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Effects of coral transplantation and giant clam restocking on the structure of fish communities on degraded patch reefs

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Abstract

Active restoration is being practiced to supplement conservation activities for the purpose of reversing the trend of reef degradation. In the last decade, the feasibility of different restoration approaches such as coral transplantation and restocking of other marine biota has been the focus of research and relatively few have examined experimentally its effects on the resultant communities. In this study, coral transplantation and giant clam restocking were applied on 25 degraded patch reefs (~25 m^2) inside a marine sanctuary in Pangasinan, northwestern Philippines to examine their effects on the community structure of reef fishes. Five interventions or treatments were employed: 1) "coral" consisted of transplantation of a combination of *Acropora* spp. and *Pocillopora* spp. on concrete blocks; 2) "clam" consisted of restocking of *Tridacna gigas*; 3) "clam+coral" consisted of restocking of *T. gigas* with *Acropora* spp. transplanted on their shells; 4) "shell" consisted of deployment of *T. gigas* shells; and 5) "control" consisted of no intervention. Fish communities on the patch reefs were monitored monthly for 3 months before the intervention and were monitored further for 11 months after the intervention, including 1 recruitment season. After the intervention, the coral cover and the "other biota" category increased in the coral and clam+coral treatments, due to the transplanted corals and deployed giant clams. Consequently, the complexity of the substrate was enhanced. A month after the intervention, a rapid increase in the abundance and species richness of reef fishes on the coral, clam+coral and clam treatments was observed compared to the shell and control treatments. A change in species composition of reef fish assemblage was also apparent in the coral and clam+coral treatments relative to the clam, shell and control, especially 4 months after the intervention. The present experiment demonstrates the feasibility of improving the condition of degraded patch reefs, which can subsequently enhance the fish community. Results also show the importance of the underlying substratum and the abundance of live corals and clams to reef fishes.

Keywords: Community structure; Coral reef fish; Coral transplantation; Giant clam restocking; Reef restoration

1. Introduction

Reef fish communities are shaped by different processes such as recruitment (Doherty and Fowler, 1994), immigration (Lewis, 1997), predation (Shulman, 1985; Beukers and Jones, 1997), competition (Jones, 1988; Robertson, 1996) and disturbance (Lewis, 1998; Syms and Jones, 2000). These processes are in turn affected one way or another by the availability of suitable habitats. Most reef fishes recruit and eventually migrate to areas with high coral cover and complex substratum for refuge and for food (Fowler, 1990; Leis and Carson-Ewart, 2002). The presence of corals that have complex configuration increases fish survivorship from predation (Beukers and Jones, 1997). Natural disturbances, such as tropical cyclones (Kaufman, 1983), crown-of-thorns starfish, *Acanthaster planci* outbreaks (Williams, 1986; Sano et al., 1987) and coral bleaching (Lindahl et al., 2001), often cause widespread coral mortality that subsequently alters fish communities. Experimental disturbance on coral communities has also been demonstrated to decrease fish species richness and abundance (Lewis, 1998; Syms and Jones, 2000).

Correlative studies show that live coral cover is positively correlated with abundance and diversity of reef fishes (Carpenter et al., 1981) but in other studies (McManus et al., 1981; Roberts and Ormond, 1987), these fish assemblage attributes are not

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influenced by coral cover and not even by coral species richness. Some authors suggest that physical complexity of the substratum is more important (Roberts and Ormond, 1987). The observed variability in the relationship between the fish and coral communities may be attributed to ecological and/or methodological factors (McCormick, 1994). Variability in fish community patterns is prevalent because different ecological factors are operating at different temporal scales: diel, lunar, seasonal, and inter-annual; and spatial scales: patch reefs, reefs, and regions (Casselle and Warner, 1996). At large spatial scales, reefs and even regions, variation is generally attributed to physical transport processes that carry larvae and juveniles (Doherty and Fowler, 1994; Casselle and Warner, 1996). At the scale of patch reefs (in meters), which is the focus in this study, substrate characteristics are believed to be the most important factor influencing fish assemblage (Roberts and Ormond, 1987).

The association of fishes with particular characteristics of the substratum can occur at different life stages: juveniles (recruits) or sub-adults to adults (post-recruits) (Tolimieri, 1995). For instance, juveniles of *Neoglyphidodon melas* are more frequently to be encountered around staghorn *Acropora* and *Pocillopora* corals, while adults are often found near soft corals and on consolidated complex substrates covered with benthic algae, on which they feed (Myers, 1999). This association can also be influenced by the ecological functions of reef fish species (Lewis, 1998; Lindahl et al., 2001) and by fish habit, whether the species is highly associated or transient in a patch reef (Lewis, 1997). The diversity of these different categories, especially the ecological functions, is important for the stability of a community (Carr et al., 2002).

Coral reefs are among the most diverse habitats in the globe (Veron, 1995), but reports show that reefs are declining in many areas around the world (Bruno and Selig, 2007). In the Philippines, particularly, only 4.3% of the total reefs surveyed have excellent coral cover (Gomez et al., 1994). Increasing concern about widespread degradation of coral reefs (Nystrom et al., 2000) has led to numerous efforts to attempt to restore reefs by restocking different marine organisms such as corals (Yap et al., 1992), giant clams (Gomez and Belda, 1988), sea urchins, and gastropods (Juinio-Meñez et al., 1998). In this way, base populations for future broodstock can be reestablished and transplanted organisms can provide immediate natural substrate for other fauna as in the case of corals and giant clams. Despite these concerns, relatively few studies (e.g., Edwards and Clark, 1992; Pamintuan, 1994) have examined the effects of transplanted benthic organisms on the associated communities. To help address this gap, this study assesses the effects of coral transplantation and giant clam restocking on the abundance, species richness, and species composition of reef fishes on degraded patch reefs in the Bolinao-Anda reef system in northwest Luzon. This study tested the hypothesis "habitat structure mediates the local organization of reef fish assemblages". If the hypothesis is true, then it is expected that after the intervention or after restoring fish habitats, there would be 1) an increase in species richness, 2) an increase in abundance, and 3) a change in species composition.

Coral transplants and giant clams have a relatively high relief which potentially allows the colonization and settlement of fish recruits and post-recruits, thus acting in the same way as many fish aggregating devices such as artificial reefs. Giant clam restocking and coral transplantation are analogous to terrestrial reforestation, and are intended to enhance biodiversity and productivity (Harriot and Fisk, 1988). This experiment can potentially provide additional insights on fish-substrate relationships and elucidate the importance of corals and other benthic organisms to reef fish communities.

2. Methods

2.1. Study location

The experiment was conducted inside the Caniogan Marine Sanctuary in Tondol, Anda, Pangasinan (northwestern Philippines). The marine sanctuary is located at the embayment of Lingayen Gulf (Fig. 1). The area has long been protected by the coastal inhabitants of Tondol, particularly by a local people's organization, Samahang Multi-sectoral ng Tondol (SAMUSETO) since 1997 until it was officially declared a marine sanctuary in 15 February 2001. The sanctuary has an area of about 9.8 ha (415 m × 236 m) and contains different-sized patch reefs that are separated by sand areas of 2 m to >5 m in diameter.

Twenty-five patch reefs (sensu Sale, 1980) in the subtidal flat were used in the experiment. They were chosen in terms of their similarity in size, depth, degree of isolation, and fish and coral community composition. Each patch consists of consolidated dead corals and a few live corals. Patch reefs that were at least 20 m from each other were selected to minimize the interaction of fish communities (Sale and Dybdahl, 1978; Syms and Jones, 2000). These are interspersed among numerous other patch reefs and <1 m above the sandy substrate.

