

# **Artificial reef structures and coral transplantation: fish community responses and effects on coral recruitment in North Sulawesi/Indonesia**

Dissertation zur Erlangung des Doktorgrades der  
Naturwissenschaften  
– Dr. rer. nat. –

im Fachbereich 2 (Biologie/Chemie)  
der Universität Bremen

vorgelegt von  
**Sebastian Christoph Alexander Ferse**

angefertigt am  
Zentrum für Marine Tropenökologie  
Center for Tropical Marine Ecology  
Bremen 2008

**Gutachter der Dissertation:**

1. Gutachter: Prof. Dr. Matthias Wolff
2. Gutachter: Dr. Andreas Kunzmann

**Mitglieder der Prüfungskommission:**

1. Prüfer: Prof. Dr. Ulrich Saint-Paul
  2. Prüfer: Dr. Uwe Krumme
- 
1. weiteres Mitglied: cand. rer. nat. Esther Borell
  2. weiteres Mitglied: Sebastian Kaspers, Diplomand

Tag des öffentlichen Kolloquiums: 9. Mai 2008

*"The bottom was absolutely hidden by a continuous series of corals, sponges, actiniæ, and other marine productions, of magnificent dimensions, varied forms, and brilliant colours. ... [T]he bottom was very uneven, rocks and chasms, and little hills and valleys, offering a variety of stations for the growth of these animal forests. In and out among them moved numbers of blue and red and yellow fishes, spotted and banded and striped in the most striking manner ... It was a sight to gaze at for hours, and no description can do justice to its surpassing beauty and interest."*

Alfred Russel Wallace, 'The Malay Archipelago', 1869

*"The diverse coral reef communities, so eloquently described by Sir Wallace during his visit to Amboyna ..., are becoming a rare sight in Ambon Bay. Most, if not all, coral communities in the vicinity of Ambon City have been destroyed mainly as a result of pollution, siltation and destructive fishing practices..."*

Tomascik et al. 1997



## Abstract

Coral reefs are a valuable asset for humanity, but are increasingly threatened by natural and anthropogenic disturbances. In many cases, destroyed reefs may not be able to recover without human intervention. In response to accelerating habitat degradation, rehabilitation of coral reefs using artificial structures or coral transplantation has received increasing attention during the last two decades. While artificial reefs have a long tradition in fisheries management, the effects of coral transplantation on the reef fish community still remain poorly studied. In the present study, artificial reefs alone and in combination with coral transplants (branching *Acropora* and *Pocillopora* species) were deployed in 100 m<sup>2</sup> plots at three locations (Gangga, Meras and Bunaken) in North Sulawesi/Indonesia in order to study the effects on the associated reef fish community and on coral recruitment dynamics. Control plots covered with coral rubble were monitored for comparison. The study was carried out between May 2005 and July 2007. Coral recruitment was studied using limestone settlement plates, which were exchanged every three months, and responses of the fish community were monitored with monthly underwater visual census. In order to assess the natural fish community in the ambient reef, an additional one-time visual census was conducted in two 100 m<sup>2</sup> plots in the natural reef at each location, and the substrate composition in these plots was measured. Fish community data were compared to census data from the experimental plots taken at the same time. Correlation analysis of the natural fish community, substrate composition, and depth at the three locations revealed that the factors depth, coralline algae, branching *Acropora* spp., foliose coral, soft coral and leather coral best explained the composition of the natural fish community at the three locations. Throughout the experiment, fish abundance, species richness and biomass remained low in the control plots. All three variables, as well as species diversity ( $H'$ ), were higher in the plots with artificial structures. Coral transplantation led to the highest increase of all variables at Gangga, the shallowest location with low natural hard coral cover (<5 %). The highest fish abundance (796 ± 36 individuals/100 m<sup>2</sup>, mean ± SE), number of species (71 ± 2 species) and biomass (107 ± 22 g m<sup>-2</sup>) were observed in the plot containing structures and corals at Gangga. Integrated over the entire duration of the experiment, fish biomass in the plot with coral transplants at Bunaken did not differ from that in the plot containing only structures. At Gangga, fish abundance, species richness, biomass and species diversity was higher in the plot with coral transplants than in the ambient natural reef, while the values from the natural reef plots were higher than or similar to those in the experimental plots at Meras and Bunaken. Observations on the condition of the ambient reef, species composition and fish recruitment indicate that the effect of coral transplantation on the fish community is strongly dependent on the reef context.

Fish community composition differed significantly between the experimental treatments, and between study locations. At all three locations, multivariate dispersion of the fish community and species turnover were lowest in the plot with coral transplants and highest in the control plots. Furthermore, coral transplantation led to increasing Bray-Curtis similarity of the fish community. The observed reduction in variability appears to be indicative of an alleviation of habitat degradation. A comparison of the relative immigration and emigration rates observed in the three treatments showed that more species were supported in the plots with coral transplants, indicating that corals provided additional habitat in comparison with the other two plots.

A crude analysis of the costs of the rehabilitation measures and the value of the standing fish stock in the experimental plots showed that transplantation may be quite expensive and could range between 450 and >5000 USD per 100 m<sup>2</sup>, depending on logistics and labor costs. The value of ornamental fishes in the rehabilitated plots (up to 26.8 ± 1.0 USD per 100 m<sup>2</sup>) was

found to be more than that of fish species caught for local consumption. However, value of the fish resources alone does not reflect the true value of a coral reef, and a more complete valuation of reef areas may yield values that warrant even the high costs of transplantation.

Coral recruitment at each location was found to be seasonal, and the highest number of recruits observed in a three month interval ( $n = 2391$ , approximately 8.7 recruits per 100 cm<sup>2</sup>) occurred at Bunaken. There was no congruent relationship between coral transplantation and coral recruitment. Results obtained during the last sampling interval indicated that recruitment may be enhanced by coral transplantation over time scales longer than the study period. At Bunaken, where the brooding species *Acropora brueggemanni* Brook was transplanted, the relative frequency of acroporid recruits was highest in the presence of the transplants, but it was not clear whether this was the result of larval production or settlement cues produced by the transplants. The species transplanted differed in their performance, with fragments of *Pocillopora verrucosa* Ellis and Solander displaying mortality rates between 75 and 80 % within the first year, while *A. brueggemanni* showed about 20 % mortality after one year. Mortality was linked to both disintegration of the transplantation substrate, which resulted in the loss of attachment, and environmental conditions such as sedimentation.

The results show that while coral fragments are an important habitat for reef fishes, the effects of transplantation and the suitability of coral species to transplantation vary depending on factors such as depth, condition and composition of the natural hard coral community, and environmental conditions. Reef rehabilitation measures need to be selected based on ecological processes and the environmental conditions at the rehabilitation site, and should be accompanied by thorough pre- and post-rehabilitation ecological monitoring. While transplantation may be warranted in some cases, in many cases resources may be better spent on improving the management and protection of a reef area.

## Zusammenfassung

Korallenriffe besitzen einen ausserordentlichen Wert für die Menschheit, sind aber zunehmend durch schädliche Umwelt- und anthropogene Einflüsse bedroht. In vielen Fällen scheint es, daß sich Riffe ohne regulierende Eingriffe durch den Menschen nicht mehr erholen können. Bedingt durch die beschleunigte Zunahme von Riffdegradierung haben Rehabilitierungsmaßnahmen unter Benutzung von künstlichen Riffstrukturen oder durch Transplantation von Korallen in den letzten beiden Jahrzehnten vermehrt an Aufmerksamkeit gewonnen. Während künstliche Riffe seit langem im Fischereimanagement und zunehmend auch in der Rifforschung zum Einsatz kommen, sind die Auswirkungen von Korallentransplantation auf die Rifffischgemeinschaft bisher kaum untersucht worden. In der vorliegenden Studie wurden künstliche Riffsegmente sowohl allein als auch in Kombination mit Korallentransplantation (verzweigende *Acropora*-Arten sowie eine *Pocillopora* Art) auf 100 m<sup>2</sup> großen Riffabschnitten an drei Standorten (Gangga, Meras und Bunaken) in Nordsulawesi/Indonesien ausgebracht und die Auswirkungen der Methoden auf die assozierte Fischgemeinschaft und die Ansiedlungsrate von Korallenlarven untersucht. Mit Korallenschutt bedeckte Kontrollabschnitte gleicher Größe wurden zu Vergleichszwecken untersucht. Die Studie erstreckte sich über den Zeitraum von Mai 2005 bis Juli 2007. Die Korallenansiedlungsrate wurde mit Hilfe von Kalksteinplatten, welche in Intervallen von drei Monaten entnommen wurden, untersucht, und ein monatlicher visueller Zensus diente der Untersuchung der Fischgemeinschaft in den jeweiligen Abschnitten. Um einen Vergleich mit der im natürlichen Riff vorkommenden Fischgemeinschaft zu ermöglichen, wurde an jedem Standort ein zusätzlicher, einmaliger visueller Zensus in zwei 100 m<sup>2</sup> großen Vergleichsquadranten im an die experimentellen Abschnitte angrenzenden Riff durchgeführt und die Substratzusammensetzung dieser Quadranten untersucht. Die Daten der Fischgemeinschaft wurden mit Zensusdaten aus den experimentellen Abschnitten aus dem selben Zeitraum verglichen. Eine Korrelationsanalyse der natürlichen Fischgemeinschaft, der Substratzusammensetzung und der Wassertiefe der einzelnen Abschnitte ergab, daß die Zusammensetzung der Fischgemeinschaft an den drei Standorten am besten durch die Faktoren Wassertiefe, kalkbildende Algen, verzweigende *Acropora*-Arten, foliose Steinkorallen, Weichkorallen und Lederkorallen erklärt wurde. Während des gesamten Experiments blieben Fischabundanz, Artenanzahl und Fischbiomasse in den Kontrollabschnitten ähnlich niedrig. In den Abschnitten mit künstlichen Strukturen nahmen alle drei Variablen, sowie die Artenvielfalt ( $H'$ ), im Vergleich zu den Kontrollabschnitten zu. Auf Gangga, dem flachsten Standort mit dem niedrigsten Anteil an natürlicher Steinkorallendichte (<5 %), führte Korallentransplantation zur stärksten beobachteten Zunahme aller Variablen. Die höchste Fischabundanz ( $796 \pm 36$  Individuen/100 m<sup>2</sup>, Mittelwert  $\pm$  Standardabweichung), Artenanzahl ( $71 \pm 2$  Arten) und Biomasse ( $107 \pm 22$  g m<sup>-2</sup>) wurden im Abschnitt mit künstlichen Strukturen und Korallenfragmenten auf Gangga registriert. In Bunaken unterschied sich auf den gesamten Studienzeitraum bezogen die Fischbiomasse im Abschnitt mit Korallenfragmenten nicht von der Biomasse im Abschnitt, der lediglich Strukturen enthielt. In Gangga waren Fischabundanz, Artenanzahl, Biomasse und Artenvielfalt im Abschnitt mit Korallentransplantation höher als in den Quadranten des angrenzenden natürlichen Riffs. An den anderen beiden Standorten hingegen waren die Werte aus den natürlichen Riffabschnitten höher als oder ähnlich hoch wie die Werte aus den experimentellen Abschnitten. Beobachtungen über den Zustand und die Zusammensetzung des angrenzenden Riffes, die Artzusammensetzung der Fischgemeinschaft und die Ansiedlung von Fischlarven lassen darauf schliessen, daß die Auswirkung von Korallentransplantation auf die Fischgemeinschaft mit dem Zustand des umliegenden Riffs zusammenhängt und stark standortbedingt ist.

Die Zusammensetzung der Fischgemeinschaft unterschied sich signifikant zwischen den drei experimentellen Ansätzen, und zwischen den untersuchten Standorten. An allen drei Standorten war die multivariate Streuung der Fischgemeinschaft und die Rate des Artenwechsels im Abschnitt mit Korallentransplantaten am niedrigsten, um in den Kontrollabschnitten am höchsten. Des Weiteren führte die Präsenz von Korallenfragmenten zu einer Zunahme des Bray-Curtis Index für Ähnlichkeit von Proben. Die insgesamt beobachtete Abnahme an Variabilität der Fischgemeinschaft scheint indikativ zu sein für eine Milderung der Habitatdegradierung. Ein Vergleich der in den drei experimentellen Ansätzen registrierten relativen Raten von Artimmigration und -extinktion ergab, daß die potentiell höchste Anzahl an Arten in den Abschnitten mit Korallenfragmenten möglich ist. Dies deutet darauf hin, daß die Präsenz von Korallen im Vergleich zu den anderen Abschnitten eine Zunahme an Habitat darstellten.

Eine grobe Analyse der mit den einzelnen untersuchten Rehabilitationsmaßnahmen verbundenen Kosten und des durch die in den experimentellen Abschnitten anwesenden Fische dargestellten Wertes ergab, daß Korallentransplantation sehr teuer sein und sich zwischen 450 und >5000 USD pro 100 m<sup>2</sup>, abhängig von Logistik und Arbeitskosten, bewegen kann. Der Wert von Zierfischen in den rehabilitierten Abschnitten (bis zu 26.8 ± 1.0 USD pro 100 m<sup>2</sup>) überstieg den dortigen Wert von Arten, die für den lokalen Verzehr gefangen werden. Allerdings spiegelt der Wert der Fischressourcen allein nicht den absoluten Wert eines Korallenriffs wieder, und eine vollständigere Evaluierung von Riffabschnitten würde möglicherweise einen Wert ergeben, der selbst die mit Korallentransplantation verbundenen hohen Kosten rechtfertigen würde.

Die Ansiedlung von Korallenlarven war an allen Standorten ausgeprägt saisonal, und die höchste in einem dreimonatigem Zeitraum beobachtete Anzahl an Larven ( $n = 2391$ , oder rund 8.7 Siedler pro 100 cm<sup>2</sup>) trat in Bunaken auf. Es gab keinen klaren Zusammenhang zwischen der Anwesenheit von Korallentransplantaten und der Ansiedlungsrate von Korallenlarven. Ergebnisse aus dem letzten Beprobungsintervall ergaben, daß ein positiver Effekt von Transplantaten auf die Wiederbesiedlung durch Larven möglicherweise in Zeiträumen erfolgt, die über den Rahmen dieser Studie hinausgehen. In Bunaken, wo Fragmente der brütenden Art *Acropora brueggemannii* Brook verpflanzt wurden, war der relative Anteil von acoporiden Larven in der Anwesenheit von Transplantaten am höchsten, aber es blieb unklar, ob dies durch Larvenproduktion oder einen durch lebenden Fragmente erzeugten Ansiedlungsanreiz bewirkt wurde. Die verwendeten Korallenarten unterschieden sich in ihrer Tauglichkeit, wobei Fragmente von *Pocillopora verrucosa* Ellis und Solander Sterblichkeitsraten zwischen 75 und 80 % im ersten Jahr aufwies, während die Sterblichkeit von *A. brueggemannii* nach einem Jahr bei rund 20 % lag. Sterblichkeit stand sowohl mit dem Zerfall des für die Transplantation verwendeten Bambussubstrates, was einen Verlust des stabilen Halts der Fragmente nach sich zog, als auch Umweltbedingungen wie Sedimentation in Zusammenhang.

Die Ergebnisse der Studie zeigen die Bedeutung von Fragmenten als Fischhabitat, belegen aber auch, daß die Wirkung von Korallentransplantation und Eignung von Korallenarten zur Transplantation abhängig von Faktoren wie Wassertiefe, Zustand und Zusammensetzung der natürlichen Steinkorallengemeinschaft und Umweltbedingungen variiert. Riffrehabilitierungsmaßnahmen müssen sich daher an ökologischen Prozessen und den Umweltbedingungen an dem zu rehabilitierenden Standort orientieren und sollten in jedem Fall durch gründliche ökologische Beobachtungen sowohl vor als auch nach Durchführung der Maßnahme begleitet werden. Während Transplantation von Korallen in einigen Fällen

sinnvoll sein mag ist es häufig zweckmäßiger, Ressourcen in eine Verbesserung des Managements und des Schutzes eines Riffgebietes zu investieren.

## Acknowledgements

This study was immensely difficult at times, and would not have been possible without the help and support of many people.

I would like to thank my supervisor Dr. Andreas Kunzmann for his support, criticism and guidance throughout the last five years. His suggestions helped to focus my thoughts and improved this manuscript considerably. Many thanks also to my second supervisor, Prof. Matthias Wolff, for agreeing to put up with yet another study on coral transplants, for helpful comments, and for pointing me to different ways of looking at my data. Thanks to Prof. Ulrich Saint-Paul and Dr. Uwe Krumme for agreeing to join the committee for my thesis defense.

In Indonesia, I thank the Indonesian Institute of Science (LIPI) for supporting my study and granting me a research visa.

Thanks to Prof. Dr. Ir. Kawilarang W.A. Masengi, MSc., dean of the Faculty of Fisheries and Marine Science, Ir. Farnis Boneka, MSc., and the other staff of the FPIK at Universitas Sam Ratulangi (UNSRAT) Manado for their interest, good will and support throughout my stay in Manado.

Special thanks are due to Ir. N. Pankie L. Pangemanan, M.Si., and Dr. Ir. Ineke Rumengan, MSc., for their help and guidance with the intricacies of Indonesian administration. I thank Dr. Fontje Kaligis and his family for their friendship and support.

Sascha Romatzki, my colleague, roommate and dive buddy in Manado, helped me enormously in many ways – the present study would not exist without him. Although the stay in Manado was not always easy, the support of Sascha helped me through several hard times. Thank you!

Many thanks to Hanne Darbol and Gaspare Davi from Gangga Island Resort and Spa and to Christiane Müller from Froggies Divers for their friendship, generosity and support. I owe this work to you and hope you will be able to enjoy the natural beauty of North Sulawesi for many years to come. Thanks to the staff of Froggies Divers and Gangga Island Resort for their keen interest and help. Space does not permit to mention you all, but your generosity is not forgotten. Thanks to Jan and Henriette Bebe for their help, friendship and good times shared.

To our roommates Birgit Berg and Sebastian Schmidt, and to Sarah Noack: thanks for your help and company, and friendship. Many thanks also to Daniel from Murex Lembeh, Tina and Nigel from Two Fish Divers, Jaakko from Living Colours, Raph from Bunaken Cha Cha, Terry and the staff from Seabreeze Resort, Jeremy Barnes, the North Sulawesi Watersport Association, and Reky Lasut and his wife. Thanks to Dr. Batuna and his wife, and to Angelique, Paul and Joanne.

Numerous students of UNSRAT helped on this project, especially Rogers, Onal, Irfi, Yodho aka. Stephen, Benny, Stiev, Dimpy, Aly, as well as several others.

Thanks to good friends in Manado – Adri, Ivon and their kids, Asti and Francesco, Marlina and Frank, Veiby and Patrice. I miss you all. And to good friends in Bogor – Unggul Aktani and family, and Ario Dammar and his wife.

Thanks to Esther Borell and Leyla Knittweis, who shared the Indonesian experience, for suggestions, extensive proofreading, and friendship. Salam Meester! Thank you also to Dr. Eberhard Krain.

At the ZMT Bremen, thank you to all the staff and students, especially Claudio Richter and Uwe Krumme for helpful comments and suggestions, Inga Nordhaus for help with PRIMER, Christiane Schnack for help with locating literature, Uli Pint and Lutz Mark for tackling the printer and other things electronic, to Jenny Leal-Florez for many helpful suggestions on the manuscript, to Susanne Eickhoff for her never-ceasing interest, and to Arturo Dominici-Arosemena, Conny Roder, Britta Grote, Malik Naumann, Sonja Rückert, Marc Taylor, Tim Migawski and Steffi Bröhl for their help and friendship.

Werner Wosniok was a tremendous help with grasping statistical concepts and selecting appropriate methods for data analysis.

Walt Jaap provided helpful comments on the first draft of the thesis proposal, Bob Clarke clarified questions regarding PRIMER and pointed me to new ways of interpreting my data, Ed Gomez brought my attention to the interesting study of Patrick Cabaitan, Makato Omori kindly provided a copy of the ‘Manual for restoration and remediation of coral reefs’ from the Japanese Ministry of the Environment, Dive & Dive’s Bali gave a generous discount on the great book, ‘Indonesian Reef Fishes’, Cody Shwaiko and his family showed a keen interest and helped on the project at Gangga, David Cheung from ScubaCam Singapore helped out with a broken housing and provided pictures, Cathy Schloss and Joyce Shaw of the Gunther Library at the University of Southern Mississippi helped to locate literature. I thank all of them.

This study was financed by a PhD scholarship from the German National Academic Foundation (Studienstiftung des deutschen Volkes). I’d like to thank Prof. Peter Richter, Dr. Hans-Ottmar Weyand and Dr. Roland Hain for their support during my time as a PhD scholar with the Studienstiftung.

Last but not least, I have received tremendous support from my parents and my brother all along the way. Having you with me, although we were separated by thousands of kilometres for most of the last three years, was and is a blessing.

Finally, thanks to Meity for making my stay in Manado a whole lot easier. Thank you for sharing good and bad times, for your companionship, for helping me to understand Manado much better, and for putting up with long weekends filled with science stuff.

I would like to dedicate this thesis to the memory of Steven Karisoh.

## Contents

	Page
<b>Abstract</b> .....	I
<b>Zusammenfassung</b> .....	III
<b>Acknowledgements</b> .....	VI
<b>List of Tables</b> .....	X
<b>List of Figures</b> .....	XIII
<b>1. Introduction</b> .....	1
<b>1.1 Coral reefs – values and threats</b> .....	3
<b>1.2 Fishes in coral reefs</b> .....	3
<b>1.3 Reef restoration</b> .....	5
<b>1.3.1 Artificial reefs</b> .....	6
<b>1.3.2 Coral transplantation</b> .....	7
<b>1.4 Coral farming and reef management</b> .....	8
<b>1.5 Research questions and hypotheses addressed</b> .....	9
<b>2. Materials and Methods</b> .....	11
<b>2.1 Study area</b> .....	13
<b>2.2 The study sites</b> .....	14
<b>2.3 Materials used in the experiments</b> .....	16
<b>2.4 Design of the experimental plots</b> .....	17
<b>2.5 Set-up of the sites</b> .....	19
<b>2.6 Transplantation of coral fragments</b> .....	19
<b>2.6.1 Gangga</b> .....	19
<b>2.6.2 Meras</b> .....	20
<b>2.6.3 Bunaken</b> .....	21
<b>2.7 Coral recruitment</b> .....	21
<b>2.8 Long-term recruitment within the experimental plots</b> .....	22
<b>2.9 Visual census of the fish community</b> .....	23
<b>2.9.1 Operational procedure</b> .....	23
<b>2.9.2 Definitions of indices used</b> .....	24
<b>2.10 Comparisons with the natural reef</b> .....	25
<b>2.11 Analysis of data</b> .....	27
<b>2.11.1. Univariate analysis of fish data</b> .....	27
<b>2.11.2 Multivariate analysis of fish data</b> .....	28
<b>2.11.3 Further analysis of fish data</b> .....	31
<b>2.11.4 Analysis of coral recruitment data</b> .....	32
<b>2.11.5 Transplant mortality</b> .....	33
<b>2.12 Prices of the materials used and value of the fish resources</b> .....	33
<b>3. Results</b> .....	35
<b>3.1 Fish community</b> .....	37
<b>3.1.1 Species observed</b> .....	37
3.1.1.1 Species composition.....	41
<b>3.1.2 Fish abundance, number of species, and biomass</b> .....	42
3.1.2.1 Fish abundance .....	42
3.1.2.2 Number of fish species .....	44
3.1.2.3 Fish biomass .....	46
3.1.2.4 Biomass distribution among species .....	48

3.1.2.5 Species diversity and evenness of the samples .....	49
<b>3.1.3 Substrate composition in the natural reef plots.....</b>	<b>51</b>
<b>3.1.4 Multivariate analysis of the fish community data.....</b>	<b>52</b>
3.1.4.1 Characteristic species .....	52
3.1.4.2 Effects of treatment .....	54
3.1.4.3 Effects of location .....	57
3.1.4.4 Comparisons with the natural reef .....	58
3.1.4.5 Responses of fish feeding guilds to treatments .....	60
3.1.4.6 Patterns in the development of the fish community over time.....	63
<b>3.1.5 General patterns in indicators among the treatments .....</b>	<b>66</b>
<b>3.2 Coral recruitment.....</b>	<b>67</b>
3.2.1 Recruitment on the settlement plates .....	67
3.2.2 Recruits on the concrete structures .....	72
<b>3.3 Survival of transplanted fragments .....</b>	<b>72</b>
<b>3.4 Synopsis of the results .....</b>	<b>75</b>
<b>4. Discussion .....</b>	<b>77</b>
<b>4.1 Fish community responses.....</b>	<b>79</b>
4.1.1 The presence of artificial structures .....	79
4.1.2 The role of corals .....	83
4.1.3 Observations on community composition .....	87
4.1.3.1 Temporal variation .....	89
4.1.3.2 Spatial variation: the importance of reef context .....	94
4.2 Trends in coral recruitment .....	96
<b>4.3 Comments on methodology, with reference to reef restoration and coral farming .....</b>	<b>101</b>
<b>4.4 The economics involved .....</b>	<b>106</b>
<b>4.5 Summary + conclusion .....</b>	<b>111</b>
<b>5. References .....</b>	<b>115</b>
<b>6. Appendix.....</b>	<b>139</b>

## List of Tables

### Materials and Methods:

<b>Table 2.1:</b> Depth ranges of the nine experimental plots.....	19
<b>Table 2.2:</b> Dates of first deployment, exchanges and final retrieval of the settlement plates at the three research locations.....	21
<b>Table 2.3:</b> Dates of the sampling campaigns at the three experimental locations. Intervals between consecutive samplings were increased towards the end at Gangga since the composition of the fish community in the experimental plots was becoming more stable over time.....	24
<b>Table 2.4:</b> Depths and monitoring dates of the comparative natural reef plots.....	25
<b>Table 2.5:</b> Overview of the categories used for the substrate census in the natural reef.....	26
<b>Table 2.6:</b> Artificial variables used to generate model similarity matrices. The Spearman rank correlations between the experimental data and the model matrices served as tests of the respective assumptions regarding the development of the fish community in the experimental plots. $t$ is the number of days since the first sampling at each location.....	31

### Results:

<b>Table 3.1:</b> List of all species observed during the experiment, showing the frequency with which they were observed in the respective plots (e.g., in 6 out of all surveys). C = Control, SC = Structures + Corals, S = Structures .....	37
<b>Table 3.2:</b> List of species contributing most to within-group similarity. For each sample group, the ten species contributing most to within-group similarity are shown. Bold species names indicate species that appear in the top ten of only one treatment at a location, or of only one of the natural plots.....	52
<b>Table 3.3:</b> Results of a crossed two-way ANOSIM for effects of Treatment and Location using all experimental fish census samples.....	54
<b>Table 3.4:</b> Relative multivariate dispersion of the average samples in each treatment at the three locations. ....	55
<b>Table 3.5:</b> Results of a crossed two-way ANOSIM for effects of Treatment and Time using all experimental fish census samples from Meras.....	56
<b>Table 3.6:</b> Results of a crossed two-way ANOSIM for effects of Location and Time using all experimental fish census samples from the Control treatment.....	57
<b>Table 3.7:</b> Results of a crossed two-way ANOSIM for effects of Location and Time using all experimental fish census samples from the Structures + Corals treatment.....	58
<b>Table 3.8:</b> Results of a crossed two-way ANOSIM for effects of Location and Time on fish species belonging to certain feeding groups, based on all samples from experimental plots in which the respective species were present.....	60
<b>Table 3.9:</b> Spearman rank correlations between the similarity matrices of the average community samples from each treatment at the three locations and model matrices. The highest correlations between a sample similarity matrix and one of the model matrices are shown in bold.....	65
<b>Table 3.10:</b> Results of the linear model testing for treatment effects, time effects and location effects on within-sample similarity.....	65
<b>Table 3.11:</b> Results from the proportional hazards model comparing the survival times among the species used.....	73

## **Discussion:**

**Table 4.1:** Relative turnover rates for consecutive censuses in the experimental plots at all three locations..... 93

**Table 4.2:** Cost of materials for the Structures plots (without additional covering of the bottom with bamboo boards) and Structures + Corals plots in Indonesian Rupiah (a) and amount of time spent on transport and underwater work at the three sites (b). Since rental conditions for transport and dive gear as well as training and expertise of the divers differed between each location, no costs are given for transportation and work. .... 107

**Table 4.3:** Average values for the fishes observed in the study plots during each census. Values are calculated based on abundances and biomass using prices obtained from local traders and the literature (see Tab. A 1). The maximum value reached in each plot is shown in bold..... 108

## **Appendix:**

**Table A 1:** Prices used to calculate the approximate average value of all fishes present in one plot at one sampling time..... 139

**Table A 2:** Results of the linear model testing for effects of treatment, time and visibility on abundance at the three sites. .... 143

**Table A 3:** Results of the linear model testing for effects of treatment, time and visibility on number of species at the three sites..... 143

**Table A 4:** Results of the linear model testing for effects of treatment, time and visibility on fish biomass at the three sites. .... 144

**Table A 5:** Results of the linear model testing for effects of treatment, time and visibility on diversity at the three sites. .... 145

**Table A 6:** Results of the linear model testing for effects of treatment, time and visibility on evenness of the samples at the three sites. .... 145

**Table A 7:** Results of a crossed two-way ANOSIM for effects of Treatment and Time using all experimental fish census samples from Gangga. .... 146

**Table A 8:** Results of a crossed two-way ANOSIM for effects of Treatment and Time using all experimental fish census samples from Bunaken. .... 146

**Table A 9:** Results of a crossed two-way ANOSIM for effects of Location and Time using all experimental fish census samples from the Structures treatment. .... 148

**Table A 10:** Results of the reduced linear model (crossed two-way ANOVA) for effects of Location and Treatment on within-sample similarity. .... 148

**Table A 11:** Results of the non-parametric Kruskal-Wallis test and pairwise Mann-Whitney U tests for effects of Treatment on within-sample similarity. .... 148

**Table A 12:** Average number of individuals observed in the Control plot at Gangga during each census, sorted by abundance in the first (descending) and last (ascending) censuses. Bold indicates late immigrants (species that appeared after the third census, were present in more than 2 censuses, and were present in > 50 % of the censuses after they appeared, n = 15). Total number of species = 89. .... 153

**Table A 13:** Average number of individuals observed in the Structures plot at Gangga during each census, sorted by abundance in the first (descending) and last (ascending) censuses. Bold indicates late immigrants (species that appeared after the third census, were present in more than 2 censuses, and were present in > 50 % of the censuses after they appeared, n = 23). Total number of species = 129. .... 154

**Table A 14:** Average number of individuals observed in the Structures + Corals plot at Gangga during each census, sorted by abundance in the first (descending) and last (ascending) censuses. Bold indicates late

immigrants (species that appeared after the third census, were present in more than 2 censuses, and were present in > 50 % of the censuses after they appeared, n = 41). Total number of species = 166..... 157

**Table A 15:** Average number of individuals observed in the Control plot at Meras during each census, sorted by abundance in the first (descending) and last (ascending) censuses. Bold indicates late immigrants (species that appeared after the third census, were present in more than 2 censuses, and were present in > 50 % of the censuses after they appeared, n = 4). Total number of species = 58. .... 160

**Table A 16:** Average number of individuals observed in the Structures plot at Meras during each census, sorted by abundance in the first (descending) and last (ascending) censuses. Bold indicates late immigrants (species that appeared after the third census, were present in more than 2 censuses, and were present in > 50 % of the censuses after they appeared, n = 4). Total number of species = 88. .... 161

**Table A 17:** Average number of individuals observed in the Structures + Corals plot at Meras during each census, sorted by abundance in the first (descending) and last (ascending) censuses. Bold indicates late immigrants (species that appeared after the third census, were present in more than 2 censuses, and were present in > 50 % of the censuses after they appeared, n = 11). Total number of species = 109..... 163

**Table A 18:** Average number of individuals observed in the Control plot at Bunaken during each census, sorted by abundance in the first (descending) and last (ascending) censuses. Bold indicates late immigrants (species that appeared after the third census, were present in more than 2 censuses, and were present in > 50 % of the censuses after they appeared, n = 7). Total number of species = 51. .... 165

**Table A 19:** Average number of individuals observed in the Structures plot at Bunaken during each census, sorted by abundance in the first (descending) and last (ascending) censuses. Bold indicates late immigrants (species that appeared after the third census, were present in more than 2 censuses, and were present in > 50 % of the censuses after they appeared, n = 18). Total number of species = 92. .... 166

**Table A 20:** Average number of individuals observed in the Structures + Corals plot at Bunaken during each census, sorted by abundance in the first (descending) and last (ascending) censuses. Bold indicates late immigrants (species that appeared after the third census, were present in more than 2 censuses, and were present in > 50 % of the censuses after they appeared, n = 14). Total number of species = 89..... 167

## List of Figures

### Materials and Methods:

<b>Figure 2.1:</b> Map of western Indonesia, showing the location of the capital of North Sulawesi province, Manado.	13
<b>Figure 2.2:</b> Map of the study area. The three experimental sites are shown by arrows. The location within Sulawesi is indicated on the map in the inset.	14
<b>Figure 2.3:</b> Aerial view of the experimental sites at Gangga (A), Meras (B) and Bunaken (C). The location of the experiments in each reef is circled. Scale bars represent 300 m.	15
<b>Figure 2.4:</b> Bases for the coral transplants were manufactured from concrete (A). The finished bases included a hole for fitting the coral transplants (B).	16
<b>Figure 2.5:</b> Concrete blocks were used to build the artificial reef structures.	16
<b>Figure 2.6:</b> Schematic drawing of the iron frames used to monitor coral recruitment. Each frame was holding three settlement plates.	17
<b>Figure 2.7:</b> Overview of the experimental set-up, showing Control (front), Structure + Coral (middle) and Structure (back) plots. Note that the grid in the Control plot is shown for illustrational purposes only.	18
<b>Figure 2.8:</b> Examples of the categories used in the categorisation of coral recruits. From left to right: Acroporids, Pocilloporids, and Others. The last photograph shows an example of an unidentified recruit. Scale bars represent 0.5 mm.	22
<b>Figure 2.9:</b> Schematic view of a Structures + Coral site. The position of the structures examined for corals is indicated by the red square.	23
<b>Figure 2.10:</b> Sketch of the census pattern used to assess the benthic composition in the natural reef plots. The substrate underneath 20 equally spaced points on 20 horizontal transects was categorized, yielding 400 data points per 100 m <sup>2</sup> .	26

### Results:

<b>Figure 3.1:</b> Relative contribution of selected families to total number of individuals (left) and biomass (right) in the Control (C), Structures + Corals (SC) and Structures (S) treatments (top to bottom) at Gangga.	42
<b>Figure 3.2:</b> Fish abundance at the three experimental sites (mean ± SE), showing the values from the natural reef plots at each site. Note the differences in time scale.	44
<b>Figure 3.3:</b> Number of fish species observed at the experimental sites (mean ± SE), showing the number of species observed in the natural reef plots for comparison.	46
<b>Figure 3.4:</b> Amount of fish biomass found in the experimental plots (mean ± SE), with the values from the natural reef plots shown for comparison.	48
<b>Figure 3.5:</b> Ranked species biomass curves based on the total biomass of each species observed in the experimental treatments at all sites over the duration of the experiment, with the four highest ranking species in each treatment shown on the right.	49
<b>Figure 3.6:</b> Diversity of the fish community (left side) and evenness of the samples (right side) in the experimental plots at three locations (mean ± SE), with the values from the natural reef plots shown for comparison.	51
<b>Figure 3.7:</b> Percent substrate cover in the natural reef plots, with percent values for all categories covering more than 3 %. A: Gangga 1, B: Gangga 2, C: Meras 1, D: Meras 2, E: Bunaken 1, F: Bunaken 2.	52

<b>Figure 3.8:</b> Non-metric Multi Dimensional Scaling (MDS) based on Bray-Curtis similarity of the average fish community data taken from all experimental sites. Red: Gangga, Yellow: Meras, Blue: Bunaken.....	56
<b>Figure 3.9:</b> Non-metric Multi Dimensional Scaling (MDS) based on Bray-Curtis similarity of all fish community samples taken at Meras.....	57
<b>Figure 3.10:</b> Non-metric Multi Dimensional Scaling (MDS) based on Bray-Curtis similarity of the average census data from the experimental plots for consecutive samplings at Meras, showing the development of the fish communities over time.....	57
<b>Figure 3.11:</b> Non-metric Multi Dimensional Scaling (MDS) based on Bray-Curtis similarity of all fish community sample replicates taken from the Control treatment.....	58
<b>Figure 3.12:</b> Non-metric Multi Dimensional Scaling (MDS) based on Bray-Curtis similarity of all fish community sample replicates taken from the Structures + Corals treatment. Note the three replicates from the first sampling at Bunaken seen in the upper right hand corner.....	59
<b>Figure 3.13:</b> Non-metric Multi Dimensional Scaling (MDS) based on Bray-Curtis similarity comparing replicates from the natural reef plots with replicates from the experimental plots taken during the same time. Red: Gangga, Yellow: Meras, Blue: Bunaken.....	60
<b>Figure 3.14:</b> Hierarchical clustering of the fish community samples from the natural reef plots and community samples from the experimental plots taken during the same time, showing subgroups at similarity = 300 ranks.	60
<b>Figure 3.15:</b> A juvenile obligative corallivore, <i>Chaetodon meyeri</i> , seeking shelter among the branches of transplanted <i>Acropora yongei</i> in the Structures + Corals plot at Gangga.....	61
<b>Figure 3.16:</b> MDS plots for all average samples from Gangga, with superimposed bubble plots showing the relative abundance of fishes in four feeding guilds in each sample.....	62
<b>Figure 3.17:</b> MDS plots for all average samples from Meras, with superimposed bubble plots showing the relative abundance of fishes in four feeding guilds in each sample.....	63
<b>Figure 3.18:</b> MDS plots for all average samples from Bunaken, with superimposed bubble plots showing the relative abundance of fishes in four feeding guilds in each sample.....	64
<b>Figure 3.19:</b> An exemplary comparison of the relative similarity of samples from the Control and Structures + Corals plots from Gangga.....	65
<b>Figure 3.20:</b> Similarity between consecutive samples from the three treatments at each location.....	65
<b>Figure 3.21:</b> Ordination by Principal Component Analysis (PCA) using normalized Euclidean distances based on indicator variables derived from number of individuals (above) and total biomass (below) in each average sample.....	67
<b>Figure 3.22:</b> Total amount of recruits counted per sampling campaign (exchange of all tiles in the experimental plots) at each location.....	68
<b>Figure 3.23:</b> Mass spawning of the mother colony of <i>Acropora yongei</i> at Lihage Island on 06. May 2007.....	68
<b>Figure 3.24:</b> Average number of recruits (mean $\pm$ SE) observed on settlement plates deployed in the experimental plots for three-month intervals at the three locations.....	70
<b>Figure 3.25:</b> Total numbers of acroporid and pocilloporid recruits counted on the 18 settlement plates deployed in each experimental plot during each sampling period.....	72
<b>Figure 3.26:</b> The total numbers of recruits counted on the eight innermost structures in the Structures + Corals [SC] and Structures [S] plots, including the portion of acroporid and pocilloporid recruits, is shown by bar the chart. The average number of recruits per structure (mean $\pm$ SE) is shown for comparison (right axis). ....	73
<b>Figure 3.27:</b> Cumulative mortality of the transplanted coral fragments at all three locations (A) and percentage of damaged boards as a function of time since first census at Meras and Bunaken (B).....	74

**Figure 3.28:** The Weibull survival of corals at a given time plotted against the Weibull survival (=absence of damage) of the bamboo substrate at the same time. Weibull parameters are shown on the right. The dashed diagonal line indicates where a linear relationship (coral survival = bamboo survival) would be located. Curves below that line translate into a higher coral mortality than bamboo disintegration; curves below that line indicate the opposite..... 75

## Discussion:

**Figure 4.1:** Juvenile and adult *Pomacentrus brachialis* moved into the concrete structures within weeks of construction..... 81

**Figure 4.2:** Browsing herbivores such as *Ctenochaetus binotatus* were common in both the Structures and Structures + Corals plots at Gangga..... 82

**Figure 4.3:** Planktivores feeding in the current above the Structures + Corals plot at Gangga..... 84

**Figure 4.4:** Juvenile and recruit damselfishes seeking shelter in the branches of an *Acropora gomezi* colony growing on an artificial reef at Gangga..... 86

**Figure 4.5:** View of the Control plot at Gangga. The fish community in the Control plots showed high multivariate variability, an indication for environmental degradation..... 88

**Figure 4.6:** An *Acropora* sp. colony growing in the Structures plot at Bunaken from natural recruitment onto larger pieces of rubble..... 89

**Figure 4.7:** Although one individual was observed during the second census, larger numbers of the honeycomb grouper *Epinephelus merra* appeared in the Structures + Corals plot at Gangga only several months after set-up of the sites at Gangga..... 91

**Figure 4.8:** The ambient reef at Gangga consisted largely of rubble and dead coral, with several soft and leather corals and few remaining hard corals..... 94

**Figure 4.9:** Sponges and a variety of hard corals comprised a large part of the substrate in the ambient reef at Meras..... 95

**Figure 4.10:** Colonies of *Acropora palifera* and *A. brueggemanni* next to the Structures plot at Bunaken..... 96

**Figure 4.11:** The colony of *Pocillopora damicornis* (arrow) growing on an iron frame used to hold three recruitment plates (**a**). A closeup of the settlement plate deployed next to the colony is shown in **b**..... 97

**Figure 4.12:** Examples of recruits other than acroporids and pocilloporids from Gangga (**a**), Meras (**b**) and Bunaken (**c**)..... 100

**Figure 4.13:** Water turbidity measured using a Secchi disc at Meras and Bunaken during the last months of the experiment. Note that small-scale variation (within days) was smaller than variability over several durations of several weeks..... 101

**Figure 4.14:** The author during a visual census in the Structures plot at Gangga in the first months after construction. Each census began in plots containing structures to allow adjustments of size estimates before moving to the Control plots..... 102

**Figure 4.15:** Underwater visibility (mean  $\pm$  SE) estimated during each visual census at the three experimental locations..... 103

**Figure 4.16:** Fragments of *Acropora formosa* had grown into colonies of up to 40 cm in height after 18 months at Meras, indicating skeletal extension rates of more than  $200 \text{ mm y}^{-1}$ ..... 104

**Figure 4.17:** Transplantation of *Acropora formosa* fragments onboard a boat at Meras using two-component epoxy..... 105

**Figure 4.18:** 30 months after construction, a diverse epibenthic community consisting of soft and hard corals, sponges, tunicates and other organisms had developed on the concrete structures, as shown here on Gangga.. 110

<b>Figure 4.19:</b> A graphical model of the population dynamics for the juveniles of a reef fish population.....	112
<b>Box 4.1:</b> Definitions of constancy, stability and resilience.....	92

## Appendix:

<b>Figure A 1:</b> Relative contribution of selected families to total number of individuals (left) and biomass (right) in the Control (C), Structures + Corals (SC) and Structures (S) treatments (top to bottom) at Meras.....	141
<b>Figure A 2:</b> Relative contribution of selected families to total number of individuals (left) and biomass (right) in the Control (C), Structures + Corals (SC) and Structures (S) treatments (top to bottom) at Bunaken.....	142
<b>Figure A 3:</b> Non-metric Multi Dimensional Scaling (MDS) based on Bray-Curtis similarity of all fish community samples taken at Gangga.....	146
<b>Figure A 4:</b> Non-metric Multi Dimensional Scaling (MDS) based on Bray-Curtis similarity of the average census data from the experimental plots for consecutive samplings at Gangga, showing the development of the fish communities over time.....	147
<b>Figure A 5:</b> Non-metric Multi Dimensional Scaling (MDS) based on Bray-Curtis similarity of all fish community samples taken at Bunaken.....	147
<b>Figure A 6:</b> Non-metric Multi Dimensional Scaling (MDS) based on Bray-Curtis similarity of the average census data from the experimental plots for consecutive samplings at Bunaken, showing the development of the fish communities over time.....	147
<b>Figure A 7:</b> Non-metric Multi Dimensional Scaling (MDS) based on Bray-Curtis similarity of all fish community samples taken from the Structures treatment.....	148
<b>Figure A 8:</b> Average among-replicate Bray-Curtis similarity for the experimental treatments at all three locations calculated by the SIMPER routine, with the similarities of the natural reef plots shown for comparison.....	149
<b>Figure A 9:</b> Average number of pomacentrid and labrid fishes $\leq 2$ cm observed at the three experimental sites in each census, with the number of recruits from the natural reef plots shown for comparison.....	150
<b>Figure A 10:</b> Relative extinction and immigration rates in the Control plots.....	151
<b>Figure A 11:</b> Relative extinction and immigration rates in the Structure plots.....	151
<b>Figure A 12:</b> Relative extinction and immigration rates in the Structure + Corals plots.....	152
<b>Figure A 13:</b> Colonization rates (immigration – extinction rates) in the experimental treatments at each location.....	152

# 1. Introduction



Coral reefs are one of nature's wonders of the world. They are home to a breathtaking diversity of life forms, brimming with colors and shapes. Carefully managed, they also are a treasure trove for humans.

Swirling Steps dive site, Gorontalo, March 2007.

## **1.1 Coral reefs – values and threats**

Coral reefs are biogenic, three-dimensional marine habitats composed of carbonate structures that are deposited by hermatypic scleractinian corals and are generally found in areas where water temperature does not fall below 18°C for extended periods of time (Vaughan 1919, Wells 1957, Ladd 1977, Achituv and Dubinsky 1990).

Often compared to tropical rainforests because of their high diversity and productivity (Connell 1978), coral reefs are one of the most valuable and threatened ecosystems on the planet. Indeed, they may be the first ecosystem perishing world-wide due to anthropogenic impacts (Cesar 2000). Coral reefs fulfill a range of ecological functions, such as shoreline protection, maintenance of biodiversity and genetic diversity, nutrient cycling and provision of habitat for a large number of organisms (Done 1995, Costanza et al. 1997, Shutler et al. 2006), but these are often difficult to quantify in monetary terms (Spurgeon 1992, Dixon 1998). Economic valuation of coral reefs is rather new (Spurgeon 1992) and usually places most emphasis on fisheries and recreational use values (Costanza et al. 1997), since these are easiest to quantify (Dixon 1998). It is estimated that in terms of sustainable fishery alone, the value of South-East Asian coral reefs is 2.4 billion USD per year (Burke et al. 2002). However, reefs also play an important role in the marine aquarium and curio trade, as coastal protection, as sources of building materials and pharmaceutical products, as environmental archives, and they have other hard-to-quantify qualities such as cultural value, high biodiversity and value for research and education (Spurgeon 1992, Cesar 2000).

South-east Asia is a center of global marine biodiversity (McManus 1985, Briggs 1999, Roberts et al. 2002, Hoeksema 2007). In this region, more than 350 million people live within 50 km of the coast, a large part of them depending on coastal resources (Burke et al. 2002). However, the increasing number of people in coastal regions are posing a rising threat to these reef systems through overfishing and the use of destructive fishing methods, river input containing waste water and pesticide as a result of heavy agriculture and development, land reclamation, and increased sedimentation rates in the vicinity of river mouths (Munro and Williams 1985, Rogers 1990, Wittenberg and Hunte 1992, McManus 1997, Erdmann 1998, Fox et al. 2001, Burke et al. 2002, Wilkinson 2004). Additionally, the effects of anthropogenic carbon dioxide emissions such as rising sea levels, increased CO<sub>2</sub> concentrations in the atmosphere and elevated sea-surface temperatures put increasing pressure on an already threatened ecosystem (Kleypas et al. 1999, Gattuso and Buddemeier 2000, Harvell et al. 2002, Buddemeier et al. 2004, Feely et al. 2004, Hoegh-Guldberg et al. 2007). Hence, the development of sustainable forms of usage of coral reef resources and the means to alleviate negative impacts (e.g. through active restoration of coral reefs, Yap 2000) is of upmost importance if the chance of continued existence of this unique ecosystem in the face of human pressure is to be improved.

## **1.2 Fishes in coral reefs**

The fish assemblages associated with coral reefs are the most speciose known today (Emery 1978, Choat and Bellwood 1991, Paxton 1995, Spalding et al. 2001). The shorefish fauna of the Indo-Pacific comprises almost 5000 species from 179 families, of which about 90 % can be considered ‘coral reef fishes’ (i.e., living on coral reefs, *sensu* Bellwood 1998) (Myers 1999). About 18 % of all extant fish species are found on the coral reefs and associated habitats of the Indo-Pacific (Choat and Bellwood 1991). The highest diversity with almost 2700 inshore fish species is found in the region of the Southern Philippines and Eastern

Indonesia, and the number of species decreases with increasing distance from this center of marine biodiversity (Myers 1999).

Although there is some degree of controversy over what constitutes a reef fish (Bellwood 1998, Robertson 1998, Bellwood and Wainwright 2006) and no families are restricted to coral-rich regions only (Robertson 1998), there is a wide range of species that rely on coral reefs at least during parts of their lives, e.g. for food or shelter (Patton 1976, Reese 1977, Glynn 1990, Choat and Bellwood 1991, Myers 1999, Jones et al. 2004). Besides being influenced by a range of physical factors that also exert an influence on the coral community, such as wave exposure, sedimentation, water depth and structural complexity (Risk 1972, Gladfelter et al. 1980, Rogers 1990, Jennings et al. 1996, Friedlander and Parrish 1998, Ferreira et al. 2001, Dominici-Arosemena and Wolff 2005, Gratwicke and Speight 2005a, Brokovich et al. 2006), reef fish assemblages have been shown to be closely correlated with certain biological attributes of the benthic biota, such as live coral cover, species composition, and diversity (Bell and Galzin 1984, Roberts and Ormond 1987, Sano et al. 1987, Chabanet et al. 1997, Garpe and Öhman 2003, Jones et al. 2004, Walter and Haynes 2006, Feary et al. 2007), although live coral cover may be correlated with physical variables and thus fail to show a significant influence on the fish community (Lecchini et al. 2003).

Two alternative theories about assemblages of fishes on coral reefs have emerged in the 1970s (see discussions by Helfman 1978, Sale 1980a, Montgomery 1990 and Greene and Shenker 1993). The ‘order’ (deterministic) theory postulates a high degree of niche partitioning and assumes a powerful role of biotic interactions such as competition and facilitation, resulting in stable and predictable fish communities (e.g., Smith 1973, Smith and Tyler 1975, Clarke 1977, Brock et al. 1979, Gladfelter et al. 1980, Ogden and Ebersole 1981). On the other hand, the ‘chaos/lottery’ (stochastic) theory was first based on the observation that several species comprising a guild with similar habitat and food requirements can co-exist within a small reef area. Rather than ecological interactions, priority in the arrival of larvae in a free habitat patch, which is becoming available largely due to stochastic processes like death and disturbance, is responsible for shaping a fish assemblage. Thus, communities are viewed as highly variable and unpredictable (e.g., Russel et al. 1974, Sale 1977, 1980b, Molles 1978; Talbot et al. 1978, Sale and Williams 1982).

