment, fertiliser and pesticide run-off as a result of changing land-use). These problems have generally been well-documented (e.g. reviews by Brown and Howard 1985; Salvat 1987; Hatcher et al. 1989) although rather fewer studies have focused either on recovery of coral communities following natural or anthropogenic disturbance (reviewed by Pearson 1981; Grigg, this issue) or on mitigation of human impacts on reefs (reviews by Hatcher et al. 1989; Woodley and Clark 1989; Miller et al. 1993).

In the atolls of the Maldives (central Indian Ocean) coral rock is extracted from shallow reef-flat areas for use as building material in the construction industry. Since the 1970s demand for coral rock has been very high in the

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vicinity of the capital island Malé in North Malé Atoll, where 26% of the country's 238 000 population live, and where tourism and urbanisation have been undergoing rapid development. Coral rock is extracted manually from shallow reef flat areas known locally as faros (submerged annular reefs). In North Malé Atoll, there are reefs which were mined over 20 years ago, that have shown virtually no recovery up to the present date (Brown and Dunne 1988). Degradation of these reef-flats by coral mining leads to loss of live coral cover and topographic diversity and to loss of reef-associated fishes (Dawson-Shepherd et al. 1992). Lack of recovery after coral mining has been tentatively attributed to the highly mobile and unconsolidated sediment which may lead to mechanical abrasion or smothering of newly settled coral larvae (Brown and Dunne 1988).

Recovery periods for damaged reefs are highly variable, and depend largely on the nature of the disturbance and how recovery is defined (Pearson 1981). Reviewing the literature, he found that recovery ("restoration of a coral assemblage to a degree comparable to its original state") from major natural or human disturbances was generally slow (several decades). Further, he concluded that recovery from man-made disturbances may be prolonged or prevented as a result of permanent environmental changes (e.g. increased sedimentation, substrate mobility, eutrophication) or continuing chronic low-level disturbance. In certain conditions (e.g. damage to acroporid dominated reefs by hurricanes) re-growth of surviving adult colonies or fragments can provide high coral cover but low species diversity a few years after the disturbance (Shinn 1976; Woodley 1992). But where the reef framework has been subject to severe mechanical damage such as ship groundings, coral mining, dredging or dynamite blasting, the reefs may recover very slowly (e.g. Alcala and Gomez 1979; Curtis 1985; Yap et al. 1990) or effectively never recover to their pre-disturbance state as viewed on a human time scale. This would appear to be the case for mined reef-flats in the Maldives. In such cases, attempts may be made to accelerate recovery by (1) stabilising cracked reef with cement (Hudson and Diaz 1988), (2) removing loose sand or rubble (Miller et al. 1993) or consolidating rubble using sponges (Wulff 1984), (3) deploying artificial structures to serve as areas for coral settlement or stable sites for transplantation (Clark and Edwards 1994), and (4) transplantation of corals to damaged areas (Auberson 1982; Yap and Gomez 1984; Hudson and Diaz 1988; Yap et al. 1990, 1992). Hatcher et al. (1989) questioned both the economics and effectiveness of restoration of reef habitat by means of transplantation, noting that countries where reef restoration is most needed can least afford it.

Recovery of degraded reefs usually occurs through recolonisation of denuded areas by settlement of coral planulae out of the plankton onto appropriate clean surfaces and by regeneration of fragments of damaged corals (e.g. Highsmith 1982; Guzman 1991). Willis and Oliver (1988) found coral planulae on the Great Barrier Reef were transported from one reef to another 26 km down current within two days of spawning and Williams et al. (1984) indicated that planulae of broadcast spawners could be transported hundreds of kilometres. Thus transplantation is only rarely likely to be useful as a means of introducing a new supply of larvae to a damaged area. However, if damage is extensive, and there is a lack of surfaces suitable for settlement and extensive rubble areas inimical to small coral survival, coral transplantation, by bypassing the early stages of the life-cycle of juvenile corals which are anyway subject to high rates of mortality (Babcock 1985), may be an appropriate option.

Coral transplantation has been studied as a potential reef management option for a range of reasons (Harriott and Fisk 1988a). In the Philippines, the potential for transplantation to aid reef recovery following dynamite fishing has been extensively studied (Auberson 1982; Yap and Gomez 1984; Yap et al. 1990, 1992). In Guam it has been used in an attempt to replace corals killed by thermal effluent from a power station (Birkeland et al. 1979) and both there and in Singapore to save species threatened by pollution or loss of habitat due to reclamation (Plucer-Rosario and Randall 1987; Newman and Chuan 1994 respectively). In Kanehoe Bay, Hawaii transplantation was used to reintroduce and study survival of two species of corals in an area polluted by sewage (Maragos 1974; Maragos et al. 1985) and in Florida to accelerate reef recovery following the *Wellwood* grounding (Gittings et al. 1988; Hudson and Diaz 1988). In the Gulf of Aqaba, Bouchon et al. (1981) transplanted large coral heads to enhance a tourism area, and in the Great Barrier Reef Marine Park, Harriott and Fisk (1988b) experimented to see whether transplantation could accelerate recovery of coral areas damaged by the crown-of-thorns starfish (*Acanthaster plancii*). At sites where environmental conditions were poor transplants suffered very high mortality (e.g. Maragos 1974; Birkeland et al. 1979), but where water quality was good transplants in relatively low energy environments tended to survive well. However, the effectiveness of transplantation is difficult to judge in some cases as few authors have carried out detailed monitoring of coral survival and growth over a number of years. An exception is the detailed long-term study by Yap et al. (1992).

The present study set out to study survivorship and growth of corals transplanted onto concrete mats laid over the unconsolidated surface of a reef flat in the Maldives severely degraded by coral mining. Methodological constraints – losses of transplanted colonies as a result of wave action – as well as comparative biological performance of different species – in situ mortality, growth rates, response to stress of transplantation – are reported. In addition recruitment of corals to concrete mats with and without transplanted corals have been compared to see if the presence of transplants enchances recruitment. The investigation formed part of a larger study evaluating the use of artificial reef structures in reef rehabilitation (Clark and Edwards 1992, 1993; Edwards and Clark 1993, 1994) and preliminary results on coral transplantation up to approximately one year after establishment were presented by Clark and Edwards (1994).