2.2. Experimental design

The twenty-five patch reefs were chosen within the Experimental Area (EA = ~10,000 m^2) (Fig. 2). Five treatments using 1) corals (coral), 2) giant clams (clam), 3) clams with corals (clam+coral), 4) clam shells (shell) as substrate and 5) control were considered in this study. Each treatment consisted of five replicate patch reefs. The treatments were randomly placed within the EA. Since interaction between the control plots and the other treatments within the EA were not known, an additional area for control patches was established to increase the number of control replicates. This is referred to as spatial hierarchy in sampling where the number of control replicates that are located away from the treated area is increased (Underwood, 1994). In the Control Area (CA = ~10,000 m^2), which is 100 m away from the EA, samplings were conducted on five 100 m-transects laid following the spatial pattern of the treatment plots in the EA. Five patch reefs were randomly chosen from the CA to represent the second set of controls (control2).

An area of 5 m × 5 m within each patch reef was demarcated with stakes at the corners and one treatment was assigned to this demarcated area. This was the core area of investigation of the effects of the different treatments. The adjacent areas within 5 and 10 m from the core area were also examined.

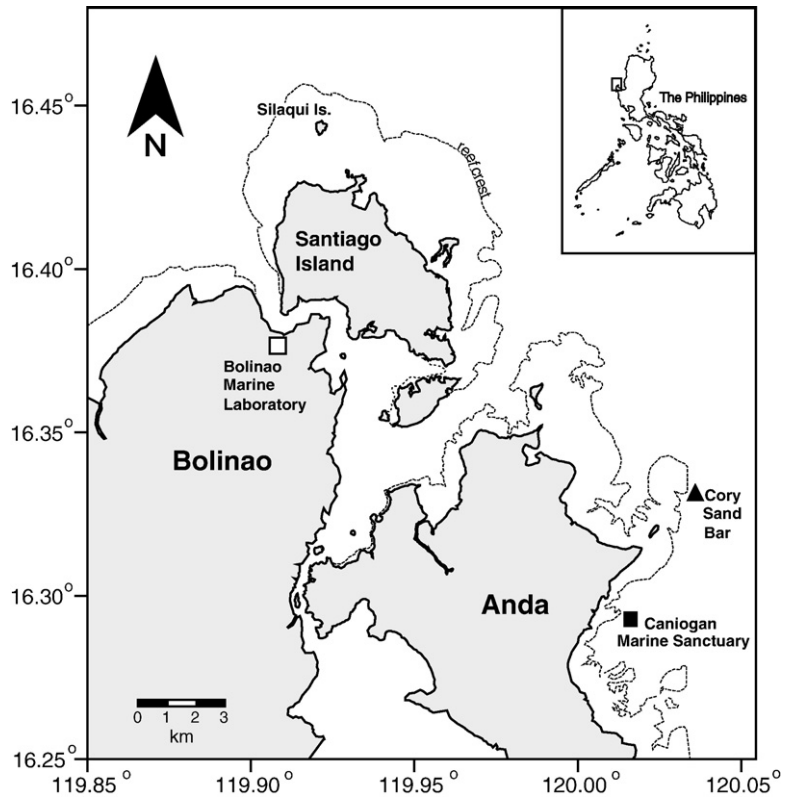

Fig. 1. Map showing study site (inside Caniogan Marine Sanctuary; square) and source site (Cory reef, triangle) in the subtidal flats off Tondol, Anda, Pangasinan (northwestern Philippines).

Fish communities on each patch reef or experimental unit were censused on 10 occasions, thrice before the intervention and 7 times afterwards. On each occasion, 4 repeated censuses were done (Table 1) in order to construct an accurate picture of fish communities, especially when dealing with transient species (Sale, 1980; Nanami and Nishihira, 2002). A temporal

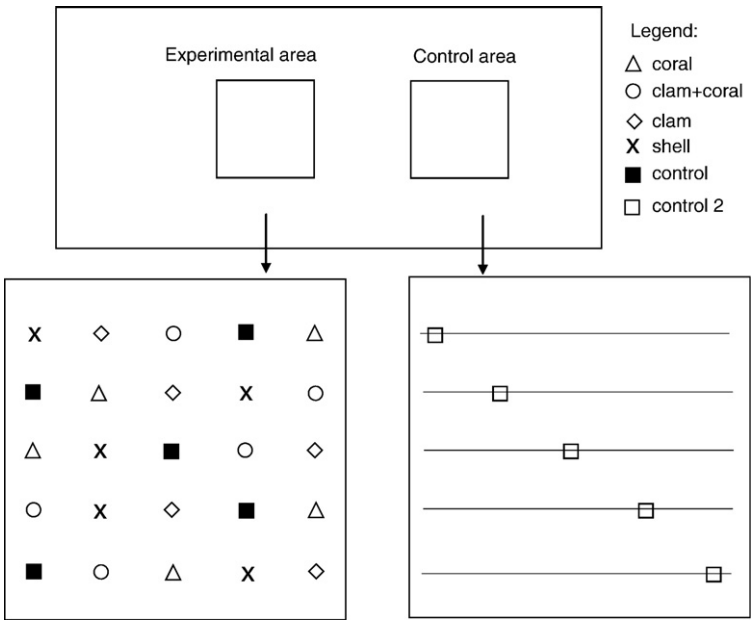

Fig. 2. Spatial configuration of the experimental design: experimental area (~10,000 m^2) – where the experimental units (patch reefs) are located, patch reefs were randomly assigned with the different treatments (coral, clam+coral, clam, shell, and control) (lower right); control area (~10,000 m^2) – this area was established to increase the number of control replicates, since it is not known whether the control treatments and the other interventions will have an interaction, sampling was conducted on the five 100 m-transects laid according to the spatial pattern of the treatment plots in the EA (lower left); Not drawn to scale.

hierarchy in sampling was followed by making 2 samplings of the fish communities at each occasion or month. Within each sampling, 2 Fish Visual Censuses (FVC) were conducted to cover small-scale variances in the location being sampled, thus, a total of 4 surveys per occasion (Underwood, 1994).

Benthic habitat characteristics such as percentage benthic cover and rugosity index at each patch reef were also assessed before, immediately after intervention was established and another during the last monitoring (Table 1).

2.3. Intervention

For each coral treatment plot, 100 coral fragments, mixture of 50 *Pocillopora* spp. and 50 *Acropora* spp., were transplanted. Coral fragments with ~15 cm width were used and were spaced at least 30 cm apart. One coral fragment was cemented to a concrete block (20 cm × 20 cm × 5 cm) to allow fast and easy replacement when dead coral transplants were noticed. Branching *Pocillopora* spp. and *Acropora* spp. corals, specifically the tabulate, bushy, bottlebrush, corymbose, and digitate growth forms (Veron, 1995), were used in the experiment. Recruitment and habitat selection studies show that most reef fishes have preferences for these two genera (Sale et al., 1984). Both coral genera have relatively more complex configuration than most corals and they are also common at the study site. Coral fragments were collected from nearby source areas such as Cory and Marcos reefs (Fig. 1).