However, it has been pointed out that some of the apparent contradictions in the two theories may have arisen due to differences in spatial and temporal scale of sampling and geographic region examined (Helfman 1978, Ogden and Ebersole 1981, Bohnsack 1983). The two theories are not mutually exclusive, and the processes they describe probably all are involved to some degree in the structuring of reef fish assemblages, although their relative importance may vary depending on the specific setting and scale of the system studied, and other processes not fully considered in the original theories such as predation or pre-settlement interactions may be responsible for the structure of an assembly (Anderson et al. 1981, Bohnsack 1983, Williams 1991, Caley and St. John 1996, Syms and Jones 2000). Recent work emphasizes that the sensory and physical capabilities of reef fish larvae are stronger than previously thought, making the process of settlement more than a matter of chance (Montgomery et al. 2001, Leis et al. 2003, Leis and McCormick 2006, Myrberg and Fuiman 2006). However, a stochastic element certainly remains and different patterns will be found depending on the availability of suitable habitat and larvae, spatial and temporal scales, and disturbance processes (e.g., Hixon 1991, Jones 1991, Sale 1991a).

By extrapolating from the Caribbean, Smith (1978) estimated the fisheries potential of the coral reef areas worldwide to be 6 million metric tons per year, which is about 7% of the

current world marine capture fisheries production (Russ 1991, FAO 2006). In an overview, Russ (1991) reported fishing yields of coral reefs ranging from 0.42 to 36.9 mt km<sup>-2</sup> y<sup>-1</sup>. Maximum sustainable yields from intensively fished coral reefs are estimated to be between 10 and 20 mt km<sup>-2</sup> y<sup>-1</sup> (Munro 1984, Bryant et al. 1998). For Indonesia and the Philippines, sustainable fisheries hold the highest potential annual economic net benefit (Burke et al. 2002).

### 1.3 Reef restoration

The discipline of coral reef restoration is rather new when compared to the restoration of other ecosystems (Precht 2006, Edwards and Gomez 2007). Within the field of reef restoration, three different approaches can be discerned (Spurgeon and Lindahl 2000):

- restoration of a reef habitat usually aims at re-creating the state of the habitat prior to an impact, e.g. in terms of its function, species composition, biological diversity or structure.
- rehabilitation involves the partial restoration of characteristic functions and qualities, or the replacement by an alternative set, usually according to pre-defined objectives, accelerating natural recovery. The resulting community is not necessarily the same as the previous one.
- creation of coral reef habitat in areas that did not previously have coral growth, either by coral transplantation or by the alteration of conditions so as to be suitable for coral survival and growth.

Miller et al. (1993) defined reef restoration in a broader sense, as ‘a proactive program designed to speed natural recovery to an end point that has aesthetic value and is functional as a coral reef ecosystem’ (cited in Clark 2002). For the sake of simplicity, all of the three approaches will be referred to as ‘reef restoration’ in this overview, although most projects undertaken to date constitute reef rehabilitation rather than restoration.

A large part of the technologies and approaches in reef restoration have been developed in the mitigation of ship groundings (e.g., Hudson and Diaz 1988, Jaap 2000, Bruckner and Bruckner 2001, Ebersole 2001, Hudson and Goodwin 2001, Miller and Barimo 2001, Tilmant et al. 2003, Bruckner and Bruckner 2006, Schmahl et al. 2006), particularly off the coast of Florida, where over 1500 vessels are estimated to scrape the reef *per annum* (Jaap 2000). Additionally, reef restoration has been attempted to counteract impacts from natural causes such as storms or crown-of-thorns starfish (Harriott and Fisk 1988a, Hudson and Goodwin 1997) and from human activities such as tourism (Rinkevich 1995), destructive fishing, dredging and coral mining (Auberson 1982, Gabrie et al. 1985, Clark and Edwards 1994, Fox et al. 2001), and coastal development and pollution (Plucer-Rosario and Randall 1987, Newman and Chuan 1994, Muñoz-Chagín 1997, Raymundo et al. 1999). In order to provide stakeholders with the scientific knowledge, tools and procedures of reef restoration, a variety of manuals on the subject have appeared since the 1990s (e.g., Harriott and Fisk 1988a, Miller et al. 1993, Heeger and Sotto 2000a, Clark 2002, Omori and Fujiwara 2004, Precht 2006, Edwards and Gomez 2007, see also Thomas 2001).

Generally, reef restoration techniques follow three distinct steps: removal of alien material, consolidation of the substrate e.g. by removal of sediments and loose fragments or cementing

and attachment of broken reef framework, and the recreation of structural complexity and benthic biota with artificial reefs and transplantation of organisms (for excellent overviews of the techniques involved, see Jaap 2000 and Clark 2002). Depending on the scale and intensity of the impact, and the scope, scale and budget of the restoration effort, all steps or a combination of some of them will be employed in restoration efforts.

Some ecological success criteria of restoration efforts that have been identified include an increase in coral cover, the reaching of large size and old age by coral colonies, the building-up of reef framework, an increase in fish biomass and other biological resources, and the accumulation of diverse populations (Clark 2002). Although a significant development of restoration techniques has occurred in response to anthropogenic impacts in the last two decades, Clark (2002) has cautioned that ‘reef restoration is largely limited by incomplete knowledge on the ecosystem processes’. Additionally, the potential benefits of coral restoration have not been adequately studied yet (Spurgeon and Lindahl 2000). One of the areas identified as in need of further research by Zimmer (2006) is the ‘determination of the scenarios under which transplantation and artificial reefs will enhance recruitment of corals [and] fish’.

### **1.3.1 Artificial reefs**

Artificial reef structures have historically been constructed primarily to enhance fishing success in recreational or commercial fishing (Grove and Sonu 1985, Mottet 1985, Stone 1985, Seaman and Sprague 1991). In Japan, artificial reefs have been constructed for centuries (Ino 1974, cited in Bohnsack and Sutherland 1985). Artificial reefs have first been employed to study coral reef fish communities in 1960 (Randall 1963). Since then, artificial reefs have been utilized in a wide range of studies on the ecology of reef fishes (see review by Bohnsack and Sutherland 1985). The primary purposes of artificial reefs in reef restoration is the provision of stability, topographic relief, shelter and refuge (Clark 2002), thus creating habitat for fishes and other biota, and the provision of hard substrate for the settlement of coral recruits (Clark and Edwards 1994, Kaufman 2006).

A large number of previous studies dealt with artificial reefs as a simple and cost-effective method of restoring partially or completely destroyed coral reefs (e.g. Fitzhardinge and Bailey-Brock 1989, White et al. 1990, Clark and Edwards 1994, Pickering et al. 1998, Lam 2003). For these reefs, a number of different materials, ranging from old tires, scrap metal and boulders to elaborate metal constructions and segments specifically made from concrete, were used. Several studies have demonstrated that concrete constitutes a suitable substrate for coral settlement (Schuhmacher 1973, Fitzhardinge and Bailey-Brock 1989, Hudson et al. 1990, Thongtham and Chansaang 1999).

Three standardized technologies for the construction of modular structures for reef restoration have been developed (Kaufman 2006). The most widely applied one is called ReefBalls and consists of hemispheres of variable sizes that are cast in special molds from a cement mixture with certain additives that result in a pH value of the substrate equivalent to that of sea water (Reef Ball Foundation 2007). The surface of the structures can be designed flexibly to include holes, crevasses and increased rugosity. According to the manufacturer, more than 500,000 structures have been deployed in over 59 countries to date (Reef Ball Foundation 2007). However, most of the published information is from the manufacturer, and few independent studies on the use of this technology are available to date (e.g., Ortiz-Prosper et al. 2001, Sherman et al. 2002). Another product consists of branching ceramic modules dubbed EcoReefs (Moore and Erdmann 2002). These mimic branching coral habitat and seem to be a

suitable substrate for the settlement of coral recruits (pers. observation). A study on the recruitment of coral larvae onto EcoReef structures is currently being carried out in Indonesia. However, the costs associated with both of these methods are considerable – according to Fox et al. (2005), ReefBalls require more than 40 USD m<sup>-2</sup> in materials and about 1000 USD per mold, while EcoReefs cost around 70 USD m<sup>-2</sup>.

The third technology has been developed by Hilbertz in the 1970s (Hilbertz et al. 1977, Hilbertz 1992) and involves electrolysis of seawater at low current densities to induce the precipitation of aragonite (CaCO<sub>3</sub>) and brucite (Mg(OH)<sub>2</sub>) onto a cathode, usually an iron structure shaped to suit a certain purpose, e.g. the creation of attractions for divers (van Treek and Schuhmacher 1998). Originally called ‘solar-generated building material’ (Hilbertz 1992), this technology has become known as Biorock (Kaufman 2006). There are observations of enhanced coral performance on this material (Goreau et al. 2000), but experimental studies have not been fully able to explain these observations (van Treek and Schuhmacher 1997, Sabater and Yap 2002, Sabater and Yap 2004, Eisinger et al. 2006, Ferse and Romatzki 2006), and further research is needed. Of the three technologies introduced here, Biorock is probably the least expensive one, but it requires the highest amount of post-construction maintenance due to the need for constant power supply.

In the end, the success criteria for the use of any artificial reef structure will be a combination of economic (e.g., costs of the method and benefits derived, Spurgeon and Lindahl 2000), ecological (e.g., increasing biomass and diversity of the reef fish population, Clark 2002) and physical (e.g., effectively stabilize the substrate or reduce wave energy, Jaap 2000, Kaufman 2006) considerations.

### **1.3.2 Coral transplantation**

Transplantation of corals has been used widely in ecological studies, first to determine the growth rates of certain species (Vaughan 1911, 1915; Mayor 1924; Edmondson 1929), and later for a range of subjects, such as the effects of environmental conditions on coral physiology (Neudecker 1982, Wellington 1982a, Yap and Gomez 1984, Clark 1997, Custodio and Yap 1997, Yap et al. 1998, Yap and Molina 2003, Dizon and Yap 2006), impacts of fish feeding on coral distribution (Neudecker 1977, Neudecker 1979, Wellington 1982b, Grottoli-Everett and Wellington 1997), the effects of transplantation and the methods used on coral growth, survival and fecundity (Yap and Gomez 1982, Alcala et al. 1982, Yap and Gomez 1985, Bowden-Kerby 1997, van Treek and Schuhmacher 1997, Yap et al. 1992, Nagelkerken et al. 2000, Lindahl 2003, Yap 2004), and to study population genetics (Bothwell 1982, Heyward and Collins 1985).

However, beginning with Maragos (1974), coral transplantation has been advocated as a tool for reef restoration. Since then, transplantation has been carried out to rehabilitate reefs affected by blast fishing (Auberson 1982, Bowden-Kerby 2003), coral mining (Clark and Edwards 1995, Bowden-Kerby 2003), sewage and thermal effluents (Maragos 1974, Birkeland et al. 1979), vessel groundings (Gittings et al. 1988, Hudson and Diaz 1988, Jaap 2000), temperature anomalies and algal blooms (Guzmán 1991), crown-of-thorns starfish (Harriott and Fisk 1988a), and tourism (Rinkevich 1995), and to rescue corals threatened by pollution and coastal development (Plucer-Rosario and Randall 1987, Newman and Chuan 1994, Muñoz-Chagín 1997) and create additional reef habitat for tourism (Bouchon et al. 1981).

According to Harriott and Fisk (1988b), the ‘primary aim of coral transplantation is to bypass the early slow growth phase by adding established colonies with a higher probability of survival and rapid growth rate’. Additional rationales for employing transplantation of corals in reef rehabilitation are the enhancement of the aesthetic value of an area for divers (Shinn 1976), enhancement of survival for locally rare species (Plucer-Rosario and Randall 1987, Edwards and Clark 1998), addition of live coral material to recruitment limited areas (Edwards and Clark 1998, Bowden-Kerby 2001), rapidly increasing the coral cover, biodiversity, and structural heterogeneity of an impacted area, thus creating habitat for reef-associated organisms like fishes (Maragos 1974, Gittings et al. 1988, Harriott and Fisk 1988b, Edwards and Clark 1998, Lindahl 1998, Bowden-Kerby 2003), and enhancement of coral recruitment to the area, either by asexual reproduction of branching transplants (Highsmith 1982, Harriott and Fisk 1988b), stimulation of settlement by the presence of transplants (Edwards and Clark 1998), or seeding of the surrounding area (Miller et al. 1993, Edwards and Clark 1998). Since several coral species brood their larvae instead of releasing gametes to the water column in a mass spawning event, it has been postulated that the use of brooding species, whose larvae are able to settle shortly after being released, could be a particularly effective form of transplantation (Rinkevich 1995, Edwards and Clark 1998). Additionally, the amount of time spent in the water column by coral larvae differs from species to species even after a mass spawning event (Harrison und Wallace 1990). Thus, even the use of spawning coral species in transplantation may lead to increased rates of larval settlement in the surrounding areas. However, the only study that had examined the effect of transplantation on recruitment did not find a significant difference in recruitment rates on artificial structures with and without transplanted corals (Clark and Edwards 1995).

Fish abundance, biomass and number of species are closely correlated with the condition of the coral community (Bell and Galzin 1984, Sano et al. 1987, Hourigan et al. 1988, Feary et al. 2007). A structural destruction of coral reefs is often followed by a dramatic decrease of both fish diversity and fish biomass (Alcala und Gomez 1987). It is unclear, however, whether this observed decrease is a result of the decreased substrate complexity (Carpenter et al. 1982) or linked to the low food availability over dead reef areas (Porter und Porter 1977). Although the potential positive effect of coral transplantation on the fish community has been widely stated, only few studies have been published that included observations on this connection (e.g., MBA International 1993 cited in Jokiel et al. 2006, Pamintuan et al. 1994a, Alfeche 2003).

## 1.4 Coral farming and reef management

The global marine aquarium trade is a multi-million dollar industry, worth more than 200 million USD year<sup>-1</sup> (Wabnitz et al. 2003). Stony corals are contributing a growing percentage to the total trade, and the trade in live stony corals has increased dramatically in the last two decades (Raymakers 1998, Green and Shirley 1999). Indonesia has surpassed the Philippines as the number one source of globally traded stony corals in the late 1980s and is now supplying over 90 % of the traded corals (O’Brien Shoup and Gaski 1995, Bentley 1998, Green and Shirley 1999). The U.S. is the major importer of corals, followed by the E.U. (Green and Shirley 1999, Wabnitz et al. 2003). Until now, the largest part of the traded corals is still harvested in the wild. However, commercial coral farming operations have begun in the Philippines, Japan, Pohnpei, Marshall Islands, Solomon Islands, Fiji and Indonesia (Heeger und Sotto 2000a, Delbeek 2001, Wabnitz et al. 2003).

As pressures on coastal resources continue to grow, the need for sustainable forms of usage and alternative, non-destructive forms of income generation becomes ever more pressing (Franklin et al. 1998, Bell et al. 2006). In Indonesia alone, losses caused by damage from destructive fishing have been estimated at several billion dollars over the last few decades (Pet-Soede et al. 2000). Coral farming has several potential advantages: it can help to reduce the pressure on wild populations by utilizing coral broodstocks, constitute a sustainable alternative means of income for coastal populations, raise awareness and a sense of belonging for reef resources, and produce fragments for the restoration of degraded reef areas (Franklin et al. 1998, Heeger et al. 1999, Heeger and Sotto 2000b, Borneman and Lowrie 2001, Bowden-Kerby 2003, Knop 2003). Conventional coral transplantation in restoration efforts usually entails considerable costs for labor and special materials for the attachment of fragments or colonies (e.g., epoxy or cement) and hence is not an option for those tropical countries where impacts on reefs are typically gravest (Kojis and Quinn 1981, Hatcher et al. 1989, Maragos 1992, Muñoz-Chagín 1997, Edwards and Clark 1998, Spurgeon and Lindahl 2000, Zimmer 2006). In coral farming, fragments of coral are usually grown in the open ocean on special culture media (e.g., bamboo boards or metal racks, Heeger and Sotto 2000a, Knop 2003, Ferse 2004). A considerable amount of time and effort could be saved if these fragments can be placed directly into areas to be rehabilitated on their culture media, without further attachment of each individual (Bowden-Kerby 1997, Lindahl 1998).

Edwards and Clark (1998) cautioned that the transplantation of coral fragments for restoration purposes is warranted only in cases where natural regeneration is either insufficient or not possible. They argued that the benefit accruing to a damaged area by the transplantation of fragments is to be weighed against the damage being caused at the source site by the collection of the corals. However, if the transplanted fragments have been reared in a coral farm, there is no damage occurring to the reef. Were it possible to increase the rate of larval recruitment in the vicinity of the rehabilitation site, this would constitute a further advantage of using living fragments in reef restoration.

## 1.5 Research questions and hypotheses addressed

In this study, the effects of artificial reef structures and farm-sized coral fragments on the fish community and on coral recruitment were examined. Specifically, the following questions were addressed:

- What are the effects of the presence of artificial structures on fish abundance, number of species, biodiversity and community composition?
- What are the effects if coral fragments are added to the artificial structures?
- Do observed effects (such as higher or lower abundance, or changes in community composition) differ between locations with different environmental conditions, e.g. different depth and substrate composition?
- Does the presence of coral transplants affect coral recruitment?
- Does the kind of coral species transplanted influence the composition of coral recruits?
- What is the survival rate of coral fragments when attached to decomposing bamboo substrates, and are there species-specific differences?
- What are the costs and quantifiable benefits of the examined methods?

Four hypotheses regarding the results were formulated:

- 1.) Coral transplants in combination with artificial structures lead to a significantly larger increase in fish abundance, number of species and diversity than artificial structures alone.
- 2.) The fish community differs in terms of species composition and their relative abundance between bare rubble plots, plots with artificial structures, and plots with structures and coral transplants.
- 3.) Between-location differences in depth and substrate composition are reflected in the composition of the fish community at each location.
- 4.) Coral transplantation enhances recruitment and alters the family composition of coral recruits in the transplant plots compared to plots containing only structures.

The results of the study are expected to

- help in the understanding of fish community responses to different restoration methods, allowing for a better selection of appropriate measures when faced with the task of restoring a specific site,
- provide information on the suitability of inexpensive culture media as a substrate for low-tech reef rehabilitation,
- give a first impression on the feasibility of using farm-sized coral fragments in medium-scale reef rehabilitation efforts,
- provide information on the performance of selected species in low-tech reef rehabilitation, and
- allow for an estimate of the associated costs and potential benefits of the described methods.

Thus, this study is meant both to give a better understanding of the involved ecological processes and to provide a reference for managers and stakeholders concerned with the rehabilitation and sustainable use of coral reef resources, allowing them to formulate a timely, adequate response to the increasingly diverse array of threats that reefs all over the globe are facing.

## 2. Materials and Methods

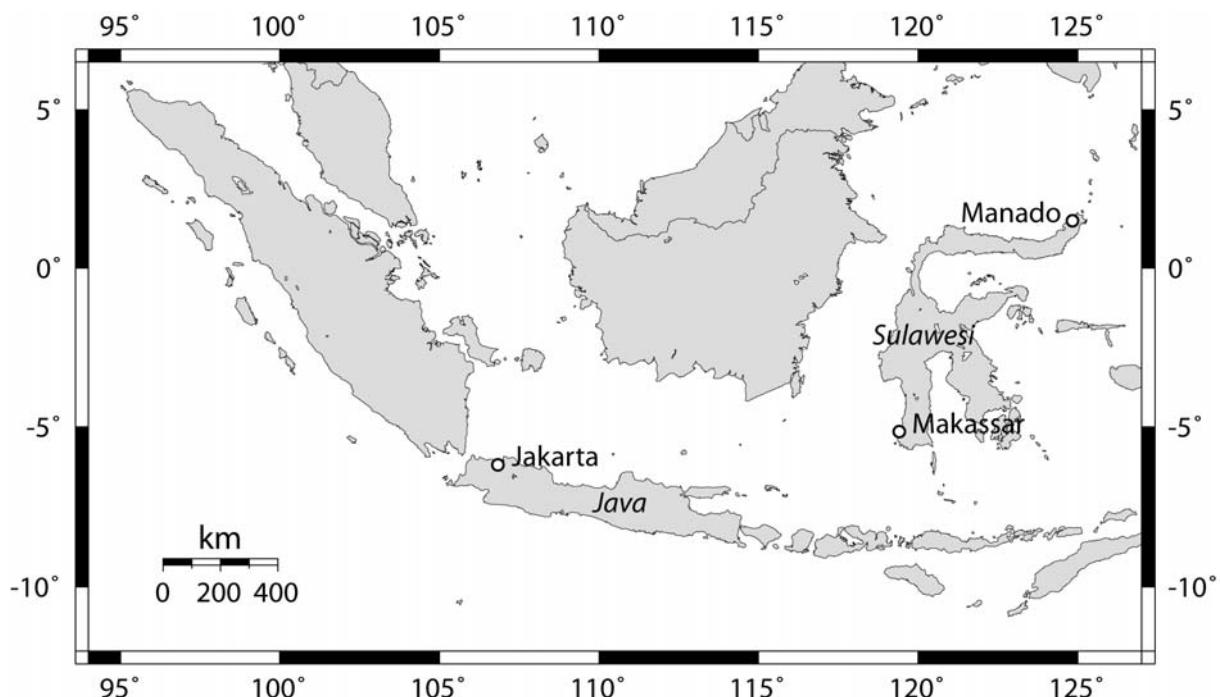


Diver attaching fragments of *Acropora yongei* in the Structures + Corals plot at Gangga, June 2005. © S. Romatzki.

## 2.1 Study area

This study was conducted at three locations in the northernmost part of North Sulawesi, Indonesia, between May 2005 and July 2007. The northern tip of Sulawesi is located slightly north of the equator, between 1° and 2° North (Fig. 2.1). The region is subject to a dry season from August to October and a wet season from November to April (Whitten et al. 2002). During the dry season, the prevailing winds are from the southeast; during the wet season, the wind is coming from the northwest. Throughout the year, average daily air temperature ranges from 22 to 32 °C (MSN 2008), surface water temperatures are from 25 to 30 °C (S. Ferse and S. Romatzki, unpubl. data), and the annual precipitation ranges from 2000 to >4000 mm yr<sup>-1</sup> (Whitten et al. 2002). Tides in the region are diurnal, with a maximum amplitude of about 1.2 m.

During the last decade, rapid economic growth and coastal development have lead to increased deterioration of the coastal environment in Manado Bay (Putra and Cottrell 2000). The capital of North Sulawesi, Manado, is a rapidly growing city of about 400,000 inhabitants. Income is derived mainly from agriculture and fishing, but tourism in the area (mostly diving) is becoming an increasingly important economic factor (DeVantier and Turak 2004).



**Figure 2.1:** Map of western Indonesia, showing the location of the capital of North Sulawesi province, Manado.  
Source: IFM Geomar 2007

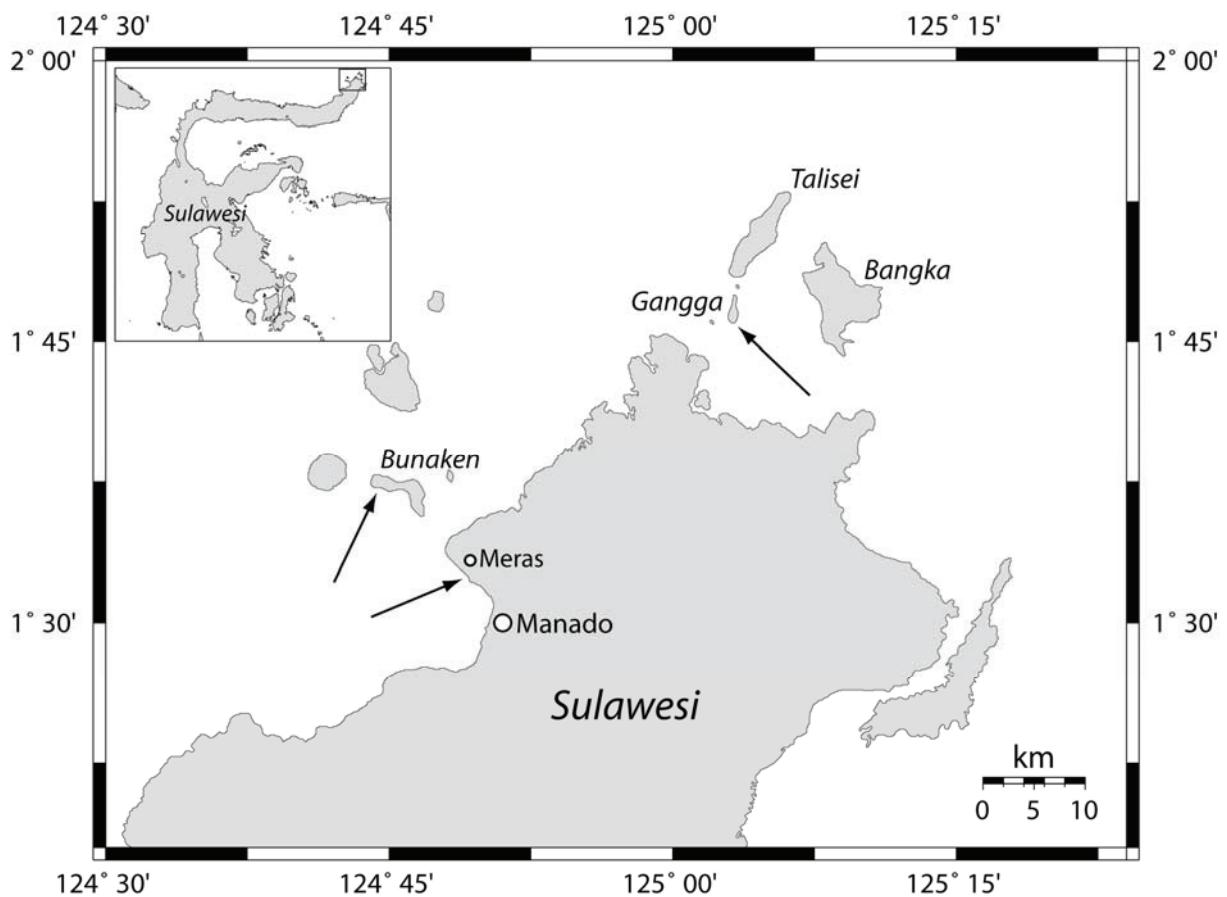
North Sulawesi is located in the middle of the South-East Asian triangle of marine biodiversity (Briggs 1999, Allen 2000). It is the convergence of the Celebes Sea to the northwest, and the Molucca Sea and Pacific Ocean to the east. It is also situated at the upper end of the Indonesian Throughflow, a vast current system connecting the Pacific and the Indian Ocean. A 2003 survey found around 390 species of stony corals and an exceptionally high level of alpha diversity in the waters around Bunaken National Park compared to other sites in the marine biodiversity triangle (Turak and DeVantier 2003). Bunaken Island (see Fig. 2.2), protected as part of the Bunaken Marine National Park since 1991, is the focal point of diving tourism in the region. A recent report stated that with more than 6000 divers per year visiting Bunaken alone, the carrying capacity of the area was likely to be exceeded soon

(DeVantier and Turak 2004). Degradation of coral reefs in the area is caused mainly by increases in pollution, land reclamation and fishing, but also tourism (Putra and Cottrell 2000). However, due to efforts of local authorities and dive operators to regulate the number of visitors and spread them more evenly over the region, more and more visitors are frequenting the nearby islands to the north of Manado, outside the borders of the national park.

Destructive fishing was widespread in the area several years ago, and although it has become less frequent during the last decade, use of homemade explosives and cyanide continues to be a problem in the more remote areas of the national park and beyond its borders (Putra and Cottrell 2000, Erdmann 2002, Turak and DeVantier 2003).

## 2.2 The study sites

The study was conducted at three experimental sites in the vicinity of Manado (Fig. 2.2). The first one was located on Gangga Island (at  $1^{\circ}45'29.0''\text{N}/125^{\circ}3'10.0''\text{E}$ ), the second one in the Bay of Manado between the villages of Molas and Meras (at  $1^{\circ}32'28.5''\text{N}/124^{\circ}49'12.0''\text{E}$ ), and the third site at Bunaken Island (at  $1^{\circ}36'53.0''\text{N}/124^{\circ}44'26.5''\text{E}$ ).



**Figure 2.2:** Map of the study area. The three experimental sites are shown by arrows. The location within Sulawesi is indicated on the map in the inset. Modified after IFM Geomar 2007

The experimental site on Gangga was situated on the southern side of the island, in front of the Gangga Island Resort (Fig. 2.3a). Here, the coast consists of a sandy beach with an adjacent seagrass bed of 50 – 100 m width, followed by a reef crest and gentle reef slope. The reef crest is covered by a mix of corals, mostly branching and foliose *Montipora* species and

other branching Acroporid and Pocilloporid species. The slope is characterized by a high amount of coral rubble and soft and leather corals, with a mix of more robust stony corals. On the southern side, the reef slopes down to about 12 m and ends on a flat seafloor covered mostly with coral rubble. In the shallow basin between the two islands of Talisei and Bangka in the north and Sulawesi in the south, water depth ranges between 20 and 30 m. Consequently, tidal currents are strong, reaching speeds in excess of  $50 \text{ cm s}^{-1}$  during spring tide (Ray et al. 2005). During the monsoon season, this site is protected from the prevailing winds from the northwest. However, at the peak of the dry season (July to September), the southern shore of Gangga is subject to strong wind and wave action from the southeast.



**Figure 2.3:** Aerial view of the experimental sites at Gangga (A), Meras (B) and Bunaken (C). The location of the experiments in each reef is circled. Scale bars represent 300 m. Modified from Google Earth™ 2007.

In Manado Bay, a set of experiments was located in the reef close to the village of Meras (Fig. 2.3b). Of the three locations used in the experiments, this site is situated closest to the city of Manado (distance to Manado Harbor and Tondano River is approximately 5 km, and distance to another major river draining into Manado Bay is 3 km). This site is located within the mainland section of Bunaken National Park. Although theoretically protected since 1991, damage from anchoring is clearly visible at this location. At Meras, the coastline is fringed with mangrove trees, followed by a reef flat of about 200 m width. The reef slope is very diverse, featuring a wide range of stony corals as well as several big sponges. Structurally, the upper reef slope is very heterogeneous, with several spurs and outcrops of coral heads. In this area, the reefs slopes down rather steep, reaching a narrow shelf covered mostly with coral rubble between 40 and 50 m depth before continuing to slope down to a depth of several hundred meters. Due to its location in Manado Bay, the Meras site is relatively well protected from the prevailing winds during the dry and wet season, but it occasionally is subject to stronger wave action when the wind is blowing from southwest. Tidal currents at this site can be strong during spring tides, but are less forceful than the currents at Gangga.

The third experimental site was located at the western part of the Bunaken Island, within Bunaken National Park, between the popular dive site ‘Fukui’ and Alung Banua village (Fig. 2.3c). Due to the close proximity to the dive site and one of the core zones of the National Park, fishing impacts were low at this spot. Here, the coast is fringed by a mangrove belt of 100 to 250 m width, followed by a wide reef flat with extensive seagrass beds. The upper reef slope features several dense thickets of branching *Acropora* species, mostly *A. brueggemannii*, interspersed with rubble sections. In the deeper parts, a mix of coral rubble, robust *A. palifera* and other stony corals as well as sponges covers the slope. Although the reefs of Bunaken generally consist of steep drop-offs, the reef in this area slopes down less steep to a series of ledges between 40 and 120 m before dropping down to a depth of more than 500 m. The site on Bunaken does not receive much wave action due to its protected location on the southern side of the crescent-shaped island. The currents here are the weakest of the three locations, although run-off from the reef flat above occasionally carries a high load of sediments and nutrients from the seagrass bed, markedly reducing visibility down to a depth of 15 m.

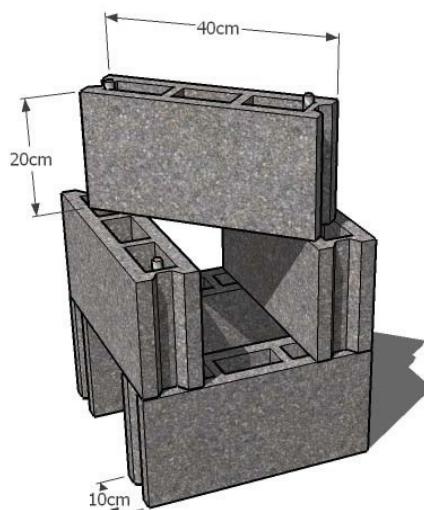
## 2.3 Materials used in the experiments

The experimental set-up had two aims: 1.) to create high structural complexity with the provision of three-dimensional structures and 2.) to imitate the use of fragments from a coral farm in a transplantation project. Materials were used that were similar to those used in coral farming projects and locally available. In coral farming, fragments are transplanted onto a basal structure (usually made from cement) before being temporarily attached to a culture substrate (e.g., bamboo boards) and reared at an accessible site in the coral reef for several months (Ferse 2004). Since it was not necessary to remove the fragments from their substrate, and since coral fragments grow better when firmly attached (Bowden-Kerby 1997, Freytag 2001, Lindahl 2003), a method of more permanent attachment was developed for the coral fragments. Bases for the fragments were manufactured by mixing one part Portland cement, four parts sand and water and pouring the mixture into PVC moulds (Fig. 2.4a). The moulds were made by cutting 4 cm pieces from a PVC pipe ( $\varnothing = 6 \text{ cm}$ ). A 200 mm cable tie was incorporated into each concrete base, and a small hole for fitting the coral fragments was made at the top of each base while the material was still wet (Fig. 2.4b). The cable tie allowed for a convenient attachment of the bases to the substrate after transplantation.



**Figure 2.4:** Bases for the coral transplants were manufactured from concrete (A). The finished bases included a hole for fitting the coral transplants (B).

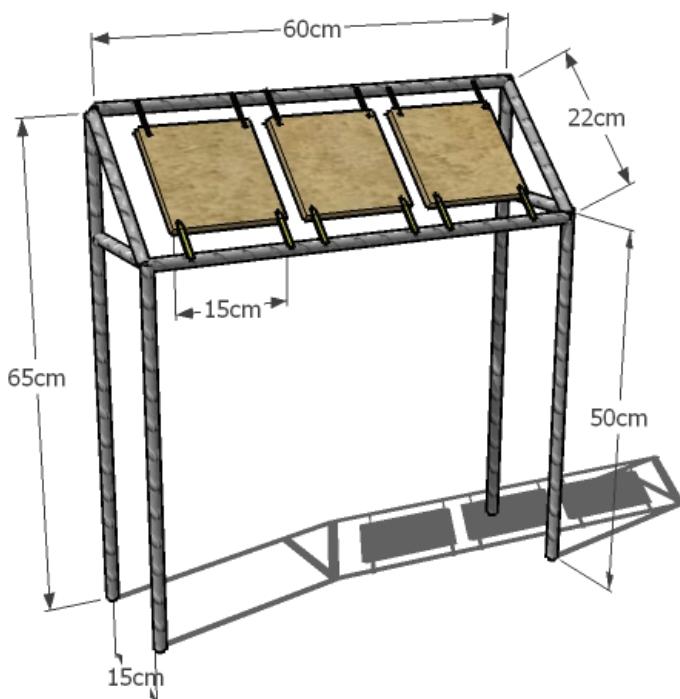
For the artificial structures, concrete blocks ( $10 \times 20 \times 40 \text{ cm}$ ) were used. Five blocks were stacked, two below, two in the middle and one diagonally on top, to form one artificial reef segment (Fig. 2.5).



**Figure 2.5:** Concrete blocks were used to build the artificial reef structures.

Boards made from bamboo strips were used as substrate for the coral transplants. These were similar to those used by a coral farming operation during a previous study (Ferse 2004). The boards were 1 x 1 m in size and consisted of seven horizontal strips of bamboo nailed onto three vertical strips. They were produced locally by craftsmen on Bunaken and Gangga.

In order to examine coral recruitment at the experimental sites, settlement plates were used. Studies on coral recruitment frequently employ unglazed ceramic settlement tiles, since they are easily obtained, are of same sizes and are a preferred substrate for coral recruits (Harriott and Fisk 1987, English et al. 1997). However, unglazed tiles could not be obtained in Manado. Thus, limestone plates were used as a ‘second best’ solution. Limestone was readily available and was considered a good substrate for recruitment, since its composition is similar to natural substrate available for recruits in a coral reef. Plates were cut to a size of 15 x 15 x 1 cm and had a hole drilled into each corner to allow for attachment using cable ties. Settlement frames holding three plates each were constructed from iron reinforcement bars (Fig. 2.6).



**Figure 2.6:** Schematic drawing of the iron frames used to monitor coral recruitment. Each frame was holding three settlement plates.

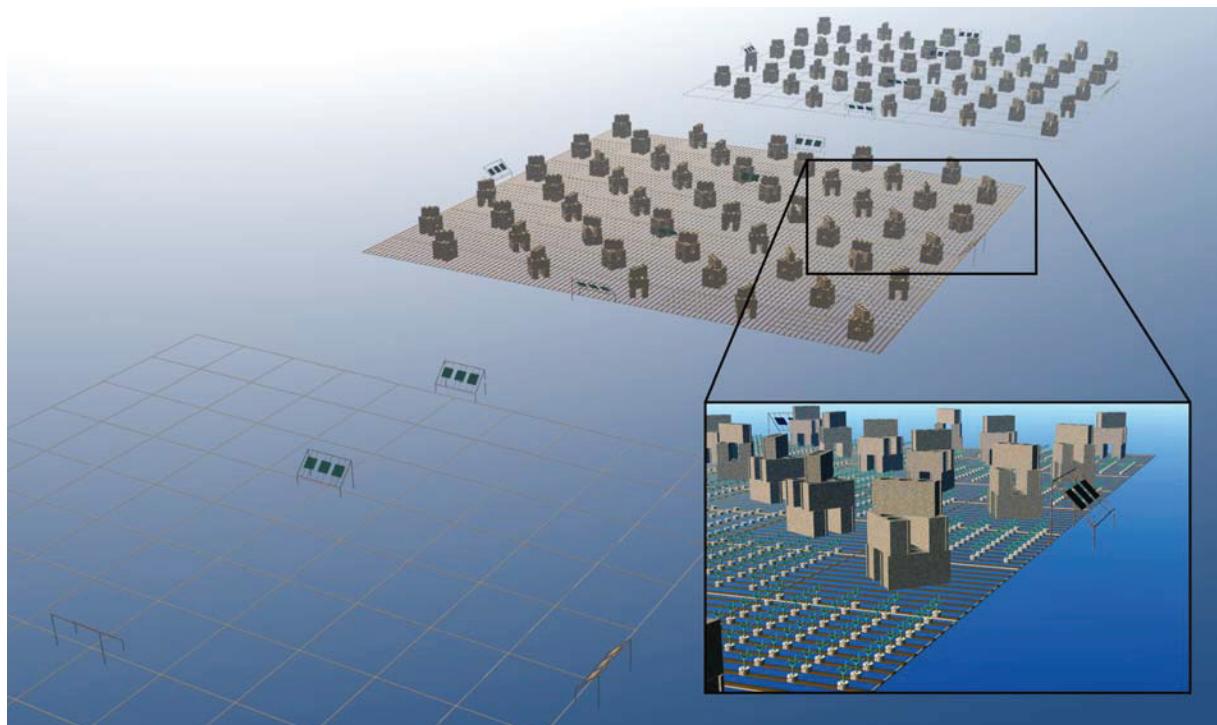
## 2.4 Design of the experimental plots

In order to examine the effects of structures alone and in combination with coral transplants, and to control for site-specific effects, a hierarchical nested experimental design was devised. Sets of experiments were deployed at each of the three locations (Gangga, Meras and Bunaken). Each set consisted of a Control plot, a Structures + Corals plot, and a Structures plot. Plots were 10 x 10 m in size (see Fig. 2.7).

The **Control** plots consisted of coral rubble. Any remaining structures (rocks, coral colonies and fragments >10 cm in size, sponges) were removed and transplanted to the outside of the plots.

**Structure** plots were treated in the same way. In addition, 100 bamboo substrates were distributed in ten by ten rows so that they covered the bottom. Then, artificial structures were constructed on top of every other bamboo board. Each structure consisted of five concrete blocks (see Fig. 2.5) and was fixed onto the reef substrate by hammering four iron stakes through the corners of the structure. The stakes had two lengths: 100 cm length on the two lower corners of the structures, and 120 cm where they were driven through the two ends of the diagonal fifth block on top of the structures. Thus, all stakes penetrated the underlying reef substrate to a depth of 60 cm. The bamboo substrates without structures were left empty and were fixed to the reef by driving 50 cm iron bars through two opposing corners of the boards.

The **Structure + Coral** plots were prepared in the same way as the Structure plots, but in addition, coral fragments were transplanted onto the boards between the concrete structures. Thus, the Structure plots consisted of 50 empty bamboo substrates and 50 concrete structures on top of bamboo boards, while the Structure + Coral plots consisted of 50 structures in combination with 50 bamboo boards holding coral transplants. At all locations, treatment levels were assigned randomly to the plots by the toss of a coin. A schematic view of the layout of a set of experimental treatments is shown in Fig. 2.7.



**Figure 2.7:** Overview of the experimental set-up, showing Control (front), Structure + Coral (middle) and Structure (back) plots. Note that the grid in the Control plot is shown for illustrational purposes only. Graphic by Ari Spenhoff.

At each experimental plot, six settlement frames were installed. One frame each was placed at the center of the shallow and deep side of the plots, and four frames were placed along the central horizontal axis, two on the side and two in the plots, four meters apart. All frames were facing inwards and were hammered into the substrate until the position of the plates was about 20 cm above the substrate. Each frame held three settlement plates, so that a total of 18 plates were deployed at each plot.

## 2.5 Set-up of the sites

In May 2005, suitable sites for the experiments were selected at the three locations using manta tows. Sites were chosen based on their location in the reef and substrate composition. In order to keep the impact from removing rocks and coral from the quadrants, plots with high initial percentage cover of rubble were selected. Also, plots were chosen to be located within an otherwise healthy reef section and at similar depths within each location. The depths for each experimental plot are shown in Tab. 2.1.

**Table 2.1:** Depth ranges of the nine experimental plots.

Location Treatment	<b>Gangga</b>			<b>Meras</b>			<b>Bunaken</b>		
	Control	Str + Cor	Structure	Control	Str + Cor	Structure	Control	Str + Cor	Structure
Shallow side	5 m	5 m	4 m	14 m	12 m	15 m	12 m	12 m	15 m
Deep side	9 m	8 m	7 m	19 m	17 m	20 m	17 m	17 m	19 m

At Gangga, construction of the structures and distribution of the bamboo substrates was done on 18-19 June 2005. From west to east, the plots were designated as Control, Structures + Corals and Structures treatments, respectively. Due to considerable logistical problems, set-up of the other two sites had to be postponed several times. The concrete blocks for the structures were placed in the reef at the experimental sites on 27 July 2005 and thus were subject to a lengthy conditioning period before structures were being assembled. Construction of the experiments at Meraas began on 8 October 2005, but the set-up of the structures was not finished until 16 December 2005. The plots at Meraas were located along the reef roughly from the northwest to the southeast, the Structures treatment being the westernmost, followed by the Structures + Corals and the Control treatments, respectively. The structures on Bunaken were being set up on 2-4 March 2006, and plots were arranged from southwest to northeast in the following order: Structures, Structures + Corals, and Control. For an overview of deployment and exchange times of the plates, see Tab. 2.2.

## 2.6 Transplantation of coral fragments

Species for transplantation of coral into the experimental plots were selected based on four criteria: Local abundance, growth at a depth comparable to the experimental plots, mode of reproduction and, where possible, desirability in the marine aquarium trade. Fragments between 5 and 10 cm were harvested using steel pliers (*Acropora* spp.) and hammer and chisel (*Pocillopora* spp.) and were transported to the transplantation site in ice coolers filled with sea water. Transport time never exceeded 10 min.

### 2.6.1 Gangga

Between 24 June and 31 July 2005, coral fragments were transplanted to the Structures + Corals plot at Gangga. Fragments were collected from the southern side of Lihage Island (1°45'35"N/125°02'14"E) and transported to Gangga for transplantation. Two species, *Acropora yongei* [Veron and Wallace 1984] and *Pocillopora verrucosa* [Ellis and Solander 1786], were selected for transplantation. *Acropora* spp. and *Pocillopora* spp. are among the most frequently traded coral genera (Raymakers 1998, Green and Shirley 1999) and thus were considered to be good representatives of fragments generated by a coral farm. *A. yongei* is a branching species that is common in shallow reef environments (Veron 2000), and the donor colony at Lihage formed a dense thicket >15 m in size. Fragments were collected from depths between 2 and 7 m. *A. yongei* is a hermaphroditic species reported to participate in mass

spawning at the Great Barrier Reef (Babcock et al. 1986), and coordinated spawning was observed in the donor colony of *A. yongei* in May 2007 (pers. observation). *P. verrucosa* is a submassive species with a dense skeleton that is widespread in most shallow water environments (Veron 2000). *P. verrucosa*, identified as a brooding species by Stimson (1978, but see Sier and Olive 1994), was common on the reef flat and upper reef slope of Lihage, with colonies occurring approximately every 5 m. Fragments were collected from depths of 2 to 5 m.

On Gangga, fragments of *A. yongei* were transplanted onto the cement bases using a mix of Portland cement and seawater. Fragments of *P. verrucosa* were attached using hot glue. Directly after transplantation, the bases with the fragments were placed in plastic boxes with approximately 90 l seawater. Each box could hold 100 fragments. Aeration was provided from small air pumps and air stones. Fragments were kept in the boxes over night to allow for the cement to cure. The following morning, the fragments were brought to the experimental site and attached to the bamboo boards using SCUBA. In this way, around 500 fragments could be processed per day.

Per bamboo board, 40 fragments of *A. yongei* and 10 fragments of *P. verrucosa* were transplanted. During the first month, since mortality of corals was still high, fragments that died were exchanged by new transplants in order to achieve a high initial coral cover of approximately 50 fragments per board in the Structures + Corals treatment. At the time of the first *in situ* count of living fragments on 3 September 2005, 1885 fragments of *A. yongei* and 475 fragments of *P. verrucosa* were alive in the Structures + Corals plot at Gangga. These numbers were used as the baseline for subsequent determinations of the mortality rate.

## 2.6.2 Meras

At Meras, fragments of *Acropora formosa* [Dana 1846] and *P. verrucosa* were transplanted. Fragments were collected from the reef area where the experimental plots were located, approximately 100 m to the southeast of the plots. *A. formosa* is a branching species that is common both in lagoons and outer reef slopes, where it can form extensive thickets with widely spaced branches (Veron 2000). It is a hermaphroditic spawning species (Harrison et al. 1984, Babcock et al. 1986, Okubo et al. 2007). The donor colonies extended over an area of more than 10 m. Fragments were collected from depths between 11 and 15 m. Colonies of *P. verrucosa* were common on the reef slope at Meras, and were collected between depths of 7 to 12 m.

The fragments were collected using SCUBA and brought to a boat for transplantation. Corals were transplanted onto the concrete bases using Pioneer Non-Sag Epoxy (Republic Chemical Industries, Inc., 731 Aurora Boulevard, Quezon City, Philippines 1112), an epoxy glue for marine applications. This glue cured faster than the cement used on Gangga and was easier to use when working on a boat. The concrete bases were soaked in salt water for several minutes prior to transplantation to drive out residual air in the material, which otherwise resulted in bubble formation underneath the epoxy, loosening the fragments.

An initial transplantation of coral fragments was carried out between December 2005 and February 2006. Fragments were distributed evenly among the boards. At the time of the first fragment count on 12 March 2006, there were 1494 living fragments of *A. formosa* and 377 fragments of *P. verrucosa*. Subsequently, more fragments were being transplanted, so that by December 2006, an additional 183 fragments of *A. formosa* and 1 fragment of *P. verrucosa* had been added to the plot.

### 2.6.3 Bunaken

Since colonies of *Pocillopora* were not very frequent at Bunaken, and since the most abundant branching *Acropora* species was the brooding *Acropora brueggemanni* [Brook 1893], only *A. brueggemanni* was transplanted at this site. *A. brueggemanni* is a species with sturdy, dense branches that is adapted to more exposed habitats (Veron 2000). It is a brooding species (Atoda 1951, Fadlallah 1983), which could thus be used instead of a brooding *Pocillopora* sp. in order to examine the effect of transplanting a brooding coral on coral larval recruitment. On 31 March 2006, the first 409 fragments of *A. brueggemanni* were collected from a depth of 8 to 10 m from an extensive thicket growing above the Structures + Corals site.

The fragments were brought to a boat, kept in ice coolers filled with seawater, transplanted using epoxy and placed in the reef again. On 7 and 8 April 2006, another 1008 fragments were transplanted and attached during the following two weeks, and by the time of the first count on 2 June 2006, 1318 living fragments were attached at Bunaken. Another 431 fragments were attached by October 2006.

### 2.7 Coral recruitment

In order to monitor coral larval recruitment rates within the experimental plots, settlement plates were deployed at the iron frames and exchanged every three months (Tab. 2.2). Plates were attached to the frames using plastic cable ties. When plates were collected, they were labelled so that the position of recruits relative to the position of the plate within each frame could be determined later. Upon retrieval, the plates were soaked overnight in a 0.2-0.3 % solution of sodium hypochlorite (NaClO), rinsed and dried. Plates were then examined using a magnifying glass, and coral recruits were counted. When in doubt, a stereo microscope with 20-fold magnification was used.

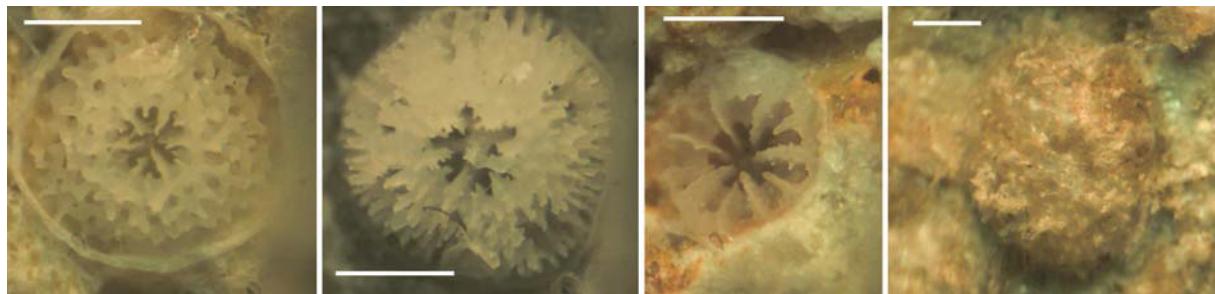
**Table 2.2:** Dates of first deployment, exchanges and final retrieval of the settlement plates at the three research locations.

Exchange of plates	Gangga	Meras	Bunaken
First deployment	27.06. – 03.07.2005	14.-17.12.2005	04.-05.03.2006
1.	01.-03.10.2005	12.03.2006	31.05.2006
2.	25.-27.01.2006	07.06.2006	25.08.2006
3.	21.-22.04.2006	01.09.2006	23.11.2006
4.	13.07.2006	25.11.2006	15.02.2007
5.	18.10.2006	16.02.2007	
6.	18.01.2007		
7.	10.04.2007		
Final retrieval	03.07.2007	11.05.2007	12.05.2007

Recruits on the upper and lower surfaces of the plates were photographed using a Bresser USB Ocular (resolution: 640 x 480 pixel, Meade Instruments Europe, Siemensstraße 6, 46325 Borken, Germany) at maximum possible magnification (20-fold or 40-fold). In cases where recruits were too large, or when they grew on the side of the plates, they were photographed at maximum resolution using a digital camera (Olympus C-5050 and Canon PowerShot A 630) and a tripod. Recruits were subsequently identified to family level, the lowest taxonomic level to which recruits could reliably be identified (English et al. 1997, Babcock et al. 2003), and sorted into three categories: Pocilloporids, Acroporids, and Others. However, there were cases where recruits could not be unmistakably assigned to one of the former three categories (Fig.

2.8). These were counted as ‘Unidentified’. Size of the recruits was measured from the photographs as their maximum diameter.