Materials and methods

Study site

The site chosen for the study, Galu Falhu, was a severely degraded faro which lies 2.4 km northwest of the capital island Malé (Fig. 1). As the reef flat at the study site is largely unconsolidated and subject to strong wave energy during storm periods it was necessary to ensure that the coral transplants would remain in position. Three replicate sets of Armorflex concrete mats (supplied by MMG Civil Engineering Systems Ltd, UK) were deployed at 0.8–1.5 m depth below LAT as platforms for the attachment of coral transplants (T1–T3 – Fig. 1). For each set, three concrete mats (2.05 × 3.06 m) and eight flooring slabs were used to give an approximate area of 36 m^2 (Clark and Edwards 1994). The flooring slabs were placed over the edges of the concrete mats to anchor them securely to the reef flat, leaving approximately 18 m^2 of surface available for coral transplantation (Fig. 2). In addition three sets of bare (without transplanted corals) Armorflex concrete mats were deployed (B1–B3, Fig. 1). To provide comparative data three unrehabilitated control areas on the mined reef flat and three donor areas from where transplanted corals were obtained (C1–C3 and D1–D3 respectively, Fig. 1) were monitored. Preliminary baseline studies in 1991 indicated that coral cover and diversity were higher at the southeasterly section of the study site near the reef crest. Four permanent transects were set up in this more consolidated area and monitored to determine whether measurable natural recovery was occurring there.

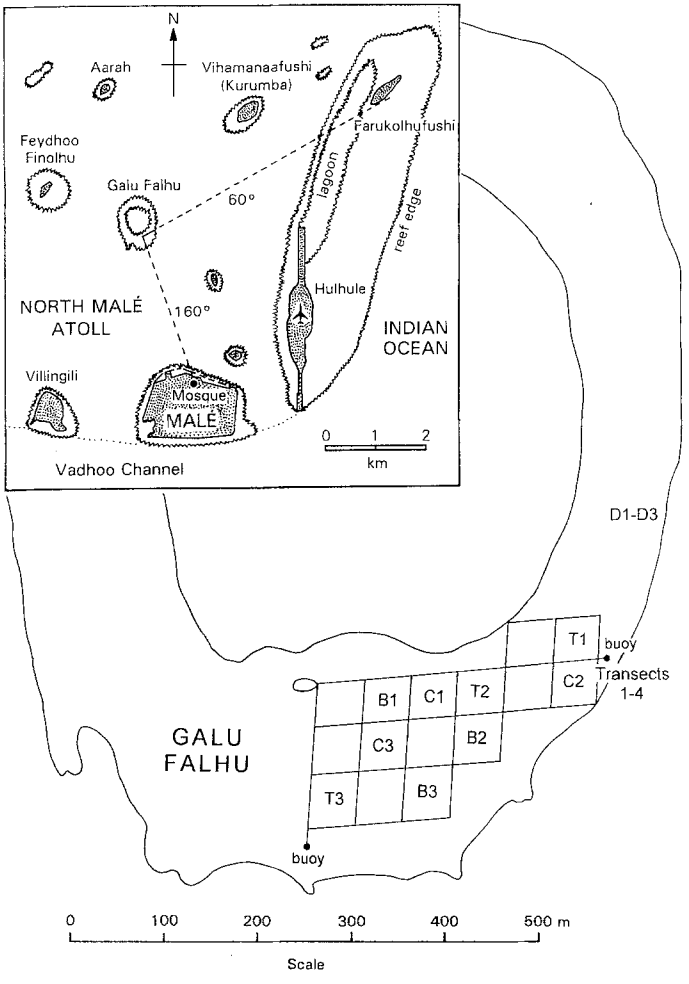

Fig. 1. Location of the three Armorflex areas transplanted with corals (T1–T3), three bare Armorflex areas without transplants (B1–B3), three non-rehabilitated control areas (C1–C3), donor areas from where corals were obtained (D1–D3), and four permanent transects on the edge of the reef flat. Structures in other sections of the 50 m grid formed part of the larger project of rehabilitation of which this study was a part. Insert shows location of the heavily mined degraded faro Galu Falhu in relation to the Maldives capital island, Malé

Transplantation methodology

Corals for transplantation were collected from three 50 m^2 areas near the reef crest within a un-mined section of the same reef and represented three random samples of the natural coral community. Using a hammer and chisel all living corals were removed from each of the donor areas D1–D3, with all corals from one donor area being transplanted to one set of Armorflex mats (T1–T3). As far as possible a dead base was left attached to serve as a means of anchoring the corals into the void spaces of the concrete mats. To minimise the stress of transplantation the detached corals were carefully placed in plastic mesh containers and transferred underwater to the transplant areas. This operation took approximately 30 minutes for each batch of corals transported. Bases of coral colonies were fixed into position as soon as possible using small polythene bags containing premixed cement with retardant (Conplast UW). Larger massive corals (> 10 cm diameter) tended to be difficult to secure using cement alone, so masonry nails were hammered into their bases and embedded in the cement bags. The three transplant areas were completed between March and June 1991.

Survey methodology

Transplanted corals were identified at least to genus, and if possible to species. The position of each coral colony transplanted onto the three areas of Armorflex matting was mapped so that the growth and fate of each coral colony could be followed. At each survey four categories of coral colony were distinguished (Table 1). A set of perspex calipers were used to measure the greatest (*GD*) and least diameters (*LD*) and heights of the colonies. Only living sections of the colonies were measured. Geometric mean diameter ($\sqrt{GD \times LD}$) was then calculated for each colony at each survey and estimates of average radial linear extension rates of colonies obtained by dividing increases in geometric mean diameter per year by two. Colonies showing negative or zero growth between surveys were not considered in calculations of average growth rates of species.

Transplanted areas were surveyed as soon as feasible after transplantation and approximately 7, 16 and 28 months later to determine survival and growth rates of the transplanted corals. One transplant area (T2, Fig. 1) suffered high losses (54 of 158 colonies) due to severe storm damage immediately after transplantation but prior to the site being mapped out in detail to record position and species of transplants. Although percentage coral cover and total number of colonies transplanted were recorded before the storm, this led to no useful data on growth rates or survival of individual colonies being obtained during the initial 7 month period following transplantation.

Natural recovery

The three bare Armorflex areas, three 50 m^2 artificially denuded donor areas near the reef crest, three 50 m^2 unrehabilitated control areas on the reef flat and four 20 m transects were monitored concurrently with the transplant areas to provide information on natural recovery and change. Quadrats laid along 5 belt transects running the length of the 5 × 10 m donor and unrehabilitated control areas were used to survey the whole of each of these areas, whilst the line intercept transect method was used to survey change on the four permanent 20 m transects. The latter were each marked by metal posts hammered into the reef at 2 m intervals.