Twenty-five *Tridacna gigas* with >40 cm shell length were deployed on each clam+coral treatment plot and were spaced at least 50 cm apart. Two fragments of *Acropora* spp. with ~10 cm width were transplanted on the shells of each live clam, one on each side. One end of the wire was glued first on clam shell with the use of cyanoacrylate adhesive, and then the wire was used to fasten the coral onto the clam shell, before gluing the other end of the wire. It was ensured that a maximal area of the coral branches was in contact with the clam shell to facilitate natural attachment.

For each clam treatment plot, twenty-five *T. gigas* with >40 cm shell length were also deployed and were spaced at least 50 cm apart. Twenty-five dead *T. gigas* shells with >40 cm shell length were also deployed on each shell treatment plot and were spaced at least 50 cm apart. No intervention was introduced in the control and control2 treatment plots. In this study, a total of 750 coral fragments, 250 live giant clams and 125 dead clam shells were used.

2.4. Fish community sampling

Fish communities on the core and the adjacent areas within 5 and 10 m from the core of each patch reef were recorded along a 25 m underwater belt transect (i.e. five 25 m^2 plots) (English et al., 1997). All fishes visible within 2.5 m on either side of the centerline were identified to the lowest possible taxon. All censuses were conducted between 0900H and 1600H. Actual counts and size estimates (to the nearest centimeter of the total length, TL) of fish were recorded. The data on total length was used to categorize fish into recruits and post-recruits. Fishes with less than 20 mm TL were considered recruits. Total fish abundance, species richness, and species composition were used in the analysis. Total fish abundance refers to the individual abundance of both fish recruits and post-recruits. Species richness is the total number of fish species. Species composition refers to the relative abundance of fish species. Fish abundance on the adjacent areas is often zero because it lies on a sandy area, so only data on the core area of each patch reef are presented in this paper.

2.5. Benthic survey

Underwater photographs were taken to document the benthic cover. On each replicate plot, ten 5 m-transects were laid parallel to each other, with a spacing of ~0.5 m. Ten regularly spaced shots or frames were then taken directly from each 5 m transect, thus, a total of 100 photos per plot. The camera was positioned to the right and perpendicular to the transect lines and fixed at a height of 0.25 m, so that the area of coverage would be the same for all photos. Photos were overlaid with 5 systematic sampling points and the benthic characteristics were

Table 1
Experimental design of the temporal sampling protocol

	2004				2005										
	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
First week				I											
Day 1	FVC	FVC	FVC	n	FVC		FVC	FVC		FVC		FVC		FVC	FVC
Day 2	FVC	FVC	FVC	t	FVC		FVC	FVC		FVC		FVC		FVC	FVC
			LIT chain transect	e r v e n t i o n	LIT chain transect										LIT chain transect
Second week															
Day 1	FVC	FVC	FVC		FVC		FVC	FVC		FVC		FVC		FVC	FVC
Day 2	FVC	FVC	FVC		FVC		FVC	FVC		FVC		FVC		FVC	FVC

FVC = fish visual census, LIT = line intercept transect.

Table 2
Benthic lifeforms and lifeform categories used in the characterization of patch reefs (modified from English et al., 1997)

Lifeform categories	Benthic lifeforms	Codes	Notes/remarks
Branching hard coral (HC)	Acropora, branching	ACB	at least 2° branching
	Acropora, digitate	ACD	no 2° branching
	Acropora, tabulate	ACT	horizontal flattened plates
	Millepora, branching	CME	fire coral
	branching coral	CB	at least 2° branching
Non-branching hard coral (HC)	Acropora, submassive	ACS	robust with knob or wedge-like form
	Heliopora coral	CHL	blue coral
	Tubipora coral	CTU	organ pipe coral
	encrusting coral	CE	major portion attached to the substrate as a laminar plate
	foliose coral	CF	coral attached at one or more points, leaf-like appearance
	massive coral	CM	solid boulder or mound
	submassive coral	CS	tends to form small columns, knobs, or wedges
	mushroom coral	CMR	solitary, free-living corals
Algae	algal assemblage	AA	consists of more than one species
	coralline algae	CA	
	macroalgae	MA	weedy/fleshy browns, reds, etc.
	turf algae	TA	lush filamentous algae, no visible characteristics, contours substrate
Other biota	other biota	OT	Ascidians, anemones, gorgonians
	soft coral	SC	soft bodied corals
	sponge	SP	
	zooanthids	ZO	examples are Platythoa, Protopalythoa
Abiotic-loose	rubble	R	unconsolidated coral fragments
	sand	S	
Abiotic-solid	dead coral with algae	DCA	this coral is standing, but no longer white
	rock	RCK	reef substrate uncolonized by living organism
Unidentified points	non-data points	DDD	undefined or unclear

quantified in terms of percentage cover of each of a series of benthic lifeform categories defined in the book of English et al. (1997) (Table 2).

The topographic complexity on each replicate plot was determined using six 2 m-chain transects laid parallel to the shore following the bottom contour. Of the six, two transects were positioned at the centerline, and two on each half of the plot. The total length covered by the chain along each patch reef was then divided by 2 m, thus producing an index of topographic complexity or "rugosity index" (McCormick, 1994). A rugosity index equal to one means that the substrate has a flat surface, while a value less than one implies that the substrate is more complex.

2.6. Data analysis

Changes in fish species richness and fish abundance were analyzed using repeated measures ANOVA (analysis of variance) (Hopkins, 2000) by means of Statistica® software. This test is used when the same experimental unit (i.e. patch reef) is being measured over a period of time (e.g. Chittaro and Sale, 2003). In each analysis, control treatment plots were compared to each of the four treatments among months. Prior to any analysis, data were tested for homogeneity of variances and normality. Fish abundance was analyzed in two ways, with and without the Apogonidae data set. In the second analysis of fish abundance, the initial data on counts of Apogonidae were not used as the counts made on this family were considered as inherent as part of the control data set. Apogonidae, which were outliers in the data, were excluded in the analysis because of their very high abundance and patchy occurrence. Nevertheless, the importance of the Apogonidae will be expounded in the discussion.

All multivariate analyses were conducted using PRIMER (Plymouth Routines In Multivariate Ecological Research) v5® software. Fish species composition was graphically presented in two-dimensional ordination plots by non-metric multidimensional scaling (nMDS) using the Bray-Curtis measure of similarity. Data were transformed to fourth root so that each species contributed evenly to each analysis. One-way ANOSIM (analysis of similarity) with pair-wise comparisons was conducted to formally test the significant differences between controls and each treatment. Similarity Percentage procedure (SIMPER) was also employed to identify the top 5 fish species that contributed to the dissimilarities (Clarke and Gorley, 2001).