After all recruits were catalogued, the plates were cleaned from all epigrowth using a chisel and a sanding machine and were then re-used again. Any remaining effect this re-usage may have had on subsequent recruitment was considered negligible, since all plates used at the different treatments were subject to the same procedure. Thus, any observed between-treatment differences in recruitment were likely to be the result of different conditions at the treatments and not of differences in the plates.

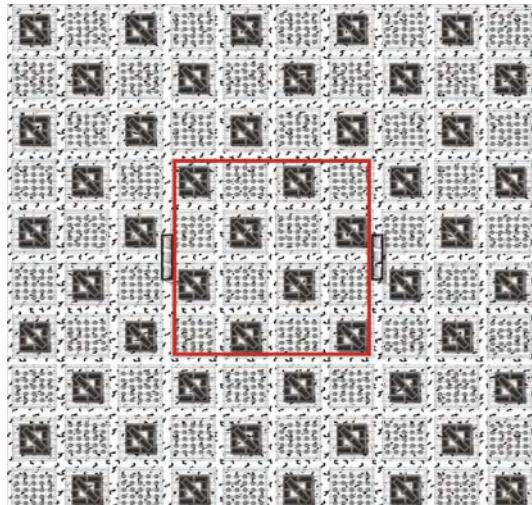


**Figure 2.8:** Examples of the categories used in the categorisation of coral recruits. From left to right: Acroporids, Pocilloporids, and Others. The last photograph shows an example of an unidentified recruit. Scale bars represent 0.5 mm.

## 2.8 Long-term recruitment within the experimental plots

Since coral recruits are subject to intense competition with other epibionts in the months after recruitment (Birkeland 1977, Sammarco and Carleton 1982), it is likely that there was a succession in the epifaunal community on surfaces within the experimental plots. However, the settlement plates were exchanged every three months, too short to allow for late successional stages to develop. Additionally, the concrete blocks comprised most of the available hard substrate within the Structures + Corals and Structures plots. Thus, the species composition on the settlement plates may not have been a good representation of the coral community that was developing on the surfaces within the plots as a result of recruitment and competition processes. In order to compare the species composition of coral recruits on the plates with the composition of corals growing on the concrete structures, the structures were examined for coral recruits in an additional census using SCUBA.

In each plot containing structures, the eight innermost structures (Fig. 2.9) were examined. On each structure, the three topmost blocks were included. For the block on top, all five outer surfaces (top, front, back and two sides) were examined, while on the two blocks below, only the front facing outwards was looked at. Thus, seven surfaces were scrutinized for each structure. On Gangga, the structures were examined on 6 and 7 May 2007, photos at Bunaken were taken at 6 June 2007, and the survey of the structures at Meras was conducted on 27 June 2007. All structures were examined *in situ* with the bare eye using SCUBA, and photos of all corals that could be detected were taken with a Canon PowerShot A 630 camera in a Canon WP-DC 8 underwater housing using maximum resolution. Recruits as small as 3 mm could be detected this way. All recruits were identified to family level and sorted into the categories described above for the recruits on settlement plates. Sizes of the corals were measured as the maximum diameter (first axis) and the maximum diameter on the axis perpendicular to the first one.



**Figure 2.9:** Schematic view of a Structures + Coral site. The position of the structures examined for corals is indicated by the red square.

## 2.9 Visual census of the fish community

### 2.9.1 Operational procedure

The response of the fish community to the experimental treatments was assessed by visual census using SCUBA. An initial list of common fish species was created based on the list given in English et al. (1997) and a number of dives at the Gangga site. The list was later augmented to include additional species occurring at Meras and Bunaken. It was then printed on waterproof paper and carried underwater for the fish census. When species that were not included in the printed list were encountered during a census, they were sketched and later identified. Identification was based on the field guides by Myers (1999), Allen et al. (2003), and Kuiter and Tonozuka (2004).

For the census of the plots, a modification of the line transect (Russel et al. 1978) was used. Each plot was divided into four imaginary horizontal transects of 2.5 m width and 10 m length. Then, a diver swam along all four transects in one plot counting the fishes within the 2.5 m wide strip and up to 2 m in the water column. All three plots at one location were monitored in turn. With the exception of the first census at Gangga, three replicate sets of censuses were carried out within one day during each sampling to account for variability and get an accurate picture of the fish community (McClanahan et al. 2007). A list of the sampling dates is shown in Tab. 2.3. Whenever possible, censuses were carried out between 9.00h and 16.00h to avoid diurnal shifts in species composition (Carpenter et al. 1982, Colton and Alevizon 1981, English et al. 1997). For ease of observation, the censuses were restricted to certain species (GBRMPA 1978). Fishes that were either cryptic (e.g., Gobiidae, Callionymidae) or pelagic (e.g., Caesionidae) were not included in the count. An exception was made for roaming herbivores (Scaridae and Siganidae) and pelagic species with ontogenetic links to the reef substrate (e.g., juvenile Lutjanidae), since their abundances were hypothesized to be related to the substrate components manipulated in the experiment. Since the juveniles of several scarid species (e.g., *Scarus flavipectoralis* and *Scarus quoyi*) were difficult to correctly identify underwater, they were collectively counted as ‘*Scarus* juvenile’.

A very numerous, small wrasse of the genus *Paracheilinus* occurred at all three locations but was particularly abundant at Meras and Bunaken. Due to its small body size and high abundance (groups of this fish sometimes comprised > 100 individuals between 1 and 6 cm)

and the cryptic coloration of the juveniles and females, the accuracy of counts for this species was considered to not be very reliable. Thus, it was excluded from the statistical analysis of the data. Spearman-rank correlation of the similarity matrices of all replicate census samples including *Paracheilinus* sp. with a similarity matrix where this species had been excluded using the RELATE function of PRIMER with 9999 permutations yielded a correlation coefficient of  $\rho = 0.96$  ( $p = 0.001$ ), which shows that removing *Paracheilinus* sp. from the samples did not have a strong impact on community structure and similarity among the samples, and the conclusions derived from the multivariate analysis are not significantly altered by excluding this species from the analysis.

In addition to fish data, visibility and time was noted during each transect. Also, the number of surviving coral fragments and damaged boards in the Structure + Coral treatment was counted during each sampling campaign. Bamboo boards were defined as being damaged when at least one of the bamboo strips was broken.

**Table 2.3:** Dates of the sampling campaigns at the three experimental locations. Intervals between consecutive samplings were increased towards the end at Gangga since the composition of the fish community in the experimental plots was becoming more stable over time.

Sampling number	Gangga	Meras	Bunaken
1	06.09.2005 <sup>†</sup>	09.02.2006	05.03.2006
2	04.10.2005	12.03.2006	02.04.2006
3	30.10.2005	10.04.2006	03.05.2006
4	04.12.2005	08.05.2006	02.06.2006
5	28.01.2006	10.06.2006	05.07.2006
6	14.03.2006	19.07.2006	21.08.2006
7	22.04.2006	25.10.2006 <sup>‡</sup>	17.10.2006
8	08.06.2006	08.11.2006	29.11.2006
9	12.07.2006	06.12.2006	02.01.2007
10	15.08.2006	15.01.2007	01.02.2007
11	19.10.2006	22.02.2007	06.03.2007
12	01.12.2006	23.03.2007	12.04.2007
13	19.01.2007	11.05.2007	23.05.2007
14	25.03.2007	11.06.2007	
15	05.05.2007		

<sup>†</sup>no replicates <sup>‡</sup>some replicates missing

## 2.9.2 Definitions of indices used

Each fish observed was identified to species level and its size was visually estimated and noted. The sizes and abundances of the fishes were used to calculate the biomass using the formulas

$$W_{ik} = a_k L_i^{b_k} \quad (1)$$

and

$$m_k = \sum_{i=1}^{n_k} W_{ik} \quad (2),$$

where  $W_{ik}$  is the biomass of the  $i$ th individual of species  $k$ ,  $a_k$  and  $b_k$  are species-specific conversion coefficients for species  $k$ ,  $L_i$  is the length of the  $i$ th individual of species  $k$ ,  $n_k$  is the number of individuals in species  $k$ ,  $s$  is the number of species in the sample, and  $m_k$  is the total biomass of species  $k$ . The total biomass  $M$  of all individuals is

$$M = \sum_{i=1}^{n_k} \sum_{k=1}^s W_{ik} \quad (3),$$

which is equal to

$$M = \sum_{k=1}^s m_k \quad (4)$$

as follows from formula (2). Conversion coefficients for each species were taken from FishBase (Froese and Pauly 2007). For ease of comparison, biomass values were standardized to  $\text{g}^*\text{m}^{-2}$ .

Biodiversity was calculated as the Shannon index  $H'$  (Shannon and Weaver 1949) using  $\log_2$  (Magurran 1988). In addition to the definitions above,  $N$  is defined as the total number of individuals in a sample:

$$N = \sum_{k=1}^s n_k \quad (5),$$

and  $p_k$  is the relative abundance of each species within a sample:

$$p_k = \frac{n_k}{N} \quad (6).$$

Then, the Shannon index is defined as:

$$H' = -\sum_{k=1}^s p_k \log_2 p_k \quad (7).$$

Following this definition of diversity,  $H'$  reaches its maximum when all species in the sampled community are equally abundant, i.e.  $p_k = 1/s$  for all  $k$  (Pielou 1975). Thus,

$$H'_{\max} = \log_2 s \quad (8).$$

Evenness of the sample was calculated using the index of evenness proposed by Pielou (1975), which defines evenness of an observed community as the ratio of the observed diversity index to the maximum diversity index value in a community with the same number of species:

$$J' = \frac{H'}{H'_{\max}} \quad (9).$$

## 2.10 Comparisons with the natural reef

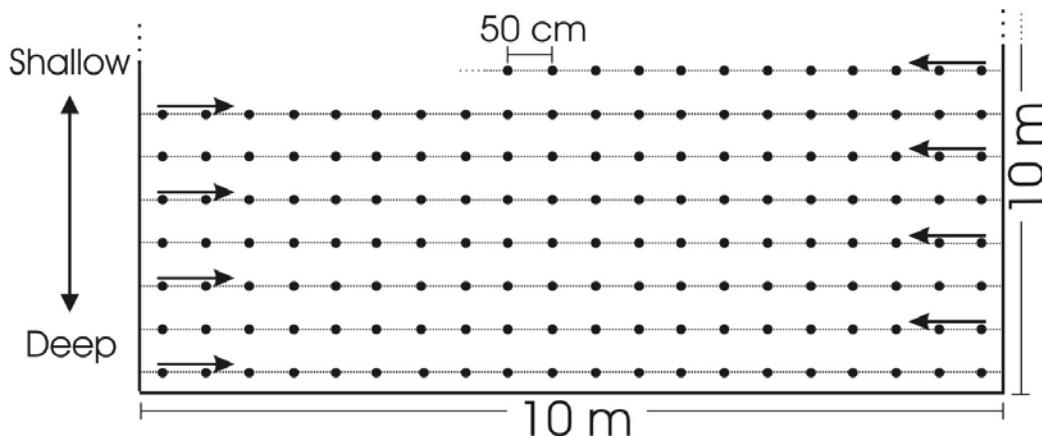
In order to be able to relate the values observed in the experimental plots to the fish community occurring naturally in the surrounding reefs, comparative censuses of plots in the natural reef were carried out. At each location, two 10 x 10 m plots were marked a depth range similar to that of the experimental plots (Tab 2.4). The selected areas were chosen so that their substrate compositions were good representatives of the natural reef at that depth at the respective locations (i.e., not to include features that were spatially rare).

The fishes in the natural plots were counted following the sampling protocol for the experimental plots, with three replicate censuses for each plot (Tab. 2.3).

**Table 2.4:** Depths and monitoring dates of the comparative natural reef plots.

Location	Depth range	Date of fish census	Date of substrate measurement
Gangga 1	4 – 7 m	21.01.2007	26.03.07
Gangga 2	6 – 9 m	27.03.2007	26.03.07
Meras 1	15 – 20 m	09.02.2007	09.02.2007
Meras 2	11 – 16 m	09.02.2007	09.02.2007
Bunaken 1	12 – 16 m	02.02.2007	02. – 03.02.2007
Bunaken 2	12 – 16 m	02.02.2007	03.02.2007

A quantitative assessment of the substrate composition was conducted in order to be able to describe the natural reef habitat at each location. To cater for the special case of a medium-sized fixed plot being surveyed, a method combining the linear point intercept (LPI; Lucas and Seber 1977, Liddell and Ohlhorst 1987) with the planar point intercept (PPI) (Kinzie and Snider 1978, see Ohlhorst et al. 1988 for a discussion of both methods) was used for the benthic census. An equidistant grid of 400 points was positioned over the plots by placing 20 horizontal lines across the plot at a distance of 0.5 m, with the initial line being placed at 25 cm distance from the lower edge of the plot. Then, a diver swam along the lines, noting the substrate type underneath the transect every 50 cm, with the first intercept being placed 25 cm from the beginning of the transect (Fig. 2.10).



**Figure 2.10:** Sketch of the census pattern used to assess the benthic composition in the natural reef plots. The substrate underneath 20 equally spaced points on 20 horizontal transects was categorized, yielding 400 data points per 100 m<sup>2</sup>.

For the characterization of substrate type, the categories of English et al. (1997) were used, with the additional division of Soft Coral into Leather Coral and other Soft Coral, since leather corals were particularly abundant at Gangga. A description of the categories used and their codes is given in Tab. 2.5.

**Table 2.5:** Overview of the categories used for the substrate census in the natural reef. Adopted from English et al. (1997).

Categories	Code	Description
<b>Abiotic</b>		
Sand	S	
Silt	SI	
Rubble	R	unconsolidated coral fragments
Rock	RCK	hard surfaces without significant epigrowth
<b>Algae</b>		
Algal Assemblage	AA	consists of more than one species
Coralline Algae	CA	
<i>Halimeda</i>	HA	
Macroalgae	MA	weedy/fleshy browns, reds, etc.
Turf Algae	TA	lush filamentous algae

<b>Hard Coral</b>			
	Dead Coral	DC	Recently dead, white to dirty white
	Dead Coral with Algae	DCA	overgrown but still standing, skeletal structure can still be seen
<i>Acropora</i>	Branching	ACB	at least 2° degree branching, e.g. <i>A. formosa</i>
	Encrusting	ACE	includes the base-plate of immature <i>Acropora</i> forms
	Submassive	ACS	robust with knob or wedge-like form, e.g. <i>A. palifera</i>
	Digitate	ACD	no 2° degree branching, e.g. <i>A. humilis</i>
	Tabular	ACT	Horizontal flattened plates, e.g. <i>A. hyacinthus</i>
Non- <i>Acropora</i>	Branching	CB	at least 2° degree branching, e.g. <i>Seriatopora hystrix</i>
	Encrusting	CE	major portion attached to substratum as a laminar plate
	Foliose	CF	coral attached at one or more points, leaf-like, or plate-like appearance
	Massive	CM	solid boulder or mound
	Submassive	CS	Tends to form small columns, knobs, or wedges
	Mushroom	CFU	solitary, free-living Fungiid corals
	<i>Heliopora</i>	CHL	blue coral
<b>Other Fauna</b>	<i>Millepora</i>	CMIL	fire coral
	<i>Tubipora</i>	CTU	organ-pipe coral, <i>Tubipora musica</i>
	Leather Coral	LC	soft bodied corals with a leathery skin and a crown or finger-like appendages on a thick stalk, e.g. <i>Sinularia</i> , <i>Sarcophyton</i> and <i>Lobophytum</i>
	Soft Coral	SC	other soft bodied corals
	Sponges	SP	
Zoanthids	Zoanthids	ZO	
	Others	OT	Ascidians, anemones, gorgonians, giant clams, etc.

## 2.11 Analysis of data

### 2.11.1. Univariate analysis of fish data

For univariate data analysis, the program JMP 7.0 (SAS Institute 2007) was used. The values of fish abundance, number of species, biomass,  $H'$  and  $J'$  at each site were analyzed using a general linear model, using the measured variables as dependent variables. Time (days since first measurement) was defined as the independent, continuous variable, treatment as a categorical variable, and the interaction term time\*treatment was included to account for differences in slope (Sall et al. 2005). Underwater visibility was included as an independent co-variable. In order to account for the possibility that the relationship between the dependent and the independent variable was not linear (i.e., the development of the measured variable over time followed a curve rather than a line), an additional model was used that included a curve factor (days<sup>2</sup>). However, this improved the fit of the model only marginally. Thus, the extended model was only used where its fit (as indicated by the R<sup>2</sup>-value) increased by more than three percent compared to the simple model, which was the case in tests of treatment effects on biomass and  $J'$  at Meras, and for number of species,  $J'$  and  $H'$  at Bunaken.

The residuals of the models were checked for normal distribution using a Shapiro-Wilk  $W$  test (Shapiro and Wilk 1965). In order to achieve normally distributed residuals, abundance data were square-root transformed, biomass data were fourth-root transformed and  $H'$  data were transformed by power transformation ( $y' = y^2$ , Zar 1999).  $J'$  data were arcsine transformed

and the curve factor was included to achieve a better fit of the model, but the residuals failed to conform to normal distribution.

Since data from each natural reef plot was only collected once, it was compared to data from the experimental plots taken at the date closest to the one when the natural reef was sampled using a one-way analysis of variance (ANOVA). Fish abundance data were square-root transformed, biomass data were fourth-root transformed and  $H'$  data were power transformed following Shapiro-Wilk  $W$  tests to achieve normal distribution. Data were checked for equal variances using Bartlett's test, and a Welch ANOVA was performed instead of a regular ANOVA in cases where variances were unequal (Zar 1999). In case of significant treatment effects, a Tukey HSD post-hoc test was performed to assess how the treatments differed from each other. For  $J'$  data, normal distribution could not be obtained by transformation. Hence, a nonparametric Kruskal-Wallis test was used instead of ANOVA (Zar 1999). Where significant effects were detected in the Kruskal-Wallis test, individual Mann-Whitney  $U$  tests were performed to assess differences among treatment pairs.

## 2.11.2 Multivariate analysis of fish data

Multivariate analysis of the fish community data was done using the program PRIMER 5.2.9 (Clarke and Gorley 2001). Fish abundance data were fourth-root transformed prior to analysis in order to decrease the influence of the few overly abundant fish species and give more weight to rare species (Field et al. 1982, Clarke and Green 1988). Similarity of the fish abundance samples was defined using the Bray-Curtis similarity coefficient (Bray and Curtis 1957), a coefficient frequently used in ecological studies since it defines similarity according to a set of criteria that generally agree well with ecological theory (for a discussion of the criteria implicit in the various similarity measures available, see Field et al. 1982, Faith et al. 1987, Cao et al. 1997, Clarke et al. 2006):

$$S_{yz} = 100 \left[ 1 - \frac{\sum_{k=1}^s |n_{ky} - n_{kz}|}{\sum_{k=1}^s (n_{ky} + n_{kz})} \right] \quad (10),$$

where  $s$  is the total number of species in all samples,  $n_{ky}$  represents the abundance (or biomass) of the  $k$ th species in the  $y$ th sample and  $n_{kz}$  correspondingly is the abundance or biomass of that species in the  $z$ th sample. The coefficient has three desirable properties (Clarke and Warwick 1994):

- $S = 0$  if two samples have no species in common, and  $S = 100$  if the samples are identical.
- The coefficient is independent of scale –  $S$  will be the same whether abundance is measured in individuals  $\text{m}^{-2}$  or in individuals  $100 \text{ m}^{-2}$ , for example.
- The joint absence of a species from both samples does not have an effect on  $S$ .

However, one additional property of the Bray-Curtis coefficient is that it acts increasingly erratic as variables become sparse, i.e., it will rate samples with few individuals per species and little species overlap as highly dissimilar. In cases where scarcity of species arises from a cause common to both samples (e.g. in the case of several impoverished samples from one biologically degraded site), it is desirable to adjust the Bray-Curtis coefficients to achieve a higher similarity between samples with many zero values (Clarke et al. 2006). Since there was a high fluctuation of observed species in the case of the Control plots, and since there were many zero values because several species observed in the other two plots were absent from

the Control plots, a ‘dummy variable’ was introduced to all samples prior to further analysis. The result is a zero-adjusted form of the Bray-Curtis coefficient (Clarke et al. 2006). This variable takes the value 1 in all samples and increases similarity between ‘impoverished’ samples, while having little effect on the similarities of ‘richer’ samples.

For analyses of differences between the treatments at one location, or between locations within one treatment, all samples taken during the experiment at a location or within a treatment (i.e., three replicates per sampling) were included. In analyses that compared data from all samplings at all locations, or that evaluated development of a community over time, averages of the three replicates per sampling were used.

The contributions of individual species to within-group similarities and between-group dissimilarities (Clarke 1993) were used to find species characteristic of the natural reef plots at the three locations, and of the three treatments at the three locations in the experiment, respectively.

Effects of treatments and sites on differences in fish community composition were examined using a crossed two-way multivariate analysis of similarities (ANOSIM) of all replicate samples, which compares the between-group and within-group similarities based on Spearman rank correlation (Kendall 1970) of the similarity matrices of the samples (Clarke and Green 1988, Clarke 1993). Significance levels were calculated using random permutations of the sample labels (Mantel 1967, Hope 1968), with 999 permutations used in each test. Were significant effects detected in the global test, pairwise tests were used to assess individual differences between the factor groups.

To get an idea of the relative variability of the community in each experimental plot over time, the multivariate dispersion of the average samples was calculated and compared for all combinations of sites and treatments using the MVDISP routine, which utilizes a similarity matrix and contrasts the average ranks of the similarities of different groups of samples (Warwick and Clarke 1993).

For each experimental location, the effects of treatment and time (sampling campaign number) on fish community composition were assessed using a crossed two-way ANOSIM. In this way, permutations of the sample labels were constrained so that replicates from one treatment were compared only to replicates from other treatments taken at the same time, and the effect of time was computed only within each respective treatment. By using this approach, the analysis was strengthened by eliminating confounding effects that could arise if the community in one treatment would over time resemble the community of another treatment at a different time. In this case, an unconstrained ANOSIM might falsely conclude that the communities of two treatments are similar, although in reality at a given time their compositions always differ. Were significant effects of treatment detected in the global test, pairwise tests were used to assess individual differences between the treatments.

Non-metric multidimensional scaling (MDS, Shepard 1962 and Kruskal 1964) based on Bray-Curtis similarity was used to visualize patterns in the multivariate similarity of the replicate samples at the three locations and the changes in average community composition over time for each location. In order to show differences between the three locations, MDS plots combining all replicate samples of one treatment were computed for each location. 30 iterations were used to compute the MDS plots.

For each treatment, differences between the locations were analyzed using crossed ANOSIM. Again, the permutations were restricted to take place only between samples taken at the same time. In order to account for the possibility that time of the year (i.e., seasonal effects on community composition) might be more important than age of the experimental plot (i.e., succession in community composition), tests were run restricted both to within-months comparisons and within-sampling-campaign-number comparisons.

In order to further analyze the similarities between samples from the experiments and the natural reef, hierarchical clustering based on the ranked similarities and average linking was used (Cormack 1971, Everitt 1980, Field et al. 1982). In the analysis, the fish community data from the natural reef plots at the three locations were used together with the data from experimental samples taken at a similar time as the natural reef samples at each location (at Gangga from sampling campaign 14, at Meras from sampling campaign 11 and at Bunaken from sampling campaign 10).

Correlation between the environmental data (substrate composition and depth) and the community composition in the natural reef plots was examined using the BVSTEP procedure (Clarke and Gorley 2001) with 50 % starting variables and 10 restarts. This procedure explores the relationship between similarity matrices for environmental and biological data using Spearman rank correlation (Clarke and Ainsworth 1993) by a stepwise selection of environmental variables resulting in the highest possible match between sample similarities based on environmental variables on the one hand and biological variables (fish community samples) on the other hand. Similarities based on environmental data were computed using normalized Euclidean distances. A new similarity matrix was then computed based on the environmental variables found in the BVSTEP procedure and compared to the similarity matrix based on the biological variables using the RELATE function, a permutation-based procedure (Clarke and Warwick 1994).

In order to examine the effect of the treatments on fishes belonging to different feeding guilds and on differences between the locations, separate crossed two-way analyses of similarity were performed including only species belonging to the groups Herbivores, Carnivores and Piscivores, and Planktivores (based on information from FishBase, Froese and Pauly 2007). Samples in which no species in a respective group were present were excluded from the analysis. Since Obligate Corallivores occurred almost exclusively in the Structures + Corals plots and were absent from all samples from the Control treatment and from Meras, a meaningful ANOSIM for corallivores could not be performed.

Patterns in the development of the fish community over time at the three experimental locations and treatments were examined with the RELATE function. The similarity matrices of the average samples for all nine combinations of treatment and location were compared to model similarity matrices that contained the same amount of samples as the experimental data from each site and used self-generated variables. For the models, Euclidean distances were used as similarity coefficients. Comparison was done using Spearman rank correlation. Models were generated for assumptions of seriation, an asymptotic increase in similarity, and periodicity. In the first case, the community is assumed to change in a regular fashion, sequentially developing away from its initial state, with every consecutive composition being more dissimilar from the composition at the beginning (Clarke et al. 1993). In the second case, the community is also developing ever further from its initial state, but with steadily decreasing steps, until a kind of new equilibrium is reached. In the third case, the community composition is assumed to change seasonally in a pattern of cyclicity. In this case, dissimilarity increases until half of the season has passed, in which case the community is

most dissimilar from its initial state. It then returns towards the initial state, which it is reaching again after one full season. Since the experimental area is located very close to the equator, the possibility exists of both an annual and a semi-annual cycle of seasonality. Thus, model matrices for 12-month and 6-month cyclicity were generated. Tab. 2.6 gives the variables used to calculate the model matrices.

**Table 2.6:** Artificial variables used to generate model similarity matrices. The Spearman rank correlations between the experimental data and the model matrices served as tests of the respective assumptions regarding the development of the fish community in the experimental plots.  $t$  is the number of days since the first sampling at each location.

Assumption examined	Variables used in model matrix	Definition of variables
Seriation	$A$	$A = 3 * \frac{t}{10}$
Increasing similarity	$A$	$A = \ln\left(\frac{t}{100} + 1\right)$
6-month cyclicity	$A, B$	$A = 1 + \sin\left(\frac{t * 720}{365}\right)$ $B = 1 + \cos\left(\frac{t * 720}{365}\right)$
12-month cyclicity	$A, B$	$A = 1 + \sin\left(\frac{t * 360}{365}\right)$ $B = 1 + \cos\left(\frac{t * 360}{365}\right)$

Differences in the multivariate dispersion of the replicate samples were examined by computing the average Bray-Curtis similarities for the three replicate samples of every combination of location, treatment, and sampling time using the SIMPER procedure and then testing for the influence of treatment, location and sampling time on within-sample similarity using a linear model. To achieve equal replication, the data from the first sampling (no replication at Gangga) and after the 13<sup>th</sup> sampling (maximum number of samples at Bunaken, see Tab. 2.3) were removed. The average similarity for the 7<sup>th</sup> sampling at Meras, where some replicates were missing, was estimated by extrapolation. Residuals from the model were checked for normality using a Shapiro-Wilk  $W$  test.

### 2.11.3 Further analysis of fish data

For a visual comparison of the fish abundance spectra in the three treatments at each site, a kind of rarefaction curves (Sanders 1968) based on biomass were produced. The log<sub>e</sub> of the total biomass of each species was plotted against its rank (Wolff and Alarcon 1993) for each combination of site and treatments. Biomass was calculated as the total biomass  $M_{total \cdot k}$  of a species  $k$  over the duration of the experiment:

$$M_{total \cdot k} = \sum_{j=1}^r \bar{m}_{kj} \quad (11),$$

where  $\bar{m}_{kj}$  is the average biomass of species  $k$  at one sampling event and  $r$  is the total number of sampling events at a location. Some biomass values were smaller than 1 due to the averaging of replicates and small body size (e.g. in cases where a species was represented only by one single, small individual in one replicate). To avoid negative log-values, data were

transformed by adding  $(1-x)$  to each value in a sample before taking the logarithm, where  $x$  was the smallest value in each respective combination of treatment and site.

In order to see whether the samples could be grouped by treatments irrespective of the fish community composition, using only descriptive variables derived from the community samples, number of individuals, species richness, diversity, and evenness of the averaged samples were used in a further multivariate analysis. Ordination by principal component analysis (PCA) (Everitt 1978, Chatfield and Collins 1980) based on Euclidean distances was applied to examine correlations between these variables and the experimental treatments. For comparison, a second PCA was done using total biomass in a sample instead of individuals. In the second analysis, diversity and evenness of the sample were calculated based on biomass. Since the variables differed in units and orders of magnitude, the data were normalized prior to both analyses.

#### **2.11.4 Analysis of coral recruitment data**

Coral recruitment numbers were square-root transformed prior to analysis to achieve normal distribution. Data were checked for normality using a Shapiro-Wilk  $W$  test. In cases where normality could not be obtained by transformation, non-parametric Kruskal-Wallis tests were used instead of ANOVA. Prior to ANOVA, data were checked for homogeneity of variances using Bartlett's test. Where unequal variances were detected, a Welch ANOVA was used instead of regular ANOVA. A significant ANOVA or Kruskal-Wallis test was followed by a Tukey HSD test, or, in the latter case, pairwise Mann-Whitney  $U$  tests in order to assess individual differences between the treatments.

For each location, mean recruitment rates in the experimental were obtained by averaging across the number of recruits found on each of the 18 plates deployed in each plot. For each sampling interval (i.e., each time the settlement plates were retrieved and recruits were counted), average numbers of recruits were compared between the three treatments at each location. Rates were standardized to number of recruits\* $100\text{ cm}^{-2}$ .

In order to assess differences in the frequency of Acroporid and Pocilloporid recruits between the treatments, the total numbers of recruits from these two families observed in one sampling interval were compared among treatments using contingency tables and Pearson's chi-square statistic (Zar 1999). This statistic tests for the null hypothesis that the relative frequencies of recruits from both families are the same for all treatments.

For recruitment on the concrete structures, mean recruitment rates were obtained by averaging across the total number of recruits found on each of the 8 structures examined in each plot. Following a Shapiro-Wilk  $W$  test, recruitment rates were fourth-root transformed to achieve normal distribution. The average numbers of recruits on structures in the Structures + Corals and Structures plots at each location were compared using a one-way ANOVA. Average numbers of recruits were also compared among locations. Again, data were checked for homogeneity of variances using Bartlett's test prior to ANOVA.

Differences between the relative frequencies of Acroporids and Pocilloporids in both treatments at each location were assessed using the Fisher exact test, which is preferable to the chi-square statistic in cases where  $2 \times 2$  categories are examined (Zar 1999). For comparisons of the relative frequencies at the three locations, Pearson's chi-square statistic was used.

## 2.11.5 Transplant mortality

Potential differences in the mortality rates of the species used were examined using JMP by fitting a survival function based on the number of new dead corals recorded for each monitoring interval and testing for homogeneity between the species using a Wilcoxon test (Kalbfleisch and Prentice 1980). The number of dead corals was determined by counting all living transplants that were still attached to their cement bases and subtracting this number from the number of live corals in the previous census. Hence, survival is a minimum estimate, as several fragments were broken off their substrates but retained a portion of living tissue. A proportional hazards model (Cox 1972) was used to set the mortality rates of each coral species in relation to the rates of each other species.

The rates of disintegration of the bamboo substrates at Meras and Bunaken were also examined with a survival function based on the number of new boards recorded as damaged in each count and tested for homogeneity with a Wilcoxon test.

In order to examine whether survival of the transplanted fragments was related to the disintegration of the bamboo substrates, the survival of corals at a given time was plotted against the disintegration of the bamboo boards at the same time. The survival curves of coral species and bamboo boards followed a Weibull function (Weibull 1951):

$$S(x) = \exp - \left( \frac{x}{\alpha} \right)^\beta \quad (12),$$

where  $S$  is the probability of survival/non-damage at time  $x$ . The Weibull parameters for each species and the bamboo boards at Meras and Bunaken were obtained by fitting a survival function in JMP, and the survival probabilities of the coral species for any given time were then plotted against the non-damage probabilities of the bamboo substrates at the respective location. A case where coral survival is linearly related to disintegration of the boards would result in a straight line in this plot.

## 2.12 Prices of the materials used and value of the fish resources

Although the artificial reef structures employed in this study were designed with primary goal of providing high topographic complexity for the fish community, and a different design may be better suited for specific rehabilitation efforts, a quantification of the costs for the methods used here was attempted to be able to put the efforts and results into perspective. Costs for the materials used are given along with the work-hours needed for set-up. A rough estimation of the value of the fishes present in a plot each month was derived from market prices for target species both of species caught for consumption and for the ornamental species trade. All prices are given in Indonesian Rupiah (exchange rate at the time of writing was around 9,000 IDR for 1 USD). Prices for materials are those paid in local hardware shops. The prices for fish species caught for consumption were derived from interviews with sellers at Manadonese fish markets in December 2007 and are usually per kg. Prices for ornamental species (per specimen) were estimated based on the export prices given by Poernomo et al. 2003. Using anecdotal information from local ornamental fish traders, the price local fishermen could expect to be paid per fish was assumed to be about one-tenth of the quoted export price. More accurate prices could not be obtained since the fish traders, mostly acting on a thin legal basis at best, were reluctant to disclose in-depth information about their trade. The value of a species in a replicate census was calculated by multiplying the biomass of that species observed in one census replicate with the price per kg of the species for species caught for consumption, and by multiplying the number of individuals observed during one replicate

count with the price per individual of that species for ornamental species. The sum of the values for each species yielded the total value of all fishes in one replicate. The prices used are shown in Tab. A 1 in the Appendix.

### 3. Results





Several transplanted fragments of *Acropora gomezi* had grown into dense thickets, harboring juvenile butterflyfishes, damselfishes and wrasses.

Structures + Corals plot, experimental site at Gangga, March 2007.

## 3.1 Fish community

### 3.1.1 Species observed

During the duration of the experiment, a total of 264 fish species belonging to 36 families were observed (Tab. 3.1). 4 species could only be identified to genus level. 22 of the species were only observed in the natural reef plots, 2 occurred only in the Control plots, 41 were exclusive to the Structures + Corals plots, and 14 were found only in the Structures plots. 9 species were present in each experimental and natural plot. However, most of the species observed only in one kind of treatment were observed only once or twice during the experiment.

**Table 3.1:** List of all species observed during the experiment, showing the frequency with which they were observed in the respective plots (e.g., in 6 out of all surveys). Note that the plots at Gangga, Meras, Bunaken were surveyed a different number of times (15, 14, and 13 times, respectively), and that the monitored natural reefs comprised two plots. Hence, the maximum possible number of observations for each species is different for each site. C = Control, SC = Structures + Corals, S = Structures. Feeding mode classification based on information from FishBase (Froese and Pauly 2007): OV = omnivore (incl. algae), OCV = obligate corallivore, OVI = omnivore invertebrate, HV = herbivore, PV = planktivore, CV = carnivore, PIV = piscivore.

No.	Family	Species	feeding mode	found in treatm.	Gangga			Meras			Bunaken			Natural reef		
					C	SC	S	C	SC	S	C	SC	S	Ga	Ms	Bn
1	Acanthuridae	<i>Acanthurus auranticavus</i>			2	3	1				2					
2		<i>Acanthurus bariene</i>	HV					1	5	1						
3		<i>Acanthurus japonicus</i>		SC							1					
4		<i>Acanthurus nigricauda</i>			3	7	5	1	6	4	5	12	12			1
5		<i>Acanthurus nigrofasciatus</i>	HV	all	9	15	15	1	6	3	3	12	12	2	1	2
6		<i>Acanthurus olivaceus</i>	HV		6	4					2			1		
7		<i>Acanthurus pyroferus</i>		all	1	15	15	8	14	13	7	13	13	2	1	2
8		<i>Acanthurus thompsoni</i>	PV			2									1	
9		<i>Acanthurus xanthopterus</i>	OV		1	1										
10		<i>Ctenochaetus binotatus</i>	HV	all	6	9	9	2	12	12	4	12	12	2	2	2
11		<i>Ctenochaetus striatus</i>	OV		2	10	13		2	2		3		1		2
12		<i>Naso annulatus</i>	PV		2	2	1									
13		<i>Naso hexacanthus</i>	PV			4	2	1						1		
14		<i>Naso lituratus</i>	HV		4	13	12		9		2	6	3	2	1	
15		<i>Naso thynnoides</i>	OV								2	6	3		1	
16		<i>Naso vlamingii</i>	OV		2	1		1			2		3			
17		<i>Zebrasoma scopas</i>	HV			10	5	5	14	7		3	5		1	2
18		<i>Zebrasoma veliferum</i>	HV								2	10	3			
19	Antennariidae	<i>Antennarius commerson</i>	PIV	Natural										1		
20	Aulostomidae	<i>Aulostomus chinensis</i>	CV		1	11	5		2	1				1	1	
21	Balistidae	<i>Balistapus undulatus</i>	CV		6	15	14		11	11	1	4	9	2	1	2
22		<i>Balistoides viridescens</i>	OVI					2								
23		<i>Melichthys vidua</i>	OV			4										
24		<i>Odonus niger</i>	PV	S		1										
25		<i>Rhineacanthus verrucosus</i>			7	15	8									
26		<i>Sufflamen bursa</i>	OVI					7	4	8		7	13		1	1
27		<i>Sufflamen chrysopterum</i>	OVI		12	2	7	2	1					1		
28	Bleniidae	<i>Meiacanthus atrodorsalis</i>	OVI						6				1			
29		<i>Meiacanthus grammistes</i>			11	3	2	3	7	2	1	2				
30		<i>Plagiotremus rhinorhynchos</i>	CV	SC		2			2							
31	Centriscidae	<i>Aeoliscus strigatus</i>	PV		1	9	10									
32	Chaetodontidae	<i>Chaetodon auriga</i>	OV		13	3	1				1		7	8		1
33		<i>Chaetodon baronessa</i>	OCV	SC		6										
34		<i>Chaetodon bennetti</i>	OV	SC									1			
35		<i>Chaetodon citrinellus</i>	OV			10	1							1		
36		<i>Chaetodon ephippium</i>	OV	SC		1										
37		<i>Chaetodon kleinii</i>	OV	all	14	15	15	6	14	14	4	12	13	2	2	2
38		<i>Chaetodon lunula</i>	OV					1	2		1				1	
39		<i>Chaetodon lunulatus</i>	OCV		1	15	10				1			2		2
40		<i>Chaetodon melannotus</i>	OCV			12	6									
41		<i>Chaetodon meyeri</i>	OCV	SC		2										
42		<i>Chaetodon ocellatus</i>	OCV			1	1									
43		<i>Chaetodon ornatus</i>	OCV												1	
44		<i>Chaetodon oxycephalus</i>	OVI	SC					1					1	1	1
45		<i>Chaetodon punctatofasciatus</i>	OV		7	2			1							
46		<i>Chaetodon rafflesii</i>	OVI		3	2										
47		<i>Chaetodon speculum</i>	OVI		7	5										1
48		<i>Chaetodon trifascialis</i>	OCV		5	2								1		

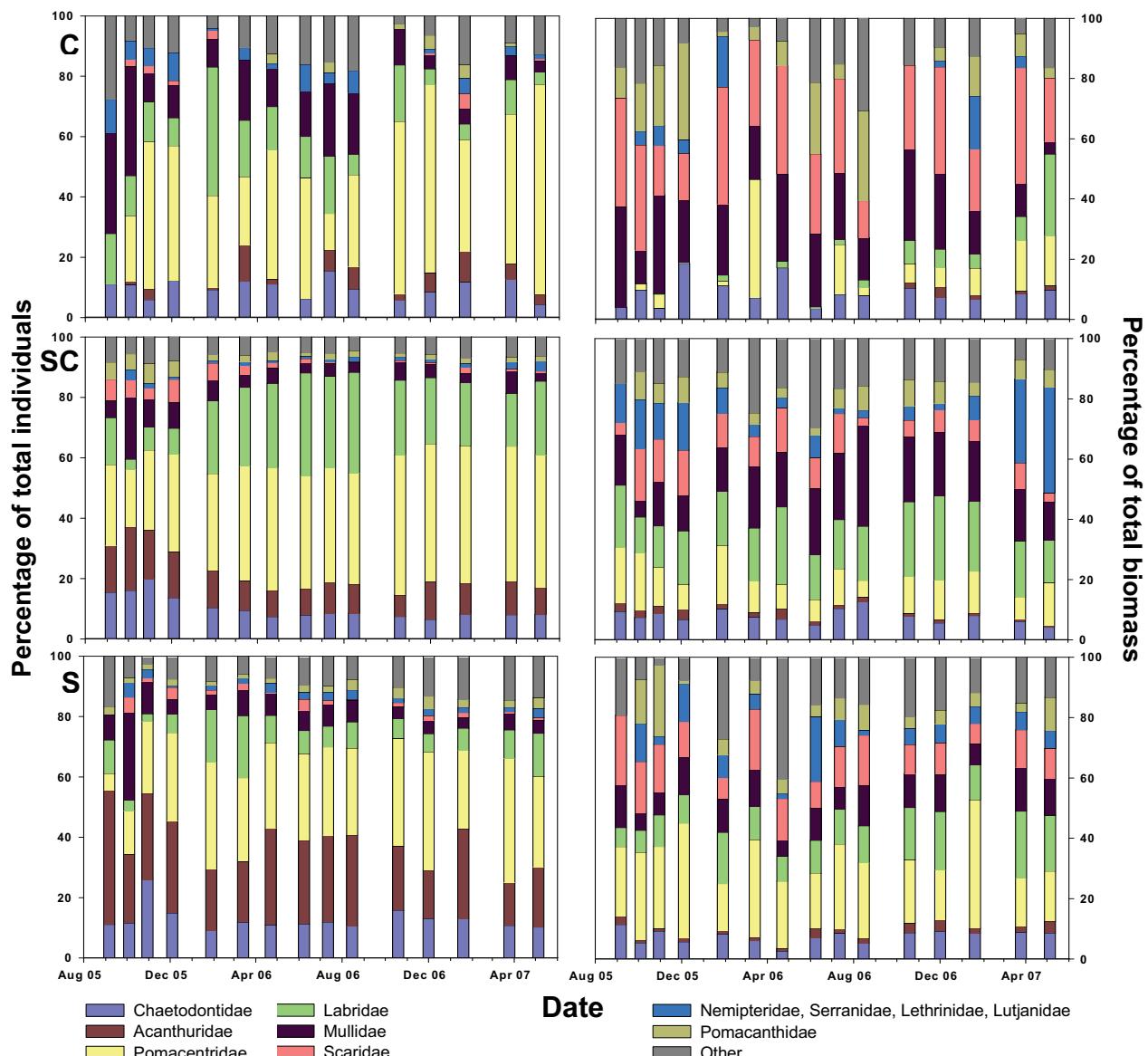






### 3.1.1.1 Species composition

Patterns in species composition at Gangga (Fig. 3.1) differed among the experimental plots. The composition in the Control plot was the most variable. When looking at the contribution of key families to total individuals, pomacentrids were the dominant family in all plots. In the Control plot, browsing mullids had a higher relative abundance than in the other two plots. One obvious feature of the community composition in time is the stability in terms of relative numbers of individuals in the Structures + Corals plot. In the Structures plot, acanthurids had a markedly higher relative abundance than in the Structures + Corals plot, while relative numbers of labrids were smaller. In terms of biomass, scarids played a much higher role than in terms of number of individuals in all plots. In the Structures + Corals plot, biomass contribution of mullids was much higher than in terms of individuals, while acanthurids and pomacentrids contributed less in terms of biomass than in numbers, indicating small body size in these two families. At Meras, the contribution of pomacentrids to total individuals was equally high in the Structures + Corals and the Structures plot. Mullids were less prominent in terms of biomass, while acanthurids contributed a much higher percentage to total biomass at the other two sites. For graphs of the data from Meras and Bunaken, see Figs. A 1 and A 2 in the Appendix.



**Figure 3.1:** Relative contribution of selected families to total number of individuals (left) and biomass (right) in the Control (C), Structures + Corals (SC) and Structures (S) treatments (top to bottom) at Gangga.

### **3.1.2 Fish abundance, number of species, and biomass**

#### **3.1.2.1 Fish abundance**

Fish abundance increased markedly in the Structures + Corals treatment at all sites, while there were only slight increases in numbers in the Control treatment (Fig. 3.2).

At Gangga, the highest number of individuals was observed in the Structures + Corals plot (up to  $796 \pm 36$  individuals/ $100\text{ m}^2$ , mean  $\pm$  SE) from the beginning on. By the end of the experiment, the number of individuals in the Structures + Corals plot had increased almost 8-fold compared to the Control. An intermediate number of individuals was observed in the Structures plot, while the Control plot, with one exception, always had the lowest number of fishes. The linear model revealed significant effects of treatment, time, treatment\*time, and visibility\*treatment (Tab. A 2, see Appendix. For a graph of average visibility, together with a discussion of potential effects of visibility, see page 103 in the discussion).

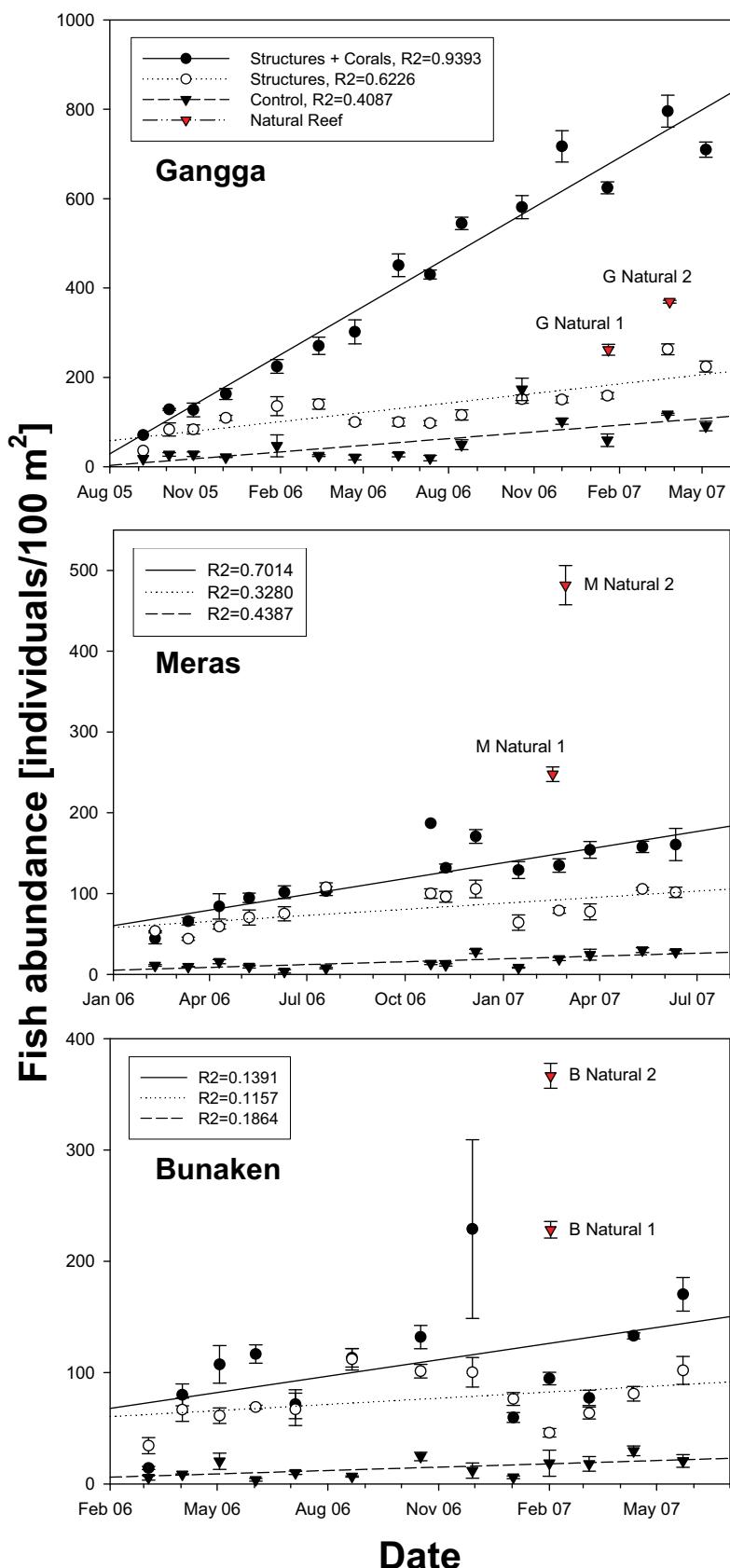
In the natural reef plots, fish abundance was lower than in the Structures + Corals plot, but higher than in the Structures and Control plots at both times the natural reef was sampled (ANOVA,  $F = 161.0741$ ,  $p < 0.0001$ ,  $df = 3,8$  and  $F = 379.0192$ ,  $p < 0.0001$ ,  $df = 3,8$  for January 2007 and March 2007, respectively). The post-hoc test showed that the differences between all treatments were significant at  $\alpha = 0.05$ .

At Meras, the trends observed were similar to those found at Gangga. However, fish abundance in the experimental plots at Meras was considerably lower. The highest number of fishes (187 individuals/ $100\text{ m}^2$ , no replication, see Materials and Methods) was observed in the Structures + Corals plot. The linear model revealed significant effects of treatment, time, visibility, treatment\*time, and visibility\*treatment\*time (Tab. A 2, see Appendix).

For the time that natural reef plots were sampled, there was a significant effect of treatment on fish abundance (ANOVA,  $F = 362.9089$ ,  $p < 0.0001$ ,  $df = 4,10$ ). Fish abundance was much higher ( $482 \pm 42$  individuals/ $100\text{ m}^2$ , mean  $\pm$  SE, in one plot) in the natural than in the experimental plots. The post-hoc test showed significant differences between all treatments ( $\alpha = 0.05$ ).

Fish abundance in the experimental plots at Bunaken reached a maximum ( $229 \pm 80$  individuals/ $100\text{ m}^2$ , mean  $\pm$  SE) in the Structures + Corals plot. During the first census, abundance was highest in the Structures plot. Fish abundance was similar in the Structures + Corals and the Structures plots, and remained low in the Control plot. In the eighth census, abundance in the Structures + Corals plot varied to a large degree because of the presence of a large amount of the wrasse *Cirrhilabrus cyanopleura* during two of the three replicate counts. The linear model was able to detect significant effects of treatment, time, visibility, and visibility\*treatment (Tab. A 2, see Appendix). Since no differences in slope between the three treatments were detected, a Tukey HSD post-hoc test was applied that confirmed significant differences between all three treatments ( $\alpha = 0.05$ ).

The highest number of individuals at Bunaken ( $367 \pm 11$  individuals/ $100\text{ m}^2$ , mean  $\pm$  SE) was observed in one of the two natural reef plots (Natural reef plot 2). Comparing the experimental and natural reef plots, there was a significant effect of treatment (ANOVA,  $F = 97.5778$ ,  $p < 0.0001$ ,  $df = 4,10$ ). The post-hoc test confirmed significant differences between the abundance in the natural reef plots and the experimental plots ( $\alpha = 0.05$ ).



**Figure 3.2:** Fish abundance at the three experimental sites (mean  $\pm$  SE), showing the values from the natural reef plots at each site. Note the differences in time scale.

### 3.1.2.2 Number of fish species

The number of fish species at Gangga followed similar trends as the fish abundance values. The linear model showed significant effects of treatment, time, treatment\*time, and visibility\*treatment\*time (Tab. A 3, see Appendix). The highest number of species ( $71 \pm 2$  species, mean  $\pm$  SE) occurred in the Structures + Corals plot, an intermediate number in the Structures plot, and the lowest number was always found in the Control plot (Fig. 3.3).