Fig. 2. An Armorflex mat (area T1) with transplanted coral colonies

Table 1. Definition of terms used to describe status of transplanted colonies at each survey and actions taken for each category

Category	Definition	Action
Live	Attached. Some to all polyps remaining alive	Status recorded. Greatest and least diameter and height measured
Dead	All polyps of colony dead	Death recorded
Lost	Detached and missing from transplant area (swept off transplant area by storms)	Loss recorded
Loose	Detached (broken away from cementation points) but still present on transplant area, some to all polyps remaining alive	Status recorded. Greatest and least diameter and height measured[a]

[a]A few massive coral colonies (*Porites*, *Favia*, *Favites* spp.) became loose and were causing significant damage to other corals at transplant area T2. These colonies could not be successfully reattached using either cement or epoxy resin and had to be removed from the area (see Results)

A survey of 'visible' coral recruits (Wallace 1983) which had settled on both the three Armorflex areas with transplanted corals and three Armorflex areas without any transplanted corals was carried out 28 months after emplacement. The entire mats (18 m^2) of the transplanted areas were surveyed and also the vertical edges of concrete paving slabs (2.4 m^2) used to anchor the mats which proved to be suitable surfaces for coral recruits. Armorflex areas to which no corals had been transplanted were surveyed, using ten randomly placed 1 m^2 quadrats over the total (36 m^2) area of these mats. The vertical edges of paving slabs (2.4 m^2) anchoring these slabs were also surveyed. Both live and dead coral recruits were recorded and their position mapped. Live coral recruits were identified to at least genus level and their greatest and least diameters and heights recorded.

Sedimentation

To obtain some background information on sedimentation rates and how they varied across the study site, they were monitored at two transplanted areas (T1 and T3, Fig. 1) from February 1994 to May 1994, during the switch from full NE monsoon to full SW monsoon conditions, using sediment traps fixed into the void spaces of the Armorflex mats. Nine sediment traps were set up at each area. The traps consisted of 30 cm long vertical PVC pipes and with a inner diameter of 4 cm. The pipes were cut in half and mesh nets were placed halfway down the pipes to prevent small fish such as gobies from taking up residence and interfering with sediment accumulation. Measurements of sedimentation rates were carried out approximately every 28 days. After collection the sediment was washed with fresh water to remove salt and the water was then removed by decantation before drying the sediment in the oven at 100 °C for 24 h. The dry sediment was weighed on an analytical balance with a precision of 0.001 g.

Results

From a management viewpoint overall survivorship of coral transplants is of paramount importance. However, survival rates depend on: (1) extrinsic methodological factors such as precisely how transplantation was carried out, (2) intrinsic biological factors such as the physiology of the coral species being transplanted, and (3) extrinsic stochastic environmental events. After reporting overall survivorship we deliberately separate consideration of the biological from the extrinsic factors influencing coral survival.

Fate of transplanted colonies

A total of 530 coral colonies belonging to ten families were transplanted to the three study areas. Three families of corals dominated the donor areas such that 31% of transplants were acroporids, 38% were poritids and 18% faviids (Table 2). However, there was considerable variation between donor areas leading to differences in the coral community structure within each transplanted area. Transplant area T1 was dominated by poritids (43% of colonies), followed by faviids (22%) and acroporids (19%), while area T3 was dominated by acroporids (41%), followed by poritids (35%) and faviids (15%). Within area T2 34% of colonies were lost due to a storm before it was possible to document the initial community structure, however, seven months after transplantation the community was dominated by poritids (37%) and acroporids (31%), followed by faviids (18%).

Changes in coral cover and density for each transplanted area over the study period show a similar trend at all three areas with both live coral cover and number of live colonies decreasing during the seven months after transplantation, from 12.9% (SE ± 2.54) to 9.1% cover (SE ± 0.98) and from 9.8 (SE ± 0.67) to 6.8 colonies m^{-2} (SE ± 0.51) respectively. Subsequently, whilst the number of live transplanted colonies declined slowly to 5.2 colonies m^{-2} (SE ± 0.38) at 28 months, percent live coral cover showed a steady increase with areas having on average 5.2% more cover at 28 months than at seven months. At two areas coral cover was higher at the end of the study than at the beginning. However, due to high rates of loss and mortality early on, area T3, although showing similar changes in coral cover and density to the other transplanted areas from 7–28 months, still had less live coral cover at the end of the study than initially (16.0% as opposed to 17.8%).

Overall survivorship of transplanted corals in terms of both attached and loose live colonies remaining on the transplanted areas indicates poor survivorship during the initial seven months with subsequent improved survival rates (Fig. 3). To compare survival rates between surveys at each transplanted area, yearly exponential rates of survival $S = 1 - \log_e(N_{t_1}/N_{t_2})/t$ (where N_{t_1} is the number of colonies alive at beginning of each survey period, N_{t_2} is the

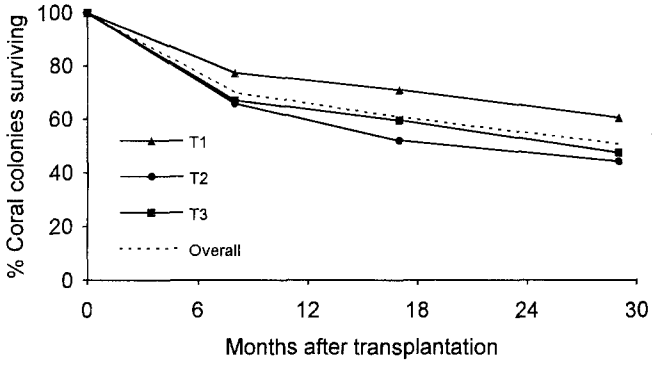

Fig. 3. Survivorship of transplanted coral colonies on the three transplanted areas over 28 months. 'Survivors' include colonies which became detached but remained on the mats

Table 2. Numbers of colonies of each coral taxon transplanted to each area at the start of the investigation and remaining alive and attached after 28 months. For area T2 a storm immediately after transplantation and before the site could be mapped in detail meant that little useful data were obtained initially and fates of individual colonies were followed from 7 months after transplantation

	Number of colonies					
	AreaT1		Area T2		Area T3	
Coral taxa	Initially	After 28 months	After 7 months	After 28 months	Initially	After 28 months
i) Pocilloporidae						
Pocillopora damicornis	0	0	0	0	1	0
P. verrucosa	14	5	7	3	6	3
ii) Acroporidae						
Acropora cytherea	3	0	5	2	6	3
A. digitifera	0	0	0	0	2	2
A. divaricata	7	6	4	4	9	4
A. gemmifera	0	0	1	0	1	1
A. humilis	4	4	3	2	9	4
A. hyacinthus	13	6	14	8	45	13
A. tenuis	1	1	2	1	4	1
Acropora indet.	2	0	3	0	1	0
Astreopora spp.	4	2	0	0	4	3
Montipora spp.	0	0	0	0	2	1
Total	34	19	32	17	83	32
iii) Poritidae						
Porites lichen	0	0	0	0	6	6
P. lobata	11	11	11	10	9	9
P. lutea	33	25	15	13	23	20
P. nigrescens	21	12	7	5	17	4
Porites indet.	9	7	5	1	16	3
Total	74	55	38	29	71	42
iv) Faviidae						
Favia spp.	13	8	4	4	10	5
Favites spp.	11	6	6	5	9	5
Goniastrea reticulosa	0	0	1	1	2	2
Goniastrea indet.	2	0	0	0	2	0
Leptastrea purpurea	0	0	0	0	2	0
L. transversa	1	0	0	0	1	0
Leptastrea indet.	6	2	7	6	0	0
Montastrea spp.	1	0	1	1	5	1
Cyphastrea sp.	5	4	0	0	0	0
Total	39	20	19	17	31	13
v) Agariciidae						
Pavona spp.	4	1	3	1	2	1
vi) Siderastreidae						
Psammacora spp.	0	0	0	0	2	0
vii) Mussidae						
Symphyllia sp.	1	1	0	0	1	1
viii) Merulinidae						
Hydnophora sp.	3	2	2	2	3	3
ix) Oculinidae						
Galaxea sp.	0	0	1	1	0	0
x) Helioporidae						
Heliopora sp.	1	1	0	0	0	0