3. Results

3.1. Patch reef benthic characteristics

All of the patch reefs ($n=25$) had comparable benthic cover compositions before the intervention (Fig. 3). Percentage cover of algae (mostly turf algae) was high in all cases (54.2–65.6%). The abiotic-loose lifeform category ranged from 18.6 to 31.7%. The remaining components generally made up a lower proportion of the benthos: non-branching hard coral (6.4–14.4%), "other biota" (1.5–2.9%), branching hard coral (1.3–1.9), and abiotic-solid (0.2–0.8%). After the establishment of interventions, the

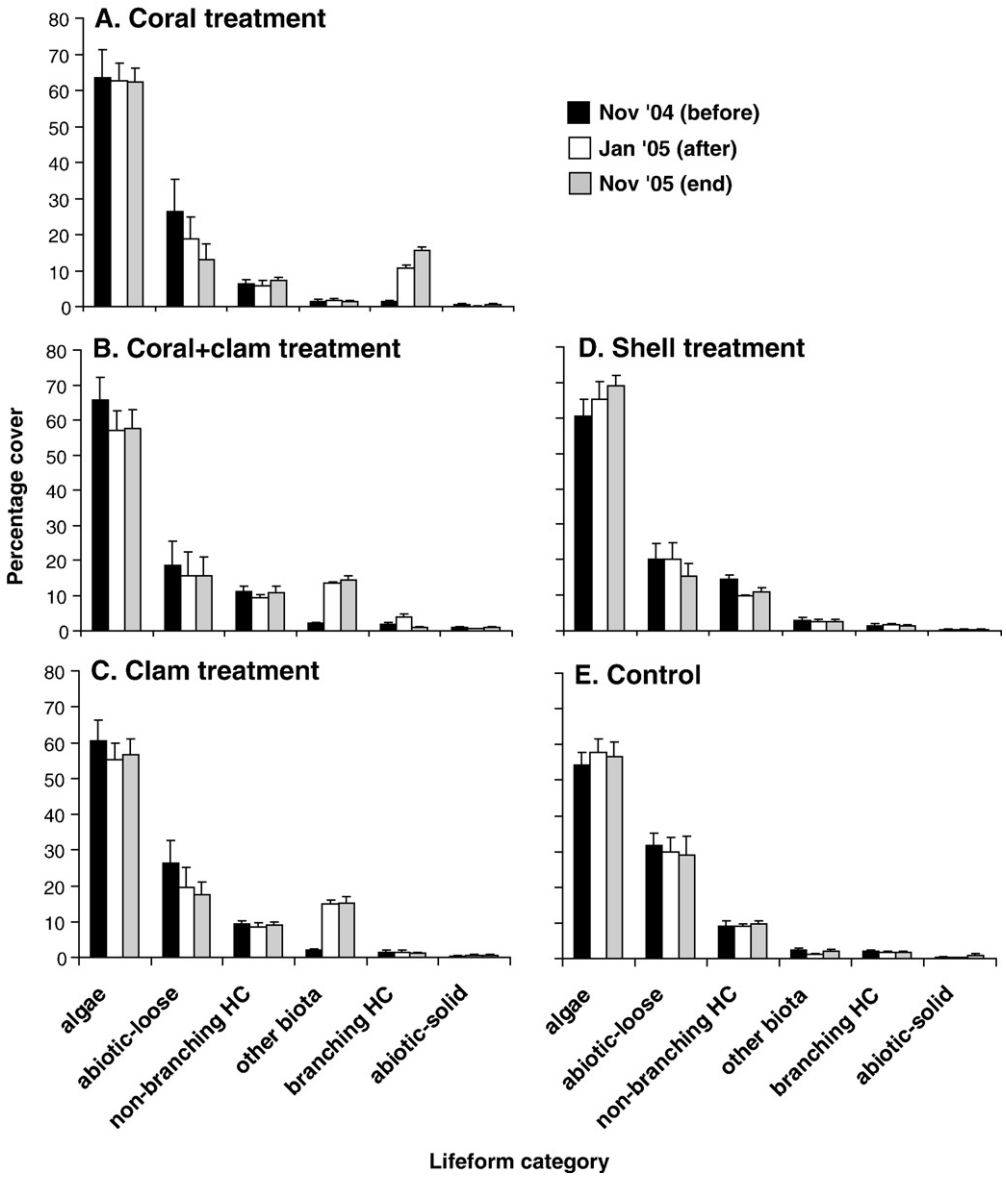

Fig. 3. Percentage cover of benthic communities of patch reefs before the intervention, after the establishment of the intervention and during the last monitoring. Error bars represent the standard error of the means.

branching hard coral cover in the coral and in the clam+coral treatments significantly increased from 1.4% to 10.8% and from 1.8% to 4.0%, respectively (repeated measures ANOVA, treatment*month $p<0.05$), indicating a perceptible effect of the intervention. Similarly, the "other biota" category also significantly increased in the clam and clam+coral treatments from 2.0% to 14.8% and from 2.0% to 13.5%, respectively (repeated measures ANOVA, treatment*month $p<0.05$). This increase was due to the addition of giant clams that were deployed on the patch reefs. During the last monitoring, the percentage cover of branching hard coral in the coral treatment further increased to 15.6% while the same declined to 1.0% in the clam+coral treatment. The "other biota" category increased by 1% in the clam and in the clam+coral treatments during the last monitoring. The shells deployed in the shell treatment were all covered with turf algae. With this, percentage cover of algae in the shell treatment increased significantly from 60.6% to 65.2% during the 2nd monitoring and to 69.2% in the last monitoring (repeated measures ANOVA, treatment*month $p<0.05$).

The increase in percentage cover of branching hard corals and "other biota" in the coral, clam+coral, and clam treatments, respectively, contributed to the significant enhancement of the topographic complexity of the substrate of each treatment plot (repeated measures ANOVA, treatment*month $p<0.05$). Subtracting the rugosity index of each treatment plot in the 2nd monitoring and in the 3rd monitoring from the 1st monitoring, coral treatment achieved the greatest change in substrate complexity followed by clam+coral and clam, then by the shell treatment.

3.2. Survival of coral transplants

Despite the frequent replacement of dead corals in the coral treatment, at least 72% survival was recorded for the coral

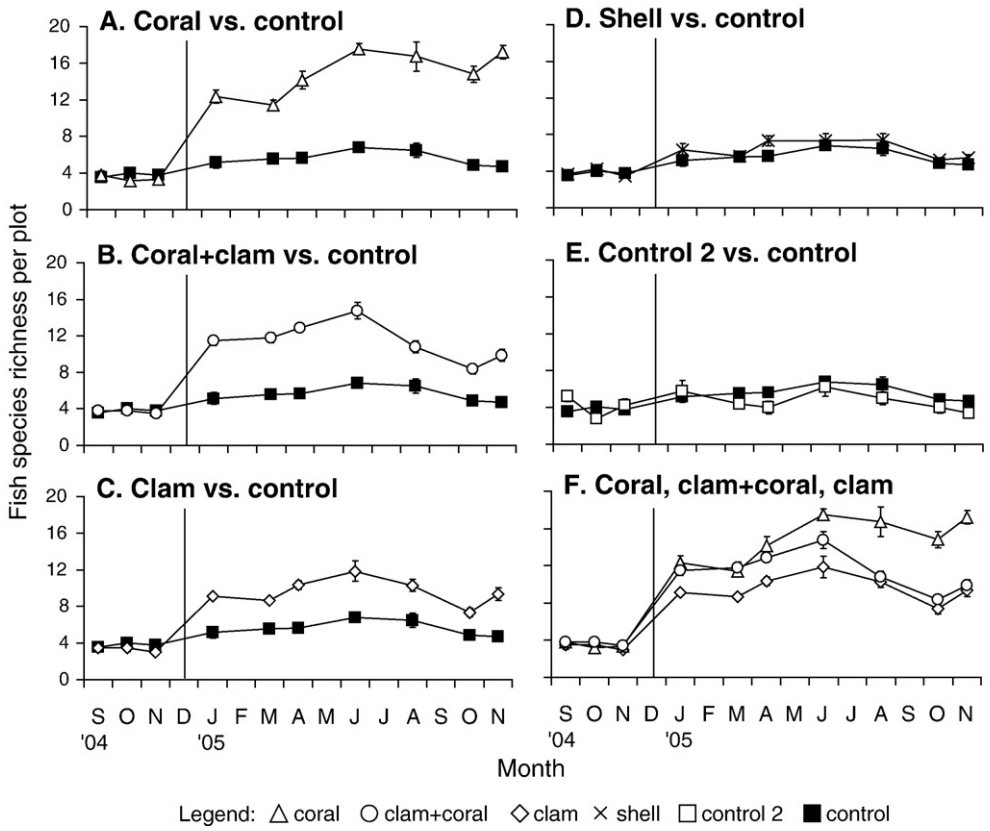

Fig. 4. Fish species richness at the control and restoration treatment patch reefs. The *x*-axis refers to the month in which a given census was taken and the bar represents the month of the application of the intervention. Error bars represent the standard error of the means.