Number of species in the natural reef plots was lower than in the Structures + Corals plot, but slightly higher than in the Structures plot. ANOVA showed significant effects of treatment both times the natural reef was sampled (ANOVA,  $F = 48.9081, p < 0.0001, df = 3,8$  and  $F = 59.5524, p < 0.0001, df = 3,8$  for January 2007 and March 2007, respectively). The post-hoc test showed that there were no significant differences between the number of species in the natural reef and in the Structures plot at both times. All other differences were significant at  $\alpha = 0.05$ .

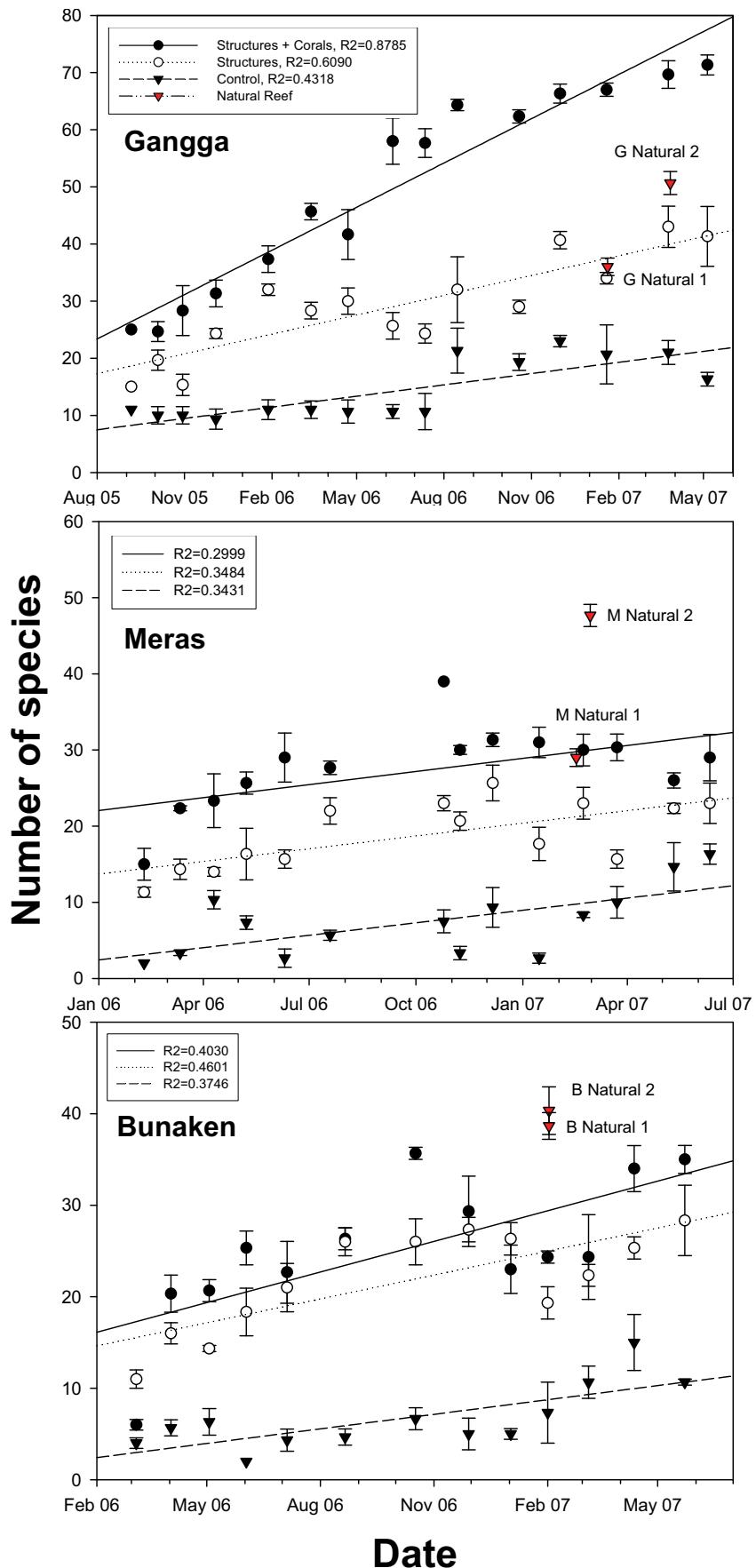
Following a storm event in August 2006, the number of species at Gangga increased in all treatments. In the Control plot, number of species slowly decreased again after the event but did not reach its former level until the end of the experiment (see Discussion).

The maximum number of species in the experimental plots at Meras (39 species, no replication, see Materials and Methods) also was observed in the Structures + Corals plot. Although there were clear linear trends visible in the first half of the experiment, some fluctuations in species numbers appeared during the final 9 months. As shown by the linear model, there were significant effects of treatment, time, visibility, visibility\*time, and visibility\*treatment\*time (see Tab. A 3, Appendix). Again, number of species was highest in the Structures + Corals plot, intermediate in the Structures plot, and lowest in the Control plot, and the post-hoc test revealed that the differences between all treatments were significant (Tukey HSD,  $\alpha = 0.05$ ).

A comparison of the number of species at the time the natural reef plots were surveyed showed a significant effect of treatment (ANOVA,  $F = 82.1000, p < 0.0001, df = 4,10$ ). The post-hoc analysis showed that the difference between the number of species in the natural reef plot 1 and the Structures + Corals and Structures plots was not significant at  $\alpha = 0.05$ . Natural reef plot number 2 had a much higher number of species ( $48 \pm 3$  species, mean  $\pm$  SE) than those found in the experimental plots.

At Bunaken, the maximum number of species in the experimental plots ( $36 \pm 1$  species, mean  $\pm$  SE) also was found in the Structures + Corals plot. In the first census, species number was highest in the Structures plot. After that, with one exception, the mean number of species was always highest in the Structures + Corals plot, although the amount in both plots was similar and markedly higher than in the Control plot. The linear model showed significant effects of treatment, time, treatment\*time,  $(time)^2$ , and treatment\*( $time)^2$  (i.e., there were different curves for each treatment that do not appear in the linear regression, Tab. A 3, Appendix).

The number of species in both natural reef plots sampled at Bunaken ( $40 \pm 3$  species, mean  $\pm$  SE, and  $39 \pm 1$  species, mean  $\pm$  SE) was higher than that found in the experimental plots. A comparison with the experimental plots sampled in February 2007 showed significant treatment effects (ANOVA,  $F = 40.4127, p < 0.0001, df = 4,10$ ). In the post-hoc test, no significant differences were detected between the numbers of species in the two natural reef plots, which were significantly higher than those in the experimental plots ( $\alpha = 0.05$ ).



**Figure 3.3:** Number of fish species observed at the experimental sites (mean  $\pm$  SE), showing the number of species observed in the natural reef plots for comparison. Note the increase in species at Gangga in August 2006.

### 3.1.2.3 Fish biomass

Trends in fish biomass were less clear (Fig. 3.4). At Gangga visible trends had emerged after one year. At Meras, there were no differences in slope between the treatments, while at Bunaken, a positive trend was evident only in the Structures treatment.

For the Gangga data, the linear model showed significant effects of treatment, time, and treatment\*time (Tab. A 4, Appendix). Again, the highest amount of biomass ( $107 \pm 22 \text{ g m}^{-2}$ , mean  $\pm$  SE) was found in the Structures + Corals plot.

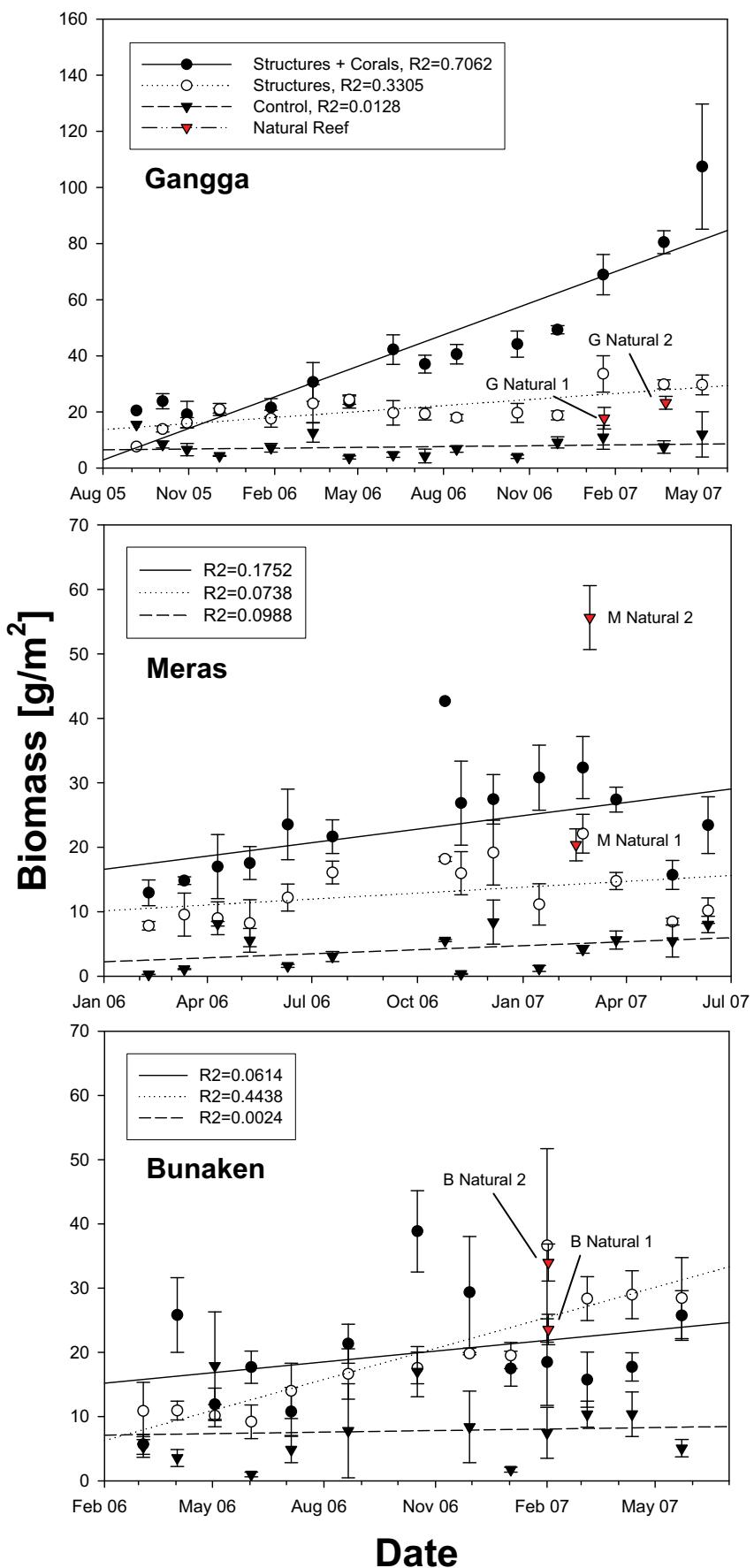
For both times the natural reef was sampled, ANOVA showed significant effects of treatment (ANOVA,  $F = 14.3754$ ,  $p = 0.0014$ ,  $df = 3,8$  and  $F = 49.6067$ ,  $p < 0.0001$ ,  $df = 3,8$  for January 2007 and March 2007, respectively). The amount of fish biomass observed in the natural reef plots was higher than that in the rubble Control plot, but lower than that found in the two other experimental plots. The post-hoc test showed that for the plots sampled in January 2007, the biomass in the natural reef plot only differed significantly from that in the Structures + Corals plot ( $\alpha = 0.05$ ). For the plots sampled in March 2007, there were no significant differences between the biomass in the natural reef plot and in the Structures plot, but these two were significantly different from both other plots ( $\alpha = 0.05$ ).

The amount of fish biomass in the experimental plots at Meras again followed the general pattern, with the amount being highest in the Structures + Corals plot, intermediate in the Structures plot, and lowest in the Control plot. As with species numbers, the amount of biomass began to fluctuate in the second half of the experiment, with biomass in the Structures + Corals and Structures plots decreasing again towards the end. The linear model showed significant effects of treatment, visibility, treatment\*time, visibility\*treatment, and treatment\*(time)<sup>2</sup>, indicating a different curvature for each treatment (Tab. A 4, Appendix).

The highest amount of biomass at Meras ( $56 \pm 5 \text{ g m}^{-2}$ , mean  $\pm$  SE) was observed in one of the natural reef plots. In the comparison of natural reef and experimental plots, a significant treatment effect was detected (ANOVA,  $F = 47.2185$ ,  $p < 0.0001$ ,  $df = 4,10$ ). In the post-hoc test, there were no significant differences between the natural plot with the lower amount of biomass and the Structures + Corals and Structures plots. The biomass in the second natural reef plot was significantly different from that in all other plots ( $\alpha = 0.05$ ).

The amount of fish biomass observed in the experimental plots at Bunaken was highly variable. The highest amount of biomass ( $39 \pm 6 \text{ g m}^{-2}$ , mean  $\pm$  SE) occurred in the Structures + Corals plot, but a similar amount was observed in the Structures plot four months later. Over the duration of the experiment, the amount of biomass in the Structures plot showed a more or less constant increase, while the biomass in the Structures + Corals plot oscillated. As revealed by the linear model, there were significant effects of treatment, time, and treatment\*time, but the model only explained a modest 47 % of the observed variability (Tab. A 4, Appendix).

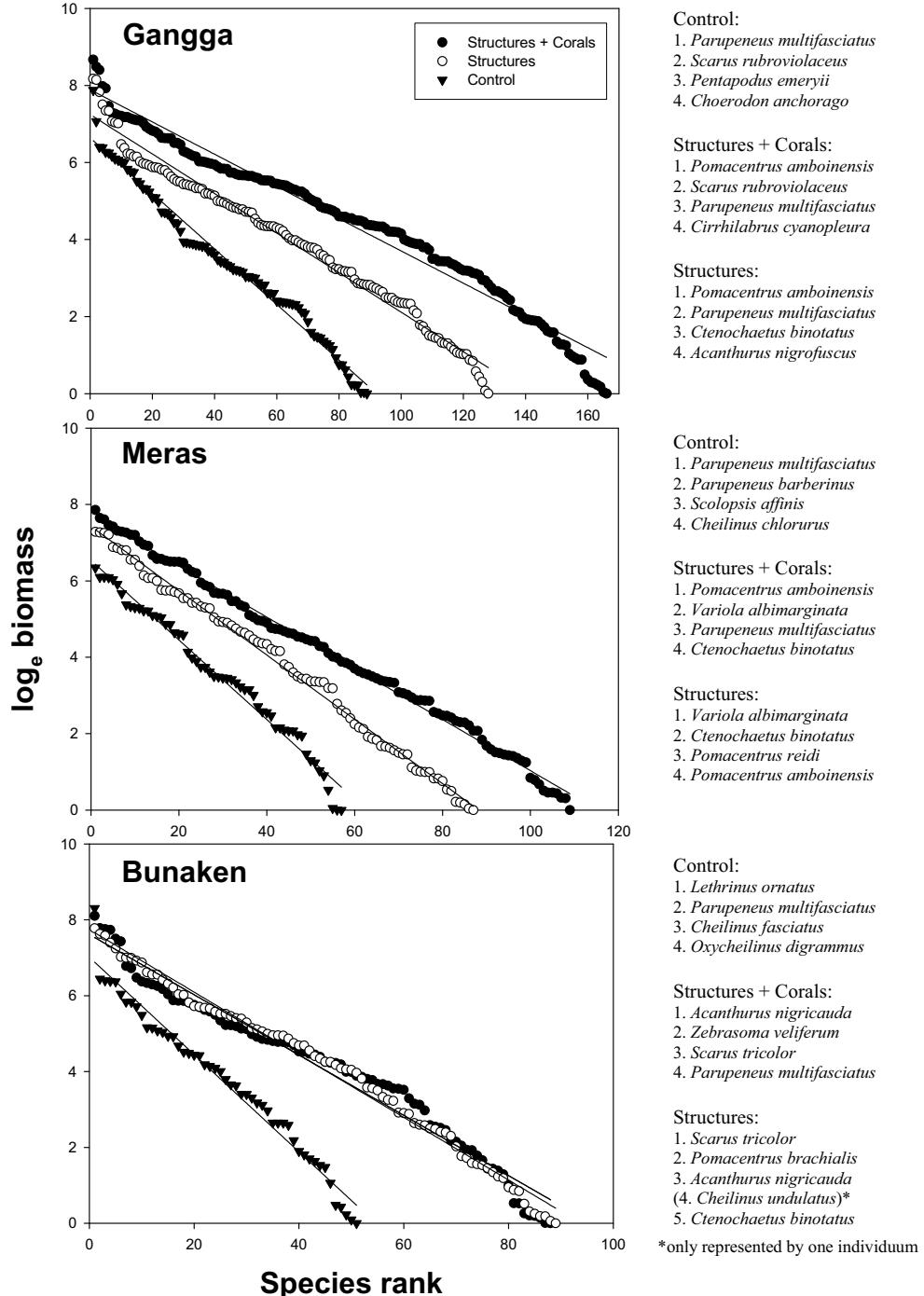
The amount of biomass found in the natural reef plots was similarly variable as that observed in the experimental plots in February 2007, and the ANOVA failed to detect any significant differences between the biomass in all of the plots.



**Figure 3.4:** Amount of fish biomass found in the experimental plots (mean  $\pm$  SE), with the values from the natural reef plots shown for comparison.

### 3.1.2.4 Biomass distribution among species

The ranked species biomass plots show differences between the three treatments (Fig. 3.5). At Gangga and Meras, the steepest ranked biomass curves are those of the Control treatment, while the curves of the Structures + Corals treatments have the least steep slopes. At Bunaken, the curve of the Control treatment also is the steepest, but the curves of the two other treatments have similar slopes. At Gangga, species on the first few ranks comprise a disproportionately high amount of the total biomass, visible in a steep head of the curves. At the other two sites, the biomass is distributed more evenly among the ranks. The x-intercept (species richness) of the Structures and Control treatment curves are very similar at Meras and Bunaken.



**Figure 3.5:** Ranked species biomass curves based on the total biomass of each species observed in the experimental treatments at all sites over the duration of the experiment, with the four highest ranking species in each treatment shown on the right.

### 3.1.2.5 Species diversity and evenness of the samples

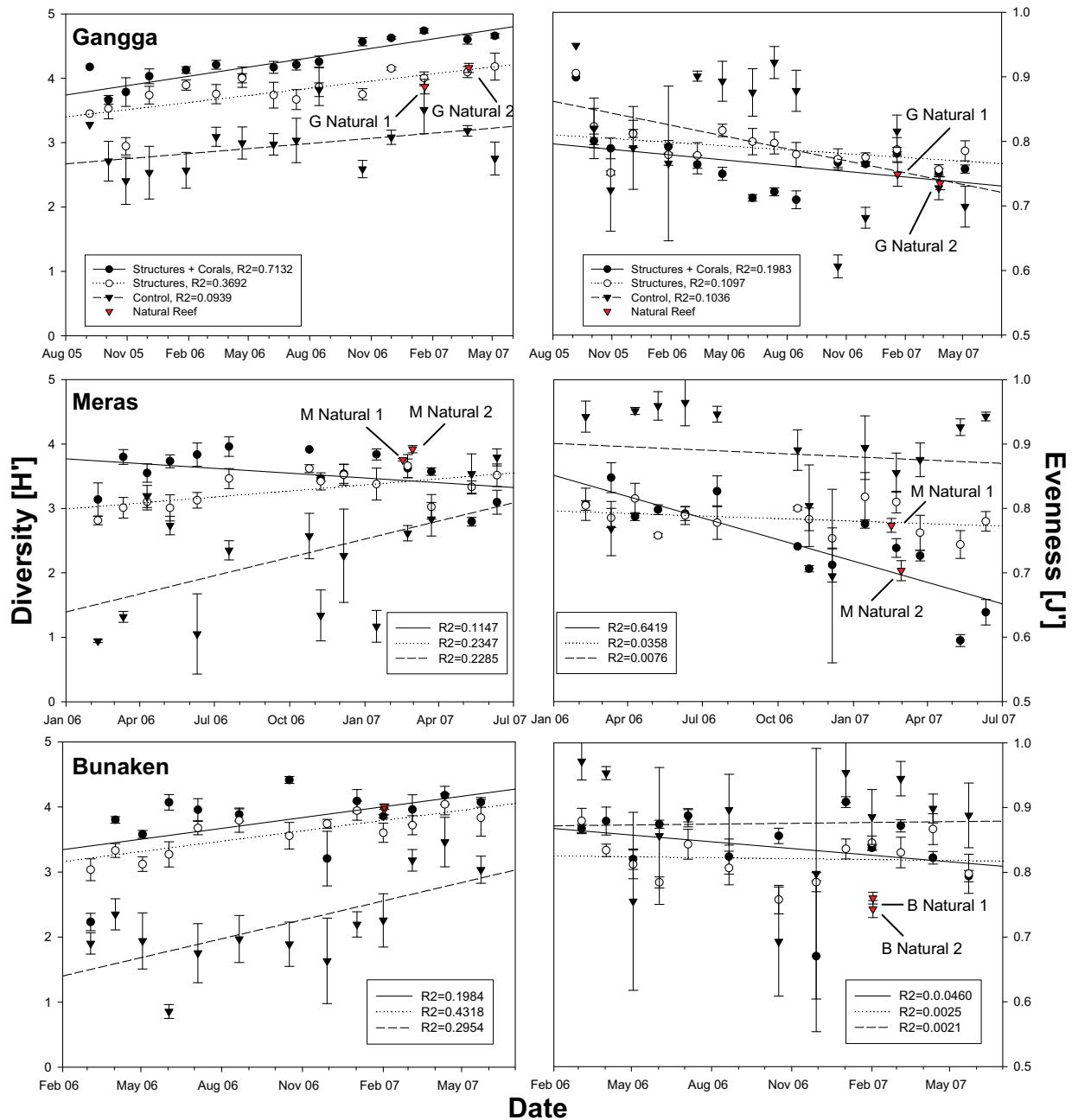
Diversity of the fish community, as measured by the Shannon-Wiener index  $H'$ , generally was higher in the Structures + Corals and Structures plots than in the Control plots at all three locations (Fig. 3.6). The highest values of  $H'$  ( $4.74 \pm 0.04$ ,  $3.96 \pm 0.15$  and  $4.41 \pm 0.05$ , mean  $\pm$  SE, at Gangga, Meras and Bunaken, respectively) all occurred in the Structures + Corals treatment. At Gangga, diversity in the Control plot hardly increased, while there was a noticeable increase in diversity in the Control plots at the other two locations. At Meras, diversity in the Structures + Corals plot apparently decreased over time, but the fit of the regression line is very poor ( $R^2 = 0.1147$ ) and hence this trend should be viewed with caution.

The linear model detected significant effects of Treatment and Time at all locations (for the results from the linear model, see Tab. A 5 in the Appendix). At Gangga and Bunaken, there were significant differences in slope (Time\*Treatment). At Meras and Bunaken, there also was a significant interaction effect of visibility\*treatment\*time. Furthermore, the model detected a significant effect of visibility at Meras, and differences in curvature (Time<sup>2</sup>\*Treatment) at Bunaken.

In the comparison of natural reef and experimental plots, a significant treatment effect was detected at all sites (Gangga: Welch ANOVA,  $F = 135.8150$ ,  $p = 0.0001$ ,  $df = 3$  and ANOVA,  $F = 58.6897$ ,  $p < 0.0001$ ,  $df = 3,8$  for January and March 2007, respectively; Meras: ANOVA,  $F = 103.5300$ ,  $p < 0.0001$ ,  $df = 4,10$ ; Bunaken: Welch ANOVA,  $F = 27.9969$ ,  $p = 0.0018$ ,  $df = 4$ ). In the post-hoc test, there were no significant differences between the natural reef and Structures plot at Gangga at both times. At Meras, there were no significant differences between the natural reef plot 1 and the Structures + Corals and Structures plots. At Bunaken, diversity in both natural reef plots did not differ significantly from that in the Structures + Corals plot, but was significantly higher than diversity in the two other experimental plots ( $\alpha = 0.05$ ).

Evenness of the samples was extremely heterogeneous at all sites. Data from the Control plots always were the most variable. Arcsine transformation of the data improved the fit of the model at Gangga and Bunaken, but even after transformation the residuals of the model did not display a normal distribution, and the results of the linear models should be regarded very cautiously. The extended linear model for Meras achieved the highest fit with  $R^2 = 0.5356$  and detected significant treatment effects (Tab. A 6, Appendix). Treatment effects were also detected for the other two sites, but fit of the models was considerably less. At all sites, there was a trend of the evenness in the Structures + Corals plots to decrease over time. This decrease was most marked at Meras, where the regression line also showed an acceptable fit ( $R^2 = 0.6419$ ).

In the comparison of natural reef and experimental plots, a significant treatment effect was detected at Bunaken and Meras (Meras: Kruskal-Wallis,  $\chi^2 = 12.6667$ ,  $p = 0.0130$ ; Bunaken: Kruskal-Wallis,  $\chi^2 = 10.4333$ ,  $p = 0.0337$ ). Individual post-hoc tests showed that at Meras, evenness in both natural reef plots was significantly lower than  $J'$  in the Control plot, and in the natural reef plot 2 was also significantly different from  $J'$  in the Structures plot (Mann-Whitney  $U$ ,  $\chi^2 = 3.8571$ ,  $p = 0.0495$ ). At Bunaken, evenness in the natural reef plots was significantly lower than in the experimental plots (Mann-Whitney  $U$ ,  $\chi^2 = 3.8571$ ,  $p = 0.0495$ ).

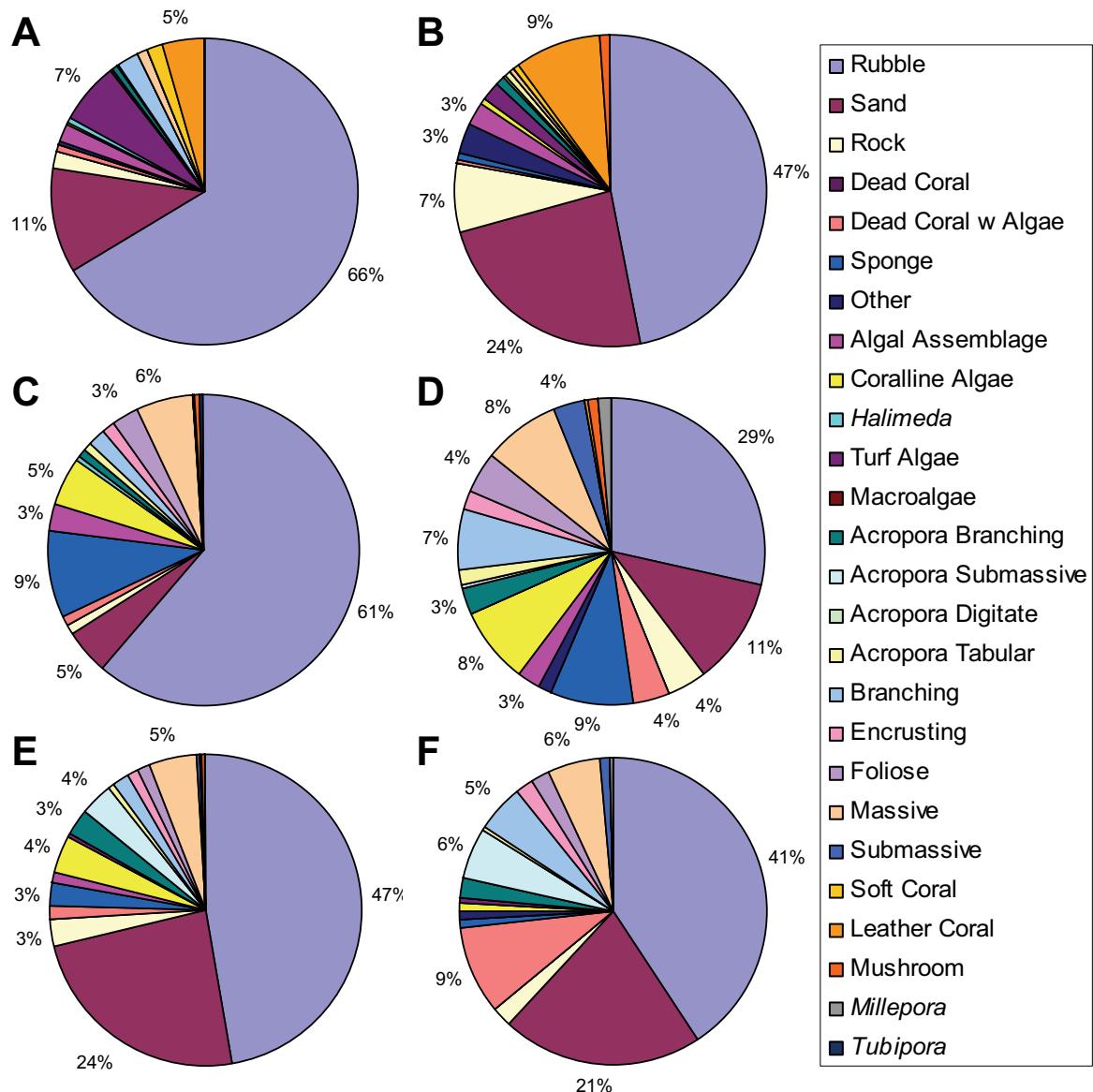


**Figure 3.6:** Diversity of the fish community (left side) and evenness of the samples (right side) in the experimental plots at three locations (mean  $\pm$  SE), with the values from the natural reef plots shown for comparison.

### 3.1.3 Substrate composition in the natural reef plots

The substrate composition in the natural reef plots, although variable, showed some general patterns at the three locations (Fig. 3.7). At Gangga, hard corals coverage was less than 5 %, and only three substrate categories were present with more than 3 % coverage in both of the plots (Fig. 3.7 A and B): Leather Coral, Sand and Rubble. At Meras, hard corals made up 13-29 % of the substrate, while sponges covered 9 % in both plots (Fig. 3.7 C and D). The seven categories Rubble, Sand, Sponge, Algal Assemblage, Coralline Algae, Foliose Coral and Massive Coral were covering more than 3 % of the substrate in both plots. At Bunaken, hard coral coverage in the natural plots was 16-23 % (Fig. 3.7 E and F). Both plots at Bunaken had a higher percentage of acroporids than the plots at Meras. Five categories (Rubble, Sand, *Acropora* Submassive Coral, and Massive Coral) were present with more than 3 % coverage in both plots.

A comparison of the similarity matrices for the natural reef plots based on fish data and on substrate data and water depth revealed that the variables Depth, Coralline Algae, *Acropora* Branching Coral, Foliose Coral, Soft Coral and Leather Coral are most closely linked to the fish community (BVSTEP,  $\rho = 0.971$ ,  $p < 0.001$ ).



**Figure 3.7:** Percent substrate cover in the natural reef plots, with percent values for all categories covering more than 3 %. **A:** Gangga 1, **B:** Gangga 2, **C:** Meras 1, **D:** Meras 2, **E:** Bunaken 1, **F:** Bunaken 2.

### 3.1.4 Multivariate analysis of the fish community data

#### 3.1.4.1 Characteristic species

The species that contributed most to within-group similarity in each treatment and in the natural reef plots are shown for each location in Tab. 3.2. The ratio of the average within-group similarity of a species to the frequency of that species in all samples of a group (the multivariate Standard Deviation) indicates how reliable that species contributes to overall within-group similarity (Clarke and Warwick 1994). The Bray-Curtis adjustment factor that takes the value 1 in each sample becomes increasingly important as species in a sample become sparse and species appear less regular within the samples of a group. Hence, it features most prominent in the Control treatment, less prominent in the Structures and Structures + Coral treatments, and does not contribute at all to within-group similarity in the natural reef plots.

**Table 3.2:** List of species contributing most to within-group similarity. For each sample group, the ten species contributing most to within-group similarity are shown. **Bold** species names indicate species that appear in the top ten of only one treatment at a location, or of only one of the natural plots.

Species	Av. abundance	Av. similarity	Similarity/SD	% Contribution	Cumulative %
<b>Gangga Control</b> , average similarity: 44.37					
<i>Pomacentrus coelestis</i>	14.9	6.33	1.43	14.27	14.27
<i>Parupeneus multifasciatus</i>	5.7	6.31	1.99	14.23	28.50
Bray-Curtis adjustment	-	5.84	3.32	13.16	41.66
<i>Chaetodon kleinii</i>	4.3	5.11	1.66	11.52	53.18
<i>Canthigaster valentini</i>	1.4	4.19	1.32	9.45	62.64
<i>Pomacentrus amboinensis</i>	11.1	2.93	0.80	6.61	69.25
<i>Halichoeres scapularis</i>	1.8	2.52	0.75	5.68	74.93
<i>Chaetodon auriga</i>	0.6	1.48	0.52	3.34	78.27
<i>Sufflamen chrysopterum</i>	1.2	1.41	0.55	3.18	81.45
<i>Pentapodus emeryii</i>	0.7	1.34	0.49	3.02	84.47
<i>Meiacanthus grammistes</i>	0.5	1.04	0.46	2.34	86.82
<b>Gangga Structures + Corals</b> , average similarity: 58.19					
<i>Pomacentrus amboinensis</i>	71.0	3.64	5.19	6.25	6.25
<i>Chaetodon kleinii</i>	26.7	3.12	3.81	5.37	11.62
<i>Parupeneus multifasciatus</i>	20.3	2.76	3.56	4.75	16.37
<i>Cirrhilabrus cyanopleura</i>	68.2	2.29	1.41	3.94	20.31
<i>Acanthurus nigrofasciatus</i>	9.8	2.29	2.61	3.93	24.24
<i>Balistapus undulatus</i>	5.7	2.02	4.02	3.47	27.71
<i>Centropyge vrolikii</i>	5.6	1.95	2.60	3.35	31.07
<i>Dascyllus reticulatus</i>	14.7	1.93	4.63	3.32	34.39
<i>Chaetodon lunulatus</i>	3.6	1.48	2.09	2.55	36.94
Bray-Curtis adjustment	-	1.48	3.29	2.54	39.48
<i>Acanthurus pyroferus</i>	4.1	1.48	1.62	2.54	42.02
<b>Gangga Structures</b> , average similarity: 51.73					
<i>Pomacentrus amboinensis</i>	31.3	5.65	5.56	10.92	10.92
<i>Chaetodon kleinii</i>	14.9	4.78	5.02	9.24	20.16
<i>Acanthurus nigrofasciatus</i>	10.7	4.34	4.60	8.40	28.55
<i>Parupeneus multifasciatus</i>	8.1	4.03	4.31	7.78	36.33
<i>Acanthurus pyroferus</i>	4.0	3.11	2.40	6.02	42.35
Bray-Curtis adjustment	-	2.70	4.56	5.21	47.56
<i>Balistapus undulatus</i>	2.0	2.14	1.54	4.14	51.70
<i>Pervagor janthinosoma</i>	4.3	2.07	1.46	4.01	55.71
<i>Canthigaster valentini</i>	1.1	1.80	1.30	3.49	59.20
<i>Pomacentrus brachialis</i>	4.1	1.69	1.07	3.28	62.47
<i>Ctenochaetus binotatus</i>	9.1	1.56	0.77	3.01	65.49

<b>Species</b>	<b>Av. abundance</b>	<b>Av. similarity</b>	<b>Similarity/SD</b>	<b>% Contribution</b>	<b>Cumulative %</b>
<b>Meras Control, average similarity: 33.77</b>					
Bray-Curtis adjustment	-	12.49	2.27	36.99	36.99
<i>Amphiprion clarkii</i>	3.3	9.09	0.93	26.92	63.91
<i>Hologymnosus doliatus</i>	2.9	2.20	0.40	6.50	70.42
<i>Pomacentrus auriventris</i>	0.7	1.27	0.27	3.76	74.17
<i>Acanthurus pyroferus</i>	0.8	1.26	0.37	3.73	77.90
<i>Scolopsis ciliata</i>	0.5	0.99	0.30	2.93	80.83
<i>Parupeneus barberinus</i>	0.3	0.83	0.31	2.45	83.28
<i>Sufflamen bursa</i>	0.3	0.69	0.26	2.03	85.31
<i>Parupeneus multifasciatus</i>	0.4	0.63	0.29	1.87	87.18
<i>Centropyge bicolor</i>	0.4	0.51	0.26	1.52	88.70
<i>Pomacentrus reidi</i>	0.5	0.51	0.26	1.50	90.20
<b>Meras Structures + Corals, average similarity: 56.05</b>					
<i>Pomacentrus amboinensis</i>	42.2	6.29	8.00	11.22	11.22
<i>Pomacentrus reidi</i>	8.7	4.62	4.35	8.25	19.47
<i>Pomacentrus brachialis</i>	12.9	4.62	5.01	8.24	27.72
<i>Chaetodon kleinii</i>	9.5	4.45	7.07	7.94	35.66
<i>Centropyge bicolor</i>	5.5	3.63	3.85	6.48	42.13
Bray-Curtis adjustment	-	2.91	5.90	5.20	47.34
<i>Parupeneus multifasciatus</i>	3.0	2.88	2.25	5.15	52.48
<i>Zebrazoma scopas</i>	1.8	2.06	1.26	3.67	56.15
<i>Ctenochaetus binotatus</i>	2.9	1.98	1.28	3.54	59.69
<i>Halichoeres hortulanus</i>	2.2	1.69	1.10	3.02	62.71
<i>Canthigaster valentini</i>	1.4	1.62	1.00	2.90	65.61
<b>Meras Structures, average similarity: 58.96</b>					
<i>Pomacentrus amboinensis</i>	24.2	8.21	7.00	13.92	13.92
<i>Pomacentrus reidi</i>	13.7	6.98	3.59	11.84	25.77
<i>Amphiprion clarkii</i>	4.7	5.72	5.72	9.71	35.47
<i>Centropyge bicolor</i>	4.7	5.25	3.41	8.91	44.38
<i>Chaetodon kleinii</i>	5.8	5.08	2.65	8.62	53.00
<i>Pomacentrus brachialis</i>	6.0	4.55	2.23	7.72	60.72
Bray-Curtis adjustment	-	4.11	5.61	6.96	67.69
<i>Halichoeres prosopaeion</i>	1.5	3.35	1.67	5.68	73.37
<i>Ctenochaetus binotatus</i>	2.7	2.77	1.20	4.69	78.06
<i>Scolopsis ciliata</i>	1.5	2.08	0.96	3.53	81.59
<i>Bodianus mesothorax</i>	0.9	1.44	0.74	2.44	84.04
<b>Bunaken Control, average similarity: 35.34</b>					
Bray-Curtis adjustment	-	13.41	2.63	37.93	37.93
<i>Pomacentrus auriventris</i>	1.8	7.35	0.84	20.80	58.74
<i>Oxycheilinus digramma</i>	0.5	3.50	0.55	9.91	68.65
<i>Lethrinus ornatus</i>	3.3	1.50	0.33	4.25	72.90
<i>Chaetodon vagabundus</i>	0.6	1.38	0.34	3.92	76.81
<i>Parupeneus multifasciatus</i>	0.8	1.38	0.39	3.91	80.73
<i>Chaetodon fasciatus</i>	0.4	1.22	0.36	3.45	84.17
<i>Canthigaster valentini</i>	0.5	1.19	0.32	3.36	87.53
<i>Pomacentrus reidi</i>	0.6	1.08	0.32	3.06	90.60
<b>Bunaken Structures + Corals, average similarity: 54.85</b>					
<i>Acanthurus pyroferus</i>	5.0	4.40	2.85	8.03	8.03
<i>Pomacentrus auriventris</i>	6.2	4.18	1.99	7.62	15.65
<i>Halichoeres chrysus</i>	10.5	4.09	2.15	7.46	23.11
<i>Pomacentrus reidi</i>	10.7	3.97	2.09	7.23	30.34
<i>Pomacentrus amboinensis</i>	12.6	3.94	2.15	7.18	37.52
Bray-Curtis adjustment	-	3.21	3.07	5.85	43.37
<i>Chaetodon kleinii</i>	4.1	2.88	1.86	5.26	48.63
<i>Centropyge bicolor</i>	4.7	2.85	1.64	5.19	53.83
<i>Acanthurus nigricauda</i>	2.9	2.42	1.34	4.42	58.24
<i>Ctenochaetus binotatus</i>	4.1	2.34	1.36	4.27	62.52
<i>Parupeneus multifasciatus</i>	3.3	1.76	0.96	3.22	65.73
<b>Bunaken Structures, average similarity: 52.15</b>					
<i>Pomacentrus brachialis</i>	17.0	6.97	6.23	13.37	13.37
<i>Pomacentrus amboinensis</i>	11.1	6.22	5.41	11.93	25.29
Bray-Curtis adjustment	-	3.75	4.93	7.19	32.49
<i>Acanthurus pyroferus</i>	2.2	3.26	1.78	6.25	38.73
<i>Sufflamen bursa</i>	1.3	2.90	1.65	5.55	44.28
<i>Ctenochaetus binotatus</i>	2.6	2.69	1.34	5.17	49.45
<i>Chaetodon kleinii</i>	2.0	2.58	1.23	4.95	54.40
<i>Pomacentrus reidi</i>	4.5	2.48	0.87	4.75	59.15
<i>Acanthurus nigrofucus</i>	3.0	2.29	1.04	4.40	63.55
<i>Oxycheilinus digramma</i>	1.2	2.07	1.07	3.97	67.52
<i>Acanthurus nigricauda</i>	1.3	1.76	0.92	3.37	70.89

Species	Av. abundance	Av. similarity	Similarity/SD	% Contribution	Cumulative %
<b>Gangga Natural Reef</b> , average similarity: 67.08					
<i>Pomacentrus amboinensis</i>	90.67	25.22	11.71	37.60	37.60
<i>Dascyllus aruanus</i>	24.50	6.10	1.90	9.09	46.69
<i>Dascyllus reticulatus</i>	20.33	6.04	5.72	9.00	55.70
<i>Chaetodon kleinii</i>	27.00	4.62	1.19	6.88	62.58
<i>Pomacentrus coelestis</i>	12.00	3.35	5.27	4.99	67.57
<i>Pomacentrus brachialis</i>	13.83	2.16	1.07	3.21	70.78
<i>Pervagor janthinosoma</i>	10.50	2.00	1.99	2.99	73.77
<i>Parupeneus multifasciatus</i>	8.00	1.94	2.63	2.89	76.67
<i>Pomacentrus moluccensis</i>	10.17	1.66	0.62	2.47	79.13
<i>Pseudochromis fuscus</i>	5.83	1.59	3.79	2.38	81.51
<b>Meras Natural Reef</b> , average similarity: 60.17					
<i>Pomacentrus brachialis</i>	46.17	12.10	1.32	20.11	20.11
<i>Pomacentrus amboinensis</i>	45.50	10.36	3.52	17.21	37.32
<i>Dascyllus reticulatus</i>	26.33	7.34	8.50	12.19	49.51
<i>Chromis retrofasciata</i>	38.00	5.59	0.92	9.29	58.81
<i>Acanthochromis polyacanthus</i>	16.67	4.38	1.49	7.28	66.09
<i>Chromis ternatensis</i>	12.33	2.78	1.32	4.63	70.72
<i>Halichoeres chrysus</i>	7.50	1.75	2.67	2.91	73.63
<i>Pomacentrus reidi</i>	4.17	1.27	4.10	2.10	75.73
<i>Chromis cf caudalis</i>	4.50	1.24	3.31	2.05	77.79
<i>Cirrhilabrus cyanopleura</i>	8.33	1.19	0.47	1.97	79.76
<b>Bunaken Natural Reef</b> , average similarity: 65.87					
<i>Pomacentrus brachialis</i>	74.17	14.59	4.79	22.15	22.15
<i>Dascyllus reticulatus</i>	41.50	11.10	3.34	16.85	39.00
<i>Acanthochromis polyacanthus</i>	64.00	10.28	2.20	15.61	54.61
<i>Chromis retrofasciata</i>	40.83	7.50	3.39	11.39	66.00
<i>Chromis amboinensis</i>	20.83	5.03	2.86	7.64	73.63
<i>Chrysiptera rollandi</i>	11.67	2.68	5.91	4.07	77.70
<i>Pomacentrus amboinensis</i>	9.17	1.56	2.23	2.38	80.07
<i>Chromis cf caudalis</i>	6.33	1.52	1.70	2.31	82.38
<i>Chaetodon kleinii</i>	5.67	1.21	1.53	1.83	84.21
<i>Chromis atripes</i>	9.67	1.18	1.23	1.80	86.01

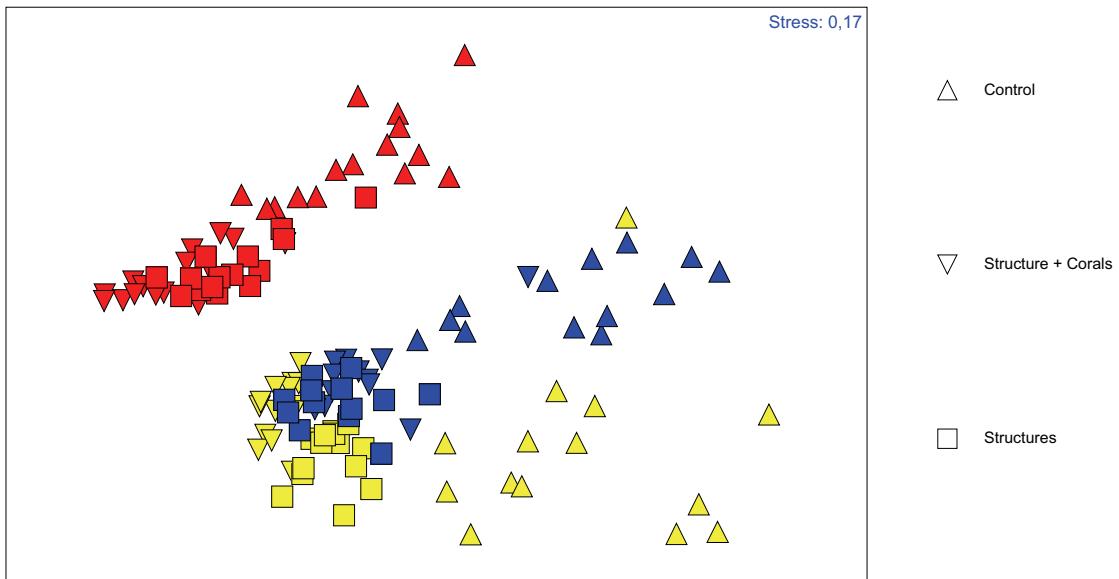
### 3.1.4.2 Effects of treatment

The crossed two-way ANOSIM revealed significant effects of both treatment and location on multivariate similarity between the community samples (Tab. 3.3). Differences between locations were more marked than differences between treatments. The fish communities in the Control and Structures + Corals treatments showed the highest dissimilarity, while the communities in the Structures and Structures + Corals treatments were the least dissimilar. In terms of location, the fish communities at Meras and Bunaken were the least dissimilar, reflecting similar environmental conditions.

**Table 3.3:** Results of a crossed two-way ANOSIM for effects of Treatment and Location using all experimental fish census samples.

Test	Factor	Test pairs	p	p(p)
Global pairwise	Treatment		0.643	0.001
		Control, S + C	0.802	0.001
		Control, Structures	0.751	0.001
		S + C, Structures	0.564	0.001
Global pairwise	Location		0.83	0.001
		Gangga, Meras	0.933	0.001
		Gangga, Bunaken	0.891	0.001
		Meras, Bunaken	0.664	0.001

In the MDS plot for the average sample data from all sites, the separation by location and treatment revealed by the ANOSIM is visible (Fig. 3.8). As indicated by the test, samples from Bunaken and Meras, and from the Structures + Corals treatment and the Structures treatment, are located close to each other in the plot.



**Figure 3.8:** Non-metric Multi Dimensional Scaling (MDS) based on Bray-Curtis similarity of the average fish community data taken from all experimental sites. **Red:** Gangga, **Yellow:** Meras, **Blue:** Bunaken.

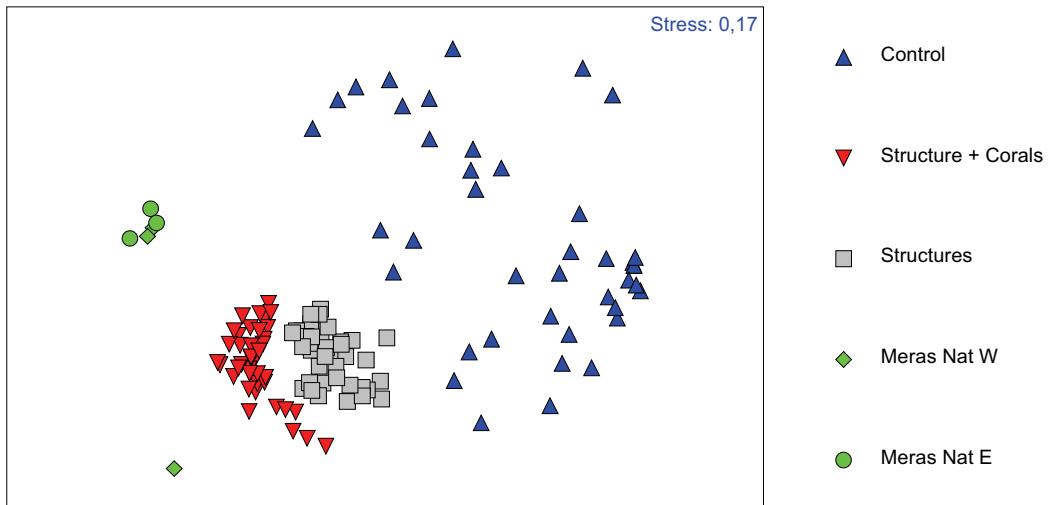
In the MDS plot, samples from the Control treatment are more widely dispersed than the samples from the other two treatments. This is confirmed by a comparison of the relative dispersion of the average samples in each sample group (Tab. 3.4): while the samples from the Structures + Corals treatment are the least dispersed, the samples from the Control treatment have the highest relative dispersion at all locations.

**Table 3.4:** Relative multivariate dispersion of the average samples in each treatment at the three locations.

Location	Treatment	Relative dispersion
Gangga	Structures + Corals	0.734
	Structures	0.919
	Control	1.247
Meras	Structures + Corals	0.672
	Structures	0.703
	Control	1.688
Bunaken	Structures + Corals	0.765
	Structures	0.807
	Control	1.489

At all three locations, there were significant effects of treatment and time on fish community composition. The effects of treatment were stronger than the effects of time at all locations. The MDS plot for the data from Meras is exemplary: it shows distinct clustering of the samples taken from the three different experimental plots, with the samples from the Control plot being most widely spaced (Fig. 3.9). Samples from the other two experimental plots show high within-treatment similarity. The samples from the natural reef plots form a distinct cluster, with the exception of one highly dissimilar sample, and appear closest (i.e., most similar) to the samples from the Structures + Corals plot.