number surviving at the end, and t is the period between surveys in years) were calculated for all survey periods. Survival rates during the first seven months after transplantation varied from 0.28–0.56 (mean 0.38, SD 0.151) and were significantly lower ($P < 0.05$, Mann-Whitney U-test) than survival rates 7–28 months after transplantation, which varied from 0.68–0.88 (mean 0.81, SD 0.072). Twenty-eight months after transplantation 44–60% of corals still survived on the concrete mats with survivorship overall being 51% (equivalent to a yearly exponential survival rate of 0.71).

Coral losses from wave action

During the initial survey period, 0–7 months after transplantation, almost one quarter of colonies were detached and swept off the transplant areas by strong wave action. Due to a storm which occurred seven days after transplantation of corals to area T2, the percentage of colonies lost there during the initial survey period (34%) was approximately twice as great as that at the other two areas (Fig. 4). From 7–28 months after transplantation only a further 5% of colonies were lost with little loss of colonies from areas T1–T2, but continuing slow loss of colonies from area T3 which was regularly subject to strong surge due to wave refraction. Overall 37% of the transplanted colonies on area T2, 28% of those on area T3 and 19% of those on area T1 were swept off the mats by wave action. Few, if any, 'lost' colonies survived on the shifting sand and rubble reef flat.

In addition to those colonies lost from the transplanted areas, about 16% of colonies on area T3 and 15% of those on area T1 became loose (see Table 1 for definition) during the study. Since many of these were subject to abrasion or breakage during storms, only those coral colonies which remained firmly attached were included in the analysis of growth and mortality rates.

For two of the transplant areas, data on losses in each well-represented family (Acroporidae, Pocilloporidae, Poritidae and Faviidae) could be compared throughout the study period. Between family comparisons of numbers of colonies lost and remaining using two-way contingency tables indicated no significant differences in loss rates (χ^2 test). Within 16 months of transplantation all acroporid colonies and most of the massive colonies had accreted at their bases and cemented themselves naturally onto the concrete mats. However, a few colonies were still lost from the transplant areas even after naturally accreting to the mats. This gives some indication of wave energy at the study site during storms.

Mortality rates of transplanted colonies

Studies of mortality rates have been based on only those transplanted colonies which remained attached to the Armorflex mats. Overall approximately 32% of coral colonies died in situ over the 28 month study period, with mortality ranging from 27.3% at T1 to 35.4% at T3 (Fig. 5). Mortality rates were generally similar between all surveys at each transplanted area with the initial apparently low rate of in situ mortality at T2 probably being an artefact of the high loss of colonies (see above). To compare mortality rates between surveys at each transplanted area, yearly exponential rates of mortality $M = \log_e (N_{t_1}/N_{t_2})/t$ (where N_{t_1} is the number of attached colonies alive at beginning of each survey period, N_{t_2} is the number alive at the end, and t is the period between surveys in years) were calculated for all survey periods. Analysis of variance indicated no significant difference between mortality rates at each area ($P > 0.7$) or between different survey periods ($P > 0.4$).

Branching corals (Acroporidae, Pocilloporidae) had significantly higher exponential mortality rates than massive corals (Poritidae, Faviidae) with a mean M of 0.33 (SD 0.261, $n = 16$) as opposed to 0.11 (SD 0.091, $n = 16$) – Mann-Whitney U-test ($P < 0.01$), one-way analysis of variance ($P < 0.005$). Acroporids had a mean exponential mortality rate of 0.31 (SD 0.225, $n = 8$), pocilloporids 0.35 (SD 0.304, $n = 8$), faviids 0.12 (SD 0.114, $n = 8$), poritids 0.09 (SD 0.067, $n = 8$). Over a two year period these mortality rates equate to the following expected percentage mortalities of transplants: Acroporidae 46%, Pocilloporidae 50%, Faviidae 22% and Poritidae 17%.

Mortality rates were individually estimated for nine coral species with more than ten colonies remaining

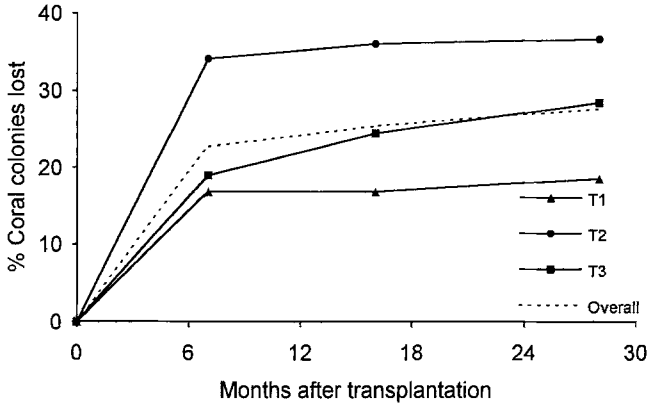

Fig. 4. Loss of transplanted coral colonies on the three transplanted areas over 28 months

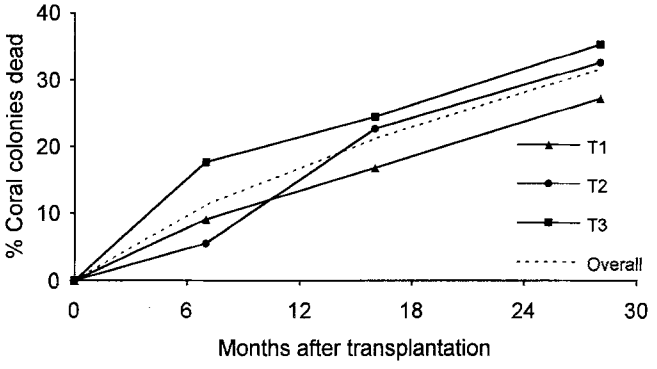

Fig. 5. In situ mortality of transplanted coral colonies (i.e. all polyps dead) over 28 months