transplants every monitoring period. In the clam+coral, a gradual decrease in the percentage survival was observed. Half of the transplants were already dead by the month of April 2005, 4 months after the intervention and the survival dropped further to near zero towards the end of the experiment, as dead coral transplants in this treatment were not replaced. Predation by *Drupella* sp. was the main reason of the mortality of the coral transplants. Generally, *Pocillopora* spp. had higher survival rates than *Acropora* spp. in the coral treatment.

3.3. Fish species richness

Overall, there were no obvious differences among the treatments and the two controls in terms of species richness before the establishment of intervention (Fig. 4). After the intervention, coral, clam+coral and clam treatments showed a significant increase relative to the control (Fig. 4, Table 3). In contrast, the shell, control and control2 had low species richness throughout the experiment.

The summary of the results of the analysis, repeated measures ANOVA (Table 3) showed that treatment comparisons (control vs coral, control vs clam+coral, and control vs clam) were significantly different in terms of treatments and treatment*months effects for species richness. On the other hand, control vs shell and control vs control2 were not significantly different in terms of treatments and treatment*months effects for species richness. All treatment comparisons were significant in the months effect; this could be attributed to the consistent increase of species richness in the month of June, which is after the recruitment period.

About a 3.5 times increase, from 3.4 + 0.6 (Standard Error of the Means) to 12.4 + 0.7, in species richness was recorded in the coral treatment, a month after the intervention (Fig. 4) and continued to increase up to 5 times higher the initial value, 17.2 + 0.7, at the end of the study. Species richness in both clam coral and clam treatments also increased a month after the intervention by 3.3 times, from 3.5 + 0.4 to 11.5 + 0.5, and by 3 times, from 3.0 + 0.3 to 9.1 + 0.1, respectively. In the period, 1–4 months after the intervention, both clam+coral and coral had significantly higher species richness than the clam treatment. However, the species richness in the clam+coral started to decline in June and became similar with the species richness found in the clam treatment by August. This occurred when the number of coral transplants suffered an almost 100 percent mortality. However, the species richness in the clam+coral, 9.9 + 0.7, and clam, 9.4 + 0.7, remained higher relative to the control.

3.4. Fish abundance

A different pattern was found in the fish abundance before the intervention. Both coral and shell treatments generally had higher fish abundance than clam+coral, clam treatments and control (Figs. 5 and 6) because one of the five patch reefs of

Table 3
Summary of repeated measures ANOVA comparing each treatment (trt) and control in terms of abundance and species richness among months (m)

Comparison of treatments		Species richness		Abundance		Abundance w/o Apogonidae	
		F	*p*	*F*	*p*	*F*	*p*
control vs coral	trt	190.3	0.000 ***	8.6	0.019 *	102.9	0.000 ***
	m	63.5	0.000 ***	1.0	0.467	54.1	0.000 ***
	m*trt	34.6	0.000 ***	0.6	0.760	30.2	0.000 ***
control vs clam+coral	trt	119.7	0.000 ***	113.3	0.000 ***	73.4	0.000 ***
	m	65.8	0.000 ***	25.1	0.000 ***	29.7	0.000 ***
	m*trt	24.9	0.000 ***	12.1	0.000 ***	13.9	0.000 ***
control vs clam	trt	37.3	0.000 ***	59.7	0.000 ***	41.2	0.000 ***
	m	48.2	0.000 ***	20.5	0.000 ***	43.7	0.000 ***
	m*trt	13.8	0.000 ***	5.7	0.000 ***	13.9	0.000 ***
control vs shell	trt	1.7	0.226	1.7	0.226	1.7	0.231
	m	20.1	0.000 ***	0.5	0.835	19.7	0.000 ***
	m*trt	1.1	0.388	0.8	0.601	1.8	0.091
control vs control2	trt	3.2	0.111	5.4	0.049 *	5.1	0.054
	m	5.1	0.000 ***	4.4	0.000 ***	4.4	0.000 ***
	m*trt	1.8	0.088	1.6	0.14	1.6	0.147

ns = not significant at $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

coral and shell treatment had newly settled juvenile *Apogon* sp. (Fig. 6). About 225 and 125 juvenile *Apogon* sp. were recorded in one of the five patch reefs of coral and shell treatments, respectively, on the first month of baseline monitoring. However, after the intervention, coral, clam+coral and clam treatments showed a significant increase in fish abundance relative to the control (Figs. 5 and 6 and Table 3), while the shell treatment, control and control2 had the lowest recorded fish abundance throughout the experiment. A slight increase in fish abundance in the control was only observed in the month of June, after the

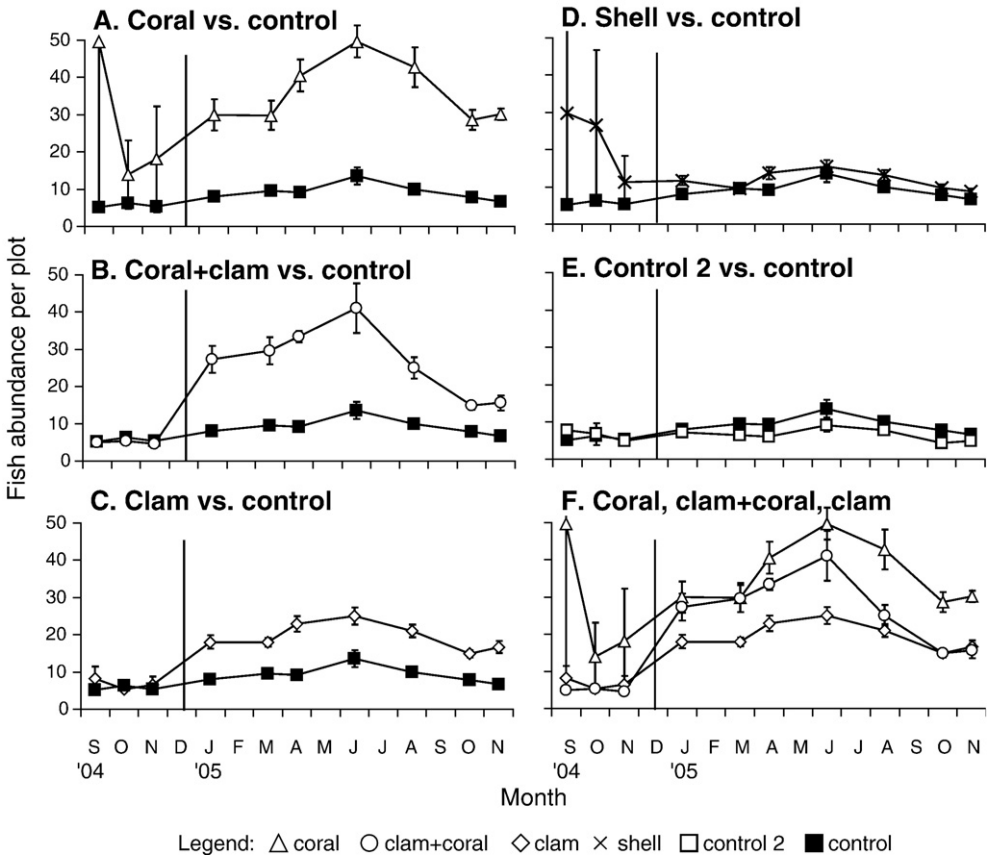

Fig. 5. Fish abundance at the control and restoration treatment patch reefs. The *x*-axis refers to the month in which a given census was taken and the bar represents the month of the application of the intervention. Error bars represent the standard error of the means.