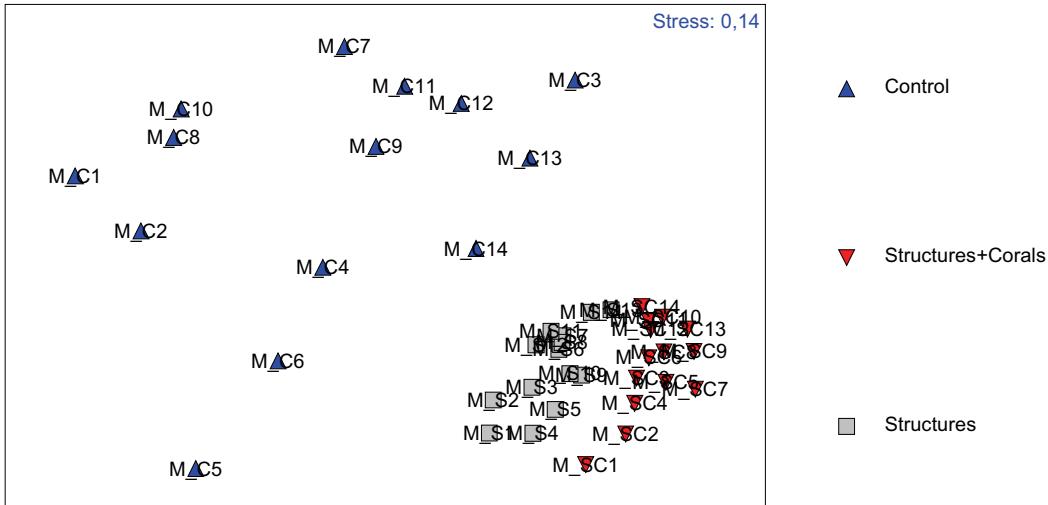
As shown by the ANOSIM (Tab. 3.5), there was a significant effect of time on community similarity. When looking at the average census data in an MDS plot, a clear trend over time becomes visible, with the community becoming more dissimilar from the original community in each experimental plot over time (Fig. 3.10). While the development of the community in the Control plot over time is somewhat random, clear trends are visible for the two other experimental plots, with the communities evolving towards an end-point over time.



**Figure 3.9:** Non-metric Multi Dimensional Scaling (MDS) based on Bray-Curtis similarity of all fish community samples taken at Meras.

**Table 3.5:** Results of a crossed two-way ANOSIM for effects of Treatment and Time using all experimental fish census samples from Meras.

Test	Factor	Test pairs	$p$	$p(p)$
Global pairwise	Treatment		0.931	0.001
		Control, S + C	0.997	0.001
		Control, Structures	0.994	0.001
		S + C, Structures	0.994	0.001
Global	Time		0.853	0.001



**Figure 3.10:** Non-metric Multi Dimensional Scaling (MDS) based on Bray-Curtis similarity of the average census data from the experimental plots for consecutive samplings at Meras, showing the development of the fish communities over time.

At the other two sites, ANOSIM revealed similar effects of treatment and time as those observed at Meras (Tabs. A 7 and A 8, see Appendix). At Gangga, the communities from the natural reef plots appear closest to the community from the Structures plot, indicating that the community in the Structures was most similar to that found in the natural reef. Also, there was some overlap between samples from the Structures + Corals and the Structures treatment. Otherwise, distinct clustering according to treatment was evident both at Gangga and Bunaken. Trends in community composition over time were similar to that seen at Meras. For MDS plots of the communities at Gangga and Bunaken, see Figs. A 3 to A 6 in the Appendix.

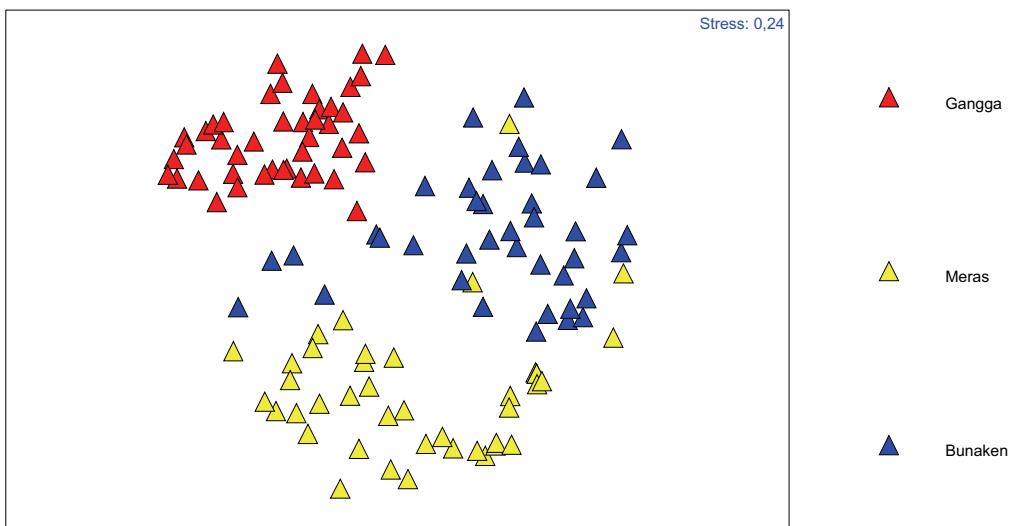
### 3.1.4.3 Effects of location

In the Control treatment, there were significant effects of location on similarity of the fish community (Tab. 3.6). When comparing only those samples taken within the same month at each location, the dissimilarity between the locations decreased. Time measured as sampling campaign number also had a significant effect, indicating some degree of succession in the community composition. However, the month in which a sample was taken also influenced similarity between the samples, hinting at the presence of some seasonality in the composition of the fish community in the Control plots.

**Table 3.6:** Results of a crossed two-way ANOSIM for effects of Location and Time using all experimental fish census samples from the Control treatment.

Using sampling campaign number as time					Using sampling month as time				
Test	Factor	Test pairs	p	p(p)	Test	Factor	Test pairs	p	p(p)
Global pairwise	Location	Gangga, Meras	0.992	0.001	Global pairwise	Location	Gangga, Meras	0.808	0.001
		Gangga, Bun.	0.959	0.001			Gangga, Bun.	0.836	0.001
		Meras, Bun.	0.909	0.001			Meras, Bun.	0.612	0.001
		Global Time	0.683	0.001			Global Time	0.31	0.001

The MDS plot for the sample replicates from the Control treatment clearly shows clustering of the samples based on the three locations (Fig. 3.11). While the samples from Gangga form one distinct cluster, there is some overlap between the samples from Meras and Bunaken. However, the relatively high stress value (0.24) indicates that the MDS plot is not a very accurate representation of the actual dissimilarities between the samples and should be viewed with caution.



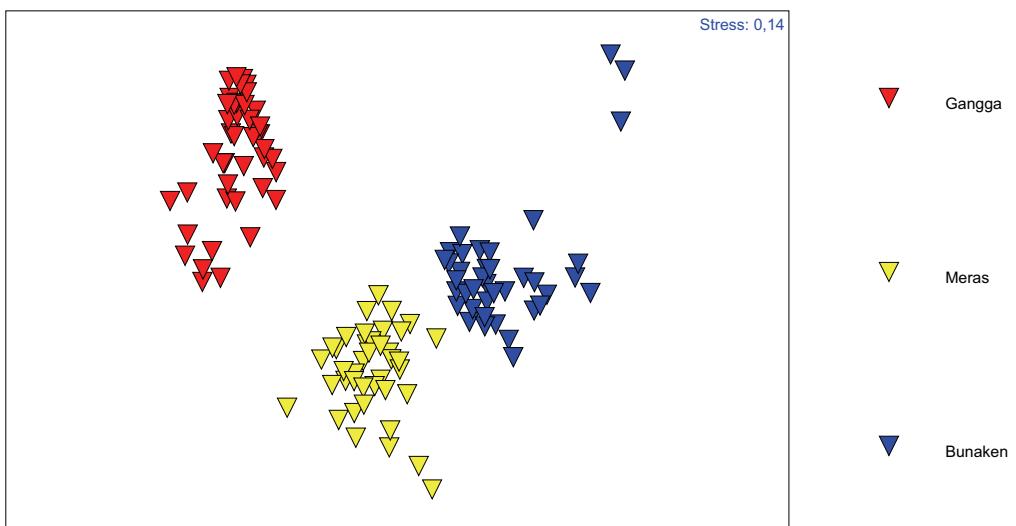
**Figure 3.11:** Non-metric Multi Dimensional Scaling (MDS) based on Bray-Curtis similarity of all fish community sample replicates taken from the Control treatment.

In the Structures + Corals treatment, differences between the communities at the three locations were most marked (Tab. 3.7). The effect of sampling campaign number was higher than in the other two treatments, while in this treatment the effect of month of sampling on community composition was the lowest of all three treatments.

**Table 3.7:** Results of a crossed two-way ANOSIM for effects of Location and Time using all experimental fish census samples from the Structures + Corals treatment.

Using sampling campaign number as time					Using sampling month as time				
Test	Factor	Test pairs	p	p(p)	Test	Factor	Test pairs	p	p(p)
Global pairwise	Location	Gangga, Meras	1.0	0.001	Global pairwise	Location	Gangga, Meras	0.919	0.001
		Gangga, Bun.	1.0	0.001			Gangga, Bun.	0.947	0.001
		Meras, Bun.	1.0	0.001			Meras, Bun.	0.982	0.001
	Time		0.889	0.001		Global	Time	0.218	0.001

In the MDS plot for samples from the Structures + Corals treatment, there is a noticeable clustering according to location (Fig. 3.12). The clustering of the location groups in this treatment is a lot denser than that in the Control treatment. The three replicates from the first sampling at Bunaken are distinctly visible in the upper right hand corner of the plot, reflecting the dissimilarity of the first replicates with those taken subsequently that was also apparent in the MDS plots of all community samples taken at Bunaken (Figs. A 5 and A 6 in the Appendix).



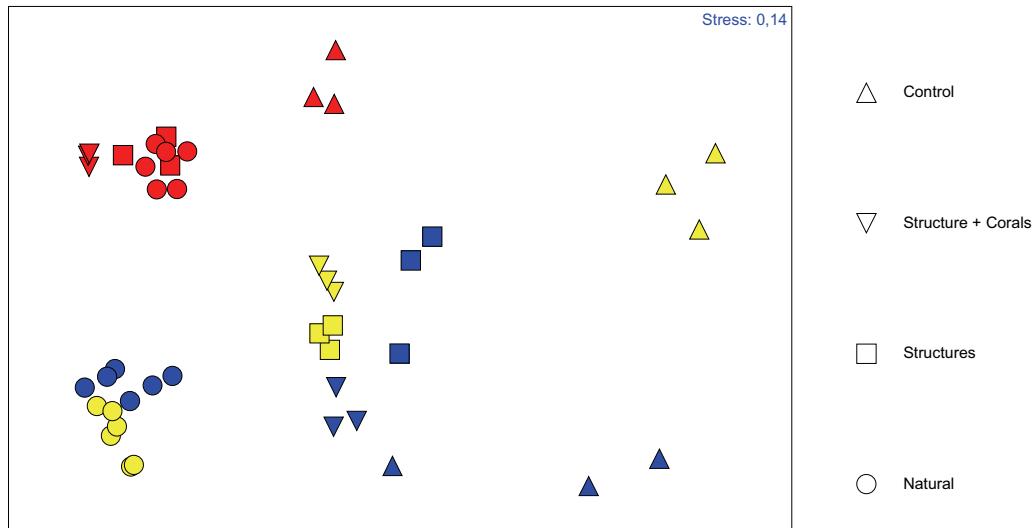
**Figure 3.12:** Non-metric Multi Dimensional Scaling (MDS) based on Bray-Curtis similarity of all fish community sample replicates taken from the Structures + Corals treatment. Note the three replicates from the first sampling at Bunaken seen in the upper right hand corner.

In the Structures treatment, there also were significant effects both of location and of time (sampling campaign number) on fish community composition. The influence of month of sampling was slightly higher than in the Structures + Corals treatment, but lower than in the Control treatment. In the Structures treatment, the clustering of samples according to sites was the most distinct of all three treatments. For the ANOSIM results and the MDS plot, see Tab. A 9 and Fig. A 7 in the Appendix.

#### 3.1.4.4 Comparisons with the natural reef

A direct comparison of the sample replicates from the natural reef plots with the experimental sample replicates taken at the same time at each location shows high similarity between the natural reef samples and the community in the Structures + Corals and Structures plots at Gangga (Fig. 3.13). While the samples from Gangga form a distinct cluster in the graph, the communities in the natural reef, Structures + Corals, and Structures plots at Bunaken and

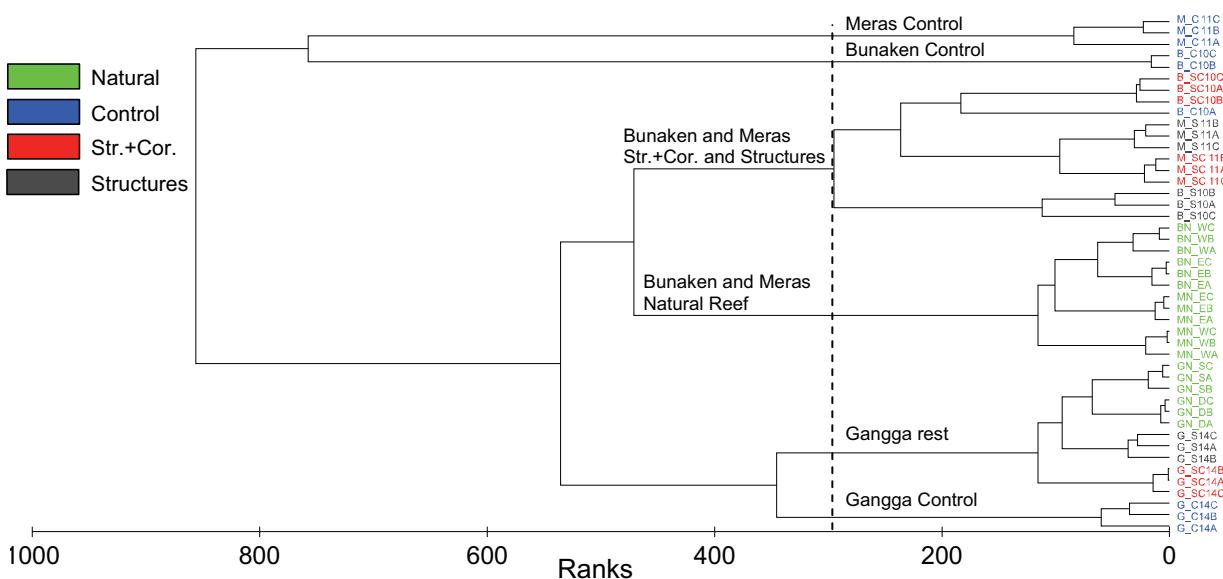
Meras are placed close to each other. The communities in the Control plots at Bunaken and Meras each form distinct clusters in the plot.



**Figure 3.13:** Non-metric Multi Dimensional Scaling (MDS) based on Bray-Curtis similarity comparing replicates from the natural reef plots with replicates from the experimental plots taken during the same time. **Red:** Gangga, **Yellow:** Meras, **Blue:** Bunaken.

Hierarchical clustering of the sample replicates underlines the patterns visible in the MDS plot (Fig. 3.14). In the dendrogram, the samples from the Control treatment group into distinct branches. The communities in the Control plots at Meras and Bunaken, although with one exception more similar to each other than to all other samples, form two distinct subgroups early on. The next branching establishes the samples from Gangga as a separate group. At Gangga, the community in the Structures plot is more similar to the natural reef plot communities than that in the Structures + Corals plot. The communities in the natural reefs at Bunaken and Meras form one distinct group. At these two locations, the communities in the Structures + Corals plots were most similar to the communities from the natural reef plots.

#### *Clustering of experimental and natural plots based on ranked similarity*



**Figure 3.14:** Hierarchical clustering of the fish community samples from the natural reef plots and community samples from the experimental plots taken during the same time, showing subgroups at similarity = 300 ranks.

### 3.1.4.5 Responses of fish feeding guilds to treatments

Obligative corallivores occurred almost exclusively in the Structures + Corals plot at Gangga (Fig. 3.15) and one of the natural reef plots at Bunaken, hence an ANOSIM for effects of treatment and location was not practicable for this group. In the three other feeding groups, effects of location were always larger than effects of treatment (Tab. 3.8). In all groups, dissimilarity was lowest between the Structures + Corals and the Structures treatment, and highest between the Structures + Corals and the Control treatment. Similarity was also higher between the samples from Meras and Bunaken than between those from these two sites and Gangga for all groups.

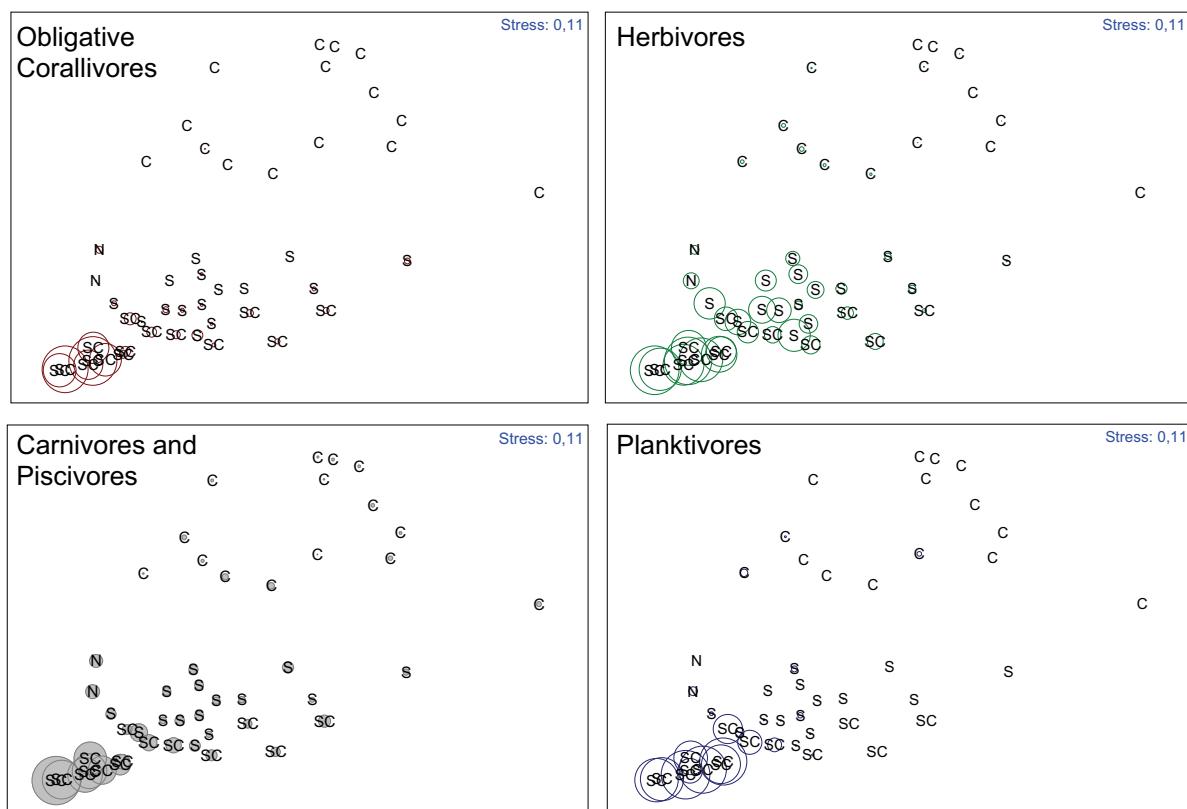
**Table 3.8:** Results of a crossed two-way ANOSIM for effects of Location and Time on fish species belonging to certain feeding groups, based on all samples from experimental plots in which the respective species were present.

Test	Factor	Test pairs	$\rho$	$p(\rho)$
<b>Herbivores</b>				
Global pairwise	Treatment		0.38	0.001
		Str+Cor, Structures	0.202	0.001
		Str+Cor, Control	0.569	0.001
		Structures, Control	0.474	0.001
Global pairwise	Location		0.518	0.001
		Gangga, Meras	0.626	0.001
		Gangga, Bunaken	0.535	0.001
		Meras, Bunaken	0.375	0.001
<b>Planktivores</b>				
Global pairwise	Treatment		0.249	0.001
		Str+Cor, Structures	0.172	0.001
		Str+Cor, Control	0.366	0.001
		Structures, Control	0.275	0.001
Global pairwise	Location		0.518	0.001
		Gangga, Meras	0.734	0.001
		Gangga, Bunaken	0.762	0.001
		Meras, Bunaken	0.175	0.001
<b>Carnivores and Piscivores</b>				
Global pairwise	Treatment		0.433	0.001
		Str+Cor, Structures	0.260	0.001
		Str+Cor, Control	0.613	0.001
		Structures, Control	0.461	0.001
Global pairwise	Location		0.712	0.001
		Gangga, Meras	0.838	0.001
		Gangga, Bunaken	0.766	0.001
		Meras, Bunaken	0.481	0.001



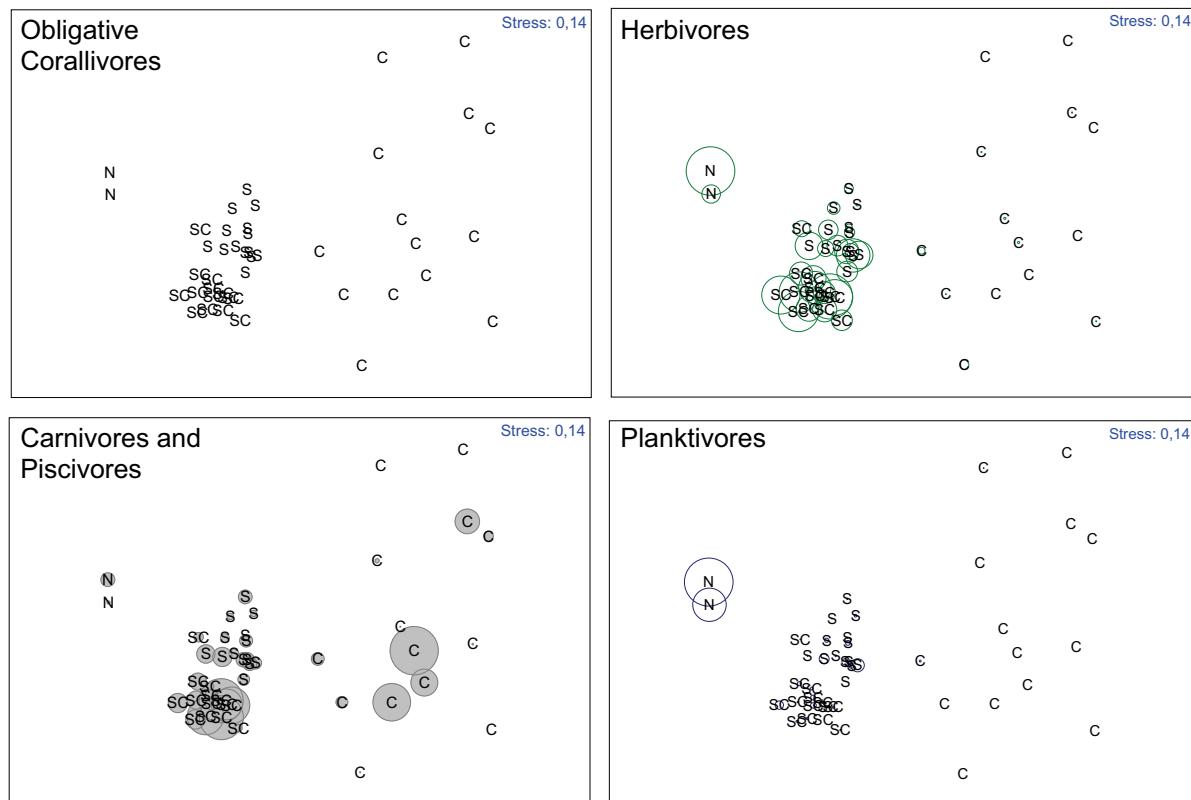
**Figure 3.15:** A juvenile obligative corallivore, *Chaetodon meyeri*, seeking shelter among the branches of transplanted *Acropora yongei* in the Structures + Corals plot at Gangga.

At Gangga, there was an obvious difference in the number of obligate corallivores in the Structures + Corals plot and in the other experimental and natural reef plots (Fig. 3.16). The largest numbers of corallivores appeared in samples taken late in the experiment (lower left corner of the MDS plot). A comparable pattern was apparent for planktivorous fishes, although they were present in high numbers earlier than the corallivores. Herbivores appeared in similar numbers in both the Structures + Corals and the Structures plots, although they were slightly more abundant in the former. Carnivores and piscivores were present in all treatments, although their relative abundance was highest in the Structures + Corals plot and lowest in the Control plot.



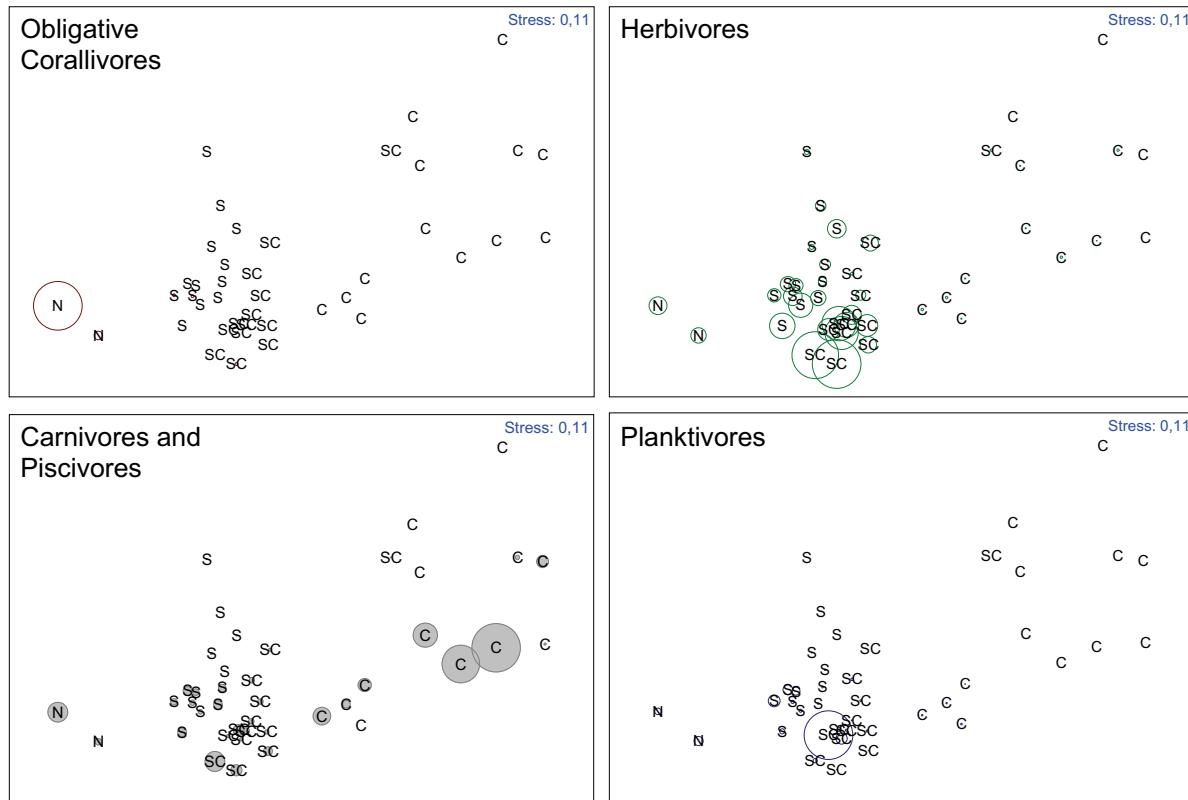
**Figure 3.16:** MDS plots for all average samples from Gangga, with superimposed bubble plots showing the relative abundance of fishes in four feeding guilds in each sample.

At Meras, no obligative corallivores were present in either the natural or the experimental plots (Fig. 3.17). Herbivores appeared in all except the Control plots in similar relative abundance. Carnivores and piscivores were most abundant in the Structures + Corals plot, but they were present in a lower abundance in all samples from the Structures plot and sometimes were very abundant in the Control plot. Planktivores were most abundant in the natural reef plots, but also occurred in the Structures + Corals and the Structures plots.



**Figure 3.17:** MDS plots for all average samples from Meras, with superimposed bubble plots showing the relative abundance of fishes in four feeding guilds in each sample.

At Bunaken, corallivorous fishes were only found in the natural reef plots (Fig. 3.18). Herbivores occurred in the natural reef plots and the Structures and the Structures + Corals plots, but relative abundance was highest in the latter one. Piscivorous and carnivorous fishes were observed infrequently in all plots, but were most abundant in the Control plot. The relative abundance of planktivores was highest in the Structures + Corals plot, but they also occurred in the natural reef and Structures plots.

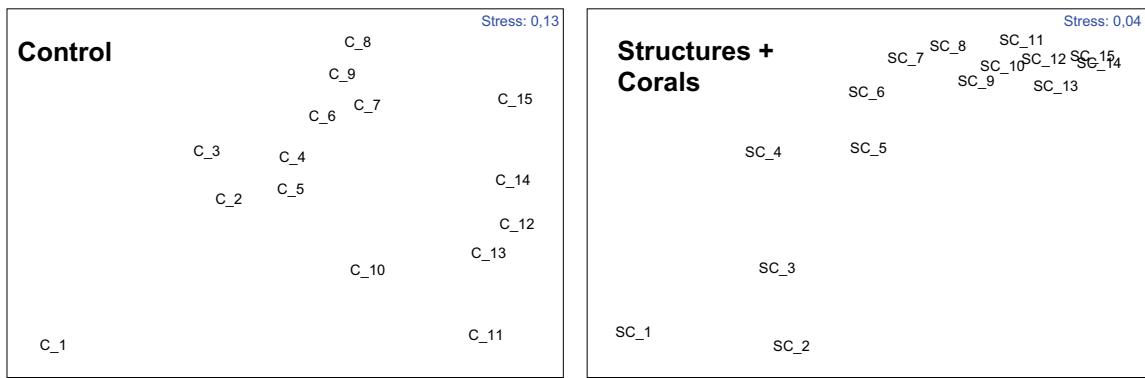


**Figure 3.18:** MDS plots for all average samples from Bunaken, with superimposed bubble plots showing the relative abundance of fishes in four feeding guilds in each sample.

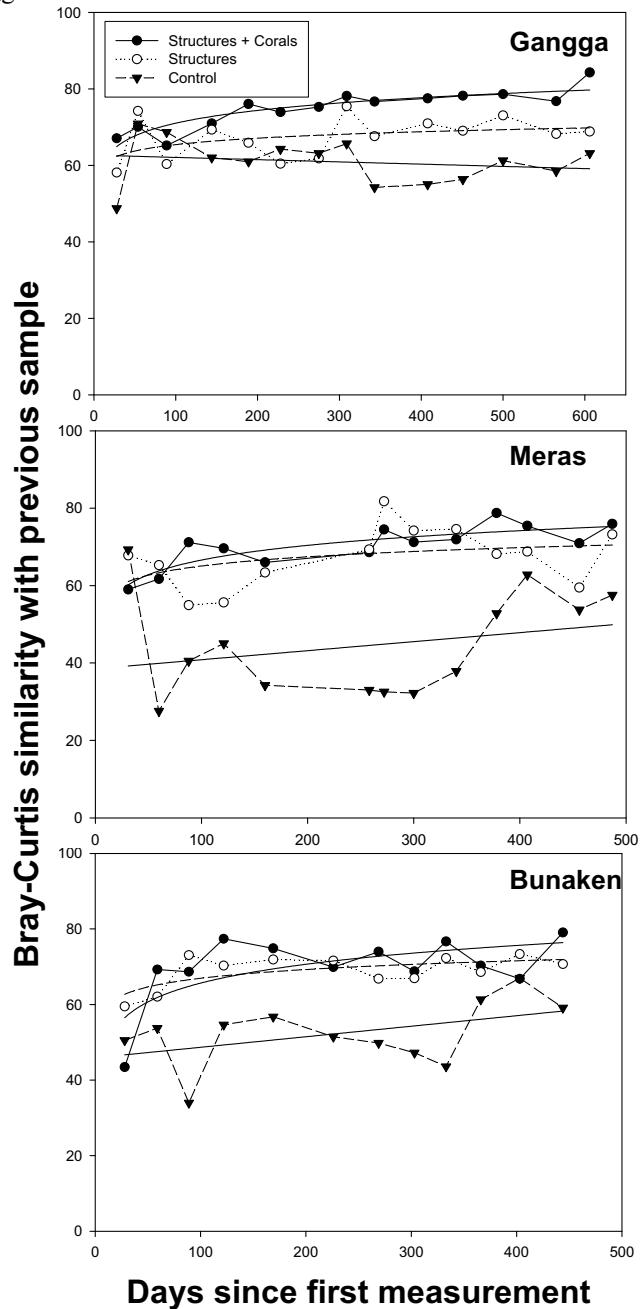
### 3.1.4.6 Patterns in the development of the fish community over time

As was shown above (see Figs. 3.10, A 4 and A 6), there were some apparent trends in the development of the fish community in the experimental plots over time. While in the Control treatment, similarity of the community in consecutive samples did not appear to follow a specific pattern over time, the communities in the Structures + Coral plots became increasingly similar to each other as time progressed and seemed to evolve away from the community composition in the initial samples (Fig. 3.19).

The similarity between consecutive samples in each treatment at the three locations, which is also incorporated in the similarity matrices underlying the MDS plots in Fig. 3.19, follows different trends over time in each treatment (Fig. 3.20). Although strictly exploratory because of interdependence of consecutive variables in the plots, it is evident that similarity between consecutive samples in the Control treatment at all locations is smaller than that between samples in the other treatments. Also, similarity between consecutive samples seems to increase over time. For illustrative purposes, regression lines are shown for each treatment.



**Figure 3.19:** An exemplary comparison of the relative similarity of samples from the Control and Structures + Corals plots from Gangga.



**Figure 3.20:** Similarity between consecutive samples from the three treatments at each location. Regression lines for each treatment are shown for illustrative purposes only. Linear regression gave the best fit for the Control treatment, while logarithmic regression yielded a better fit for the other two treatments.

A statistical analysis of similarity of the fish communities in consecutive samples over time was performed by comparing the similarity matrices of each treatment at the three locations with model matrices (Tab. 3.9). The results show that while in the Control plot at Gangga similarity between consecutive community samples was best explained by a serial model (i.e., similarity did not increase over time), the model assuming increasing similarity best explained the similarity patterns observed in the other experimental plots. The correlation with the increasing model matrix was markedly higher in the Structures + Corals plots than in the other two at Gangga and Meras. At Bunaken, the increasing similarity matrix correlated equally well with the sample matrices from the Structures and the Structures + Coral plots. There were no significant correlations between any of the sample matrices and either one of the two cyclicity model matrices, indicating that seasonality did not play a significant role in the composition of the fish community in all treatments.

**Table 3.9:** Spearman rank correlations between the similarity matrices of the average community samples from each treatment at the three locations and model matrices. The highest correlations between a sample similarity matrix and one of the model matrices are shown in **bold**.

Location	Treatment	Model matrix used							
		Seriation		Increasing similarity		Annual cyclicity		6-month cyclicity	
		$\rho$	p( $\rho$ )	$\rho$	p( $\rho$ )	$\rho$	p( $\rho$ )	$\rho$	p( $\rho$ )
Gangga	Control	<b>0.683</b>	0.001	0.625	0.001	0.100	0.112	-0.101	0.895
	Str + Cor	0.849	0.001	<b>0.973</b>	0.001	0.070	0.184	-0.108	0.961
	Structures	0.758	0.001	<b>0.877</b>	0.001	0.118	0.940	-0.117	0.942
Meras	Control	0.500	0.001	<b>0.733</b>	0.001	0.003	0.439	0.127	0.111
	Str + Cor	0.726	0.001	<b>0.903</b>	0.001	0.033	0.324	0.036	0.306
	Structures	0.646	0.001	<b>0.734</b>	0.001	-0.095	0.810	0.044	0.315
Bunaken	Control	0.583	0.001	<b>0.673</b>	0.001	-0.004	0.459	0.060	0.238
	Str + Cor	0.697	0.001	<b>0.903</b>	0.001	0.020	0.397	-0.028	0.615
	Structures	0.803	0.001	<b>0.918</b>	0.001	0.017	0.391	-0.065	0.725

In addition to the similarity between consecutive community samples, the similarity between the replicates in one sample differed according to treatment. In the linear model testing for effects on within-sample similarity, significant effects of Treatment, Location\*Time and Location\*Treatment were detected (Tab. 3.10). A post-hoc test (Tukey HSD,  $Q = 2.3831$ ,  $\alpha = 0.05$ ) confirmed that within-sample similarity was lowest in the Control treatment and highest in the Structures + Corals treatment, and that differences between all treatments were significant. However, the results should be treated carefully, since the Shapiro-Wilk test revealed that the residuals of the model were not normally distributed ( $p = 0.0147$ ), and normality of residuals could only be achieved by removing Time from the model. The significance of the other factors remained similar in the simplified model (see Tab. A 10). As the data from the Structures treatment did not conform to normality even after transformation, an additional non-parametric Kruskal-Wallis test followed by pairwise Mann-Whitney tests was applied to confirm the significant effects of Treatment (Tab. A 11). For graphs of the average similarities in the three treatments at each location, see Fig. A 8 in the Appendix.

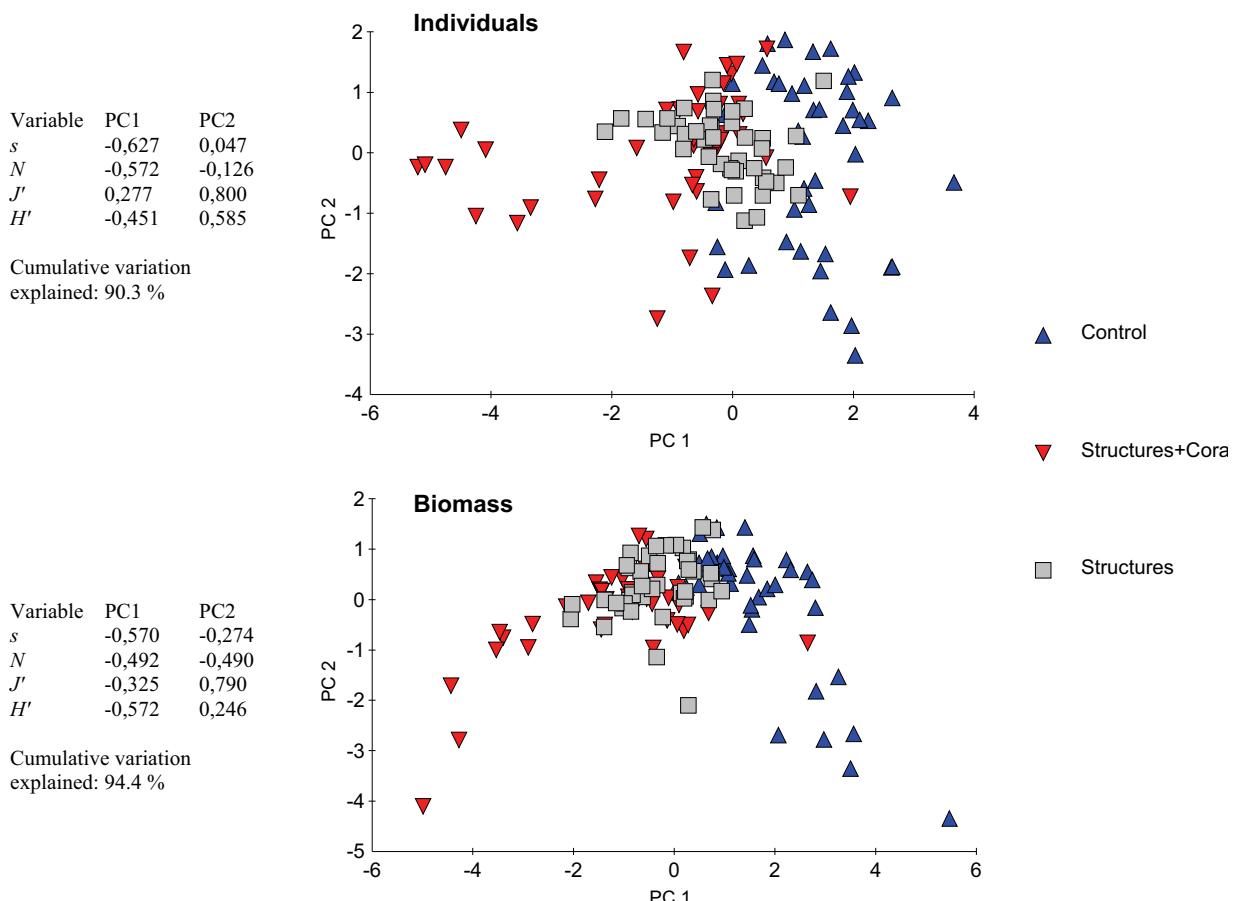
**Table 3.10:** Results of the linear model testing for treatment effects, time effects and location effects on within-sample similarity.

Test	Source	df	F	p
ANOVA	Model ( $R^2 = 0.6751$ )	17,90	11.0007	< 0.0001
Effect Test	Location	2	2.8534	0.0629
	Time	1	0.9198	0.3401
	Treatment	2	73.7140	< 0.0001
	Location*Time	2	5.9557	0.0037

Location*Treatment	4	4.5452	0.0022
Time*Treatment	2	0.9218	0.4015
Location*Time*Treatment	4	0.3567	0.8387

### 3.1.5 General patterns in indicators among the treatments

Using only four indicator variables derived from each averaged sample (species richness  $s$ , total sample content  $N$  (number of individuals and total biomass, respectively), diversity  $H'$ , and evenness  $J'$ ), differences among the three treatments could be discerned (Fig. 3.21). While the first principal component axis clearly divides the samples into those from the Structures + Corals treatment (on the left) and those from the Control treatment (on the right), the second axis does not distinguish between treatments. Both for indicators based on number of individuals and for those based on biomass, samples from the Structures + Corals treatment are positively correlated with  $s$ ,  $N$  and  $H'$ , while samples from the Control treatment are found on the opposite end of the PC 1 axis. The eigenvector of  $J'$  for the PC 1 axis are rather small for both analyses. An ordination based in indicators derived from numbers of individuals resulted in dispersal of the samples, while ordination based on indicators from biomass lead to denser clustering and stretching of the Structures + Corals and Control samples along a kind of arch: while high values of  $J'$  coincide with intermediate  $s$ ,  $N$  and  $H'$  in the center of the graph, lower values of  $J'$  occur in samples with high  $s$ ,  $N$  and  $H'$  in the Structures + Corals treatment and with low  $s$ ,  $N$  and  $H'$  in the Control treatment. In both plots, samples from the Structures treatment are clustered in the center of the graph at the intersection of both principal component axes.

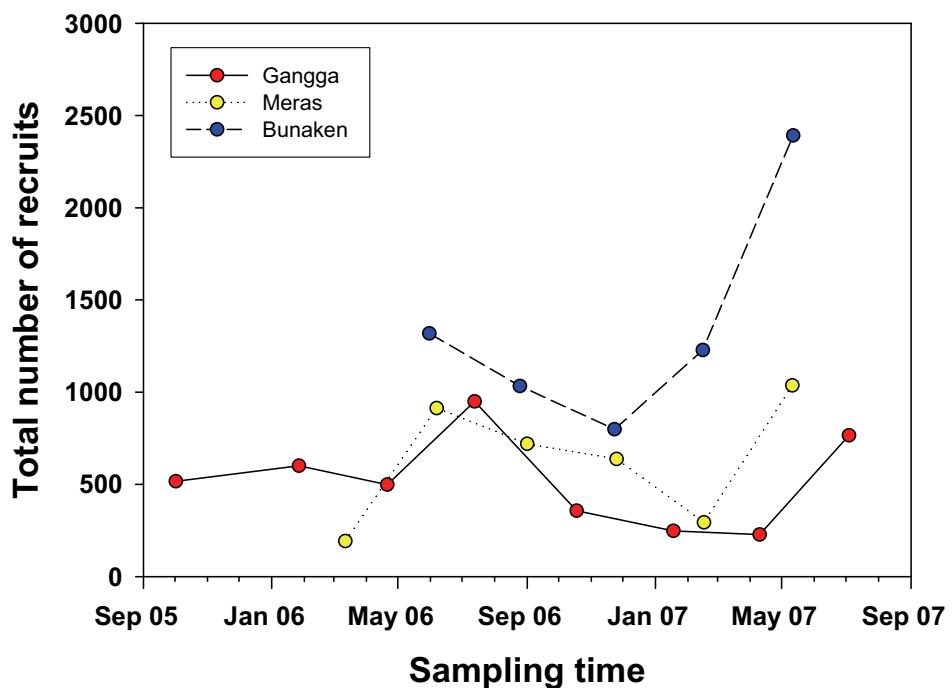


**Figure 3.21:** Ordination by Principal Component Analysis (PCA) using normalized Euclidean distances based on indicator variables derived from number of individuals (above) and total biomass (below) in each average sample.

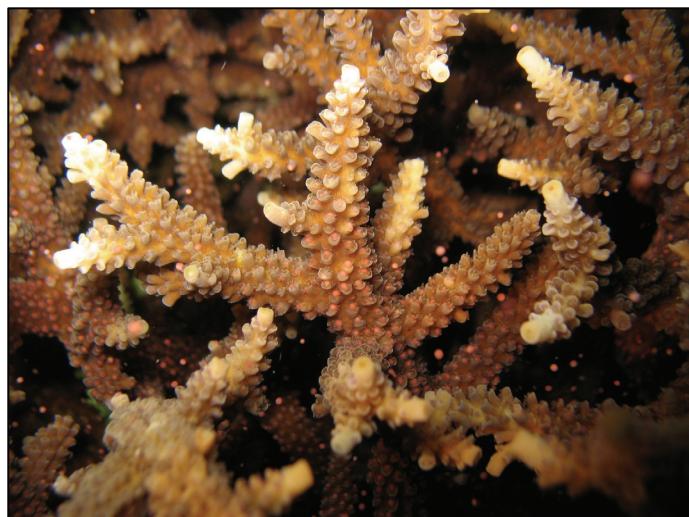
## 3.2 Coral recruitment

### 3.2.1 Recruitment on the settlement plates

The total number of recruits counted for each location every time the settlement plates were collected indicates a major recruitment event taking place each year between March and June (Fig. 3.22). The highest total number of recruits ( $n = 2391$ , approximately 8.7 recruits per 100 cm $^2$ ) were observed during the final sampling period at Bunaken. Generally, the number of recruits occurring at Bunaken was higher than that observed at Meras and Gangga at comparable times. While the number of recruits reached a low before each major recruitment event at Meras and Gangga, recruitment at Bunaken increased in two steps in 2007. The second major recruitment event indicated by the high number of recruits observed coincided with a mass spawning observed at the donor colony of *A. yongei* at Lihage Island from which the coral transplants used at Gangga were collected (Fig. 3.23).



**Figure 3.22:** Total amount of recruits counted per sampling campaign (exchange of all tiles in the experimental plots) at each location. At each location, 54 plates with a total surface area of about 27,540 cm $^2$  were deployed.



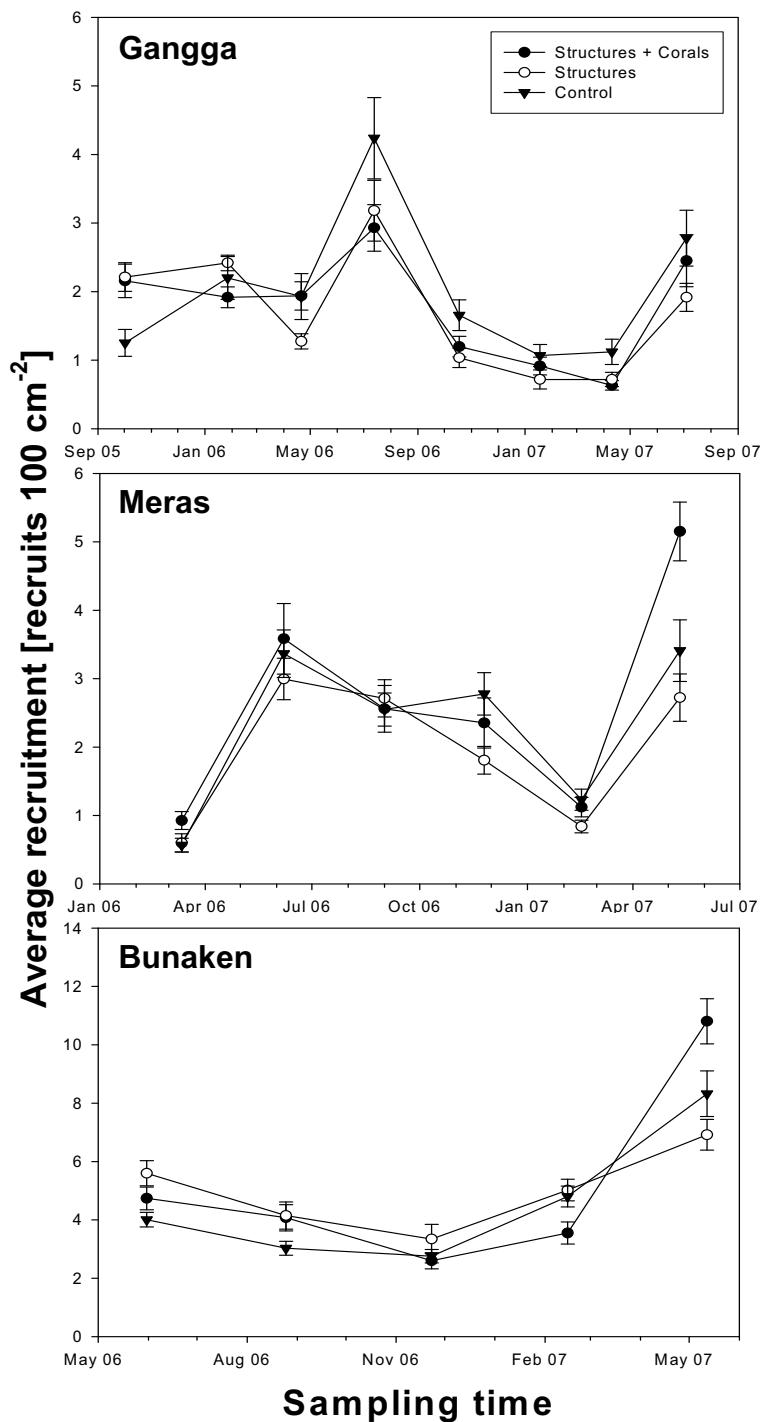
**Figure 3.23:** Mass spawning of the mother colony of *Acropora yongei* at Lihage Island on 06. May 2007.

At all locations, there were little differences between the treatment plots in the average number of recruits observed every time the settlement plates were collected (Fig. 3.24).

At Gangga, an unusually high number of recruits were observed on one of the settlement plates in the Control treatment after the plates were collected for the last time. Since there was reason to suspect that this high number was caused by the presence of a coral colony growing on the settlement frame (see discussion), data from this plate was excluded from the subsequent analysis. A significant effect of treatment was detected only after the first period (ANOVA,  $F = 7.1783$ ,  $p = 0.0018$ ,  $df = 2,51$ ). The Tukey HSD test confirmed significant differences between recruitment in the Control and the higher rates in the other two plots ( $\alpha = 0.05$ ). In the third period, Bartlett's test detected unequal variances (Bartlett,  $F = 9.0168$ ,  $p = 0.0001$ ,  $df = 2$ ) and the subsequent Welch ANOVA was significant ( $F = 3.7903$ ,  $p = 0.0338$ ,  $df = 2,30.577$ ), but the post-hoc test did not find significant differences between the treatments.