Table 3. Mortality rates over 28 month study period among transplants of main coral species. Only those colonies which remained attached to Armorflex mats are considered

Species	Number of colonies		Mean M	% dying in 2 years
	At start	Dead at 28 months		
Acropora divaricata	18	4	0.11	19.4
Acropora humilis	13	3	0.11	20.1
Acropora hyacinthus	62	35	0.36	51.0
Favia sp.	22	5	0.11	19.8
Favites sp.	22	6	0.14	23.9
Pocillopora verrucosa	25	14	0.35	50.5
Porites lobata	31	1	0.01	2.8
Porites lutea	64	6	0.04	8.1
Porites nigrescens	30	9	0.15	26.3

attached to the Armorflex mats (Table 3). Intra-family variation is apparent with *Acropora hyacinthus* having a significantly higher mortality rate than either *A. humilis* or *A. divaricata* ($P < 0.05$ and $P < 0.025$ respectively, χ^2-test), and *Porites nigrescens* having a significantly higher mortality rate than either *P. lobata* or *P. lutea* ($P < 0.005$ and $P < 0.025$ respectively, χ^2-test). Although faviid transplants as a whole did not have a significantly different mortality rate to poritids, *Favia* spp. and *Favites* spp. as a group suffered significantly greater mortality than *Porites lobata* or *P. lutea* ($P < 0.0025$ and $P < 0.05$ respectively, χ^2-test). The overall high acroporid mortality was largely due to *Acropora hyacinthus*, with *A. divaricata* and *A. humilis* having very similar mortality rates to the massives *Favia* and *Favites* (Table 3).

Growth rates of transplanted colonies

Linear extension rates of colonies of eleven species of transplanted coral yielding over ten growth estimates during the study are summarised in Table 4. Colonies which showed negative or zero growth rates because of partial mortality, breakage or predation were excluded from mean growth rate calculations. Growth rates varied widely between colonies within one species and between congeneric species as well as between families (Table 4). The fastest growing species were the branching acroporids *Acropora cytherea, A. hyacinthus* and *A. divaricata* followed by the pocilloporid *Pocillopora verrucosa.* The slowest growth rates were found in the massive faviids (*Favia, Favites*) and poritids (*Porites lobata, P. lutea*). Within the Acroporidae, *A. cytherea, A. hyacinthus* and *A. divaricata* had significantly higher mean growth rates than *A. humilis* ($P < 0.01$), whilst within the Poritidae, *Porites nigrescens* had a higher mean growth rate than *Porites lobata* and *P. lutea* ($P < 0.05$, Student-Newman-Keuls test). Growth rates did not vary significantly between transplant areas.

Stress as a result of being transplanted might be reflected in depressed growth rates in the initial period

Table 4. Estimated mean colony radial extension rates in cm y^{-1} for principal species of coral transplanted

Species	Mean growth rate	Standard error	Minimum growth rate	Maximum growth rate	Number of estimates obtained
Acropora cytherea	5.81	0.850	0.09	10.39	12
A. hyacinthus	4.33	0.291	0.32	11.55	69
A. divaricata	4.15	0.269	0.13	7.84	42
A. humilis	1.93	0.227	0.07	4.24	25
Favia sp.	0.75	0.100	0.06	3.02	40
Favites sp.	0.96	0.185	0.05	3.40	22
Pocillopora verrucosa	2.51	0.182	0.61	5.95	38
Porites lichen	1.63	0.320	0.43	4.34	13
P. lobata	1.21	0.091	0.15	3.30	55
P. lutea	1.12	0.059	0.07	3.59	115
P. nigrescens	1.78	0.204	0.09	4.84	40

after transplantation. To determine whether growth rates might have been affected by transplantation, growth rates for each species in each survey period were compared using analysis of variance. To allow for possible effects of colony size on growth rates average geometric mean diameters of each colony during each survey period were used as covariates. The acroporids *Acropora hyacinthus* ($P < 0.005$), *A. divaricata* ($P < 0.01$), *A. humilis* ($P < 0.05$) and the poritid *Porites lutea* ($P < 0.005$) showed significant positive correlations between growth rate and colony size. Of the four families comprising most of the transplants, only acroporids showed significantly slower mean growth rates during the initial seven months after transplantation than thereafter ($P < 0.01$, analysis of variance with average colony diameter as covariate). Among the main *Acropora* species, mean growth rates (adjusted for colony size) of *A. hyacinthus, A. humilis* and *A. cytherea* were significantly less during the initial seven months after transplantation than thereafter ($P << 0.001$, $P < 0.05$, $P < 0.001$ respectively, t-test), but growth rates of *A. divaricata* showed no such change.

The numbers of transplanted colonies showing negative as opposed to positive growth were compared for each survey period to test whether relatively more colonies were failing to thrive in the seven month period after transplantation than later. There were significantly fewer colonies showing negative growth (relative to those showing positive growth) 16 and 28 months after transplantation than seven months after ($P < 0.001$ and $P < 0.025$, χ^2-test), but in all surveys, from a quarter to a third of colonies had shown negative growth over the preceding inter-survey period. Faviids were the most affected with 32–49% of colonies showing negative growth and acroporids least affected with only 12–23% of colonies showing negative growth between surveys. While 84 colonies showed negative growth seven months after being transplanted (data only available for areas T1 and T3), after 16 months 56% showed positive growth, 20% still showed negative

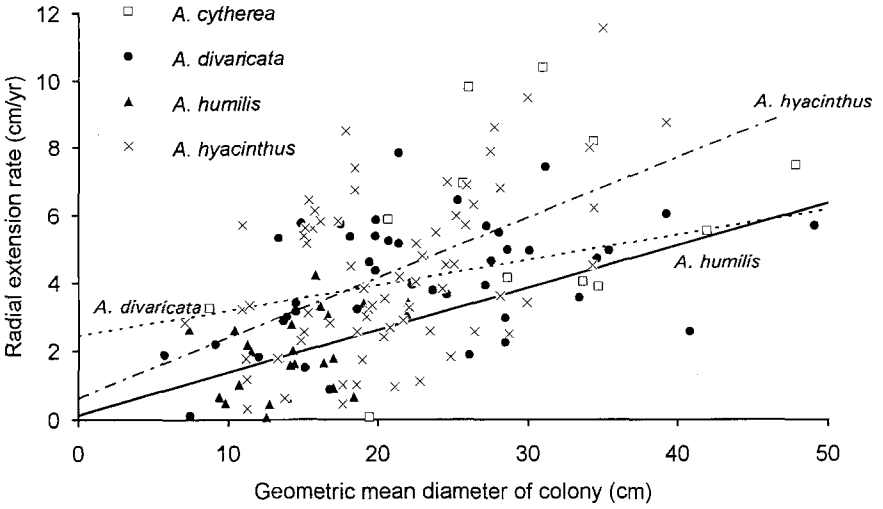

Fig. 6. Relationship between mean colony diameter and radial linear extension rate for four species of *Acropora* transplanted onto the Armorflex mats

growth and 24% had died. Of the 17 colonies still showing negative growth 16 months after transplantation, a further seven showed positive growth by 28 months, three had died and seven still showed negative growth. Thus 64% of colonies showing negative growth early on recovered eventually.