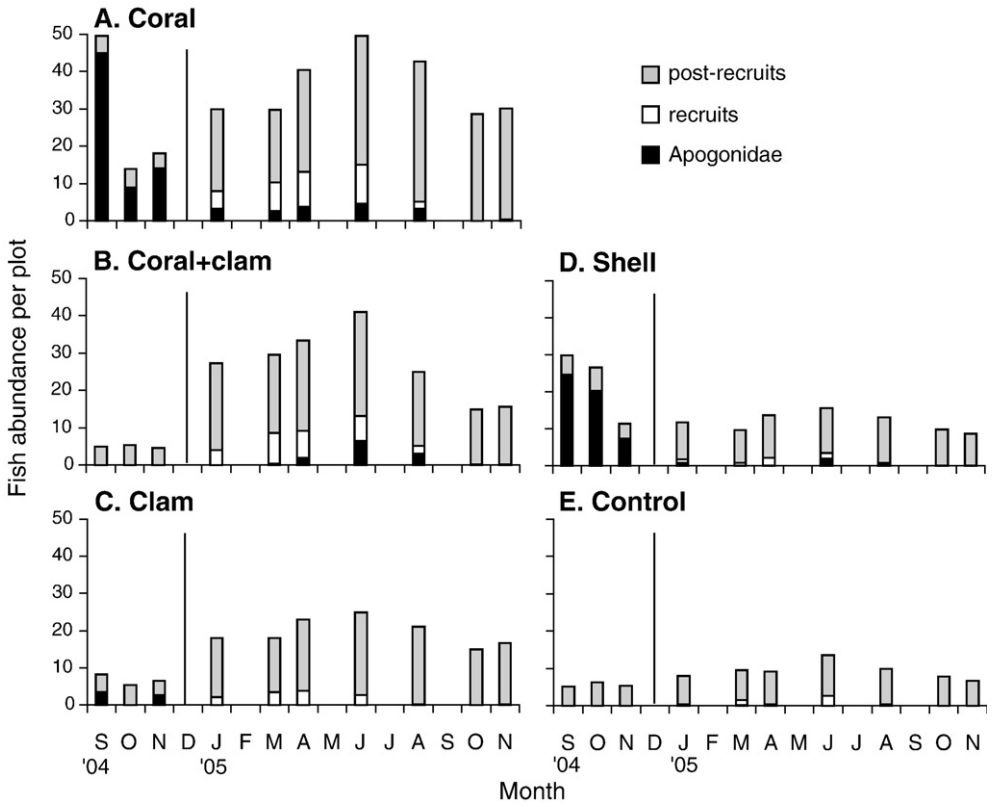

Fig. 6. Mean abundance of post recruits, recruits and Apogonidae at the control and restoration treatment patch reefs. The *x*-axis refers to the month in which a given census was taken and the bar represents the month of the application of the intervention.

recruitment season, which seems to be a general trend to all of the interventions. Generally, a large proportion of post-recruits to recruits contributed to the increase in fish abundance. Recruits were also significantly higher in the coral, clam+coral, and clam treatments than in the shell treatment and control (Fig. 6) plots (repeated measures ANOVA, treatment*month $p < 0.05$).

Results of the analysis, repeated measures ANOVA (Table 3) on fish abundance (with Apogonidae) showed that treatments (control vs coral treatment and control vs shell treatment) were non-significant in terms of treatment*months and months effects. When fish abundance (without Apogonidae) was analyzed using repeated measures ANOVA, results showed that treatments (control vs coral, control vs clam+coral, and control vs clam) were significantly different in terms of treatments and treatment*months effects for abundance. On the other hand, control vs shell and control vs control2 were not significantly different in terms of treatments and treatment*months effects for abundance. All treatment comparisons were significant in the month's effect; this could be attributed to the consistent increase of fish abundance in the month of June, which is after the recruitment period.

Total fish abundance (without Apogonidae) increased, from 4.1 + 0.6 to 26.7 + 1.9, in the coral treatment a month after the intervention (Fig. 5). It reached up to 11 times higher, after four months 45.2 + 2.4, but subsequently declined back to 30.2 + 1.5 (i.e., 7.3 times higher), relative to the total abundance before the intervention. The total abundance in both clam+coral and clam treatments also increased a month after the intervention by 6.0 times, from 4.6 + 0.6 to 27.4 + 3.6, and by 4.6 times, from 4.0 + 0.5 to 18.0 + 1.8, respectively. The abundance of fish at both coral and clam+coral treatments were also significantly higher than the clam treatment in the 1–4 months after the intervention. The total abundance in the clam+coral started to decline by June and became similar to the total abundance found in the clam by August. At the end of the study, the total abundance in the clam+coral, 15.6 + 2.0, and clam, 16.7 + 1.6, remained higher relative to the control.

3.5. Fish species composition

Reef fish assemblages, in the treatment plots and in the control plots, displayed no clear distinction in the three months prior to the intervention (Fig. 7). This was confirmed by the analyses. One-way ANOSIM and pairwise comparisons showed no significant differences in fish species composition between each treatment and the control (see Table 4). After the intervention, fish assemblages in the treatment plots started to separate out from the control plots, although the pattern was variable among the following months.

Only the fish species composition in the coral treatment consistently exhibited a significant difference from the control in all the months (see Fig. 7 and Table 4). The clam+coral treatment also showed a significant difference in fish species composition from the control right after the intervention, but reached similar values during the last two months of monitoring. The clam treatment was significantly different in fish species composition only in April