At Meras, significant differences between the treatments were detected after the first and sixth period. For the first data set, transformation failed to achieve normal distribution in the Control treatment (Shapiro-Wilk,  $W = 0.8372$ ,  $p = 0.0054$ ). Hence, a nonparametric test was applied, which detected significant treatment effects (Kruskal-Wallis,  $\chi^2 = 6.4610$ ,  $p = 0.0395$ ,  $df = 2$ ). Pairwise tests revealed that recruitment in the Structures + Corals plot was higher than that in the Control plot (Mann-Whitney,  $\chi^2 = 5.5660$ ,  $p = 0.0183$ ,  $df = 1$ ) and in the Structures plot (Mann-Whitney,  $\chi^2 = 4.0369$ ,  $p = 0.0445$ ,  $df = 1$ ). In the final sampling interval, there again was a significant treatment effect (ANOVA,  $F = 9.4631$ ,  $p = 0.0003$ ,  $df = 2,51$ ). The post-hoc test confirmed that recruitment in the Structures + Corals plot was higher than in the other two plots, which did not differ from each other ( $\alpha = 0.05$ ).

At Bunaken, significant treatment effects were detected after the first, fourth and fifth sampling interval (ANOVA,  $F = 4.3749$ ,  $p = 0.0176$ ,  $df = 2,51$ ; ANOVA,  $F = 5.3279$ ,  $p = 0.0079$ ,  $df = 2,51$ ; ANOVA,  $F = 7.8161$ ,  $p = 0.0011$ ,  $df = 2,51$ , respectively). After the first period, the post-hoc test found significant differences between the Control and the Structures treatment. In the fourth period, recruitment was significantly lower in the Structures + Corals plot than in the other two plots. In the last interval, recruitment rates reversed and a significantly higher number of recruits were found in the Structures + Corals plot than in the other two plots (all post-hoc tests at  $\alpha = 0.05$ ).



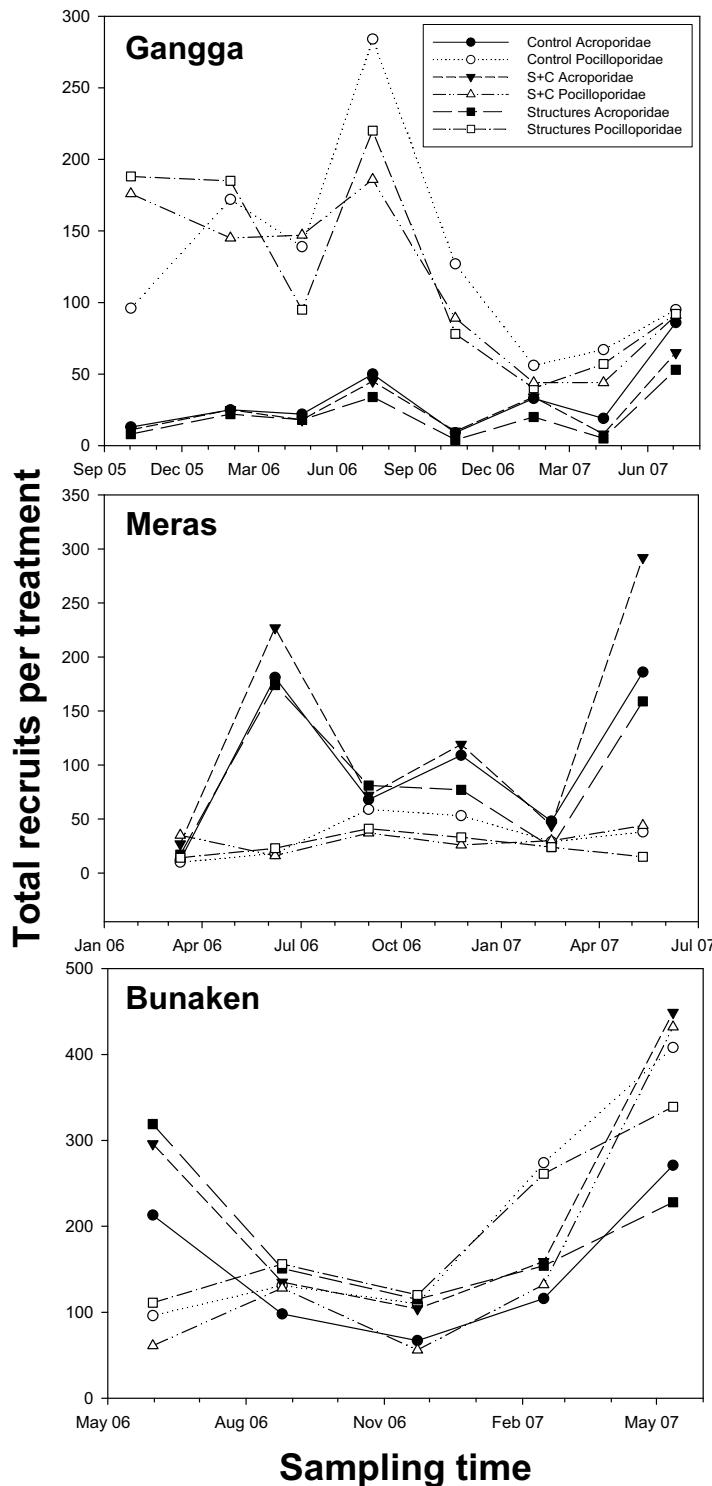
**Figure 3.24:** Average number of recruits (mean  $\pm$  SE) observed on settlement plates deployed in the experimental plots for three-month intervals at the three locations.

In terms of recruits belonging to the families Acroporidae and Pocilloporidae, different patterns were observed at the three locations (Fig. 3.25).

At Gangga, the total number of acroporids observed in each plot did not vary much, while the number of pocilloporids fluctuated a lot in the first year of the experiment, and relative abundances in the three treatments changed with each sampling. Only during the last three samplings did the trends stabilize. A significant difference in the relative frequencies of both families among the treatments was detected only for the first sampling interval (Pearson chi-square,  $\chi^2 = 7.281$ ,  $p = 0.0262$ ,  $df = 2$ ), where relative frequency of acroporids was highest in the Control plot. The total number of acroporids increased during both observed mass recruitment events, while the number of pocilloporids showed a major peak only during the first event but increased only slightly in the final interval.

At Meras, the number of pocilloporids in the three treatments did not vary much over the experiment, while acroporids fluctuated and reached peak abundances during the two mass recruitment events. Relative frequencies of the families differed significantly between the treatments only in the fourth sampling interval (Pearson chi-square,  $\chi^2 = 9.265$ ,  $p = 0.0097$ ,  $df = 2$ ), with relative frequency of acroporids being highest in the Structures + Corals plot.

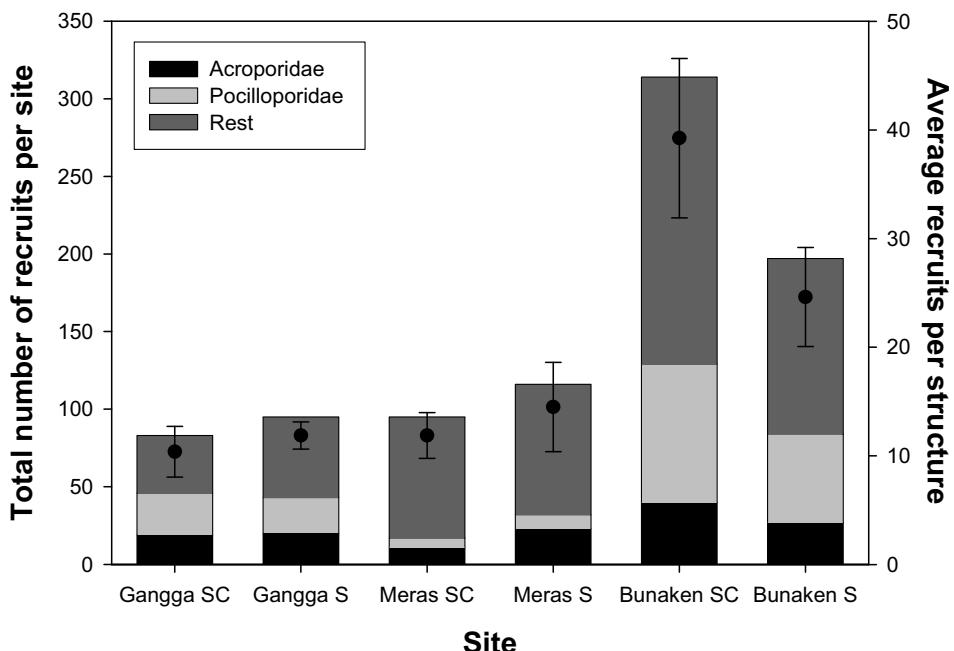
At Bunaken, the amount of acroporids was markedly higher than that of pocilloporids in all treatments in the first sampling interval. In the two subsequent intervals, pocilloporids and acroporids occurred in similar abundances. Relative frequency of acroporids was highest in the Structures + Corals plot during all sampling intervals, and significant differences between the treatments were detected in all but the second interval (Pearson chi-square, 1<sup>st</sup> interval:  $\chi^2 = 18.236$ ,  $p = 0.0001$ ,  $df = 2$ ; 3<sup>rd</sup> interval:  $\chi^2 = 24.953$ ,  $p < 0.0001$ ,  $df = 2$ ; 4<sup>th</sup> interval:  $\chi^2 = 44.520$ ,  $p < 0.0001$ ,  $df = 2$ ; 5<sup>th</sup> interval:  $\chi^2 = 24.907$ ,  $p < 0.0001$ ,  $df = 2$ ).



**Figure 3.25:** Total numbers of acroporid and pocilloporid recruits counted on the 18 settlement plates deployed in each experimental plot during each sampling period.

### 3.2.2 Recruits on the concrete structures

The total numbers of recruits counted on the eight innermost concrete structures in the Structures + Corals and Structures plots as well as the average number per structure were similar at Gangga and Meras (Fig. 3.26). Both total and average numbers were higher at Bunaken. The difference in average number of recruits between locations was significant (ANOVA,  $F = 14.9761$ ,  $p < 0.0001$ ,  $df = 2,45$ ). The post-hoc test confirmed significant differences between average number of recruits at Bunaken and the other two sites ( $\alpha = 0.05$ ). There was no significant effect of treatment on average number of recruits at any of the sites. Although there were differences in the relative frequencies of acroporid and pocilloporid recruits at the three locations (Pearson chi-square,  $\chi^2 = 24.675$ ,  $p < 0.0001$ ,  $df = 2$ ), there were no significant effects of treatment on relative frequencies at any of the locations. Relative frequency of acroporids was highest at Meras and lowest at Bunaken.



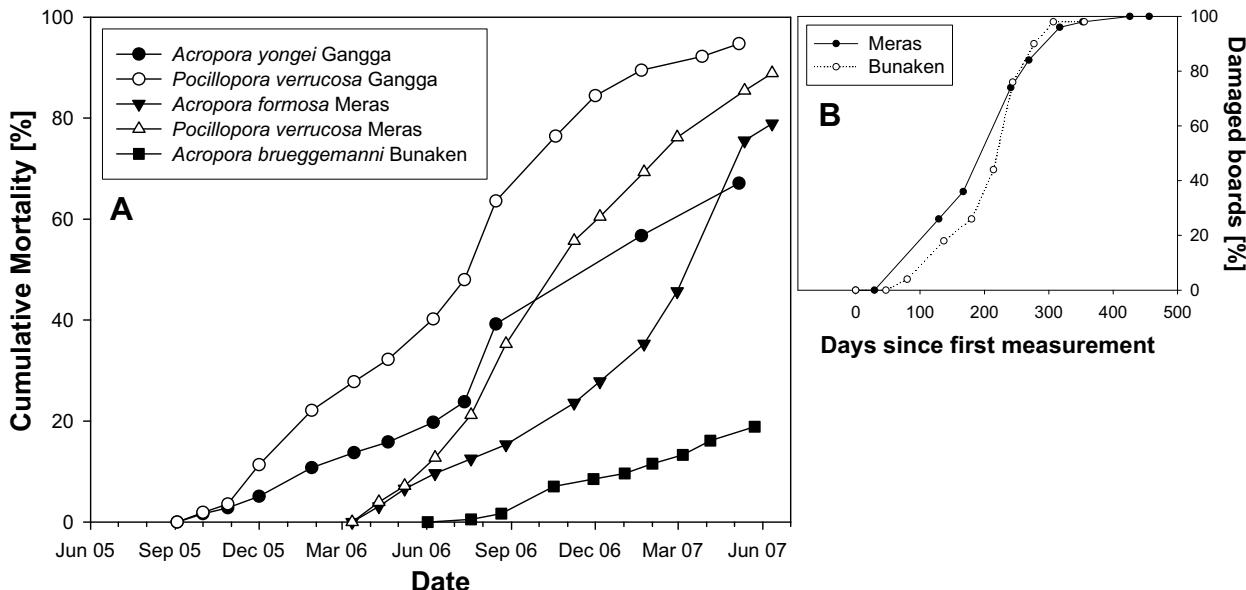
**Figure 3.26:** The total numbers of recruits counted on the eight innermost structures in the Structures + Corals [SC] and Structures [S] plots, including the portion of acroporid and pocilloporid recruits, is shown by bar the chart. The average number of recruits per structure (mean  $\pm$  SE) is shown for comparison (right axis).

### 3.3 Survival of transplanted fragments

The increase in number of damaged boards at Meras and Bunaken followed a sigmoid curve (Fig. 3.27 B). After about 200 days in the water, half of the bamboo boards were damaged in some way. At Bunaken, one board was still intact at the end of the experiment after 330 days, while at Meras, all boards were damaged after 410 days. There was no significant difference between the damage rates at both sites. Data on damaged boards from Gangga was too sparse for analysis.

The mortality curves of the coral transplants also were sigmoidal (Fig. 3.27 A). There were significant differences between the mortality curves of each species (Wilcoxon test,  $\chi^2 = 935.0502$ ,  $p < 0.0001$ ,  $df = 4$ ). The transplanted fragments of *P. verrucosa* reached a mortality of more than 80 % both at Meras and Gangga within the duration of the experiment. Mortality of the *Acropora* fragments was less than that of *Pocillopora*. *A. formosa* at Meras had the steepest increase in cumulative mortality, while the number of dead *A. yongei*, with the

exception of a marked increase following the storm event in August 2006, increased more slowly but did not seem to level off towards the end of the experiment. Mortality was lowest in fragments of *A. brueggemanni*.



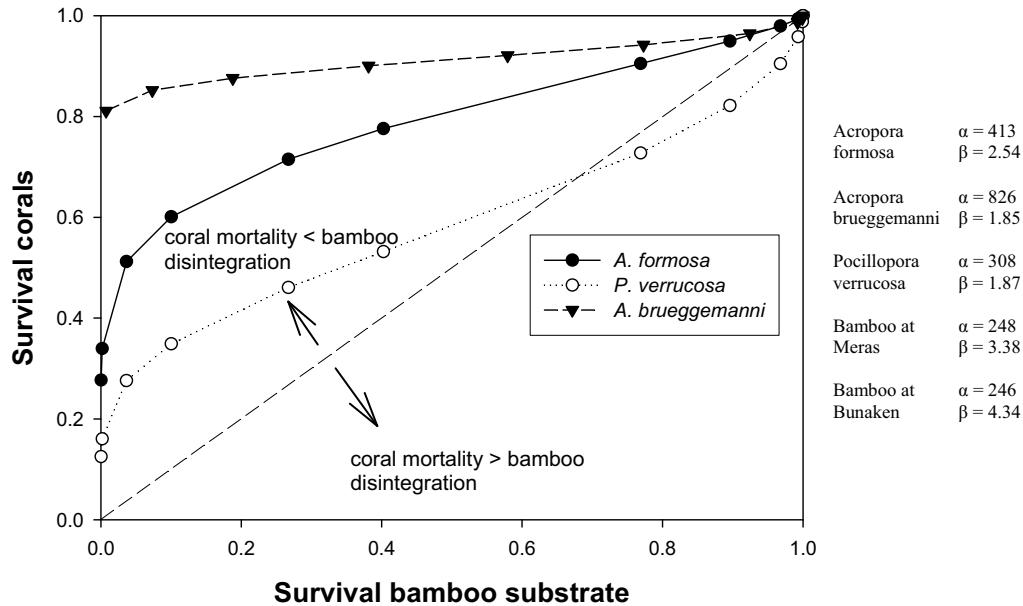
**Figure 3.27:** Cumulative mortality of the transplanted coral fragments at all three locations (A) and percentage of damaged boards as a function of time since first census at Meras and Bunaken (B).

The proportional hazards model confirmed differences in the mortality rates between the coral species (Effect Likelihood Ratio Test,  $\chi^2 = 1051.5417$ ,  $p < 0.0001$ ,  $df = 4$ ). The hazard parameter was lowest for *A. brueggemanni* and highest for *P. verrucosa* at Meras, and the risk ratio for these two species shows that survival time of *A. brueggemanni* was about 6 times higher than that of *P. verrucosa* at Meras (Tab. 3.11). Survival time also differed, albeit slightly, between the fragments of *P. verrucosa* transplanted at Meras and at Gangga, indicating that factors other than species influenced survival of fragments.

**Table 3.11:** Results from the proportional hazards model comparing the survival times among the species used.

Species	Hazard Parameter Estimate	95 % Confidence Limit
<i>Acropora brueggemanni</i>	-1.0377	$\pm 0.0944$
<i>Acropora yongei</i>	-0.5205	$\pm 0.0650$
<i>Acropora formosa</i>	0.2302	$\pm 0.0584$
<i>Pocillopora verrucosa</i> at Gangga	0.5102	$\pm 0.0818$
<i>Pocillopora verrucosa</i> at Meras	0.9102	$\pm 0.0925$
<b>Risk Ratios</b>		
Species		Ratio
<i>P. verrucosa</i> Meras / <i>A. brueggemanni</i>		6.3946
<i>P. verrucosa</i> Gangga / <i>A. brueggemanni</i>		4.7013
<i>P. verrucosa</i> Meras / <i>A. yongei</i>		3.8123
<i>A. formosa</i> / <i>A. brueggemanni</i>		3.5534
<i>P. verrucosa</i> Gangga / <i>A. yongei</i>		2.8028
<i>A. formosa</i> / <i>A. yongei</i>		2.1185
<i>P. verrucosa</i> Meras / <i>A. formosa</i>		1.7996
<i>A. yongei</i> / <i>A. brueggemanni</i>		1.6774
<i>P. verrucosa</i> Meras / <i>P. verrucosa</i> Gangga		1.3601
<i>P. verrucosa</i> Gangga / <i>A. formosa</i>		1.3230

The relationship between disintegration of the bamboo substrate and mortality of the coral fragments differed between the species (Fig. 3.28). While the survival of *Acropora brueggemanni* remained high even when all bamboo boards showed some degree of damage, survival of *P. verrucosa* at Meras was reduced almost at the same rate as the boards disintegrated. The relationship was curved rather than linear in all species: while coral survival decreased at a slower rate than bamboo ‘survival’ between 0.2 and 0.8 on the x axis, coral survival decreased increasingly rapid towards the end. However, correlation does not imply causality, and the comparably lower survival rate of *P. verrucosa* is not necessarily (only) caused by a more negative impact of substrate disintegration on this species than on the others.



**Figure 3.28:** The Weibull survival of corals at a given time plotted against the Weibull survival (=absence of damage) of the bamboo substrate at the same time. Weibull parameters are shown on the right. The dashed diagonal line indicates where a linear relationship (coral survival = bamboo survival) would be located. Curves below that line translate into a higher coral mortality than bamboo disintegration; curves below that line indicate the opposite.

### **3.4 Synopsis of the results**

The presence of artificial structures led to increases in the number of fish individuals, species and biomass. Transplantation of corals further increased these numbers, although the difference between the Structures + Corals plot and the Structures plot was not very prominent at Bunaken. The trends were most obvious at Gangga. Differences in these values were detected between treatments (usually, the highest values were found in the Structures + Corals treatment) and in time (e.g., number of observed species increased over time at all locations). The increases in time also differed between the treatments: at Gangga, the strongest increase in abundance, species and biomass occurred in the Structures + Corals treatment, while increases in the Control treatment were very slight. However, the small increases observed in the Control treatment indicate that a recovery process took place here following the removal of rocks and remaining coral from the plots at the beginning of the experiment.

Shannon-Wiener diversity  $H'$ , which depends on both the total number of species observed and their relative abundances, usually was highest in the Structures + Corals treatment. Clear increases in  $H'$  over time were visible at Gangga. Evenness  $J'$  of the fish community was the most variable univariate parameter examined. Since a low value of  $J'$  means that a few very abundant species dominate a sample, the high standard error of several average samples indicates the presence of species with high abundances in some replicates. Indeed, schools of planktivores such as the wrasse *Cirrhilabrus cyanopleura* or groups of the damselfish *Pomacentrus brachialis* hovered above the plots in highly variable numbers, thus impacting the evenness. The ranked species biomass plots showed that in addition to dominant species in terms of numbers of individuals, some species were dominant in terms of biomass although they only occurred with few individuals, such as Scarids or Serranids. In the ranked species plot, there was no difference between the Structures + Corals and the Structures treatment at Bunaken in terms of number of species and biomass distribution, although the species composition was different.

As shown in the multivariate analysis, the composition of the fish community differed both between the three locations and between the three treatments. That is to say, the diversity, species composition, and relative abundance of species were different for each location, and at a given location also for each treatment. Again, the communities at Gangga were more distinct from those at Meras and Bunaken than these were from each other. Time also influenced community composition – in each experimental plot, the kind and amount of fish species and their relative abundances differed over time, again indicating time-driven processes such as recovery and colonization. Interestingly, similarity between the three replicate censuses conducted for each plot during a sampling campaign was highest in the Structures + Corals treatment and lowest in the Control treatment. This indicates a less constant community in the Control plots, i.e., when sampling these plots several times in one day, the chances of observing a similar number of species and of individuals is much lower than when sampling the Structures + Corals plot. While similarity within a sample (comprising three replicates) was not influenced by time at all sites, the similarity between consecutive samples increased over time. Thus, while at a given time the fish community remained most constant in the Structures + Corals treatment, the community in all plots also became more constant over time – the chance increased that when sampling a community again in the following month, its composition would still be the same as in the previous month.

Both in terms of depth of the plots and composition of the ambient reef, there were marked differences between Gangga, where hard corals were almost absent and soft corals a prominent feature, and the other two locations with higher amounts of hard corals. At all locations, the fish community in the natural reef differed from that in the experimental plots. At Bunaken and Meras, the community in the Structures + Corals plot was most similar to that in the natural reef, but number of individuals and number of species remained higher in the latter. At Gangga, the composition of the community, numbers of individuals and amount of species in the natural reef were most similar to that in the Structures plot, and the Structures + Corals treatment was populated by a much higher number of fishes and fish species by the end of the experiment. The transplanted corals at Gangga had also attracted a high number of corallivores, which was not the case at the other two locations.

Transplantation of corals did not have a detectable effect on coral recruitment within the time frame of the experiment at Gangga. During the second peak in recruitment, the number of recruits was highest in the Structures + Corals plots at Bunaken and Meras. The family composition of the recruits indicates that the presence of *Acropora* corals does attract other acroporids to settle in the area.

Post-transplantation survival of the coral fragment differed between the species. While some acroporids showed low mortality within the first year after transplantation, almost all pocilloporids had died by the end of the experiment. The similarity of the rate of decay of the bamboo substrate and the cumulative mortality of all species but *A. brueggemanni* indicates that the coral species differ in their ability to cope with unstable substrate. While pocilloporids die almost at the same rate as the boards they have been attached to fall apart, *A. brueggemanni* maintains an almost linear mortality rate even after most bamboo boards have begun to disintegrate.

## 4. Discussion





A mixed group of cardinalfishes and wrasses hovers above a colony of branching *Porites* sp. that they use for shelter.

Pulau Taipi, Togean Islands, March 2007.

The effects of artificial structures and coral transplants on the associated fish community and on coral recruitment to the manipulated plots were examined during a two-year field study in North Sulawesi, Indonesia. A range of univariate and multivariate methods were used to assess the observed patterns. The fish community showed some clear and immediate responses to the experimental treatments, while effects on coral recruitment were less obvious.

## 4.1 Fish community responses

Coral reefs are complex biogenic habitats, combining both physical (e.g., high structural heterogeneity) and biological (e.g., live coral cover, diversity of benthic lifeforms) characteristics (Jones 1991, Ebeling and Hixon 1991). As several fishes are directly dependent on live coral for food (Randall 1974, Reese 1977, Hourigan et al. 1988) or shelter (Patton 1976, Lassig 1977), and structural heterogeneity increases available habitat, provides refuge from predation and attracts fish recruits (Shulman 1984, Steele 1999, Kawasaki et al. 2003), both the structural and biological component potentially exert an influence on the composition of the associated fish community. Furthermore, different reef zones such as reef flat, reef crest and reef slope, or reef areas with different current regimes and exposure are home to distinct fish communities (Hiatt and Strasburg 1960, Talbot and Goldman 1972, Goldman and Talbot 1976, Williams 1991). Thus, a range of environmental factors necessarily interacts in shaping the fish community in a given reef area. The effect of structures, coral transplants, and location will be examined separately before discussing potential interactions and the question of how differences in reef context will affect to which extent structures and transplants are shaping the resulting fish community.

### 4.1.1 The presence of artificial structures

The plots with artificial reef units made from concrete blocks had significantly higher fish abundance, species richness, biomass and diversity ( $H'$ ) than control plots containing only coral rubble at all three locations (Figs. 3.2 – 3.6). Similarly, several studies on fish community structure in coral reefs have found positive correlations of structural complexity and abundance (Carpenter et al. 1982, Grigg 1994, McCormick 1994, Lirman 1999, Friedlander et al. 2003, Chittaro 2004, Gratwicke and Speight 2005a), number of species (Luckhurst and Luckhurst 1978, Molles 1978, McCormick 1994, Friedlander et al. 2003, Chittaro 2004, Dominici-Arosemena and Wolff 2005, Gratwicke and Speight 2005b, Dominici-Arosemena and Wolff 2006, Wilson et al. 2007), biomass (Carpenter et al. 1982, Friedlander et al. 2003) and species diversity (Risk 1972, Molles 1978, McCormick 1994, Öhman and Rajasuriya 1998, Friedlander et al. 2003, Dominici-Arosemena and Wolff 2005, Dominici-Arosemena and Wolff 2006). However, other authors reported only a weak or no correlation at all (Talbot et al. 1978, Roberts and Ormond 1987, Booth and Beretta 1994, Galzin et al. 1994, Ferreira et al. 2001). The artificial reef units altered habitat complexity in several ways: Since hollow blocks were used, the number of holes acting as refuges increased. Additionally, the vertical relief, available surface area and interstitial space between the blocks in each structure increased habitat heterogeneity. Accordingly, artificial reefs of high structural complexity have been observed to yield higher fish densities, species numbers and biomass than artificial reefs of less complexity or degraded natural reef areas (Edwards and Clark 1993, Rilov and Benayahu 2000, Sherman et al. 2002, Lingo and Szedlmayer 2006, see review by Bohnsack and Sutherland 1985).

One important potential aspect of habitat complexity is the provision of refuges from predation (Clarke 1977, Shulman 1984). That refuge from predation (and hence, structural complexity) indeed plays an important role in structuring a fish community by modifying post-recruitment mortality in reef fish has been shown both for natural reefs (Buchheim and Hixon 1992, Beukers and Jones 1997, Willis and Anderson 2003) and artificial reefs (Hixon and Beets 1989, Caley 1993, Caley and St. John 1996, Eklund 1997). However, Steele (1999) found that in some fishes, recruits may respond directly to the presence of shelter and higher post-recruitment abundance thus is a function of habitat selection rather than reduced predation.

The presence of artificial structures led to a two- to three-fold increase in the maximum amount of biomass observed compared to the Control plots at all three sites (Fig. 3.4). The highest biomass values in the Structures plots ranged from  $222 \pm 30 \text{ kg ha}^{-1}$  (mean  $\pm$  SE) at Meras to  $367 \pm 151 \text{ kg ha}^{-1}$  (mean  $\pm$  SE) at Bunaken. However, while the biomass observed in the natural reef plots at Gangga ( $178 \pm 38 \text{ kg ha}^{-1}$ , mean  $\pm$  SE, and  $233 \pm 23 \text{ kg ha}^{-1}$ , mean  $\pm$  SE) was somewhat lower than in the Structures plot, it was similar in both plots at Bunaken and one of the plots at Meras. The biomass of reef fish communities varies widely depending on factors such as reef location, habitat condition and fishing pressure. Goldman and Talbot (1976) give estimates from  $175 \text{ kg ha}^{-1}$  to  $1950 \text{ kg ha}^{-1}$ , depending on reef zone. Comparing several reports from natural and artificial reefs, Stone et al. (1979) stated that the average biomass on artificial reefs ( $2199 \text{ kg ha}^{-1}$ ) was higher than that on natural reefs ( $735 \text{ kg ha}^{-1}$ ). In Indonesia, fish biomass in the Komodo area ( $3820 \text{ kg ha}^{-1}$ ) was found to be more than four times higher than in the Spermonde archipelago ( $860 \text{ kg ha}^{-1}$ ), where fishing intensity was eight times higher (Pet-Soede et al. 2001). While the biomass values observed in the natural reef and Structures plots are on the lower end of the range of values reported from elsewhere, they may be explained partially by the high fishing pressure in the region, the condition and exposure of the ambient reef (see below), and the fact that certain large-bodied and numerous transient fish species (such as caesionids, carangids and adult unicornfishes) were not included in the censuses.

Central to the assessment of artificial reef performance is the so-called production-attraction issue (Lindberg 1997), i.e., the question of whether they serve to produce new fish biomass or simply re-distribute existing biomass by attracting individuals from the ambient reef. Artificial reefs may increase production by providing additional food, shelter from predation, and habitat for fish recruits that would otherwise have been lost to the population (Bohnsack 1989). Alternatively, fishes may be attracted to the artificial reefs by behavioral preferences (Bohnsack 1989). The basic premise underlying the production hypothesis is that available benthic resources are limiting (Bohnsack 1989, Grossman et al. 1997). However, although available shelter in the face of predation has been found to be limiting the abundances of resident fishes in some cases (Shulman 1984, Caley and St. John 1996, Eklund 1997), the determinants of fish communities are likely to be a combination of available habitat, pre-settlement and post-settlement processes, the relative importance of each varying according to the species studied, reef locale and other factors (Wellington and Victor 1985, Hixon 1991, Grossman et al. 1997, Jennings and Polunin 1997, Hixon 1998). In an intact reef, available habitat usually is not in short supply and fish populations are limited by recruitment or density-independent post-settlement mortality (reviews by Doherty and Williams 1988a, 1988b). As Sale (1991b) observed, ‘the coral reef is not always filled with fish’, hence competition for space seldom occurs. However, in a degraded reef environment such as a rubble field, habitat may indeed become the limiting resource. On the other hand, Stone et al. (1979) observed that a fish community developed on artificial reefs in Florida that was similar to that of the nearby natural patch reef and that the increase in fish numbers on the artificial

reefs was not accompanied by a decrease in the natural reef. They concluded that the artificial reefs increased production by providing additional habitat for individuals that would have been lost to the biota otherwise (see Bohnsack 1989).

Whether the artificial reef structures used in this study increased fish abundance and biomass due to attraction or to production can not be determined with certainty without knowledge of the four basic demographic parameters underlying the population dynamics, that is, birth (more accurately, recruitment of larvae from the plankton), mortality, immigration and emigration rates (Hixon 1998), and both attraction and production probably play a role to some extent (Bohnack 1989). There are, however, some indications. Labrid and pomacentrid fishes were the families with the highest relative abundance in all plots, except the Structures plot at Gangga (Figs. 3.1, A 1 and A 2), and species of both families have been observed to display habitat preferences during settlement (Eckert 1985, Caselle and Warner 1996, Booth and Wellington 1998, Holbrook et al. 2000). When assuming that individuals with a body size of  $\leq 2$  cm can be considered as recruits from the plankton rather than immigrants (Lewis 1997a), the number of small individuals observed in each census gives an approximation of relative settlement rates for these families in each experimental plot. These rates show that settlement in the Structures plot was lower than in the Control plot at Gangga, but higher than in the Control plot at Meras, and at Bunaken until the eighth census, respectively (Fig. A 9, Appendix). Additionally, while high initial numbers of settlers were observed in both plots with artificial structures at Bunaken, settlement in the Structures and Structures + Corals plots increased over time at Gangga and Meras.

These data show that while more fish larvae may have settled in the Structures plots than in the Control plots at Meras and Bunaken, the higher number of individuals in the Structures plot at Gangga can not simply be explained by higher settlement rates. However, post-recruitment immigration plays an important role in affecting the fish population size in natural reefs, and for some pomacentrid and labrid species, it may account for up to 100 % of the individuals appearing in a reef patch (Lewis 1997a). Pomacentrids comprised a major part of the ichthyofauna in the Structures plots at all three locations. Thus, in addition to recruitment, a large amount of juvenile and adult individuals probably moved into the plots to make use of the new, unoccupied habitat formed by the Structures (Fig. 4.1). The rapid response of fishes to the new structures became most obvious at Bunaken. Here, the structures had been completed two days prior to the first visual census in the Structures plot, but in the Structures + Corals plot, they had been set up on the day before the census.

While the number of individuals in the S + C plot ( $14 \pm 1$  individuals  $100 \text{ m}^{-2}$ , mean  $\pm$  SE) was only slightly higher than that in the Control plot ( $6 \pm 2$  individuals  $100 \text{ m}^{-2}$ , mean  $\pm$  SE), fish abundance in the Structures plot ( $34 \pm 7$  individuals  $100 \text{ m}^{-2}$ , mean  $\pm$  SE) had already increased markedly.



**Figure 4.1:** Juvenile and adult *Pomacentrus brachialis* moved into the concrete structures within days to weeks of construction.

Groups of browsing herbivores frequently were observed at Gangga. Two of the most abundant species in the Structures plot were the acanthurids *Acanthurus nigrofasciatus* and *Ctenochaetus binotatus* (Fig. 4.2), both of which occurred in similar numbers in the Structures + Corals plot but not in the Control plot (see Tabs. A 12 – A 14 in the Appendix).



**Figure 4.2:** Browsing herbivores such as *Ctenochaetus binotatus* were common in both the Structures and Structures + Corals plots at Gangga.

individuals comes from the theory of island biogeography (MacArthur and Wilson 1967). Several features of this theory are applicable to aspects of reef fish community structure (Bohnsack 1983). It predicts that the number of species found on an island will increase in relation to its area (other factors such as climate and topography being equal). The rates of extinction and immigration, both of which are dependent on the number of species present, reach a dynamic equilibrium at a point that varies according to habitat variables such as area and isolation. In terms of a patch of reef, area may be equated with suitable habitat. As structural complexity is enhanced, the amount of available habitat increases, allowing more species to be present (Sale 1991b). For two subsequent fish community censuses, an approximation of the immigration and extinction rates can be obtained by the number of species gained in the second census ('immigration') and the number of species lost since the first census ('extinction', Cairns et al. 1969, Talbot et al. 1978, Smith 1979). A comparison of the relative immigration and extinction rates for the Control and Structures treatments shows that the number of species at which a dynamic equilibrium is reached is about twice as high in the Structures treatment as in the Control treatment (see Figs. A 10 and A 11 in the Appendix).

As shown by the multivariate analysis, the composition of the fish community differed significantly between the Control and Structures plots (Tab. 3.3). These differences could be caused by differences in fish abundance and species richness in each sample as well as by characteristic species restricted to each treatment. Two species, *Anampsese melanurus* and *Halichoeres hartzfeldii*, were restricted to the Control plots (see Tab. 3.1), but only *H. hartzfeldii* occurred with more than one individual and was present in several censuses both at Meras and at Gangga. Since this species inhabits sand and rubble areas (Myers 1999), it probably can be regarded as truly characteristic of the Control treatment. Although 14 of the identified species occurred only in the Structures treatment, almost all of these were observed in only one single census, comprised only single individuals, or were transient species such as lutjanids or siganids. Several species were observed in similar frequencies in the Structures and Structures + Corals plots which were absent from the Control plots or were present with

These species showed little site fidelity and roamed a wider area of reef browsing for food. Additionally, they were increasing in numbers throughout the experiment, which indicates that they responded to a resource that was getting more abundant with time – such as algae growing on the structures. Hence, the availability of additional food on the structures probably helped to attract a significant amount of the individuals observed in the Structures plot at Gangga.

A further support of the Structures providing additional habitat able to accommodate a higher number of

only a few individuals (e.g., *Ctenochaetus striatus*, *Balistapus undulatus*, *Chaetodon unimaculatus*, *Paracirrhites forsteri*, *Plectorrhinchus chaetodonoides*, *Thalassoma hardwicke*, *Ostracion cubicus*, *Centropyge tibicen*, *Chromis scotochiloptera*, *C. weberi*, *Pomacentrus brachialis* and *P. nagasakiensis*). In total, at least 20 species seemed to occur preferentially in the presence of structures, although in most cases their abundances were further increased by the presence of corals.

#### 4.1.2 The role of corals

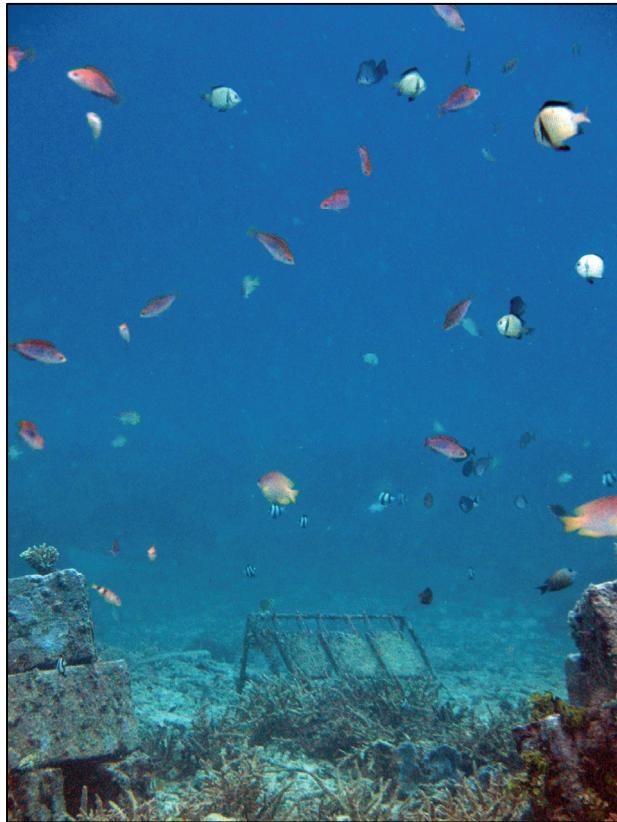
Transplantation of coral fragments lead to a further increase in fish abundance, species richness, biomass, and species diversity. While these trends were clear at Gangga, the increases were only slight at Bunaken. Here, fish abundance was similar in the Structures and the Structures + Corals plots during several censuses, and biomass in the Structures + Corals plot sometimes was lower than that in the Structures plot, although a tendency became apparent in the final three censuses for the Structures + Corals plot to develop the fish community with the highest abundance and biomass (Figs. 3.2 and 3.4). The positive correlation between live coral cover and fish abundance, number of species and diversity has been observed in a number of previous studies (Carpenter et al. 1982, Bell and Galzin 1984, Sano et al. 1987, Gomez et al. 1988, Chabanet and Faure 1994, Walter and Haynes 2006), while some authors only observed a weak correlation (Luckhurst and Luckhurst 1978, Bell et al. 1985a, Roberts et al. 1988, Fowler 1990) or no correlation at all (Risk 1972, McManus et al. 1982, Roberts and Ormond 1987). A positive relationship has usually been described for species that depend on coral for food or shelter, such as chaetodonts or gobiids, with other groups being more related to variables such as water depth or algal abundance (Jones and Kaly 1996, Nanami et al. 2005, Feary et al. 2007). Yet, some studies found more general associations between coral cover and species richness (Carpenter et al. 1982, Bell and Galzin 1984, Garpe and Öhman 2003, Walter and Haynes 2006). However, Chabanet et al. (1997) observed that the relationship between species richness of an associated fish community and diversity or abundance of coral is less apparent in the literature than a relationship with habitat complexity due to difficulties in coral classification.

A number of fish species feed on live coral (Randall 1974, Reese 1977, Hourigan et al. 1988, Cox 1994), and others are obligate coral dwellers (Lassig 1977) or display recruitment preferences for live corals (Eckert 1985, Booth and Beretta 1994, Holbrook et al. 2000, Feary et al. 2007), so that the richer fish communities in the Structures + Corals plots observed in this study are not unexpected. Again, the question of attraction versus production arises. For corallivores, attraction to a food resource obviously is an important factor. Consequently, at Gangga the large majority of corallivores were found in the Structures + Corals plot. However, no obligate corallivores were observed at Meras, and at Bunaken they only occurred in the natural reef plots. Moreover, the relative abundance of chaetodonts (which comprised the large majority of obligate corallivorous species) was similar in the Structures and Structures + Corals plots at Gangga (Fig. 3.1), showing that the increase in fish abundance in the presence of coral transplants was not simply due to the increased presence of corallivorous species.

Other fishes may indirectly depend on live coral as a food resource, e.g. through coupling of coral mucus and benthic production (Wild et al. 2004) or plankton (Richman et al. 1975, Gottfried and Roman 1983). Planktivores were another feeding guild that was more abundant in the Structures + Corals treatment than in the Structures treatment and the natural reef plots at Gangga (Fig. 4.3). This observation agrees with the findings of Porter and Porter (1977), who during the day observed a higher abundance of demersal plankton above branching live coral than above tabulate coral and coral rubble. Similarly, Alldredge and King (1977) reported higher abundances of demersal plankton from live coral substrates than from coral rubble or solid rock. However, at the other two sites, coral transplantation did not have a marked effect on planktivores, and abundances were similar or higher in the natural reef plots.

For herbivores, and carnivores and piscivores, there were also significant differences between the treatments. While carnivores and piscivores were most abundant in the Structures + Corals plot on Gangga and at Meras, probably due to the higher amount of food available there, the difference between the Structures + Corals and Structures plots was less marked at Bunaken. Additionally, large numbers of carnivores and piscivores were observed in the Control plots at Meras and Bunaken on several occasions. However, while this group comprised mostly territorial individuals (juvenile and sub-adult serranids and wrasses) in the Structures + Corals and Structures plots, transient groups of lethrinids benefiting from the lack of shelter to search for easy prey were responsible for most of the observed carnivores in the Control plot on Bunaken, and the high abundance of carnivores in the Control plot at Meras was due to a large number of juvenile *Hologymnosus doliatus*.

The amount of food available for herbivores in the form of epigrowth on the structures was similar in the Structures + Corals and Structures treatment. Consequently, these treatments were the least dissimilar in terms of herbivores (Tab. 3.8). However, herbivores were more abundant in the Structures + Corals plots at all three locations. Studies of the reef fish communities following coral mass-mortality after temperature anomalies and crown-of-thorn outbreaks have reported increases in the abundance of herbivores which were attributed to an increase in available food, as filamentous algae began to grow on the dead coral skeletons (Wass 1987, Lindahl et al. 2001). Conversely, Hart et al. (1996) reported that on *Acanthaster*-affected reefs, herbivorous fishes were negatively correlated with turf algae but positively correlated with live coral cover. Moreover, Sano et al. (1984) found that an increase in filamentous algae did not always increase the number of herbivores and that the structural complexity offered by coral colonies was more important than the available food. An increase in algal growth on dead coral skeleton could account for the larger abundance of herbivores in the Structures + Corals plots at Gangga and Meras, where around 40 % of the *Acropora* fragments were dislodged or killed within one year, providing additional substrate for



**Figure 4.3:** Planktivores feeding in the current above the Structures + Corals plot at Gangga.

filamentous algae to grow on. However, herbivores also were more abundant in the Structures + Corals plot on Bunaken, where coral mortality was less severe. Hence, the higher abundance of herbivores seems to be the result of both an increase in available food, and the additional habitat provided by the coral fragments.

Identifying fish species characteristic for the plots containing corals is not as straightforward as for the other two treatments, as different coral species were used at each location and each of these potentially was attractive for different fish species. Of all species observed in this study, 41 occurred only in the Structures + Corals treatment. However, 26 of these were observed only during one single census. Of the remaining species, only five (*Plagiotremus rhinorhynchos*, *Hologymnosus annulatus*, *Pseudocoris yamashiroi*, *Pseudomonacanthus macrurus* and *Scorpaenopsis diabolus*) were observed at more than one location. None of these were dependent on corals for food. Five species were present in three or more censuses, four of which occurred only on Bunaken. The most frequently encountered species restricted to the Structures + Corals plot at Gangga was the obligate corallivore *Chaetodon baronessa*. Among the nine species that occurred in all experimental and in the natural reef plots (see Tab. 3.1), six were observed less frequently in the Control than in the Structures + Corals and Structures plots, where they were encountered with similar frequency (*Acanthurus nigrofasciatus*, *A. pyroferus*, *Ctenochaetus binotatus*, *Chaetodon kleinii*, *Centropyge bicolor* and *Pomacentrus amboinensis*). While the acanthurids in general were similarly abundant in the Structures + Corals and Structures plots (Tabs. A 13 to A 20), the other three species (two omnivores and one planktivore/herbivore) had markedly higher abundances in the Structures + Corals plots. These patterns reinforce the notion that other factors beside the direct dependence of fishes on corals for food led to increases in fish abundance and species richness in the Structures + Corals plots.

When comparing the numbers of fish recruits, one potential effect of the presence of corals becomes obvious: recruitment was highest in the Structures + Corals plots at Gangga and Bunaken (Figs. A 9). A recent long-term study in Papua New Guinea found that about two-thirds of the observed fish species, including many that were not directly associated with live coral, settled preferentially into corals (Jones et al. 2004). For Meras, the data suggests that post-recruitment immigration was mainly responsible for the higher abundance of fishes in the Structures + Corals plot (Lewis 1997a). At all sites, recruits were observed year-round, with peaks in recruitment in spring and fall that were most noticeable at Meras. Two peaks in recruitment have been reported from Hawaii, the Philippines and the southern Caribbean, while recruitment is restricted to a single season e.g. in the Great Barrier Reef, Micronesia, Japan and Florida (Doherty and Williams 1988a). Generally, recruitment of reef fishes is highly variable over time (both within and between seasons, Doherty and Williams 1988a, Doherty 1991). The relatively constant increase in individuals in the Structures + Corals plots despite fluctuations in recruitment points to a limitation by available habitat and post-recruitment processes (food and shelter from predation, and interaction between the individuals), rather than availability of fish larvae, being predominant in shaping the community structure. This agrees with the conclusion of Ault and Johnson (1998), who suggested that while patterns in recruitment may explain the variability of fish communities on patch reefs, the relationship between population density and habitat structure is enhanced on continuous reefs by post-settlement migration.

A further sign for the role of coral fragments became apparent after a storm impacted the experimental site at Gangga in August 2006, destroying a large amount of the branching coral (mostly acroporids) on the shallow reef top and shifting several large branches and entire dislodged colonies into the experimental plots. As a result, the abundance and species

richness of fishes increased in all three plots. The impact was most apparent in the Control plot, where the number of species increased both due to a larger number of roaming fishes that were browsing for food among the remnants of the coral colonies and boulders being dislodged by the storm (e.g., *Cantherhines pardalis* and *Ctenochaetus binotatus*), and a few species that were absent from the Control plot prior to the storm and colonized the larger relocated branches of coral (*Dascyllus aruanus*, *D. reticulatus*, *P. moluccensis*, *Centropyge tibicen* and *C. bicolor*, see Tab. A 12 in the Appendix). Additionally, recruits of *Pomacentrus amboinensis* appeared in the coral branches after the storm while previously, only a few adult individuals of this species had been observed in the Control plot. Such a shift in habitat use following storms has been reported e.g. from Hawaii and Jamaica (Kaufman 1983, Walsh 1983). Although several of the coral fragments in the Structures + Corals plot became dislodged and broke off their bases, a large part of them actually survived this impact and continued to grow, with a large number of loose fragments being piled up into thickets rather than being transported out of the plot by the storm. That the observed increase in species richness and abundance was least marked in the Structures + Corals plot probably is due to the fact that live coral had been present there already before the storm, and since a large number of fragments survived the event, the habitat was less significantly altered than in the other two plots, where live coral had been largely absent prior to the storm.

Further support of the limiting function of available habitat again comes from the comparison of the relative immigration and extinction rates (see above). In the Structures + Corals treatment, the number of species at which a dynamic equilibrium is reached is again higher compared to the Structures treatment, and is almost thrice the number of species supported in the Control treatment at equilibrium. It is interesting to note that the increase in number of species at equilibrium between the Control and the Structures + Corals treatments is caused mostly by a shallower slope of the relative immigration rate, since the relative extinction rate correlates only poorly with the number of species present in all three treatments (Figs. A 10 – A 12, Appendix). That a higher number of species can be supported by the Structures + Corals treatment underlines the function of coral fragments in providing additional habitat. This observation agrees with the findings of Galzin et al. (1994), who concluded that, as postulated by the MacArthur and Wilson theory, ‘more area gives more habitat complexity, which in turn supports higher fish diversity’.



**Figure 4.4:** Juvenile and recruit damselfishes seeking shelter in the branches of an *Acropora gomezi* colony growing on an artificial reef at Gangga.

Since the presence of corals not only increased the abundances of obligate corallivores and planktivores, the coral fragments apparently played an important role in providing habitat and shelter (Fig. 4.4). Several species of the most abundant families in the Structures + Corals plots, pomacentrids and labrids, frequently use coral branches for shelter (Clarke 1977, Sweatman 1983, Green 1996, Lewis 1997b, Holbrook et al. 2000). As the coral transplants in the plots were

growing, they necessarily also increased the complexity of and amount of space available in the habitat. Accordingly, some authors have linked the abundance of non-corallivorous fishes in areas with high coral coverage to the amount of protection or additional habitat provided by the coral (Sano et al. 1987, Beukers and Jones 1997, Lirman 1999, Friedlander et al. 2003). Since the complexity of the substrate in the Structures plots was somewhat lower due to the absence of coral transplants, it is difficult to say how much of the observed increase in the Structures + Corals plots was due to the live coral cover and how much was due simply to the increased structural complexity. However, Cabaitan et al. (2008), who monitored trends in the fish community after coral transplantation, reported a decrease in fish abundance and species richness following high mortality in the transplants, and Pamintuan (1994, cited in Cabaitan et al. 2008) found higher numbers of fishes on artificial structures with live coral compared to artificial structures onto which dead corals were transplanted. Emery (1978) emphasized the role of reef-building corals as an ‘organic matrix’ and stressed the importance of a living surface in addition to the topographic complexity created by the corals. As an example, he cited outbreaks of crown-of-thorns starfish in the Pacific, which were followed by a rapid reduction in fish diversity although the topographic diversity of the reef was not immediately affected. This rapid reduction in fish diversity points to a response of certain species to a lack of food in dead reef areas, rather than reduced settlement rates or protection. However, the higher fish abundance, species richness and diversity in the presence of corals observed in this study probably are the results of a range of factors. In commenting on the effects of predation, Jennings and Polunin (1997) argued that one single dominant process does not govern the structure of a fish community, but that a range of processes operating on different scales and in different circumstances are at work, which helps to explain why the effect of the three treatments differed in magnitude between the three locations.