The relationship between geometric mean colony diameter and growth rates for four transplanted *Acropora* species is shown in Fig. 6 with regression lines displayed for those species showing a significant increase in growth rate with increasing size.

Natural recruitment of corals to Armorflex mats

The first coral recruits recorded within the transplant areas belonged to the genera *Acropora* and *Pocillopora.* These recruits were first observed in December 1991, approximately 10 months after the mats had been emplaced. Initially, the coral recruits were observed only on the vertical edges of the large flooring slabs anchoring the mats, but subsequently settlement was observed on vertical surfaces of the concrete mats themselves between February and July 1992. About 15 months after emplacement a small number of *Porites* recruits were first observed on the horizontal surfaces of the mats within one area (T1). Twenty-eight months after emplacement, coral recruitment on each of the transplant sites (T1–T3) was compared to that observed on bare Armorflex mats (B1–B3) without coral transplants (Table 5).

Coral recruits which had settled on the surfaces of the concrete mats and those settled on the vertical edges of the concrete flooring slabs were analysed separately (Table 5). The numbers of visible recruits per unit area established on the Armorflex mats and on the vertical edges of the flooring slabs did not differ significantly between areas with and areas without transplanted corals. However, mortality of recruits on the vertical edges of the flooring slabs was far higher on the areas without transplanted corals than those with transplants ($P < 0.001$, χ^2-test) with only 9 out of 128 recruits recorded as dead on the latter compared to 56 out of 129 on the former. Cushion stars (*Culcita* sp.) appeared to be implicated in the relatively high mortality of recruits on the vertical edges of flooring slabs within the bare Armorflex areas.

Coral recruits on both transplanted and bare Armorflex areas were dominated by branching species. *Acropora* species were dominant on areas B3 (56% of recruits), T3 (52%) and T1 (44%) and *Pocillopora* species dominant on T2 (69% of recruits), B1 (42%) and B2 (41%). Detailed data on the survival rates and growth of these recruits were not collected and no measurements of coverage are available beyond 28 months, however, preliminary observations indicated that survival was high and growth rates

Table 5. Visible recruitment of juvenile corals to (1) Armorflex with transplanted coral colonies (area surveyed = 18 m²) and to bare Armorflex mats (area surveyed = 10 m²), and (2) vertical edges of concrete paving slabs (area surveyed = 2.4 m²) within the transplanted Armorflex and bare Armorflex areas, 28 months after emplacement. Means ± standard errors are given for transplanted areas (T1–T3) and bare Armorflex areas (B1–B3)

Mats	Total no. of recruits/m²	No. live recruits/m²	% mortality	% cover
(1) Armorflex matting				
Transplanted Armorflex	3.8 ± 1.8	3.3 ± 1.4	10.0 ± 4.1	0.56 ± 0.26
Bare Armorflex	3.2 ± 1.0	2.9 ± 0.9	9.1 ± 3.1	0.47 ± 0.03
(2) Paving slabs				
Transplanted Armorflex	17.8 ± 3.9	16.6 ± 3.1	5.8 ± 3.0	4.70 ± 1.61
Bare Armorflex	17.9 ± 0.7	10.2 ± 0.6	43.5 ± 1.1	2.20 ± 0.38

Fig. 7. An Armorflex area (B3) to which no corals were transplanted 3.5 years after emplacement. Several *Acropora* and *Pocillopora* recruits have grown into substantial colonies

fast, with some *Acropora cytherea* colonies attaining a colony diameter approaching 20 cm within 12 months of first being recorded. Figure 7 illustrates the extent of recruit growth on an Armorflex mat to which no corals had been transplanted, 3.5 years after it was deployed.

Natural reef recovery

After seven months there was little natural recovery at the artificially denuded coral donor areas, but after 16 months a small number of *Acropora* recruits were found in each of these areas. After 28 months, coral cover in the denuded donor areas was 0.22–0.71% (mean 0.40%, SE 0.15%), with 9–12 genera present. There was no evidence of significant recovery in the unrehabilitated mined control areas over three years nor at the permanent transects near the reef edge (Table 6). Overall these data suggest that natural recovery rates on the mined reef flat at Galu Falhu, as measured by changes in coral cover and species richness, are very slow.

Sedimentation

Sedimentation rates near the reef edge on the northeast side of the study site (area T1) ranged from 1.09 mg $cm^{-2}d^{-1}$ (SE 0.16) during the calm NE monsoon to 2.81 mg $cm^{-2}d^{-1}$ (SE 0.24) during the stormier SW monsoon. At the southwest of the study site, where the sea was often turbulent due to refracted waves meeting (area T3), the sedimentation rates were 6–20 times greater, being 6.97 mg $cm^{-2}d^{-1}$ (SE 0.24) during the NE monsoon and 57.35 mg $cm^{-2}d^{-1}$ (SE 5.99) during the SW monsoon. Differences in sedimentation rates between both the two monsoon seasons and the two sites were highly significant ($P<0.001$). Although it was noted that several *Acropora cytherea* and *A. hyacinthus* colonies at area T3 were regularly coated in fine sediment and that branches appeared stunted compared to other transplant areas, no significant quantifiable effects on mortality or growth were found. One effect of the sedimentation was that most of the void spaces of the concrete mats in area T3 were rapidly filled with sand and small pieces of coral rubble reducing the vertical surfaces available for settlement. This seemed to be reflected in records of only 25 recruits on the mats at T3 compared to 133 at T1. Also, T3 was the only site where coral cover was less at 28 months than at the beginning of the study.

Discussion

If the results of a given transplantation study apply only to a restricted environment in a restricted geographic area,

Table 6. Changes in coral cover and diversity (mean ± standard error) at transects on southeast Galu Falhu and at non-rehabilitated mined control areas (C1–C3) over two and a half years

Site	1991		1992		1993	
	% coral cover	Number of genera	% coral cover	Number of genera	% coral cover	Number of genera
Transects on SE Galu Falhu	5.63 ± 2.43	4.7 ± 0.25	5.61 ± 1.43	6.0 ± 0.82	6.4 ± 1.01	6.5 ± 0.50
Mined control areas (C1–C3)	0.80 ± 0.69	6.0 ± 3.46	0.09 ± 0.06	3.3 ± 1.76	0.19 ± 0.12	3.3 ± 1.76

they are of very limited benefit to managers. We discuss our results in some detail in relation to previous studies of transplantation to see whether some general principles emerge from the studies which may be useful to managers. Comparisons are difficult due to the different objectives, methodologies and time scales of the transplantation studies carried out to date. However, some general conclusions and some specific areas where additional research is required are highlighted.