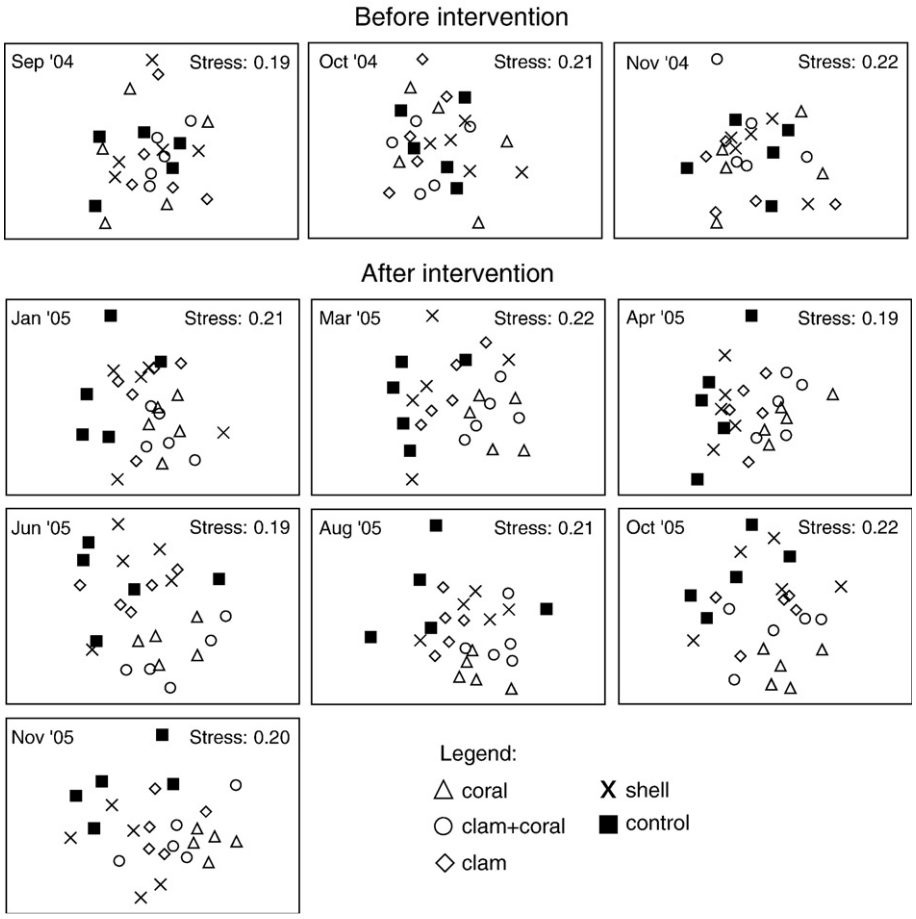

Fig. 7. Non-metric multidimensional scaling (nMDS) ordination of the fish communities in the restoration treatments and control before and after the intervention.

while the shell plots consistently remained similar with the control throughout the duration of the study. The fish species composition in control2 became significantly different from control in the first 4 months after the intervention and then eventually became similar with the control in the succeeding months.

Fish species that contributed to the significant differences between two treatments were identified using SIMPER tests (Table 5). For illustration, only the dataset for April was used since there were more comparisons (between each treatment plot and the control plots) that resulted in significant differences. The corallivores, *Chaetodon trifasciatus*, *C. octofasciatus*, *C. auriga*, juvenile wrasse *Halichoeres* sp., juvenile cardinalfish *Apogon* sp. and the coral-dependent damselfish *Amblyglyphidodon curacao*, consistently provided a greater percentage contribution when the coral treatment was compared with the control, shell and clam treatments and when the clam+coral treatment was compared with the control. The relatively higher numbers, as shown in the average abundance column, of the wrasses *Halichoeres* sp., *H. chloropterus*, *Cheilinus chlorourus*, herbivorous damselfish *Plectroglyphidodon lacrymatus* and *C. trifasciatus* in the clam treatment made this different from the control.

4. Discussion

The results of this study show that reef fish respond rapidly to changes to their habitat in terms of species richness, abundance and species composition, as a result of restoration activities. The coral treatment generated the highest increase in abundance and species richness. The clam+coral treatment exhibited a comparable increase with the coral treatment right after the intervention, but fish abundance and species richness declined when all the coral transplants in this treatment died. Consequently, the clam+coral treatment became similar in fish species richness and abundance with the clam treatment and displayed comparable numbers towards the end of the experiment. Only shell treatment remained similar in fish species richness and abundance to the control throughout the experiment (Figs. 4 and 5).

Multivariate analysis also showed that there is a significant change in community composition of reef fishes between the control and the restoration treatments, especially the coral treatment and, to some extent, the clam+coral treatment. On the other hand, the clam treatment showed no significant effect as seen on the multivariate analyses of its community structure (Fig. 7), which means that a similar set of species were associated with this treatment. Both univariate and multivariate analyses elicit varying insights as to the importance of the treatments vis-à-vis their associated fish communities. Changes in the aggregate measurements, total abundance and species richness are obtained without apparent overall the multivariate community structure differences in the case of clam treatment.

As expected, the coral treatment attained the highest increase in coral cover after the establishment of the intervention, followed

Table 4
Summary of one-way analyses of similarity (ANOSIM) with pairwise comparisons of the assemblages of reef fishes among treatments before and after the intervention

Pairwise comparisons	Before					
	Sep		Oct		Nov	
	r	*p*	*r*	*p*	*r*	*p*
control vs coral	−0.13	ns	−0.10	ns	−0.15	ns
control vs clam+coral	0.08	ns	−0.15	ns	−0.15	ns
control vs clam	−0.14	ns	0.04	ns	−0.27	ns
control vs shell	−0.16	ns	−0.02	ns	−0.15	ns
control vs control 2	0.12	ns	0.26	ns	0.02	ns
among treatments	0.022	ns	0.016	ns	−0.034	ns

Pairwise comparisons	After													
	Jan		Mar		Apr		Jun		Aug		Oct		Nov	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
control vs coral	0.464	**	0.572	**	0.508	**	0.536	*	0.388	**	0.780	**	0.792	**
control vs clam+coral	0.404	**	0.540	*	0.516	**	0.588	**	0.384	*	0.344	ns	0.344	ns
control vs clam	0.268	ns	−0.072	ns	0.320	**	0.200	ns	0.056	ns	0.300	ns	0.376	ns
control vs shell	−0.104	ns	0.036	ns	−0.068	ns	−0.032	ns	0.208	ns	0.040	ns	0.180	ns
control vs control 2	0.284	*	0.268	*	0.248	*	0.160	ns	0.116	ns	0.204	ns	0.028	ns
among treatments	0.255	**	0.295	**	0.305	**	0.331	**	0.320	**	0.373	**	0.412	**

ns = not significant at $p>0.05$, * $p<0.05$, ** $p<0.01$.

by clam+coral treatment (Fig. 3). The highest change in the complexity of the substrate was also observed in the coral treatment, followed by clam+coral and clam, then by the shell treatment. The coral treatment, which enhanced both coral cover and the complexity of the substrate, generated the highest increase in total fish abundance and species richness. It is difficult to

Table 5
Summary of the results of SIMPER (Similarity percentage procedure), showing the top 5 species that are responsible for the differences between two treatments

Species list		Ave. abundance	Ave. abundance	% contribution
Coral vs control		coral	control	
Chaetodon trifasciatus	o	1.2	0.0	4.3
Chaetodon octofasciatus	o	2.5	0.0	4.1
Chaetodon auriga	o	1.1	0.0	4.0
Halichoeres sp.	zb, j	1.6	0.0	3.9
Amblyglyphidodon curacao	o	1.5	0.4	3.2
Coral vs shell		coral	shell	
Chaetodon trifasciatus	o	1.2	0.0	4.8
Chaetodon auriga	o	1.1	0.0	4.5
Chaetodon octofasciatus	o	2.5	0.1	4.2
Amblyglyphidodon curacao	o	1.5	0.4	3.5
Apogon sp.	zp, j	3.8	0.0	3.3
Coral vs clam		coral	clam	
Chaetodon octofasciatus	o	2.5	0.1	3.8
Amblyglyphidodon curacao	o	1.5	0.6	3.2
Apogon sp.	zp, j	3.8	0.0	3.1
Scolopsis margaritifer	c	0.7	0.2	3.0
Chaetodon auriga	o	1.1	0.3	2.9
Clam+coral vs control		clam+coral	control	
Chaetodon trifasciatus	o	1.1	0.0	4.5
Chaetodon auriga	o	0.8	0.0	4.2
Halichoeres sp.	zb, j	1.3	0.0	4.0
Halichoeres chloropterus	zb	0.8	0.3	3.2
Amblyglyphidodon curacao	o	1.3	0.4	3.2
Clam vs control		clam	control	
Halichoeres chloropterus	zb	1.2	0.3	4.1
Halichoeres sp.	zb, j	0.9	0.0	4.0
Plectroglyphidodon lacrymatus	h	1.2	0.6	4.0
Chaetodon trifasciatus	o	0.4	0.0	3.7
Cheilinus chlororous	Zb	0.2	0.3	3.5