#### **4.1.3 Observations on community composition**

Although no more than a few species were restricted to only one of the experimental treatments, significant differences between the compositions of the fish community in the experimental plots were detected at all three locations (Tabs. 3.5, A 17 and A 8). At all locations, the average similarity among all replicate samples taken during the experiment was lowest in the Control plots, and at Gangga and Bunaken, it was highest in the Structures + Corals plots (Tab. 3.2). Additionally, the within-group similarity in the natural reef plots was higher than that of the experimental treatments at all sites, although the replicates from two different natural plots, with different abundances and occurrences for several species, were combined for each site. A lower similarity in the experimental plots can partially be explained by the long time span over which the samples in those plots were taken. Any successional patterns in the community there are reflected in increasing dissimilarity between samples taken at the beginning and at the end of the experiment. However, the within-group similarities of the samples from Bunaken are comparable to or lower than those from Gangga, which encompassed almost twice the time span of the samples from Bunaken. Thus, higher within-group similarity of the fish community generally appears to be indicative of a more complex, or luxurious (*sensu* Sale 1991b), reef habitat.

When comparing the samples from all three locations within one treatment (Figs. 3.11, 3.12 and A 7), another effect of the treatments becomes apparent: the samples are forming clusters according to location that become more clear-cut as complexity increases. Consequently, the ANOSIM completely separates samples from the three locations in the Structures + Corals treatment (Tab. 3.7), while overlap of samples between locations is highest in the Control treatment. Letourneur (1996a) observed that fish communities in a degraded habitat may be less separated than communities in a complex, healthy reef. In the latter case, more

opportunities exist for a characteristic local fauna to develop, while a degraded habitat provides space for fewer specialists and attracts more opportunistic and browsing species (such as *Parupeneus multifasciatus*) and some rubble-associated species found at all three locations, such as *Pomacentrus auriventris*. On the other hand, the use of a different *Acropora* species at each location is likely to also have contributed to the distinct separation of the communities in the Structures + Corals plots. That the communities in the experimental plots at Bunaken and Meras were more similar to each other than to those in the respective natural reefs, which formed one distinct cluster (Fig. 3.14), shows that the coral fragments alone were insufficient to provide a habitat similar to that found in the ambient reef (see below).

The observed effect of the experimental treatments on the multivariate similarity among the fish communities was one of the most intriguing results of this study. The relative multivariate dispersion, which increases as *a priori* defined groups of samples exhibit higher within-group dissimilarity, was highest for the Control plots and lowest for the Structures + Corals plots at all locations (Tab. 3.4). In studies of benthic communities, increased multivariate variability has been linked to environmental impacts and used as a symptom of stress (Warwick and Clarke 1993, Chapman et al. 1995). Warwick et al. (1990) observed increased variability in the coral community following an El Niño event in Indonesia. Fish communities over mined reef flats in the Maldives showed higher multivariate dispersion than those found over non-mined flats (Dawson Shepherd et al. 1992). Thermal-stress induced mass mortality of corals in Tanzania also was followed by increased variability in the fish community (Lindahl et al. 2001). Similarly, Garpe and Öhman (2003) reported the highest dispersion in the multivariate ordination of fish assemblages from sites with the highest proportion of dead coral, while Öhman et al. (1997) observed higher multivariate dispersion in an area that had been impacted by destructive fishing compared to undisturbed habitats.



**Figure 4.5:** View of the Control plot at Gangga. The fish community in the Control plots showed high multivariate variability, an indication for environmental degradation. Photo courtesy of David Cheung.

Hence, the higher variability observed in the Control treatments at all three sites corresponds to a fish community living in a degraded area (Fig. 4.5). According to this interpretation, the stepwise decrease in multivariate dispersion is a sign of reduced stress of the fish community in the Structures and Structures + Corals treatments and shows that the treatments are re-creating a more natural, undisturbed state. However, the relative multivariate dispersion only gives an overall measure of the comparative spread of all samples within a treatment at each location, which is also influenced by how much a community evolved from its initial composition over time. Thus, the average similarity of the three replicate samples during each census is a more appropriate measure of relative variability among the treatments. Again,

significant treatment effects were detected (Tab. 3.10). On average, among-replicate similarity was lowest in the Control plots and highest in the Structures + Corals plots (Fig. A 8). The similarity among replicate censuses varied over time, and this variability was most marked in the Control plots at all three locations.

Although one should be careful when drawing general conclusions from a localized study, especially when only one replicated census has been made in each natural reef plot, the similarity of these results at all three sites is intriguing. Thanner et al. (2006) showed consistently high Bray-Curtis similarities (0.61 to 0.73) among natural reef fish communities in Florida. However, the limitation of this index as a measure of health rather than stress becomes apparent. Based on the values from the natural reef plots, a similarity index around 0.8 seems to be the maximum value that will be reached in the study area under natural conditions, and while moderate to severe impacts will be detected by comparisons among replicate censuses, improvements of the reef substrate beyond the state of the ambient reef following rehabilitation are likely to remain unnoticed in cases where the surrounding reef already is severely degraded. However, censuses of the fish community should be part of a regular post-rehabilitation monitoring protocol. Variability appears to be a good indicator of a stressed fish community in a degraded habitat, and an analysis of the multivariate dispersion and average similarity of replicate censuses could serve as an additional yardstick to assess the performance of the measures employed.

#### 4.1.3.1 Temporal variation

In the MDS plots of all average samples from the experimental plots at each location, changes in the community composition over time became visible. Rank-correlation between the similarity matrices of the samples from each experimental plot and model matrices with equal and stepwise increasing similarity between consecutive samples showed that the fish communities in the experimental plots were becoming increasingly similar as time progressed, and that this trend was least pronounced in the Control plots at all sites and most pronounced in the Structures + Corals plots at Gangga and Meras (Tab. 3.9). While limited



**Figure 4.6:** An *Acropora* sp. colony growing in the Structures plot at Bunaken from natural recruitment onto larger pieces of rubble.

development of a different benthic community (and hence the associated fish assemblage) may have been possible in the Control plots, e.g. by the establishment of new coral recruits on larger pieces of rubble (Fig. 4.6) or fragments of live coral being shifted into the plots by storms, the recovery of a rubble area generally is extremely slow. In the Philippines, hard coral had recolonized only around 1-3 % of a denuded rubble plot after one year (Aliño et al. 1985), and full recovery of a dynamited reef area has been estimated to take well over 100 years (Riegl 2001). On the other hand, the

presence of hard substrate allows for a more rapid development of the benthic community, which is reflected in the development of the fish community. In the presence of coral fragments, a successional state that would otherwise take several years to reach is created

early on. That the fish community in the Structures plot at Bunaken developed similarly to that in the Structures + Corals plot may be due to an influence of the ambient reef on the community in the Structures plot (see below).

At Gangga, the impact of the storm after the ninth census is reflected in the MDS plot as well, with samples from the Control plot being located further from the other Control samples and closer to samples from the other plots from the tenth census on (Fig. A 4). Although seasonal changes in community composition have been noted for fish communities on artificial and natural reefs (Molles 1978, Fowler 1990, Aktani 2003, Chittaro and Sale 2003), only weak seasonal effects were detected in this study apart from seasonal peaks in recruitment (e.g., Tab. 3.9). However, seasonal effects differ among species (Green 1996, Thompson and Mapstone 2002), and since similarity values of the fish community as a whole were used in the analysis, some seasonal patterns may have existed for individual species that remained undetected. A major part of seasonal variability in fish communities has been attributed to variations in recruitment (Letourneur 1996b, Ault and Johnson 1998). As recruitment only had minor effects on the fish communities in the experimental plots (other than ‘filling up’ available space) and the development of the communities seems to have been driven largely by post-settlement immigration, temporal patterns in community composition mainly reflect successional patterns and the development of a mature fish community following set-up of the sites. Since all plots were cleared from remaining live coral and larger rocks at the beginning of the experiment, some patterns of succession are to be expected even in the Control plots.

According to Talbot et al. (1978) an increased similarity of the fish communities is to be expected in cases where post-settlement processes order the structure of the community. Hence, the patterns observed in the Structures and Structures + Corals plots indicate the higher importance of post-settlement processes over limitation from recruitment. Since the increasing between-census similarity of the fish community over time appears to indicate the development of a mature community, this property could also be applied in the follow-up monitoring of reef rehabilitation projects to assess the performance of the measures. It should be kept in mind, though, that a less-variable, mature community may develop with a composition that reflects the new habitat, but which is not necessarily the one that existed prior to an impact or that was supposed to be achieved by the rehabilitation measure.

Similar to other studies of fish communities on artificial reefs (Russel et al. 1974, Molles 1978, Bohnsack and Talbot 1980, Walsh 1985, Clark and Edwards 1994), the first colonizing species appeared rapidly from the surrounding habitat, within hours to days after deployment of the structures. Since no censuses were made in each plot prior to the set-up of the experiments, no data are available on the original fish communities, but from observations during the marking of the plots, the slope of the abundance, species richness and diversity curves, and the multivariate distribution of samples at Bunaken, where the time-interval between construction of the sites and first census was shortest, it is fair to assume that the communities were similar to those in the Control plots in all experimental plots prior to the experiment. The similar initial increases in fish abundance and species richness at all three locations, which were set up at different times of the year, indicate that there were no seasonal differences in colonization, which contrasts with findings from higher-latitude locations (Russel et al. 1974). However, in the study by Russel et al. (1974), juvenile recruits were responsible for almost all of the observed colonization of artificial reefs.

Several species appeared in the plots more than three months after the initial set-up (Fig. 4.7). It is likely that a number of the ‘secondary colonizers’ required a certain level of biological

maturity of the habitat (e.g., the growth of food items on the artificial structures), and that their appearance is sign of a succession towards a more mature state of the community.

Species appearing after the third census that were present in more than two censuses during the experiment were defined as ‘late immigrants’. While the third month was selected arbitrarily as a benchmark, only those species consistently present within a plot were considered. The number and percentage of late immigrants was lowest in the Control plots at all three locations (between 4 and 15 species, or 6.8 to 16.8 % of all species), and highest in the Structures + Coral plots at Gangga and Meras (41 and 11 species, or 24.7 and 10.1 % of all species, respectively,

see Tabs. A 12 – A 20 in the Appendix). The higher number of ‘late immigrants’ observed in all plots at Gangga may have been a result of the longer duration of the experiment there, as there was more time for a natural benthic community to develop. However, it probably was also due in part to the low structural complexity and hard coral cover of the surrounding reef, which might have made the experimental plots more attractive to immigrants from the ambient reef (see below). Again this supports the notion that the higher complexity generated by the combination of artificial structures and corals seems to have provided more available habitat and suitable niches for a larger range of species to settle in the Structures + Corals plots, a view that is also supported by the immigration rate versus number of species plots for each treatment.



**Figure 4.7:** Although one individual was observed during the second census, larger numbers of the honeycomb grouper *Epinephelus merra* appeared in the Structures + Corals plot at Gangga only several months after set-up of the sites at Gangga.

Observed variability depends to some degree on the experimental methods used (Talbot et al. 1978, Bohnsack 1983, Tupper and Hunte 1998), which helps to explain the dichotomy of results from earlier studies. In any natural setting, community structure will depend on the composition of the available habitat, size and location of the reef, and recruitment and post-recruitment processes, and the interaction of these factors will vary between different locations (Sale 1991a, Tupper and Hunte 1998), which makes the comparison of results from different studies difficult. The studies that commented on the variability of the fish community (or lack thereof) have usually failed to compare variability in several habitats of different complexity. However, in this study treatments of different habitat composition and complexity were employed within the same reef area, which makes comparisons of variability more meaningful without the pitfalls of comparing among reefs of different size and location, or monitored at different time intervals (Tupper and Hunte 1998). Additionally, the apparently small importance of recruitment relative to post-recruitment processes in driving fish abundance and species richness diminishes the stochastic influence of variable recruitment on variability of the fish community in the experimental treatments.

During early studies of fish community composition, a dispute evolved over whether community composition is variable or predictable over time (Helfman 1978). While some studies observed the development of stable, predictable communities on artificial or denuded natural reefs (Smith and Tyler 1975, Brock et al. 1979, Ogden and Ebersole 1981), others described the development of a community as rather stochastic (Russel et al. 1974, Sale and Dybdahl 1975, Sale 1978, Talbot et al. 1978). Walther and Kolasa (1996) argued that both stochastic processes in the form of variable larval supply and non-stochastic processes in the form of habitat characteristics interact to a varying degree, and that stochastic processes exert a higher influence on habitat generalists. Additionally, the dependence on a stochastic larval supply influences the degree of variability. While recruitment-limited assemblages tend to be more variable, habitat-limited assemblages show a lesser degree of variability. Previous authors have used low turnover rates as indicators of ‘predictable’ fish communities, while high species turnover was equated with stochastic and variable assemblages (Bohnsack 1983). In the present study, turnover rates tended to decrease over time, and this trend was most pronounced at Gangga (Tab. 4.1). At all locations, though, the average turnover rate was lowest in the Structures + Corals and highest in the Control plot.

Judging both from the increasing between-census similarity over time and the lower relative multivariate dispersion and species turnover rates of communities in the Structures + Corals plots compared to the other two treatments, the fish communities show a higher degree of *constancy* (see Box 4.1) in the presence of artificial structures and coral transplants. Similar to the results of Talbot et al. (1978), colonization rates (the difference between immigration and extinction rates) in the experimental plots remained highly variable throughout the experiment, indicating that an equilibrium community was not reached (see Fig. A 13 in the Appendix). It has been suggested that populations are kept below equilibrium by predation, and that frequent extinction is important in maintaining high diversity (Sale 1977, Helfman 1978, Talbot et al. 1978). According to the MacArthur and Wilson island biogeographic theory, immigration and extinction continue even at species equilibrium, leading to a dynamic equilibrium with continuous biotic turnover (Smith 1979, Bohnsack 1983). Ongoing immigration in the presence of small-scale disturbance and predation then acts to maintain both the stability and high diversity of an assemblage (Connell 1978). High diversity has been shown to increase community stability, without necessarily increasing population stability (Tilman 1996). Thus, coral transplantation seems to increase the *stability* of the associated fish community. This view is supported by the observation that trends in Bray-Curtis similarity of the fish communities in the Structures + Corals treatment persisted even in the face of considerable disturbance in the form of storms at Gangga and Meras. It should be noted that stability is used here in a multivariate community sense, relating to species richness, composition, and relative abundance of species.

#### Box 4.1

**Constancy:** The tendency of a system to remain unchanged when not disturbed (Lewontin 1969).

**Stability:** The ability of a system to return to an equilibrium state after a temporary disturbance (Holling 1973).

**Resilience:** The ability of a system to persist despite perturbation (Holling 1973).

**Table 4.1:** Relative turnover rates for consecutive censuses in the experimental plots at all three locations. Relative turnover rates were calculated as:

$$\bar{T}_{ov} = 0.5 \left( \frac{E_x}{S_{x-1}} + \frac{I_x}{S_x} \right) \left( \frac{30}{t} \right)$$

following a modification of the formula given by Smith (1973) and used by Talbot et al. (1978) to measure turnover between consecutive monthly censuses.  $E_x$  denotes the number of species lost since the previous sample,  $I_x$  is the number of species not present in the previous sample,  $S_{x-1}$  is the number of species in the previous sample,  $S_x$  is the number of species in the present sample, and  $t$  is the number of days between the two samples.

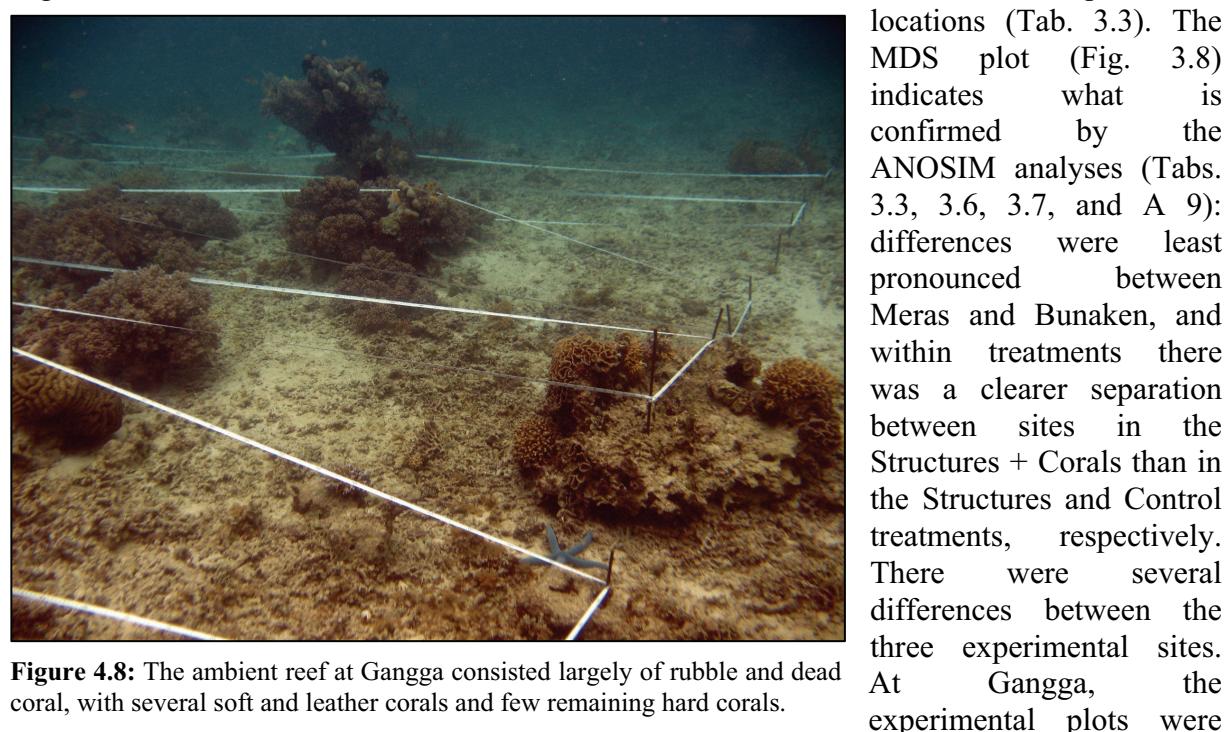
Census	Gangga			Meras			Bunaken		
	Control	S+C	Structures	Control	S+C	Structures	Control	S+C	Structures
2	0,522	0,345	0,356	0,323	0,416	0,341	0,493	0,385	0,493
3	0,342	0,346	0,282	0,685	0,411	0,383	0,462	0,295	0,374
4	0,284	0,314	0,362	0,668	0,336	0,577	0,667	0,332	0,292
5	0,211	0,168	0,169	0,433	0,273	0,508	0,432	0,196	0,281
6	0,258	0,174	0,256	0,508	0,268	0,326	0,273	0,164	0,176
7	0,303	0,211	0,317	0,204	0,080	0,098	0,239	0,166	0,152
8	0,262	0,153	0,230	1,416	0,540	0,382	0,358	0,163	0,238
9	0,303	0,202	0,322	0,753	0,385	0,281	0,473	0,212	0,272
10	0,365	0,218	0,282	0,367	0,206	0,179	0,533	0,204	0,244
11	0,189	0,108	0,135	0,271	0,143	0,254	0,324	0,279	0,276
12	0,320	0,171	0,219	0,394	0,265	0,336	0,233	0,260	0,186
13	0,235	0,139	0,160	0,260	0,175	0,277	0,279	0,136	0,220
14	0,182	0,112	0,137	0,383	0,235	0,293			
15	0,282	0,110	0,247						
Mean	<b>0,290</b>	<b>0,198</b>	<b>0,248</b>	<b>0,513</b>	<b>0,287</b>	<b>0,326</b>	<b>0,397</b>	<b>0,233</b>	<b>0,267</b>
± SE	<b>± 0,023</b>	<b>± 0,022</b>	<b>± 0,021</b>	<b>± 0,089</b>	<b>± 0,035</b>	<b>± 0,035</b>	<b>± 0,039</b>	<b>± 0,022</b>	<b>± 0,027</b>

The lower turnover rates observed in the Structures + Corals treatment do not necessarily mean a higher stability in terms of individual species and their absolute abundances, but rather reflect the ability of the more complex plots to retain a higher proportion of species. As Caley and St. John (1996) observed, the availability of refuges does not influence which species are present, only how many (although it is likely that certain coral species have a higher effect in retaining specific fishes than others, and that this property goes beyond a sheer ‘refuge function’). This property, together with the higher biodiversity and the higher possibility for functional redundancy (Walker 1992) of the fish communities in the Structures + Corals plots, as more available habitat permits the coexistence of species with similar requirements (Clarke 1988, Galzin et al. 1994), may also render them more *resilient* to change (Tilman 1999, Fonseca and Ganade 2001).

The results of this study show that while equilibrium may not be reached, multivariate stability and increased resilience are still possible. In this respect, it is interesting to note that similarity between subsequent samples remained high in the Structures + Corals treatments in spite of an increasing mortality of the coral transplants. While this does not mean that the fish community will remain similar over a longer period of time (it could gradually evolve away from the species composition observed in the presence of high coral cover), the fact that fish abundance, species richness and diversity remained highest in the Structures + Corals treatment until the end of the experiment at all three locations shows that coral transplantation helped in the creation of a rich fish community that persisted even though a large number of fragments did not survive, possibly because a natural benthic community was beginning to develop on the artificial structures.

#### 4.1.3.2 Spatial variation: the importance of reef context

Significant differences were detected between the fish communities at the three experimental locations (Tab. 3.3). The MDS plot (Fig. 3.8) indicates what is confirmed by the ANOSIM analyses (Tabs. 3.3, 3.6, 3.7, and A 9): differences were least pronounced between Meras and Bunaken, and within treatments there was a clearer separation between sites in the Structures + Corals than in the Structures and Control treatments, respectively. There were several differences between the three experimental sites.



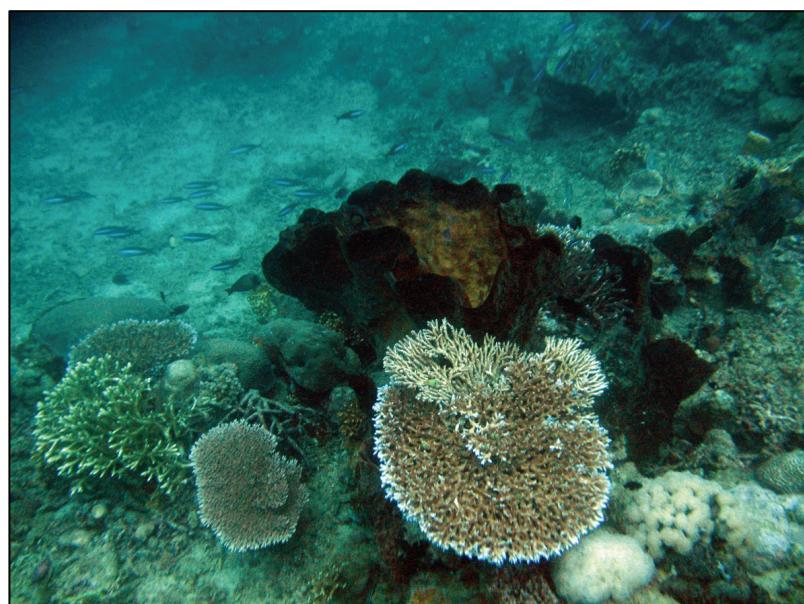
**Figure 4.8:** The ambient reef at Gangga consisted largely of rubble and dead coral, with several soft and leather corals and few remaining hard corals.

At Gangga, the experimental plots were located at a shallower depth than at Meras and Bunaken. Additionally, the shallow slope at Gangga was covered mostly with coral rubble and had little structural complexity, which was in the form of larger boulders or intact massive corals. Soft and leather corals comprised the highest proportion of live coral (Fig. 4.8). Anecdotal information from local villagers suggests that destructive fishing with drag nets and explosives may be responsible for the low coral coverage and structural complexity (see also Turak and DeVantier 2003). Meras had the highest spatial heterogeneity of the three sites. Sponges and hard coral comprised the majority of living benthic substrate (Fig. 4.9), which covered more than 50 % in one of the two natural reef plots (Fig. 3.7). Species of hard corals had a mixed distribution, with few monospecific patches. The site at Bunaken had less topographic complexity than the site at Meras, but had a higher percentage cover of branching acroporids, which formed several monospecific thickets (mostly *Acropora brueggemannii*) that sometimes measured tens of meters across.

A comparison of the fish communities in the natural plots with the substrate composition and depth of the plots showed that some of the major living benthos categories (soft and leather corals, branching *Acropora* sp., foliose coral, and coralline algae) as well as depth of the sites were closely related with the fish community composition. Although no data on topographic complexity is available, results from previous studies (Gladfelter and Gladfelter 1978, Grigg 1994, Chittaro 2004, Wilson et al. 2007) indicate that complexity of the habitat probably also influenced the abundance and composition of the fish assemblage at each site.

Depth has been shown to exert a major influence on fish community composition (McCormick 1994, Green 1996, Friedlander and Parrish 1998, Khalaf and Kochzius 2002). For example, McCormick found a strong relationship between depth and abundance of *Pomacentrus moluccensis*. In the present study, *P. moluccensis* was present in all of the shallow plots at Gangga, but occurred only in one natural reef plot at Meras. Similarly, artificial reefs deployed at different locations or different depths were colonized by different fish communities (Walsh 1985, see review by Sherman et al. 2001).

Since different coral species were transplanted at each location, and the species were selected in part based on their abundance in the ambient reef, it seems probable that the different coral species attracted specific fish species, which were a reflection of the natural assemblages at each site and thus reinforced differences between the fish communities in the Structures + Corals plots at the three locations. As soft coral, which is the dominant form of coral at Gangga, has been found to exert no direct influence on the fish community (Syms and Jones 2001), and since the respective natural and experimental plots at Meras and Bunaken were relatively similar to each other while the shallower communities from Gangga formed one distinct cluster, it appears that depth and amount of hard coral was the overriding factor in shaping the different fish communities at the three locations.



**Figure 4.9:** Sponges and a variety of hard corals comprised a large part of the substrate in the ambient reef at Meras.

As a major part of the fishes observed in the experimental plots was comprised of post-recruit juveniles and adults that had immigrated into the plots from the surrounding reefs, the faunal composition within the plots necessarily is a reflection of the species present in the ambient reef. This is reflected in the cluster analysis of samples from the natural and experimental plots at similar times, where the samples from Gangga form one distinct cluster, while the samples from the Structures+ Corals and Structures plots from Meras and Bunaken form one cluster with the natural reef samples (Fig. 3.14). An indication of the small importance of hard corals in the natural reef at Gangga is the fact that the samples from the natural reef there are more similar to the samples from the Structures than those from the Structures + Corals plot, and the fish abundance and species richness is similar in the Structures and natural reef plots. On the other hand, the samples from the Structures + Corals plots at Meras and Bunaken are more similar to those from the Structures than those from the natural reef plots. This shows that the coral fragments transplanted there were not sufficient to re-create the conditions of the ambient reef, and the higher numbers of fish abundance in the natural than the Structures + Corals plots are a further indication that fishes were not overly attracted to these plots, maybe because they failed to offer the same amount of habitat diversity and complexity as the ambient reef.

A higher number of species were observed in the Structures + Corals plots than in the Structures plots for the entire duration of the experiment at Meras and Gangga, but the total



**Figure 4.10:** Colonies of *Acropora palifera* and *A. brueggemanni* next to the Structures plot at Bunaken.

number of species in these two plots was similar at Bunaken. Here, several species were observed only in the Structures plot, which was located in close proximity to a large thicket of branching *Acropora* sp. and several mixed coral patches (Fig. 4.10), and it seems that the species exclusive to the Structures plot (e.g., *Bodianus mesothorax*, *Cheilinus oxycephalus* and *Chromis ternatensis*, all of which occur in areas with patches of live coral, Myer 1999) were the result of spill-over from the ambient reef.

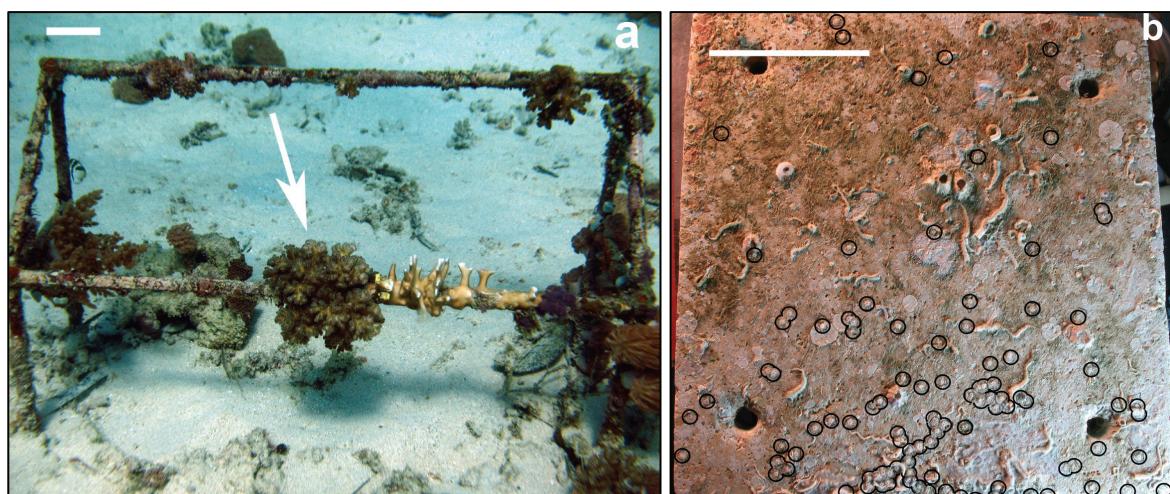
While there were few hard corals and little structural complexity in the ambient reef at Gangga, the reef at Meras was more heterogeneous both in terms of habitat complexity and diversity of hard corals and sponges, and several large thickets of branching *Acropora* sp. as well as big single colonies of *Acropora palifera* occurred in the vicinity of the experimental plots at Bunaken. As noted above, artificial reefs placed in an area of low structural complexity and live coral cover frequently show very high fish abundance and biomass compared to the ambient reef (Randall 1963, Edwards and Clark 1993, Rilov and Benayahu 2000), while in those cases where the values were lower than in the natural reef, the artificial structures had been placed in biologically rich and structurally complex natural settings (Burchmore et al. 1985). This may help to explain why artificial structures and coral transplantation was able to match, and surpass, the abundance and species richness of the ambient reef at Gangga, but did not have such a marked effect at the other two sites.

Bohnsack (1989) as well as Bohnsack et al. (1994) concluded that artificial reefs may create additional habitat in areas with reef damage or loss, thus increasing production, while attraction should be predominant in areas with high natural reef availability. This seems to explain the observed dichotomy between Gangga and the other two sites. If the reef at Gangga has indeed been subject to anthropogenic impacts, causing reduced structural complexity and hard coral cover and thus habitat limitation, the provision of artificial structures and coral transplants would have served both to attract fishes from the ambient reef and increase production, leading to the observed higher fish abundance in the Structures + Corals plot than in the natural reef. The higher structural complexity and benthic diversity in the natural reef at Meras seems to explain the lower number of recruits in the experimental than the natural plots, while low attractiveness of the experimental compared to the natural plots are the reason for the higher fish abundance and diversity in the natural reef plots. At Bunaken, the large patches of branching *Acropora brueggemanni* in the vicinity probably attracted the majority of fish recruits, and the transplanted fragments of *A. brueggemanni* helped to re-create settlement substrate similar to that in the natural reef plots, leading to similar amounts of recruits in the natural reef and Structure + Corals plots.

## 4.2 Trends in coral recruitment

Coral recruits were found on the settlement plates year-round. However, two peaks in recruitment were observed between April and July in 2006 and 2007 (Fig. 3.22). Seasonal peaks in recruitment have been described from other areas in the Indo-Pacific region, with the majority of spawning usually occurring in late spring and early summer (Wallace and Bull 1982, Harrison et al. 1984, see reviews by Fadlallah 1983 and Harrison and Wallace 1990). While mass spawning of corals has first been described from the Great Barrier Reef and was thought to be restricted to reefs in higher-latitude regions (Harrison and Wallace 1990), it has since been observed in places at low latitudes with less pronounced seasonal fluctuations (Baird et al. 2001, Guest et al. 2002). The occurrence of mass spawning events at low latitudes was confirmed in the present study, where a large patch of several branching *Acropora* sp. (mostly *A. yongei*) was observed during spawning in May 2007. In contrast to the results of Wallace (1985), who found higher recruitment variability at shallow rather than deep sites, the maximum annual variation in recruitment was observed in the deep plots at Bunaken. For both pocilloporids and acroporids, peaks in recruitment were observed in late spring at Gangga and Bunaken, although recruitment of pocilloporids remained the same throughout the year at Meras. Wallace (1985) and Fox (2004) described patterns similar to those observed at Meras, with seasonal peaks for acroporids, while recruitment of pocilloporids occurred in all seasons. The peaks in recruitment of acroporids are not unusual, as more than 80 % of the species in this family for which data are available spawn during seasonal mass spawning events (Willis et al. 1985).

A direct seeding effect by the transplanted fragments (Rinkevich 1995) most likely only occurred for the brooding species, as brooded planulae are capable of settling within a few hours after being released, sometimes within meters of their parent colony (Harrison and Wallace 1990, Tioho et al. 2001, Harii et al. 2002). An indication that brooding corals are capable of seeding their vicinity with larvae came from an incidental observation towards the end of the experiment. A colony of the brooding *Pocillopora damicornis* had settled onto one of the iron frames deployed in the Control plot at Gangga and grown to a diameter of 13.5 cm by the end of the experiment. When the settlement plates were collected for the last time in July 2007, 123 recruits were observed on the plate adjacent to the colony of *P. damicornis*, 97.6 % of which were comprised of pocilloporids (Fig. 4.11).



**Figure 4.11:** The colony of *Pocillopora damicornis* (arrow) growing on an iron frame used to hold three recruitment plates (a). A closeup of the settlement plate deployed next to the colony is shown in b. Recruits are circled in black (scale bars = 5 cm).

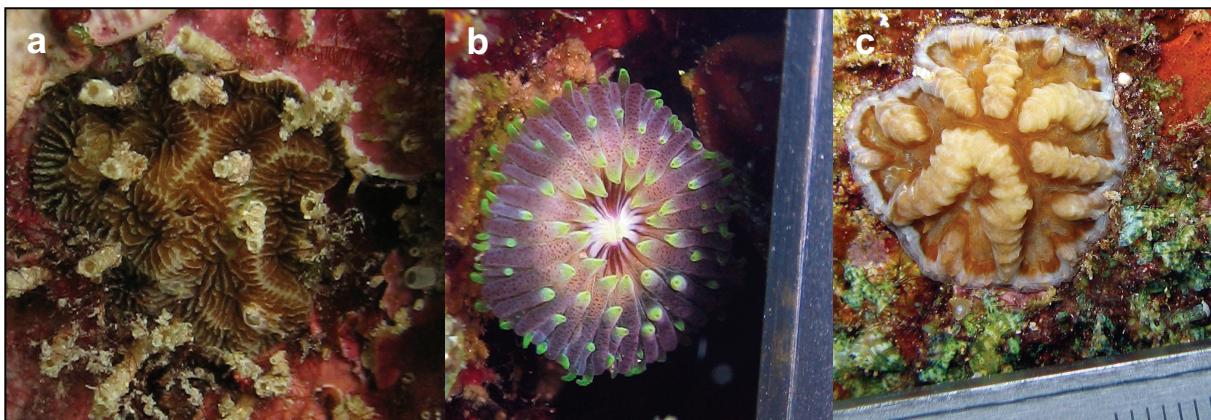
Although spawning was not observed in this case, the aggregation of the recruits in close proximity to the location of the colony on the frame indicates that larvae had settled onto the closest suitable substrate available upon release. If the recruits on the plate indeed originated from the colony growing on the frame, this observation shows that coral colonies are capable of reproduction even at small sizes similar to that of the transplanted fragments. Although corals (almost all of them *Pocillopora* sp.) were observed growing on some of the other frames, this was the only case where a high number of recruits were observed in the vicinity of an adult colony, and data from this plate were thus excluded from the analysis. The lack of an effect of colonies on the other frames indicates that the presence of *Pocillopora* sp. colonies did not serve to attract coral larvae and generally influence the settlement rates on the plates, and is an additional indication that the increase in settlement observed in this case was caused by larvae released from the colony next to the plate.

Another observation from Gangga provides an indication of a potential secondary effect of the coral transplants on settlement. The three settlement plates from the outermost upcurrent settlement frame in the Control plot only had between 0 and 3 recruits each during all of the eight sampling periods, while the average amount per plate for the other frames in that treatment ranged from  $5.4 \pm 1.8$  to  $21.6 \pm 3.5$  (mean  $\pm$  SE). A cloud of several dozen to  $> 100$  juvenile planktivorous fish, mostly pomacentrids, frequently was observed within 1 m upcurrent of the frame. Kingsford and MacDiarmid (1988) found that high densities of planktivorous pomacentrids were capable of significantly reducing the amount of zooplankton drifting past. A reduction of planktivorous fishes could help to explain the higher rates of recruitment observed by Hughes (1985) in quadrats cleared of all benthic biota compared to control plots left intact, although he did not provide data on fish abundance in his study. Despite the fact that no data exists to substantiate this observation and conclusions about a potential correlation between planktivore abundance and larval supply thus have to remain speculative, it seems possible that a higher abundance of planktivores occurring in the presence of coral transplants removes a certain amount of coral larvae from the water column. Any such effect could counteract potential positive effects of the transplants on coral recruitment, and mask differences in recruitment between plots with and without coral transplants.

Significantly higher numbers of recruits were observed in the Structures + Corals plots only during the final sampling period at Meras and Bunaken, and it is possible that these were caused by the presence of the transplanted fragments. Of the transplanted species at Meras, *P. verrucosa* was the only potential source of larvae (but see Sier and Olive 1994). However, there was no difference in the relative frequency of pocilloporids between the plots in the final treatment. Attraction of coral larvae by the live fragments remains as a possible explanation for the higher recruitment in the Structures + Corals plot. Gittings et al. (1988) reported higher recruitment rates in the vicinity of living adult colonies from damaged reef areas, but did not elaborate whether this was due to attraction or seeding by the adults. Baggett and Bright (1985) attributed small-scale variability in coral recruitment patterns to the proximity of adult colonies, and Reyes and Yap (2001) found significantly higher numbers of recruits on settlement plates placed among live corals than on bare sand  $> 5$  m away from coral. However, other studies found no connection between coral cover and recruitment (Fitzhardinge 1985) or detected a negative correlation (Hughes 1985). Edwards and Clark (1998) did not observe any effect of coral transplants on recruitment. Moreover, there was no significant difference between the number of recruits and the species composition on the concrete structures in the Structures and the Structures + Corals plots. Thus, the data at hand do not conclusively support a positive effect of the transplanted coral fragments on coral recruitment at Meras.

At Bunaken, where only fragments of the brooding species *A. brueggemanni* had been transplanted, the highest number of recruits was again detected in the Structures + Corals plot during the final sampling period. The relative frequency of acroporids was also highest on the settlement plates from the Structures + Corals plot. As large monospecific thickets of *A. brueggemanni* were prominent in the vicinity, it is likely that, if localized recruitment from brooding species took place, a large portion of the acroporid recruits belonged to this species. At any rate, of the three Structures + Corals plots in this study, the plot at Bunaken constituted the closest imitation of the ambient hard coral composition with the exclusive transplantation of *A. brueggemanni*, which also had the lowest mortality of all species used. The observed higher rates of recruitment in the Structures + Corals plot again could be the result of attraction via settlement cues or seeding by brooded larvae produced by the transplanted fragments. As no spawning was observed in transplanted fragments at any of the sites and no histological data on the fecundity of the transplants is available, conclusions about the effect of coral transplantation on recruitment have to remain speculative. A trend, although not statistically significant, is however apparent in recruitment on the concrete structures at Bunaken. Here, a higher number of recruits was observed on the structures in the Structures + Corals plot. As the relative frequencies of pocilloporids and acroporids did not differ significantly between the Structures and the Structures + Corals treatment, generally increased settlement rates of recruits from all species (i.e., non-selective attraction by the living fragments) is a better explanation for the observed numbers of recruits on the concrete structures than increased seeding of the plot by the coral transplants. However, since increases in recruitment on the settlement plates in the Structures + Corals plots at Meras and Bunaken were observed only during the final sampling period, these patterns would not necessarily be reflected in the coral recruit community on the concrete blocks, which were examined some months before the end of the study.

The amount of recruits on the concrete structures generally reflected the recruitment patterns observed on the settlement plates, but differences existed in terms of the observed composition. At Gangga, pocilloporids comprised the majority of the recruits on the settlement plates. The percentage of recruits from other families and unidentified recruits ranged from 2 to 31 %, with an average of  $11 \pm 1\%$  ( $\pm$  SE). However, on the concrete structures, acroporid and pocilloporid recruits comprised only about half of the observed recruits (around 13 % could not be identified). At Meras, the percentage of recruits from other families and unidentified recruits (Fig. 4.12) on the plates was higher than at Gangga ( $37 \pm 2\%$ , mean  $\pm$  SE), but not as high as the percentage on the concrete structures (around 77 %, including around 8 % unidentified recruits). At Bunaken, recruits from other families and unidentified recruits comprised  $18 \pm 2\%$  ( $\pm$  SE) on the settlement plates, but almost 60 % on the concrete structures, including about 3 % of unidentified recruits.

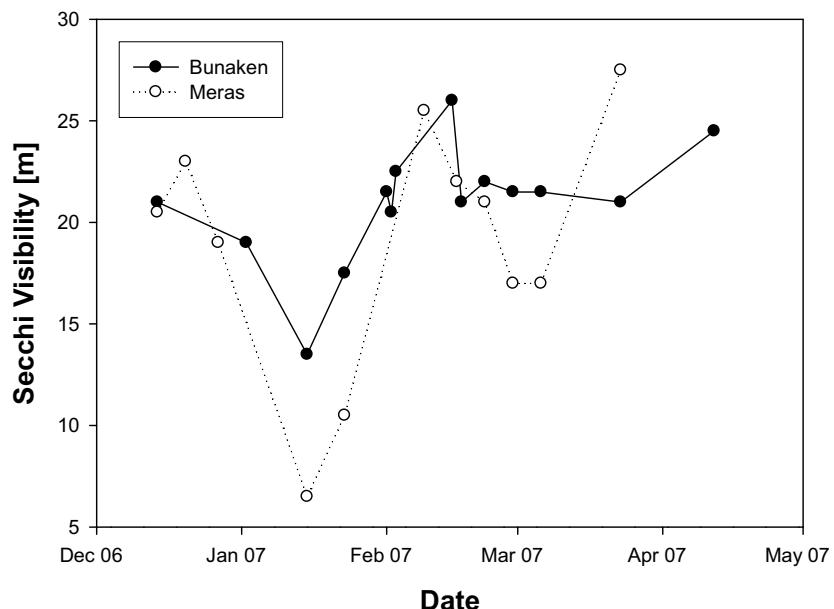


**Figure 4.12:** Examples of recruits other than acroporids and pocilloporids from Gangga (a), Meras (b) and Bunaken (c).

Concrete has been observed to be a suitable substrate for coral settlement in a number of previous studies (Schuhmacher 1973, Fitzhardinge and Bailey-Brock 1989, Clark and Edwards 1994, Reyes and Yap 2001), and Fitzhardinge and Bailey-Brock (1989) recommended the use of concrete for artificial reefs because it has a texture and chemical composition similar to coral. Reyes and Yap (2001) found no significant differences between the number of recruits on concrete and coral limestone substrates. On the other hand, Miller and Barimo (2001) found higher numbers of recruits on embedded limestone than on the surrounding concrete material. The concrete structures in this study had been in the water for a much longer time than the deployment time of the limestone plates by the time they were censused. The developmental stage of the epifaunal community necessarily differs with immersion time (Russel 1975, Schuhmacher 1977, Pamintuan et al. 1994b), and a conditioning period has been deemed necessary for a biofilm to develop before coral recruitment takes place (Schuhmacher 1977, Keough and Raimondi 1995). However, a separate study at Meras using limestone plates similar to the ones used in this study found settlement of coral recruits within one week of immersion (Schmidt 2007). Recruits from different species display differences in mortality over time (Babcock 1985, Smith 1992, Smith 1997, Glassom and Chadwick 2006) and in relation to orientation and available light levels (Babcock and Mundy 1996, Mundy and Babcock 2000). Some species, such as the pocilloporid *Stylophora* spp. and various acroporids, have been described as weedy *r* strategists with high recruitment and growth rates, but low survival compared to other, more slow-growing species (Smith 1992, Glassom and Chadwick 2006). Thus, any differences observed between the recruitment on settlement plates and concrete structures are probably due to a combination of differences in settlement preferences for the two materials and the successional state of the epifaunal community. Furthermore, it is possible that a methodological bias influenced the results, as the concrete structures were censused *in situ* without any technical aides, while the settlement plates were examined *ex situ* using a stereo microscope.

Since the concrete blocks had been in the water for different amounts of time at the three locations, the differences in composition and abundance of recruits among the sites could reflect different successional states. However, the blocks at Meras and Bunaken had been placed at the respective plots in the reef on the same day, although construction of the structures was completed several months apart. Thus, in terms of immersion time, the differences between these two sites should be less pronounced. Moreover, the composition of recruits on the settlement plates also differed between the sites. Hence, differences in composition on the structures between the locations most probably were caused by differences in the larval pool and environmental conditions such as depth, turbidity and

current regime. Depth and current regime were similar at Meras and Bunaken, but data on water turbidity, as measured with a Secchi disc during the final months of the experiment, shows a different pattern for the two sites (Fig. 4.13).



**Figure 4.13:** Water turbidity measured using a Secchi disc at Meras and Bunaken during the last months of the experiment. Note that small-scale variation (within days) was smaller than variability over several durations of several weeks.

Coral recruits show species-specific settlement preferences regarding depth, microhabitat and light levels (e.g., Morse et al. 1988, Babcock and Mundy 1996, Mundy and Babcock 1998, Baird et al. 2003). Thus, while the observed differences in species composition between the settlement plates and the structures seem to be caused largely by settlement preferences and successional state, the different environmental conditions between the sites probably were causing the observed differences in composition and number of recruits between the three locations. Similar to the data from the settlement plates, the patterns in recruits observed on the concrete structure do not support a general positive effect of coral transplants on recruitment.

### 4.3 Comments on methodology, with reference to reef restoration and coral farming

Underwater visual census (UVC) was the main tool of collecting data on the fish community in this study. UVC has been used widely in coral reef research since the method was first introduced to estimate reef fish populations (Brock 1954). Since then, a number of standardized procedures have been developed (e.g. GBRMPA 1978, Bohnsack and Bannerot 1986, English et al. 1997). However, estimates of fish abundances can be biased by a range of factors, such as fish movement patterns and behavior, transect size, visibility and diver experience level (Russel et al. 1978, English et al. 1997, Sale 1997, Kulbicki 1998, Williams et al. 2006). Estimates of fish size may vary in accuracy depending on size of the individual and experience of the observer, and may be systematically affected by the optical properties of the surrounding medium (Bell et al. 1985b, Harvey et al. 2001, Edgar et al. 2004). Species with cryptic behavior are frequently missed or underestimated (Sale 1980b, Sale and Douglas 1981, Brock 1982), and the impact of experience level on estimates of abundance is more

pronounced in cryptic fishes (Williams et al. 2006). Both time of day (Colton and Alevizon 1981, Carpenter et al. 1982, Unsworth et al. 2007) and tidal phase (Thompson and Mapstone 2002) can influence observations on fish community composition. Additionally, instantaneous variability caused by fish mobility patterns affects fish community observations, especially for more mobile species such as acanthurids and scarids (McClanahan et al. 2007), and several replicate counts conducted per day are recommended to minimize within-day variability and achieve accurate estimates of fish densities (Samoilys and Carlos 2000, Willis et al. 2006, McClanahan et al. 2007).

In the present study, it was attempted to keep potential sources of systematic bias to a minimum. All census data was collected by the same observer, which eliminated between-diver differences in size estimation and fish identification (Sanderson and Solonsky 1986, Samoilys and Carlos 2000, Edgar et al. 2004). Cryptic and small species, such as gobiids, trypterygiids, callionymids, pinguipedids and most blenniids, were excluded as well as several transient and pelagic species, such as caesionids and carangids. Estimates of fish size could have been systematically biased, and no collections of fish were made to compare size estimates with actual sizes of individuals. However, since several objects of known dimensions (the concrete blocks, settlement frames and settlement plates) were present in each plot and allowed for direct comparisons of size for individuals at several distances, the sizes used in this study probably were reliable estimates of the true sizes. In order to increase the accuracy of size estimates in the Control plots, they were always censused last within each replicate (Fig. 4.14). Moreover, several dives were conducted at the experimental sites at Gangga after the set-up of the experiments to train fish identification and size estimation prior to the first visual census. Bell et al. (1985b) found that length estimates improve rapidly after repeated training, and reported that divers were able to achieve reasonably accurate estimates of fish size after five repeated trials.

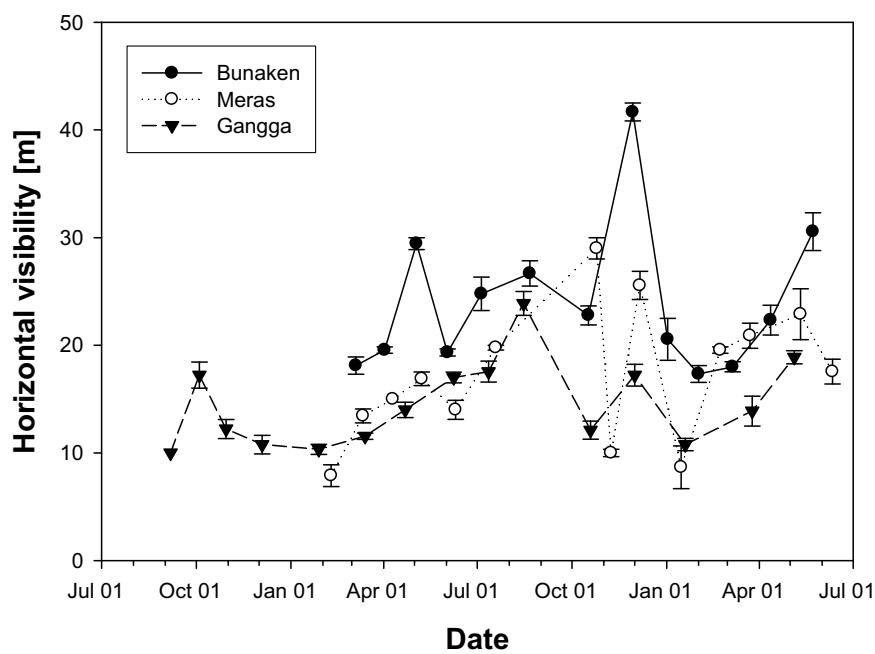


**Figure 4.14:** The author during a visual census in the Structures plot at Gangga in the first months after construction. Each census began in plots containing structures to allow adjustments of size estimates before moving to the Control plots. Photo courtesy of David Cheung.

However, experienced divers have been shown to count more fishes per transect, and counts of acanthurids, labrids and pomacentrids tend to be affected by observer experience level (Williams et al. 2006). Although the relative observations of community composition for each individual census will not be affected by experience level, it is possible that there was an effect of increasing experience of the observer on fish community observations over time. However, more than 350 individual censuses of experimental plots were carried out during the present study, and since censuses at Meras and Bunaken commenced about 6 months after the beginning of monitoring at Gangga, increases in experience had little potential effect at these sites. Williams et al. (2006) reported that the most experienced divers in their study, with more than 300 surveys conducted previously, counted between 40 and 130 % more fishes for some taxa than the least experienced observers with less than 10 previous dives. On

the other hand, fish abundance at Gangga increased by up to one order of magnitude during the experiment, an increase much higher than any that could be attributed solely to experience gained throughout the study. It can not be ruled out, though, that increased experience over the course of the study was partially responsible for the observed increase in within-census similarity over time.