Overall survivorship of transplanted coral colonies of 51% at 28 months (equivalent to about 75% survival over one year) compares favourably with other studies – see Table 1 in Hariott and Fisk (1988a) for a summary of previous work. For example, in the Philippines Alcala et al. (1982) recorded 40% survival of transplants in 1.2–1.5 m depth over one year in a study at Sumilon Island, Cebu whilst Auberson (1982) recorded 70% survival on average over one year in the same locality for transplants placed at depths of 1.5–10.5 m. However, at relatively high energy shallow sites comparable to our study site, he reported only 20–50% survival over a year. Comparisons between studies should be made with care because authors do not always make it clear whether survival is just the inverse of in situ mortality or is the inverse of this plus losses due to other factors. Survivorship figures suggest that transplantation reduces average life-expectancy of the colonies transplanted, although Plucer-Rosario and Randall (1987) and Yap et al. (1992) appear to be the only researchers who have tested this hypothesis rigorously. In addition transplantation impacts donor areas by removing live coral colonies or segments of them. Any benefits likely to accrue from transplantation need to be balanced carefully against these environmental impacts.

In this study most losses of transplanted colonies occurred during the initial seven months following transplantation when about 25% of cemented colonies were torn loose by wave action. Birkeland et al. (1979) had greater loss problems in studies in Guam where 505 out of 643 transplanted colonies (79%) belonging to nine genera were lost from an open coast site at Tanguisson whilst 39 out of 87 *Porites* transplants (45%) were lost at a relatively sheltered site in Apra Harbor. Plucer-Rosario and Randall (1987) also mention the problem of high losses of transplants particularly from their more exposed transplant site. This emphasises the need to attempt to attach colonies securely in areas with even moderate wave energy. However, whether one uses underwater cement, epoxy resin, cable ties, nylon strings, or plastic coated wires it appears that losses in high energy environments can be substantial (Birkeland et al. 1979; Alcala et al. 1982; Auberson 1982; this study), although rigorous comparative tests of a range of attachment methods under the same environmental conditions have yet to be made.

Once transplanted colonies had naturally accreted to the concrete mats, losses were significantly reduced and in the present study only 5% of colonies were lost after seven months. We observed natural accretion of some *Acropora* colonies (i.e. *A. humilis, A. divaricata, A. hyacinthus* and *A. cytherea*) within seven months of transplantation, and by 16 months all *Acropora* colonies and those of some massive species had naturally accreted at their bases and firmly attached themselves to the concrete mats. These results are in contrast to those of Birkeland et al. (1979) who found no natural accretion of transplanted corals onto the substrate. In their study natural attachment only occurred when underlying corals grew over transplants.

We recorded 32% mortality of transplanted colonies which remained attached to the concrete mats over the 28 month study period. This in situ mortality rate is considerably higher than the 5% over one year (equivalent to about 14% over 28 months under an exponential model) recorded by Birkeland et al. (1979) for the mixed community of transplants at Tanguisson. However, one must be very cautious in comparing the studies because of the high loss rates recorded by Birkeland et al., as death may have predisposed coral transplants to being lost to wave action.

Although in situ mortality of colonies was not significantly greater during the initial seven months after transplantation than thereafter, there was evidence of sublethal effects which we tentatively ascribe to the stress of transplantation. First, growth rates of *Acropora hyacinthus, A. humilis* and *A. cytherea* transplants were significantly slower during the seven months after transplantation than thereafter (after allowing for colony size effects). Second, the proportion of transplanted colonies as a whole which showed negative growth was significantly greater during the initial seven month period. The net result was an overall decrease in % live coral cover on the transplanted areas over the first seven months with the initial level of live coral cover not being regained until some time between 16 and 28 months after transplantation.

The ideal coral species for transplantation would grow fast, survive the stress of transplantation well, and have low mortality rates once established in their new environment. Unfortunately, such a combination of characteristics is unlikely as life-history strategies tend to involve a trade-off between growth rates and longevity. This was broadly reflected in significantly higher growth and mortality rates of branching species (Acroporidae, Pocilloporidae) compared to massive growth forms (Poritidae, Faviidae). However, there was considerable variability in life-history characteristics within these broad groupings and it is worth examining our growth and mortality data together to see whether any species particularly suited or unsuited to transplantation may be identified.

We found *Acropora hyacinthus, A. cytherea* and *A. divaricata* to be the fastest growing species among those transplanted (Table 4). However, *A. hyacinthus* showed significantly greater mortality than *A. divaricata,* with an exponential rate of natural mortality M of 0.33 compared to 0.11 for the latter species, suggesting that among the acroporid species examined *A. divaricata* offers the best combination of life-history characteristics. Among the poritids *Porites nigrescens* grew significantly faster than *P. lobata* or *P. lutea* but also suffered significantly higher mortality (Table 3) with a mortality rate similar to faviids and some acroporids (*Acropora divaricata* and *A. humilis*). The trade-offs are such that no single poritid stands out as being particularly suited or unsuited to transplantation,

although if longevity and low wastage of transplants, as opposed to rapid growth of coral cover, are an objective then *Porites lobata* and *P. lutea* with very low mortality rates (Table 3) would be clear choices.

Pocillopora verrucosa combined high mortality (M = 0.35) similar to *A. hyacinthus* with an intermediate growth rate (significantly less than the fastest growing acroporids, and significantly more than faviids and the slowest growing poritids, Table 4). It thus does not appear particularly suited to transplantation. The faviids for which we have adequate data (*Favia* and *Favites*) had mortality rates similar to *Acropora divaricata, A. humilis* and *Porites nigrescens* but the lowest mean growth rates of any of the transplanted taxa. Further, faviids seemed to be the family worst affected by being transplanted with between 32 and 49% of colonies showing negative growth between surveys. On all criteria the *Favia* spp. and *Favites* spp. appeared unsuitable for transplantation.

Auberson (1982) had two species of *Acropora* among his transplants (*A. brueggemanni* and *A. prominens*). Mortality rates were far higher than those recorded by us (equivalent to exponential rates of 0.81 and 0.66 respectively for the two species, compared to 0.11–0.36 for *Acropora* spp. in the present study) whilst mean radial extension rates calculated from his data were 2.5 and 1.2 cm y^{-1} respectively, broadly similar to our value for *A. humilis*. He transplanted fragments of colonies rather than whole colonies which may explain the higher mortality rates. Harriott and Fisk (1988a, 1988b) reported that small fragments (<10 cm length) of *Acropora* suffered very high mortality (around 90% in 3–6 months) although larger fragments (>25–30 cm length) survived much better with only 10–40% mortality over the same time period. Auberson (1982) found best survival over one year (all of 24 fragments transplanted) in *Heliopora coerulea* but this species also had the slowest growth. However, slow growing corals may take longer to respond to disturbance and so may need longer observation times to determine effects of transplantation.