Average abundance refers to the average number of individuals of certain species in a treatment. o = omnivores, zb = zoobenthivores, zp = zooplanktivores, c = carnivores, h = herbivores, j = juveniles.

separate the influence of live coral cover and of the coral structure that enhances substrate complexity on the fish community, in this treatment. However, in the clam+coral treatment, it is interesting to note that the mortality of the coral transplants produced a concurrent decrease in the total abundance and species richness in this treatment, which may be due to the decline of the omnivores, specifically the corallivores. Pamintuan (1994) was able to demonstrate that AR modules with live coral transplants allow more fish recruits to settle compared to AR modules with dead coral transplants and with no coral transplants. Clam+coral and clam treatments also generated higher total abundance and species richness of fish compared to the shell treatment and control. The addition of dead clam shells did not allow any further settlement of new fish species. The extent of deviation of the structure of fish communities in restored areas, from those in the control patches is related to the degree of alteration of their habitats. This denotes that fish–habitat interaction could be the primary mechanism affecting the structure of fish communities.

There have been varying ideas over how fish communities are related to their habitat. According to Carpenter et al. (1981) and Ault and Johnson (1998), live corals are positively correlated with the abundance and species richness of reef fishes while Roberts and Ormond (1987) and Fowler (1990) maintain that the physical complexity of the habitat is more important. Moreover, results of some experimental manipulation of fish habitat have shown concurrent changes in the fish community structure. Massive reduction of coral cover brought about by an outbreak of *Acanthaster planci* in Ryukyu Islands, Japan decreased the abundance of coral-associated fish species. After infestation of *A. planci*, the dead corals were degraded into coral rubble within two years that further reduced the species richness and abundance of other fish taxa (Sano et al., 1987). The 1997–1998 mass mortality of corals due to abnormally high water temperatures caused a shift in the structure of fish communities on a Tanzanian reef, from corallivores to herbivores, although diversity was not affected. The algae that overgrew on the standing dead corals apparently attracted herbivorous fish (Lindahl et al., 2001). The disturbance experiment by Syms and Jones (2000) resulted in a rapid decline of total fish abundance on patch reefs after coral cover was reduced by 15% by deliberately breaking corals with a hammer.

Omnivores specifically the coral-associated species contributed to the separation of fish assemblage in the coral treatment, and to some extent the clam+coral treatment, from the control (Table 5). The coral-associated fish species are both habitat-linked (e.g., juvenile *Halichoeres* sp. and juvenile *Apogon* sp., and *Amblyglyphidodon curacao*) and trophic linked (e.g., *Chaetodon trifasciatus*, *C. octofasciatus*, and *C. auriga*). On the other hand, no significant separation of fish assemblage in the clam and shell treatments from the control, but the clam treatment generated a higher abundance of zoobenthivores and herbivores.

Development of the structure of fish communities at the study site was facilitated by the immigration of post-recruits from neighboring reefs more than by the settlement of recruits from the plankton (Fig. 6). Reef fishes settle onto suitable habitat during their larval stage and they are known to move and select another habitat depending on their requirements during a particular age (Fowler, 1990; Leis and Carson-Ewart, 2002). Although the patch reefs are at least 20 m away from each other, they are not totally isolated from one another because other patch reefs that are interspersed between them may act as stepping-stones for fishes. Habitat choice (Sale et al., 1984) is responsible for the differences in fish communities between treatments and the similarities among patch reefs treated with the same intervention, and this works in the scale of meters. Another factor that can influence the structuring of fish communities is predation (Hixon and Beets, 1993). Predation could explain the decline in the total abundance of fish at the treatment and control plots after the spawning season. However, the enhancement of the habitat complexity at the coral, clam+coral, and clam treatments could neutralize the effect of predation, as demonstrated in other studies (Beukers and Jones, 1997).

It has been suggested previously that reef fish assemblages are unpredictable because they are structured by stochastic factors such as recruitment (Sale, 1980). However, this study demonstrates that reef fish assemblages are to a certain degree predictable. A modification of their habitat produces a change in the community structure which seems to be driven by the habitat requirements of the fish populations. Thus, both stochastic and deterministic factors should be recognized to influence the development of the structure of fish communities. Biological interactions, such as predation (Beukers and Jones, 1997) and competition (Robertson, 1996) that stabilize fish assemblages, may also be mediated by the presence of habitat attributes such as live coral and substrate complexity. Definitely, stochastic processes such as recruitment and immigration can create a considerable variability in community structure; however, limits to this variability are set by the nature of the habitat. The recruitment of hundreds of juvenile Apogonids (Fig. 6) on one of the 5 patch reefs of coral and shell treatment before the intervention produced a high variability among the patch reefs in terms of total abundance. However, the juvenile Apogonids rapidly decreased within a month, which may have been brought about by the intensified effect of predation due to the bare feature of the patch reef. After the intervention, more *Apogon* sp. were able to sustain their presence in the coral than in the shell treatment, which was brought about by the differences in the complexity of the substrate.

Restoration treatments, applied for a duration of one year, contributed to the rapid increase of fish total abundance and species richness and to the enhancement of the fish species composition. This means that reef fishes are ably to re-colonize restored habitats. Thus fish monitoring should be included in standard restoration monitoring schemes especially since part of its rationale is to help replenish fish abundance. The effects of the restoration treatments may be unique to a particular area; this will be influenced by the current condition of the reef. It would be interesting to see the outcome of the application of the restoration treatments on other reefs such as areas outside marine protected areas that experience different levels of disturbance. Reefs outside protected areas or more depleted fish stocks may have relatively less supply of recruits and post-recruits that could potentially alter the development of fish communities. The quick recovery of the patch reefs in terms of fish abundance and species richness could be attributed to the aggregating power (i.e. “openness or closeness”) of the patch reefs and supply of recruits and post-

recruits from neighboring reefs. The maximum increase of total abundance recorded in the patch reef was about 50/25 m^2 or 2/m^2, which was in the month of August at the coral treatment. This figure is far from the number of abundance of fish recorded in pristine reefs (Russ and Alcala, 1998) at the Apo Island reserve, which ranges from 10,000 to 15,000/1000 m^2 or 10 to 15/m^2. This study recorded the response of fish communities to restoration treatments for only about a year. Long term monitoring should also be considered to document the further development of the fish communities and their habitats.

Restoration efforts like coral transplantation and giant clam restocking should be regarded as secondary to conservation and management initiatives such as establishment of marine reserves. Restoration would be ineffective if not applied on areas protected from constant human disturbance. The outcome of this study supports the idea of how marine reserves are selected, where percentage coral cover and substrate complexity are the primary consideration as these habitat features often produce a concurrent enhancement in structure of fish communities.

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