Only three studies appear to have rigorously assessed the impact of transplantation on growth and mortality rates of corals. Yap and Gomez (1985) showed that growth rates of transplanted *Acropora pulchra* colonies were less than those of undisturbed controls and Yap et al. (1992) carried out a particularly thorough study of growth and mortality of transplants of three ecologically dominant species in the Philippines. They compared growth and mortality of transplanted 10–12 cm diameter segments of *Acropora hyacinthus, Pocillopora damicornis* and *Pavona frondifera* colonies attached with epoxy resin, to those of undisturbed control colonies of each species growing close to the transplant source colonies. Transplants of both *A. hyacinthus* and *P. damicornis* suffered higher mortality than controls. No *Pavona* died in either group. Among control colonies *A. hyacinthus* and *P. frondifera* had higher growth rates than *P. damicornis*, whilst among transplants *P. frondifera* and *P. damicornis* grew faster than *A. hyacinthus*. Mortality rates of control colonies did not differ between the three species but *A. hyacinthus* transplants suffered greater mortality than those of *P. frondifera* or *P. damicornis*. They concluded that of the three species, *A. hyacinthus* was the least amenable to transplantation whilst *Pavona frondifera* was the most amenable with transplants both maintaining good growth rates and suffering very low mortality. Plucer-Rosario and Randall (1987) studied effects of transplantation on growth and mortality of four coral species (*Pavona cactus, Acropora echinata, Leptoseris gardneri* and *Montipora pulcherrima*) in Guam. They found that mortality rates of transplants averaged 1.6–9.6 times those of controls under various treatments whilst growth rates of transplants averaged 50–75% of those of controls. Like Yap et al. (1992) they found *Pavona* to be most amenable to transplantation among their species with the lowest mortality and highest growth rate. *Pavona* was uncommon at our study reef in the Maldives with only nine colonies among the transplants. Five were lost due to wave action and one of the remaining four died in situ by the end of the study. With such a small sample size however it was not possible to assess whether it was amenable to transplantation in the Maldives. Both the Guam and Philippines studies clearly demonstrate a generally negative impact of transplantation on growth and mortality of corals.

The mortality rates recorded by Yap et al. (1992) for *A. hyacinthus* were extremely high, averaging about 40% per month over the period July 1983 to July 1984. This is equivalent to an exponential annual mortality rate of about 11 or annual percentage mortality of over 99% and is about 30 times the mortality rate we recorded for transplanted *A. hyacinthus* (Table 3). The most obvious difference between the studies was that we transplanted whole colonies (average diameter 17 cm) whilst Yap et al. transplanted segments of colonies. This suggests that if *A. hyacinthus* is chosen for transplantation, which both studies suggest is unwise because of the relative susceptibility of transplants to dying, then whole colonies should be transplanted. In general, where fragments survive poorly relative to whole colonies, their decreased survivorship should be weighed against the increase in number of transplants obtainable by fragmenting colonies in order to decide the least destructive method of reintroducing corals into an area.

'Visible' recruits were first noted on the Armorflex areas ten months after emplacement of the concrete mats. Most recruits were species of *Acropora* or *Pocillopora* and had settled on vertical or near vertical surfaces where densities reached about 18 m^{-2}. The difference in densities of recruits between the Armorflex mats and vertical edges of concrete paving slabs (Table 5) largely reflected the preponderance of vertical surfaces over the former. Preliminary data from studies of recruitment to other concrete structures over 3.5 years on the same reef flat indicated < 2 recruits m^{-2} on horizontal surfaces but on average 27 m^{-2} on vertical surfaces. From a management perspective the important point is that where suitable surfaces for settlement are available and water quality is conducive to coral growth then natural recruitment can deliver substantial restoration within 3–4 years.

Harriott and Fisk (1988a, 1988b) have reviewed the use of coral transplantation as a management option in some detail. Whether transplantation should be adopted

in a particular situation depends on objectives, site characteristics, available funding and manpower, and degree of concern about the environmental impact of obtaining donor colonies or fragments. Our study site was in a relatively high energy environment with potential sources of recruits on nearby healthy reefs in all directions. Because of the wave energy, transplantation was particularly time consuming (and thus costly) with all colonies having to be cemented in place. Environmental impact of collection might have been reduced by using segments or fragments rather than whole colonies but the discussion above and Harriott and Fisk (1988b) and Plucer Rosario and Randall (1987) suggest that any benefits gained in terms of more effective utilisation of donor colonies would likely be nullified by higher mortality of transplants. There was no enhancement of recruitment on transplanted areas or a reduction in life-expectancy of those colonies transplanted. Once stable substrate in the form of concrete mats was available for settlement, significant recovery as a result of growth of corals recruiting from the plankton occurred over 3.5 years (Fig. 7). We expect that within 5–7 years of emplacement, transplanted areas will only be distinguishable from untransplanted ones by the greater amount of dead coral on the former. Thus, for our site in the Maldives, transplantation did not appear a cost-effective option to aid reef rehabilitation, there being significant costs but no clear benefits over a 5–10 year time scale.

However, with different objectives and site characteristics transplantation may be a useful management option, particularly at low-energy, recruitment-limited sites. The lessons from the present study, taken in combination with the experiences of Birkeland et al. (1979), Harriott and Fisk (1988a,b), Plucer-Rosario and Randall (1987) and Yap et al. (1992), are that: (1) species for transplantation should be selected with care as certain species are significantly more amenable than others to transplantation, (2) for some species the choice of whether fragments, segments or whole colonies are transplanted may profoundly influence survival, (3) considerable loss of transplants is likely from higher energy sites whatever methods of attachment, (4) transplantation should, in general, be undertaken only if recovery following natural recruitment is unlikely.

Acknowledgements. This research was funded by the UK Overseas Development Administration's Renewable Natural Resources Research Strategy and Engineering Research Programmes. We would like to thank Mr Hassan Maniku Maizan, Director of the Marine Research Section and all his staff who have assisted with this project. We also acknowledge the invaluable assistance of Mr Abdullah Kamaludeen and the staff of the Ministry of Public Works and Labour in the reef emplacement programme. In addition, we are most grateful to Mr. Ahmed Shareef, Mr Ismael Haleem, Mr Ahmed Shathir, Dr Charles Anderson, Mr William Allison, Dr Alec Dawson Shepherd and Mr Chris Sier for their contributions to the field work and to three anonymous reviewers for their helpful comments.

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