Turbidity, as approximated by horizontal visibility during each census (Fig. 4.15), had significant effects at Meras and Bunaken. This observation contrasts with the findings of Bohnsack and Bannerot (1986), who did not observe any significant effects of visibility on fish abundance and species richness. A potential effect of visibility could be reduced accuracy of the diver in counting the fishes present. Sale and Douglas (1981) concluded that increased water clarity was at least partially responsible for higher numbers of fishes and fish species recorded in some of their censuses. It is likely that the presence of a diver had an effect on certain fishes or fish species, e.g. causing some species or larger individuals to avoid the diver (e.g., Chapman et al. 1974, Kulbicki 1998). In this case, species or individuals more wary of a diver would be more likely to be detected from a distance, leading to higher counts of individuals, species and biomass in conditions of increased visibility. Additionally, as light levels were higher at the shallower sites at Gangga, the effect of visibility on vision of the diver probably was less marked here than at the deeper sites at Meras and Bunaken, which would explain why effects of visibility were more marked at the latter two sites. Additionally, turbidity could be correlated with the change of tides, and increased currents could have resulted in higher numbers of planktivores (Bray 1981, Kingsford and MacDiarmid 1988). Both of these factors are likely to have affected the results of the present study, although the relative effect of each is difficult to determine with the data at hand and is beyond the scope of this study.



**Figure 4.15:** Underwater visibility (mean  $\pm$  SE) estimated during each visual census at the three experimental locations.

As some time was required to accurately examine each structure and coral colony, the time spent in each plot increased with increasing complexity from the Control to the Structures + Corals plots. About 5 to 10 minutes were usually spent in each Control plot, while a census of the Structures + Corals plot at Gangga required up to one hour. More time spent in a plot also increases the number of individuals and species counted (Sale 1997). The 26 species restricted

to the Structures + Corals plots observed only once during the study could be an artifact of the larger amount of time spent in these plots. Addressing the effect of sampling time, Bohnsack and Bannerot (1986) showed that the cumulative number of species counted by a stationary diver leveled off after about five minutes. They reported that the increase in number of species observed with additional time was larger in more complex habitats. Since a larger area of the plot could be seen and the species present recorded at a given time in the Control than in the more complex plots, the effect of different amounts of time spent in each plot were presumably small. Differences in observation time could have had another impact, however. Dive time in the deeper plots at Meras and Bunaken was necessarily limited by decompression constraints. Although there was no instance when censusing had to be aborted due to decompression limits and care was taken to examine all plots equally thorough for all fishes present, it is possible that there was a psychological effect of the potentially limiting bottom time at Meras and Bunaken that lead to less accurate counts than at the shallower sites at Gangga. However, the relative data on community composition for each location would have been subject to a similar bias, and comparisons among the treatments at each site would not be affected.

As replicate censuses were used to assess the fish community in each plot, effects of within-day variation were reduced, which increased the ability to statistically detect spatial and temporal variation in the fish community (Thompson and Mapstone 2002, Willis et al. 2006, McClanahan et al. 2007). Furthermore, the MDS plots showing all replicate samples from one location (Figs. 3.9, A 3 and A 5) display distinct clusters of replicates according to treatment, showing that within-day variability of replicate samples from one experimental plot was less pronounced than differences in community composition between the different plots.

Hence, with the above-mentioned weaknesses in mind, it can be concluded that the quadrat census method used is a reasonably accurate and suitable method for the monitoring of the fish community in each plot and for addressing the questions posed in this study.

As survival was the only variable measured for the coral transplants, measurements of the growth rates of the transplanted fragments are not available. However, in a parallel study at



**Figure 4.16:** Fragments of *Acropora formosa* had grown into colonies of up to 40 cm in height after 18 months at Meras, indicating skeletal extension rates of more than  $200 \text{ mm y}^{-1}$ .

Gangga using the same methods as those used here, *A. yongei* was observed to grow between  $1.2 \pm 0.3$  and  $4.7 \pm 0.3 \text{ mm } 30 \text{ d}^{-1}$  (mean  $\pm$  SE), depending on season (S. Romatzki and S. Ferse, unpublished data). These rates are equal to or slightly lower than growth rates of colonies of *A. yongei* reported from subtropical Australia (Marsh 1993, Harriott 1999). For *P. verrucosa*, increments in diameter between 25 and 30  $\text{mm y}^{-1}$  were reported for fragments attached to bamboo sticks in the Philippines (Alcala et al. 1982), while Clark and Edwards (1995)

observed a similar rate of mean linear radial extension ( $25.1 \text{ mm y}^{-1}$ ) in fragments transplanted onto concrete mats in the Maldives. From Thailand and the Great Barrier Reef, growth rates between  $80$  and  $120 \text{ mm y}^{-1}$  linear extension have been observed *in situ* for colonies of *A. formosa* (Oliver et al. 1983, Charuchinda and Hylleberg 1984). At Samoa, Mayor (1924) reported annual growth rates of  $185 \text{ mm}$  for transplanted fragments of *A. formosa*. Personal observation of the fragments at Meras indicates that transplants of *A. formosa* grew at least as fast as the rates reported by previous authors, and that some fragments may have been growing more than  $200 \text{ mm y}^{-1}$  (Fig. 4.16). For *A. brueggemanni*, a comparison of the fragments at Bunaken with those transplanted at the other two sites showed that *A. brueggemanni* had the slowest growth rates of the three *Acropora* species used in this study, and it is estimated that this species grew less than  $100 \text{ mm y}^{-1}$  (personal observation). Auberson (1982) reported annual increases in height from  $41$  to  $75 \text{ mm}$  for transplanted fragments of *A. brueggemanni* from the Philippines.

Cement has been used to attach corals without apparent negative effects on survival in a number of previous studies (e.g., Mayor 1924, Alcala et al. 1982, Auberson 1982, Franklin et al. 1998, Ferse 2004). At Gangga, *A. yongei* did not seem to be affected by the use of cement, as mortality in the days after transplantation remained low (<5%). However, fragments of *P. verrucosa* suffered mortality of up to 90% in response to cement. Thus, hot glue subsequently was used to attach *P. verrucosa*, and mortality in the first week after transplantation decreased to <5%. At Meras and Bunaken, the cement was discarded in favor of two-component epoxy glue, which did not cause residual particles to accumulate in the water and cured much faster than cement, a logistical advantage when working on a boat (Fig. 4.17). However, as the epoxy was about 30 times as expensive per fragment as the cement, using epoxy should be considered only in small-scale studies of coral ecology or physiology, while the high costs do not warrant the use in reef rehabilitation or coral farming projects. Inexpensive cement should be used instead, and placing the fragments directly into the reef environment or a flow-through system with running sea water most likely will keep mortality caused by the cement <5%.

Attachment of coral fragments has been identified as a key factor for post-transplantation survival, especially in high-energy environments (Edwards and Clark 1998, Lindahl 2003). The importance of attachment became particularly apparent at Meras, where a number of additional fragments were transplanted after completion of the set-up of the site. Since they could not be attached to the bamboo boards right away due to logistical problems, the fragments were placed individually onto rubble patches next to the Structures + Corals plot for four months before being attached. By then, transplants had been moved, probably by currents and reef organisms, and only 45.8% of *A. formosa* and 1% of *P. verrucosa* were still alive. On Bunaken, too, a number of fragments could be transplanted



**Figure 4.17:** Transplantation of *Acropora formosa* fragments onboard a boat at Meras using two-component epoxy.

only some time after the plots had been set up. The fragments were placed individually and upright onto rubble next to the Structures + Corals plot. After two months, 76.3 % had survived and were attached to the bamboo boards. Assuming a stable mortality rate, survival of *A. brueggemanni* after 4 months would have been around 56 %, indicating that without further attachment of the concrete bases, survival was higher in *A. brueggemanni* than in *A. formosa*. This concurs with the observation that there was no strong correlation between survival rate of *A. brueggemanni* and disintegration of the bamboo substrate (Fig. 3.28).

Fragments of *A. brueggemanni* had the highest survival rate in the present study and thus appeared to be most amenable to the transplantation method applied here, i.e., attachment to a substrate that will disintegrate within 1 – 2 years. On the other hand, Auberson (1982) found that *A. brueggemanni* had the lowest annual survival rate (44 %) among six species examined. Moreover, Lindahl (1998) observed 73 % survival in unattached fragments of *A. formosa* after 11 months in 3 m water depth, suggesting that the high mortality of *A. formosa* observed at Meras was partially caused by factors other than attachment, such as sedimentation or predation by *Acanthaster*. Bruno (1998) suggested that survival of unattached fragments is highly context and species specific, a conclusion that is supported by the results of this study. *Pocillopora verrucosa* appears to require a more permanent, stable attachment, but Edwards and Clark (1998) observed that even when cemented to the substrate, this species had the second highest mortality of nine species transplanted, and suggested that massive species may be more amenable to transplantation than pocilloporids and acroporids.

The results presented here show that selection of a coral species suitable for transplantation is not the only aspect to be considered in reef rehabilitation. While the fragments at Bunaken had the highest rate of survival, the impact of the Structures + Corals plot in terms of fish abundance, species richness and biomass was least pronounced compared to the natural reef and Structures plots at that site. Moreover, coral recruitment rates were highest at that site, showing that the provision of hard structures as settlement substrate is probably sufficient to aid the natural recovery of the rubble plots in that reef environment, and resources should be directed to managing the reef rather than to transplantation (Kojis and Quinn 2001). On the other hand, low remaining hard coral cover and lower rates of recruitment at Gangga, and the remarkable response of the fish community there, seem to warrant coral transplantation in addition to artificial structures there. These observations underline that long-term monitoring is needed to judge the effectiveness of any rehabilitation measure. Artificial reefs may concentrate fish biomass, especially when in close proximity to natural reefs, and thus increase the vulnerability of a fish population rather than serve to increase the population (Bohnsack 1989, Abelson 2006). Also, coral transplants may be detached or damaged by human activities in the rehabilitation area, e.g. fishing with nets or weighted lines, throwing of anchors, or careless diving. Thus, a protection of the rehabilitation area from fishing, at least temporarily, is highly recommended. Combining rehabilitation efforts with the creation of an MPA may be a successful approach (see Cabaitan et al. 2008).

#### 4.4 The economics involved

The experimental set-up in this study consisted of inexpensive, locally available materials. The material costs for the construction of the Structures and Structures + Corals plots, based on local prices, are shown in Tab. 4.2a. Costs for tools and gear (e.g., pliers for the collection of coral fragments, plastic boxes and air pumps for the temporary maintenance of coral transplants, dive gear) are not included. Transportation costs and work hours for set-up of the sites and coral transplantation differed between the three locations and are shown in Tab. 4.2b.

**Table 4.2:** Cost of materials for the Structures plots (without additional covering of the bottom with bamboo boards) and Structures + Corals plots in Indonesian Rupiah (**a**) and amount of time spent on transport and underwater work at the three sites (**b**). Since rental conditions for transport and dive gear as well as training and expertise of the divers differed between each location, no costs are given for transportation and work.

<b>a</b>	<b>Materials (amount per plot)</b>	<b>Structures plot</b>	<b>Structures + Corals plot</b>
Bamboo Boards* (100)		-	595,000
Cinder Blocks (250)		430,000	430,000
Metal bars, ø 14 mm (220 m)		1,780,000	1,780,000
Concrete bases <sup>†</sup> (2500)		-	950,000
Total IDR		2,210,000	3,755,000
Total USD <sup>°</sup>		245.6	417.2
<b>b</b>	<b>Type of transportation/work</b>	<b>Gangga</b>	<b>Meras</b>
- boat (9 m wooden boat with 3x115 hp engines) <sup>‡</sup>	32 h (16 d, 2 h each)	16 d (boat rented per day)	8 d (boat rented per day)
- vehicle (7.5 ton truck)	12 h (3 d, 4 h each)	2 h	2 h
- dive time:			
• construction	44 h	69 h	ca. 35 h
• coral transplantation	57 h	50 h	ca. 32 h

\*includes manufacture and material costs (bamboo and nails), <sup>†</sup>includes manufacture and material costs (cement, sand and cable ties), <sup>°</sup>based on an exchange rate of 9,000 IDR = 1 USD, <sup>‡</sup>used for transport of materials and workers, and for coral transplantation

In the present study, corals were collected and transplanted specifically for the experiments. However, size of the fragments, culture substrates and transplant bases were chosen based on specimens and material used in coral farming (e.g., Heeger and Sotto 2000a, Ellis and Ellis 2002, Knop 2003, Ferse 2004). Thus, the coral transplants in the Structures + Corals could also have been supplied by a coral farming operation, and in that case the costs for transplantation could be substituted by the production costs or breakeven prices of coral fragments available from farming projects. Heeger et al. (1999) gave a total cost of 11.9 USD per 100 fragments, which included material and labor costs for collection, transplantation and ocean-based grow-out. One large national exporter in Indonesia was willing to buy fragments produced by local farming operations at a maximum price of 1,200 IDR (0.125 USD at that time) per fragment (personal communication). Ellis and Ellis (2002) calculated a breakeven price of 2.04 USD per fragment at a production of >2000 fragments month<sup>-1</sup>. Thus, the cost of the 2500 fragments in the Structures + Corals plots ranges between 298 USD (based on Heeger et al. 1999) and 5100 USD (based on Ellis and Ellis 2002). At Meras, where transplantation was most expensive due to difficult logistics, the total costs for transplanting the fragments in the Structures + Corals plot (including all incurred costs for materials, transportation, gear rental, food and labor) was around 9,965,000 IDR or about 1110 USD. In this study, all diving was done by unpaid volunteers, and most of the time private equipment was used. If costs for underwater labor and dive gear rental were added, the total costs would be markedly higher. However, even assuming that less expensively produced fragments pre-attached to substrates where available from a nearby coral farm, these would still have to be transported to the rehabilitation site and distributed underwater. For example, Heeger et al. (1999) calculated an additional cost of 6.8 USD per 100 fragments for reef rehabilitation (consisting of transport and labor). Hence, the costs for covering 100 m<sup>2</sup> with 2500 coral fragments should be expected to range between about 450 and 5300 USD, but could be much higher in places of high labor costs.

The calculations above necessarily constitute a simplification that does not reflect all the costs of rehabilitating 100 m<sup>2</sup> coral reef. It should be kept in mind that further costs are likely to occur, such as site surveys, project planning, training and management, and monitoring (Spurgeon and Lindahl 2000). Furthermore, the removal of coral fragments may have serious impacts on the donor site (Edwards and Clark 1998), and these should be included in the

planning and evaluation of any transplantation project (Spurgeon and Lindahl 2000). The use of farmed fragments could help to avoid negative impacts to donor sites (Clark 2002, Epstein et al. 2001, Rinkevich 2005).

In order to arrive at a comparable measure of value for the experimental plots, average values for all fishes observed in one plot during each census were calculated based on prices for food fishes and ornamental fishes collected from interviews on local fish markets, with traders, and available literature (Tab. A 1). The calculated prices are shown in Tab. 4.3. For the calculation of the values, the biomass and abundance of all individuals, irrespective of size, were used. Also, it was not possible to obtain price estimates for all species observed, and several species are neither sold in the aquarium trade, nor do they feature prominently on the fish markets. Furthermore, since the values were calculated based on all individuals observed, they would only be realized if every individual in a plot could be removed and sold. Using a net, this may be possible for the food fishes in the Control plots, but it clearly is not feasible for all fishes of ornamental value in the Structures + Corals plots. Hence, the values are given primarily for reasons of comparison.

**Table 4.3:** Average values for the fishes observed in the study plots during each census. Values are calculated based on abundances and biomass using prices obtained from local traders and the literature (see Tab. A 1) and are given in Indonesian Rupiah. The maximum value reached in each plot is shown in **bold**.

Census	Gangga Control				Gangga Structures + Corals				Gangga Structures			
	Ornamental value	SE	Food fishery value	SE	Ornamental value	SE	Food fishery value	SE	Ornamental value	SE	Food fishery value	SE
1	7000	-	9428	-	42000	-	10826	-	14000	-	5304	-
2	5167	726	4863	2272	54500	1607	21063	3922	20167	2421	16897	530
3	4167	1333	2790	2187	66833	7452	11340	3389	28667	8074	19491	6497
4	6167	441	1410	718	74833	7424	18223	5415	33833	6496	20452	2698
5	8833	1764	6270	2169	61500	13420	11181	1467	26167	3632	7405	157
6	7167	1014	15320	6688	66333	6930	10111	3154	28000	3329	20122	9041
7	7667	2167	2037	476	80667	8946	10172	770	19167	4003	13696	606
8	6000	289	2256	72	119667	12063	17561	5689	29000	7147	15732	5494
9	6833	1014	3393	2630	127333	4226	21944	2916	31000	3775	14720	874
10	14667	1590	2319	790	169667	8012	12684	6242	32833	6692	11901	487
11	23667	1202	2046	756	189167	34552	31722	2109	54500	764	10899	2332
12	23000	6874	6272	1844	199333	13932	28495	4711	50333	4936	8889	252
13	<b>24667</b>	7860	7258	1708	226667	11170	38232	7547	53333	3283	<b>31726</b>	11665
14	22167	2848	7126	1797	222000	10054	78514	15103	<b>70167</b>	3245	23490	7135
15	7333	1691	<b>28772</b>	26314	<b>241500</b>	8836	<b>124151</b>	41629	69667	12170	19584	2144
Census	Meras Control				Meras Structures + Corals				Meras Structures			
	Ornamental value	SE	Food fishery value	SE	Ornamental value	SE	Food fishery value	SE	Ornamental value	SE	Food fishery value	SE
1	17500	2500	0	0	18667	3609	8945	3467	38333	2728	2768	770
2	15000	1443	289	289	21667	1453	13923	2710	18667	2186	8413	6436
3	9833	3844	7502	2910	21833	6167	20407	7547	31833	2205	4569	3313
4	8000	500	1986	1444	28667	1333	19308	4436	36833	5134	3755	2468
5	1167	1167	1300	661	35000	4041	26361	5577	38667	5674	11647	3538
6	1000	577	3207	1014	27000	2646	26551	7329	48333	2522	13165	3817
7	11500	2500	6719	2099	<b>75000</b>	-	<b>58334</b>	-	53250	4250	23833	5510
8	8000	500	0	0	47500	4252	26272	12536	42000	577	9116	2587
9	19500	4311	6826	5597	67167	441	27807	8423	57000	4368	18775	6121
10	12500	0	0	0	55333	10748	24916	11030	39333	5630	6524	2156
11	15000	1607	1728	549	62500	8694	24128	6169	46833	13368	<b>25751</b>	8804
12	16167	4531	4005	2628	64667	5199	29612	6074	41000	9251	22352	6536
13	<b>20500</b>	5752	5017	1969	60667	9203	10310	1146	50500	1803	3636	626
14	16500	2500	<b>8088</b>	2429	46333	13007	18062	1954	<b>60667</b>	6888	4111	633

Census	Bunaken Control				Bunaken Structures + Corals				Bunaken Structures			
	Ornamental		Food fishery		Ornamental		Food fishery		Ornamental		Food fishery	
	value	SE	value	SE	value	SE	value	SE	value	SE	value	SE
1	333	333	5754	2934	2667	1764	7292	2906	7833	4693	10271	4450
2	1667	882	4227	2827	15167	2682	26433	4435	3667	1691	14795	1201
3	4667	3712	30477	15500	13000	1443	14345	3203	5000	1000	11439	3258
4	0	0	1700	971	42333	4885	14807	2701	8833	726	7570	3777
5	1667	882	5075	3152	25167	6405	9715	4365	17000	5204	10561	3712
6	5333	2906	2087	2087	43333	1590	20167	1415	15667	4631	15418	6277
7	1667	1667	<b>31282</b>	7821	69333	1641	<b>42405</b>	12798	21333	3383	14885	4535
8	500	500	14453	11293	59000	6384	28779	7299	22167	11348	18047	2259
9	4167	1453	1396	1396	48500	6110	17415	2595	22000	3464	14239	2947
10	9333	7097	5887	3749	40333	5732	29305	17370	8167	2804	23713	5277
11	5000	1528	15000	3310	36667	10232	18937	4860	18500	6245	<b>31400</b>	7376
12	<b>14667</b>	6064	12607	3242	54167	14007	21483	2144	15500	3122	21348	7296
13	3667	1590	4565	2525	<b>72667</b>	6870	38374	16383	<b>31500</b>	11846	29512	7453
	Natural Reef plots											
	Ornamental		Food fishery									
	value	SE	value	SE								
G Nat. 1	71167	3193	11135	3657								
G. Nat 2	117000	4726	7686	606								
M Nat. 1	62000	5679	7296	3309								
M Nat. 2	121500	5107	10224	3600								
B Nat. 1	80000	5204	11441	5542								
B Nat. 2	121000	8694	21919	7694								

Assuming an annual sustainable yield of 15 t km<sup>-2</sup> (Munro 1984), which Cesar (1996) found to be a reasonable average estimate, Pet-Soede et al. (1999) calculated a gross revenue of 15,000 USD km<sup>-2</sup> from sustainable fisheries in Indonesia, while White and Cruz-Trinidad (1998) arrived at a somewhat higher estimate of 20,000 to 55,000 USD km<sup>-2</sup> in potential annual revenues for sustainable fisheries (both for consumption and live export) in the Philippines. These values translate to a value from 1.5 to 5.5 USD 100 m<sup>-2</sup> from sustainable fishery for intact reefs. Assuming an exchange rate of 9,000 IDR = 1 USD, the calculated values of the standing stock in this study reached a maximum of  $26.8 \pm 1.0$  USD (mean  $\pm$  SE) for ornamental fishes and  $13.8 \pm 4.6$  USD (mean  $\pm$  SE) for food fishes in the Structures + Corals plot at Gangga. The values for food fishes in the Structures and Structures + Corals plots exceeded those in the natural reef plots at all locations, while the values for ornamental species were higher in the natural reef plots at Meras and Bunaken.

None of the studies mentioned above have explicitly included the value of ornamental fishes in their assessment, although White and Cruz-Trinidad (1998) assumed a higher market price to fishers for fishes caught for live export (10 USD kg<sup>-1</sup>) than for fish caught for local consumption (1.5 USD kg<sup>-1</sup>). Per weight, the value of ornamental species may be 1 to 2 orders of magnitude higher than the value of food fish (Green 2003). The valuation of the standing stocks in this study, although simplified, shows that ornamental fishes may add a significant amount to the potential value of a reef area. However, the operational and labor costs also are higher in the ornamental than in the food fishery. As mentioned before, the total value calculated for all fishes in a plot would only be realized, even under the assumption that all individuals were of a tradeable size, if every individual was caught. Clearly, this would not be sustainable. However, as most ornamental species are traded at a much smaller size than food fishes, a higher number of ornamental fishes could be removed sustainably per year than for food fishes, resulting in a higher realized proportion of the potential value for ornamental species. Thus, the potential annual revenues from sustainable fisheries cited above can be expected to be at least twice as high when ornamental species are included.

A comparison of the potential values of the Structures + Corals plots shows that the value at Gangga is up to three times as high as that of the plots at Meras and Bunaken. During the last census, the fish value of the Structures + Corals plot at Gangga was about 30 USD higher than that of the Structures plot. Based on fisheries value alone, assuming that all fishes from the plots could be removed and sold after the two years of the experiment and that fish production rather than attraction would produce an identical fish community that could be sold for the same price every two years, it would take between 30 and 350 years (with transplantation costs between 450 and 5300 USD) for the cost of transplantation to be offset by the value of the fishes in the plot. However, fishery constitutes only a part of the potential value of a reef area, and other values such as tourism and research potential, coastal protection, biodiversity, production of building materials etc. have been identified (Spurgeon 1992, White and Cruz-Trinidad 1998, Cesar 2000) and should be included in determining the benefits of reef rehabilitation (Spurgeon and Lindahl 2000). For example, in the calculation of Costanza et al. (1997), food production constituted only 3.6 % of the total annual value of coral reefs. A more inclusive calculation of the actual value of a rehabilitated reef area may thus show that even costs for coral transplantation of around 5000 USD 100 m<sup>-2</sup> are offset by the benefits derived from an intact reef within a few years.



**Figure 4.18:** 30 months after construction, a diverse epibenthic community consisting of soft and hard corals, sponges, tunicates and other organisms had developed on the concrete structures, as shown here on Gangga.

justified at Bunaken, where the amount of branching *Acropora* in the vicinity was high, and at Meras, where the ambient reef was diverse and transplants did not survive well. Although survival of fragments at Meras may have been increased to some degree by using other means of attachment, this would also have further increased the costs. In the case of Meras, where sedimentation seems to have been partially responsible for the high coral mortality, funds would be better spent on improved land management and schemes to reduce terrestrial run-off and sedimentation than on coral transplantation (Edwards and Clark 1998). Similarly, Spurgeon and Lindahl (2000) concluded that ‘coral restoration may not always be the most appropriate or efficient way to enhance damaged coral reefs’. The results presented here support their assertion that ‘prevention may well be more cost-effective than cure’ (Spurgeon and Lindahl 2000).

It should be kept in mind that coral transplantation may not always be warranted or appropriate (Edwards and Clark 1998). In the present study, recruitment rates of corals were sufficient to re-establish a natural epibenthic community at all three locations, provided that suitable hard substrate was available (Fig. 4.18). While the additional cost of transplanting coral fragments may have been justified by the remarkable increases in fish abundance and species richness at Gangga, where natural hard coral cover was low, the high costs of transplantation do not seem

## **4.5 Summary + conclusion**

In comparison to Control plots covered with coral rubble, plots with artificial structures had significantly higher fish abundance, species richness, biomass, and species diversity at all three study locations. Coral transplantation led to a further increase in fish abundance and number of species. Similar trends were observed for biomass and species diversity, although the effect of coral transplants on fish biomass at Bunaken and on species diversity at Meras was ambiguous.

Hence, the first study hypothesis that ‘coral transplants in combination with artificial structures lead to a significantly larger increase in fish abundance, number of species and diversity than artificial structures alone’ can not be accepted, since the null hypothesis is not clearly rejected at all three locations.

An analysis of similarity however showed that there were significant differences between the compositions of the fish community in each experimental plot at all three locations. The second hypothesis is thus accepted. A specific fish community developed at each site in response to the treatments. Although some fish species were identified as being correlated to coral rubble or live coral, there was no common characteristic community in either one of the experimental treatments. Differences between the three locations in water depth and substrate composition of the ambient reef were reflected in the composition of the fish community.

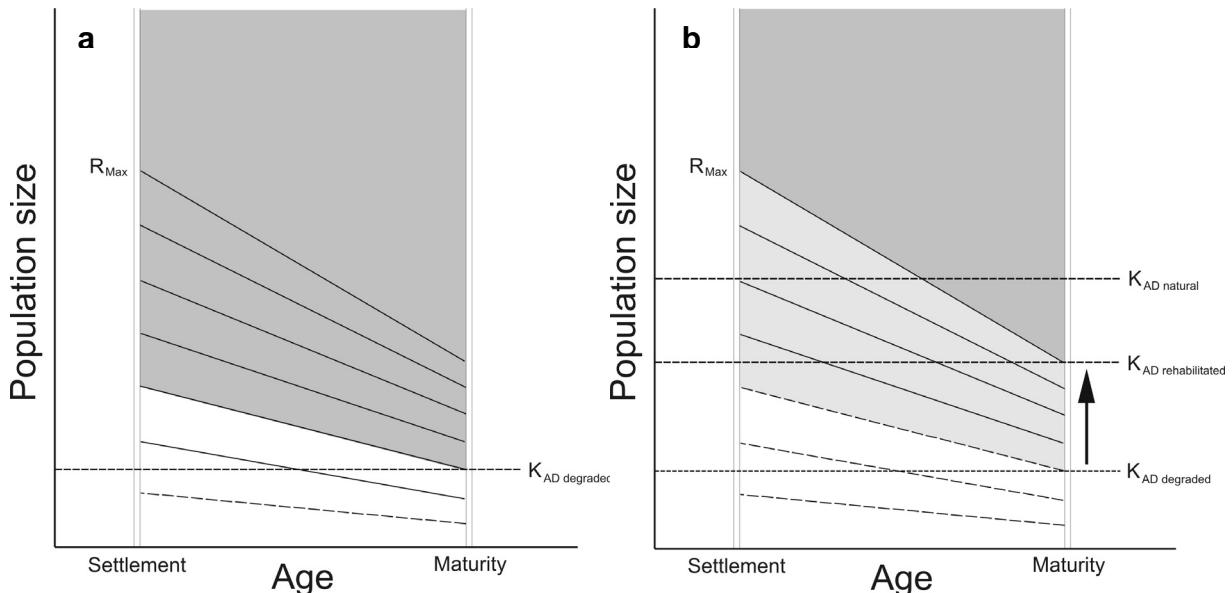
Differences in depth and hard coral cover were found to be the factors responsible for most of the observed variations in the composition of fish communities in the natural reef plots. In addition, differences in the natural fish communities between the three sites were reflected in the composition of the communities in the experimental plots. In each treatment, significant differences between the three sites were detected. The third study hypothesis is therefore accepted as well.

The observation of the fish community in response to two levels of rehabilitation revealed some trends of general applicability, but also showed that the response elicited by a chosen method is highly context-dependent. The processes structuring a fish community are manifold, vary depending on species and context, and interact. As coral reefs are patchy habitats with a high degree of spatial variability, it is important to understand that there is no single correct approach for reef rehabilitation efforts, but that efforts must be tailored to meet the situation at hand.

Similar to the responses of fish abundance and species richness, the observed trends in multivariate variability and similarity show that coral transplants may lead to a more stable fish community, but that the increase compared to the provision of artificial structures may be negligible in areas of high natural coral cover. Similarly, artificial reefs may lead to higher number of fishes and biomass by attracting fishes from the surrounding reef without actually contributing to fish production if places are in close proximity to intact natural reefs. Nonetheless, they may be useful in stabilizing loose substrate and provide coastal protection in areas of localized damage. In addition to reef context, the selection of an appropriate method for rehabilitation thus also depends on the desired ecological function of the method.

A comparison of the immigration and extinction rates of the three treatments showed that more species could be sustained by the more complex habitats, indicating an increase in the carrying capacity of the plots following rehabilitation. Although fish communities in natural reefs appear to be recruitment limited in most cases (e.g., Doherty and Williams 1988b) and

overfishing may further reduce the number of fishes below carrying capacity of the habitat (Lindberg 1997), the increasing habitat destruction in coral reefs, e.g. by destructive fishing or bleaching events, may lead to situations where, even at constant larval supply, the fish community is being limited by resources rather than recruitment. In this case, the appropriate degree of reef rehabilitation could be defined as increasing the carrying capacity of the habitat to the point beyond which recruitment becomes limiting again (Fig. 4.19), even though the capacity of the natural system may have been higher. This approach requires knowledge of the recruit dynamics at a location prior to rehabilitation.



**Figure 4.19:** A graphical model of the population dynamics for the juveniles of a reef fish population (a). The juvenile mortality of 50 % is assumed to be density-independent and linear.  $K_{AD}$  represents the carrying capacity of the habitat for adults. The dashed lines represent population decay in a primarily recruitment-limited population, where the number of recruits entering a population is below the carrying capacity for adults. The solid lines in the dark shaded area represent population decay in a habitat limited population. Secondary recruitment limitation occurs when the number of juveniles entering the population is above the carrying capacity, but post-settlement mortality reduces the number below carrying capacity. If degradation leads to a habitat-limited population, rehabilitation can be used to increase the carrying capacity of the habitat (b). As a result, the threshold for secondary recruitment-limitation is increased, and population decay lines of formerly habitat-limited populations now end below the carrying capacity of the habitat (light shaded area). Rehabilitation beyond the point where the decay line corresponding to maximum recruitment ( $R_{max}$ ) ends will not lead to a further increase in adult population size. The carrying capacity of the natural reef may be higher than that aimed at by a rehabilitation project. Modified from Victor (1986).

Johnson (2007) found that habitat complexity influences the relative importance of recruitment and post-recruitment processes in structuring the adult community. At low levels of complexity, density-independent mortality had the strongest effect on local population sizes. As habitat complexity increased, recruitment became more important. These results support the original model of Victor (1986) adapted in Fig. 4.5. However, these concepts deal with populations of a single species, and it should be borne in mind that the dynamics of a multi-species community potentially are influenced by intraspecific interactions and may vary depending on reef context. Nonetheless, the selection of appropriate rehabilitation measures should be based on ecological processes, and careful pre- and post-rehabilitation monitoring should be an integral part of all rehabilitation efforts (Miller 2002, Abelson 2006).

In contrast to an expected seeding effect of the transplanted brooding coral species, no general increase in coral recruitment was observed in the presence of coral transplants. Also, there were no differences in composition of recruits at the family level at Gangga and Meras. Thus,

the hypothesis that 'coral transplantation enhances recruitment and alters the family composition of coral recruits in the transplant plots compared to plots containing only structures' must be rejected. However, at Meras and Bunaken, recruitment in the last sampling period was highest in the presence of transplants. Hence, it may be that transplants require a certain period to recover from transplantation stress before they will resume spawning (Edwards and Clark 1998, Smith and Hughes 1999) and that the time frame of this study was not sufficient to cover this period. At Bunaken, the highest relative abundance of acroporids occurred in the plot into which *A. brueggemanni* was transplanted, but it is not clear whether this is the result of attraction to or larval release by the transplants. As the origin of recruits on the settlement plates could not be determined, this method may not be suitable to resolve the issue and additional histological examination of the transplants is needed.

For the census of fish communities in fixed quadrats, a modified version of underwater visual census was developed. Four adjacent transects per quadrat were used to cover the entire quadrat area. Monthly census of the 100 m<sup>2</sup> sized plots using three replicate counts proved to be both a feasible and reasonably accurate method for the comparison of experimental treatments and the collection of data from natural reef plots. The method is recommended as census protocol for similar studies of fixed plots of comparable size. However, nine replicate counts were the maximum number that could be conducted by a single observer per day. If experimental replication is to be increased per site, or if only natural reef plots are censused, replicate counts will have to be spread over more than one day.

The method adopted to assess substrate composition was better suited for surveying the quadratic plots than line intercept transects, which usually survey substrate strips of >30m length. Three divers working together were able to collect substrate data of one natural reef plot in about 30 min. As it allows for rapid surveys of fixed areas, his method is well-suited for studies of permanent transects with >5 m width, especially when a number of replicate plots are used. A thorough study of the accuracy of this method will help to determine the level of resolution required to address a specific question.

A comparison of the costs associated with the construction of the structures and transplantation of coral fragments showed that plots containing structures and coral transplants are at least twice as expensive per area as plots containing only structures. The costs incurred may vary considerably depending on available logistics and labor costs. The value of ornamental fishes constituted the largest portion of the calculated value of fish standing stock in the rehabilitated plots, and it is recommended that ornamental species be included in the valuation of the fisheries value of a reef. Even the highest projected returns from sustainable harvesting of the fishes in the plots containing coral fragments were not enough to balance the high costs of coral transplantation within a time frame of 30 years. However, the true economic value of an intact reef is much higher than the value represented by fishes alone, and in cases where larval supply is insufficient, hard coral cover has been severely reduced and the cause of degradation has stopped or been removed, coral transplantation may be ecologically and economically sensible.

In conclusion, the effects of the rehabilitation methods examined in this study differed in their extent between sites.

- The low-tech approach of transplanting coral fragments attached to bamboo boards was initially successful, but species differed in their ability to cope with subsequent disintegration of the substrate.
- Comparisons with other studies showed that local environmental factors may have impacted the performance of each species, and the choice of whether or not to transplant and which species to use must depend on the local conditions in the reef.
- More complex habitats had higher fish abundances and supported more fish species, but the strength of the response was different at each site.
- Live coral substrate appeared to exert an influence beyond a simple increase in structural complexity, but this effect differed between the locations as well.
- The highest increase in value of the standing stock in response to the experimental treatments occurred at the location with the lowest ambient hard coral cover. Ornamental species may constitute a higher potential value than food fishes.

## Outlook

In this study, the effects of corals transplanted at high densities (40-50 fragments m<sup>-2</sup>) in combination with artificial reefs on the fish community were examined for the first time. Thus, the results necessarily are still mostly descriptive in nature, and follow-up studies should augment the study design for a more detailed examination of the processes underlying the observed patterns (Miller 2002). Although the results indicate differences in the relative importance of recruitment, habitat limitation and attraction on fish community structure at the three sites, the potential contribution of these factors in correlation with habitat variables such as depth, substrate composition or exposure has yet to be determined. A higher amount of replication at each site, and multiple fish removal together with observation of the subsequent recolonization of the plots, are needed to determine the degree of stochasticity and site-dependent effects. Further analysis of the size cohorts of the fish community may help to shed more light on the dynamics in each plot. To date, evidence supporting the importance of live coral cover for the most part comes from ‘natural experiments’, where coral mortality caused by temperature anomalies or crown-of-thorn starfish reduced the amount of live coral while leaving colonies structurally intact. For a more in-depth examination of the importance of living coral substrate versus habitat complexity, and of species-specific effects, large-scale transplantation of single coral species accompanied by the transplantation of dead coral fragments should be used. The potential of using variability of the fish community and the concept of carrying capacity in the monitoring and design of reef rehabilitation projects also should be examined further.

## 5. References

- Abelson A. 2006. Artificial reefs vs coral transplantation as restoration tools for mitigating coral reef deterioration: benefits, concerns, and proposed guidelines. *Bulletin of Marine Science* 78(1): 151-159.
- Achituv Y. and Z. Dubinsky 1990. Evolution and zoogeography of coral reefs. In: Dubinsky Z. (ed.) 1990. *Ecosystems of the World, Volume 25 — Coral Reefs*. Elsevier Science, New York and Amsterdam: 1-9.
- Aktani U. 2003. Fish communities as related to substrate characteristics in the coral reefs of Kepulauan Seribu Marine National Park, Indonesia, five years after stopping blast fishing practices. PhD thesis, Zentrum für Marine Tropenökologie (ZMT), University of Bremen. 101 pp.
- Alcala A.C. and E.D. Gomez 1987. Dynamiting coral reefs for fish: A resource-destructive fishing method. In: Salvat B. 1987. *Human Impacts on Coral Reefs: Facts and Recommendations*. Antenne Museum, École Pratique des Hautes Études, French Polynesia: 51-60.
- Alcala A.C., E.D. Gomez and L.C. Alcala 1982. Survival and growth of coral transplants in Central Philippines. *Kalikasan, Philippines Journal of Biology* 11(1): 136-147.
- Alfeche L.R. 2003. Coral reef restoration through coral transplantation: the case of Duka Bay, Medina, Misamis Oriental. Second International Tropical Marine Ecosystems Management Symposium (ITMEMS), March 24-27 2003, Manila.
- Aliño P.M., P. Viva Banzon, H.T. Yap, E.D. Gomez, J.T. Morales and R.P. Bayoneto 1985. Recovery and recolonization on a damaged backreef area at Cangaluyan Island (Northern Philippines). *Proceedings of the 5<sup>th</sup> International Coral Reef Congress* 4: 279-284.
- Alldredge A.L. and J.M. King 1977. Distribution, abundance, and substrate preferences of demersal reef zooplankton at Lizard Island Lagoon, Great Barrier Reef. *Marine Biology* 41: 317-333.
- Allen G.R. 2000. Indo-Pacific coral-reef fishes as indicators of conservation hotspots. *Proceedings of the 9th International Coral Reef Symposium* 2: 921-926.
- Allen G.R., R. Steene, P. Humann and N. DeLoach 2003. Reef Fish Identification. Tropical Pacific. New World Publications, Inc., Jacksonville, Florida, USA. 457 pp.
- Anderson G.R.V., A.H. Ehrlich, P.R. Ehrlich, J.D. Roughgarden, B.C. Russell and F.H. Talbot 1981. The community structure of coral reef fishes. *American Naturalist* 117(4): 476-495.
- Atoda K. 1951. The larva and postlarval development of the reef-building corals. III. *Acropora brüggemannii* (Brook). *Journal of Morphology* 89(1): 1-15.
- Auberson B. 1982. Coral transplantation: an approach to the reestablishment of damaged reefs. *Kalikasan, Philippines Journal of Biology* 11(1): 158-172.
- Ault T.R. and C.R. Johnson 1998. Spatially and temporally predictable fish communities on coral reefs. *Ecological Monographs* 68(1): 25-50.
- Babcock R.C. 1985. Growth and mortality in juvenile corals (*Goniastrea*, *Platygyra* and *Acropora*): the first year. *Proceedings of the 5<sup>th</sup> International Coral Reef Congress* 4: 355-360.
- Babcock R.C. and C. Mundy 1996. Coral recruitment: consequences of settlement choice for early growth and survivorship in two scleractinians. *Journal of Experimental Marine Biology and Ecology* 206(1-2): 179-201.
- Babcock R.C., G.D. Bull, P.L. Harrison, A.J. Heyward, J.K. Oliver, C.C. Wallace and B.L. Willis 1986. Synchronous spawnings of 105 scleractinian coral species on the Great Barrier Reef. *Marine Biology* 90(3): 379-394.

- Babcock R.C., A.H. Baird, S. Piromvaragorn, D.P. Thomson and B.L. Willis 2003. Identification of scleractinian coral recruits from Indo-Pacific reefs. *Zoological Studies* 42(1): 211-226.
- Baggett L.S. and T.J. Bright 1985. Coral recruitment at the East Flower Garden Reef (Northwestern Gulf of Mexico). *Proceedings of the 5<sup>th</sup> International Coral Reef Congress* 4: 379-384.
- Baird A.H., C. Sadler and M. Pitt 2001. Synchronous spawning of *Acropora* in the Solomon Islands. *Coral Reefs* 19(3): 286.
- Baird A.H., R.C. Babcock and C.P. Mundy 2003. Habitat selection by larvae influences the depth distribution of six common coral species. *Marine Ecology Progress Series* 252: 289-293.
- Bell J.D. and R. Galzin 1984. Influence of live coral cover on coral-reef fish communities. *Marine Ecology Progress Series* 15: 265-274.
- Bell J.D., M.L. Harmelin-Vivien and R. Galzin 1985a. Large scale spatial variation in abundance of butterflyfishes (Chaetodontidae) on Polynesian reefs. *Proceedings of the 5<sup>th</sup> International Coral Reef Congress* 5: 421-426.
- Bell J.D., G.J.S. Craik, D.A. Pollard and B.C. Russell 1985b. Estimating length frequency distributions of large reef fish underwater. *Coral Reefs* 4(1): 41-44.
- Bell J.D., B.D. Ratner, I. Stobutzki and J. Oliver 2006. Addressing the coral reef crisis in developing countries. *Ocean & Coastal Management* 49(12): 976-985.
- Bellwood D.R. 1998. What are reef fishes? – Comment on the report by D. R. Robertson: Do coral-reef fish faunas have a distinctive taxonomic structure? (*Coral Reefs* 17: 179-186). *Coral Reefs* 17(2): 187-189.
- Bellwood D.R. and P.C. Wainwright 2006. The history and biogeography of fishes on coral reefs. In: Sale P.F. (ed.) 1991. *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego and London: 5-32.
- Bentley N. 1998. An overview of the exploitation, trade and management of corals in Indonesia. *TRAFFIC Bulletin* 17(2): 67-78.
- Beukers J.S. and G.P. Jones 1997. Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia* 114(1): 50-59.
- Birkeland C. 1977. The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. *Proceedings of the Third International Coral Reef Symposium* 1: 15-21.
- Birkeland C., R.H. Randall and G. Grimm 1979. Three methods of coral transplantation for the purpose of reestablishing coral community in the thermal effluent area of the Tanguisson Power Plant. *University of Guam, Marine Laboratory Technical Report* 60. 24 pp.
- Bohnsack J.A. 1983. Species turnover and the order versus chaos controversy concerning reef fish community structure. *Coral Reefs* 1(4): 223-228.
- Bohnsack J.A. 1989. Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? *Bulletin of Marine Science* 44(2): 631-645.
- Bohnsack J.A. and F.H. Talbot 1980. Species-packing by reef fishes on Australian and Caribbean reefs: an experimental approach. *Bulletin of Marine Science* 30(3): 710-723.
- Bohnsack J.A. and D.L. Sutherland 1985. Artificial reef research: a review with recommendations for future priorities. *Bulletin of Marine Science* 37(1): 11-39.
- Bohnsack J.A. and S.P. Bannerot 1986. A Stationary Visual Census Technique for Quantitatively Assessing Community Structure of Coral Reef Fishes. *NOAA Technical Report NMFS* 41. 15 pp.

- Bohnsack J.A., D.E. Harper, D.B. McClellan and M. Hulsbeck 1994. Effects of reef size on colonization and assemblage structure of fishes at artificial reefs off southeastern Florida, U.S.A. *Bulletin of Marine Science* 55(2-3): 796-823.
- Booth D.J. and G.A. Beretta 1994. Seasonal recruitment, habitat associations and survival of pomacentrid reef fish in the US Virgin Islands. *Coral Reefs* 13(2): 81-89.
- Booth D.J. and G. Wellington 1998. Settlement preferences in coral-reef fishes: effects on patterns of adult and juvenile distributions, individual fitness and population structure. *Australian Journal of Ecology* 23(3): 274-279.
- Borneman E.H. and J. Lowrie 2001. Advances in captive husbandry and propagation: an easily utilized reef replenishment means from the private sector? *Bulletin of Marine Science* 69(2): 897-913.
- Bothwell A.M. 1982. Fragmentation, a means of asexual reproduction and dispersal in the coral genus *Acropora* (Scleractinia: Astrocoeniidae: Acroporidae) – a preliminary report. *Proceedings of the 4<sup>th</sup> International Coral Reef Symposium* 2: 137-144.
- Bouchon C. J. Jaubert and Y. Bouchon-Navaro 1981. Evolution of a semi-artificial reef built by transplanting coral heads. *Tethys* 10(2): 173-176.
- Bowden-Kerby A. 1997. Coral transplantation in sheltered habitats using unattached fragments and cultured colonies. *Proceedings of the 8<sup>th</sup> International Coral Reef Symposium* 2: 2063-2068.
- Bowden-Kerby A. 2001. Low-tech coral reef restoration methods modelled after natural fragmentation processes. *Bulletin of Marine Science* 69(2): 915-931.
- Bowden-Kerby A. 2003. Coral transplantation and restocking to accelerate the recovery of coral reef habitats and fisheries resources within no-take Marine Protected Areas: hands-on approaches to support community-based coral reef management. Second International Tropical Marine Ecosystems Management Symposium (ITMEMS), March 24-27 2003, Manila.
- Bray J.R. and J.T. Curtis 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs* 27: 325-349.
- Bray R.N. 1981. Influence of water currents and zooplankton densities on daily foraging movements of blacksmith, *Chromis punctipinnis*, a planktivorous reef fish. *Fishery Bulletin* 78(4): 829-841.
- Briggs J.C. 1999. Coincident biogeographic patterns: Indo-west Pacific Ocean. *Evolution* 53: 326-335.
- Brock R.E. 1982. A critique of the visual census method for assessing coral reef fish populations. *Bulletin of Marine Science* 32(1): 269-276.
- Brock R.E., C. Lewis and R.C. Wass 1979. Stability and structure of a fish community on a coral patch reef in Hawaii. *Marine Biology* 54(3): 281-292.
- Brock V.E. 1954. A preliminary report on a method of estimating reef fish populations. *Journal of Wildlife Management* 18: 297-308.
- Brokovich E., A. Baranes and M. Goren 2006. Habitat structure determines coral reef fish assemblages at the northern tip of the Red Sea. *Ecological Indicators* 6: 494-507.
- Bruckner A.W. and R.J. Bruckner 2001. Condition of restored *Acropora palmata* fragments off Mona Island, Puerto Rico, 2 years after the *Fortuna Reefer* ship grounding. *Coral Reefs* 20(3): 235-243.
- Bruckner A.W. and R.J. Bruckner 2006. Restoration outcomes of the *Fortuna Reefer* grounding at Mona Island, Puerto Rico. In: Precht W.F. 2006. *Coral Reef Restoration Handbook*. CRC Press/Taylor and Francis, Boca Raton, Florida, USA: 257-269.
- Bruno J.F. 1998. Fragmentation in *Madracis mirabilis* (Duchassaing and Michelotti): how common is size-specific fragment survivorship in corals? *Journal of Experimental Marine Biology and Ecology* 230(2): 169-181.

- Bryant D., L. Burke, J. McManus and M. Spalding (eds.) 1998. Reefs at Risk. A Map-Based Indicator of Threats to the World's Coral Reefs. World Resources Institute (WRI), Washington, D.C., USA. 56 pp.
- Buchheim J.R. and M.A. Hixon 1992. Competition for shelter in the coral-reef fish *Acanthablemaria spinosa* Metzelaar. *Journal of Experimental Marine Biology and Ecology* 164(1): 45-54.
- Buddemeier R.W., J.A. Kleypas and R.B. Aronson 2004. Coral reefs & global climate change. Potential contributions of climate change to stresses on coral reef ecosystems. Pew Center on Global Climate Change, Arlington, USA. 56 pp.
- Burchmore J.J., D.A. Pollard, J.D. Bell, M.J. Middleton, B.C. Pease and J. Matthews 1985. An ecological comparison of artificial and natural rocky reef fish communities in Botany Bay, New South Wales, Australia. *Bulletin of Marine Science* 37(1): 70-85.
- Burke L., E. Selig and M. Spalding (eds.) 2002. Reefs at Risk in Southeast Asia. World Resources Institute (WRI), Washington, D.C., USA. 76 pp.
- Cabaitan P.C., E.D. Gomez and P.M. Aliño 2008. Effects of coral transplantation and giant clam restocking on the structure of fish communities on degraded patch reefs. *Journal of Experimental Marine Biology and Ecology* 357(1): 85-98.
- Cairns J., Jr., M.L. Dahlberg, K.L. Dickson, N. Smith and W.T. Waller 1969. The relationship of fresh-water protozoan communities to the MacArthur-Wilson equilibrium model. *American Naturalist* 103(933): 439-454.
- Caley M.J. 1993. Predation, recruitment and the dynamics of communities of coral-reef fishes. *Marine Biology* 117(1): 33-43.
- Caley M.J. and J. St. John 1996. Refuge availability structures assemblages of tropical reef fishes. *Journal of Animal Ecology* 65(4): 414-428.
- Cao Y., W.P. Williams and A.W. Bark 1997. Similarity measure bias in river benthic Aufwuchs community analysis. *Water Environment Research* 69(1): 95-106.
- Carpenter K.E., R.I. Miclat, V.D. Albaladejo and V.T. Corpuz 1982. The influence of substrate structure on the local abundance and diversity of Philippine reef fishes. *Proceedings of the 4<sup>th</sup> International Coral Reef Symposium* 2: 497-502.
- Caselle J.E. and R.R. Warner 1996. Variability in recruitment of coral reef fishes: the importance of habitat at two spatial scales. *Ecology* 77(8): 2488-2504.
- Cesar H.S.J. 1996. Economic Analysis of Indonesian Coral Reefs. *Working Paper, "Work in Progress Series"*, Environment Department, World Bank, Washington DC, USA. 97 pp.
- Cesar H.S.J. 2000. Coral reefs: their functions, threats and economic value. In: Cesar H.S.J. (ed.) 2000. *Collected Essays on the Economics of Coral Reefs*. CORDIO, Kalmar University, Kalmar, Sweden: 14-39.
- Chabanet P. and G. Faure 1994. Relationship between benthic and ichthyological communities on coral reefs. *Comptes Rendus de l'Académie des Sciences Paris, Sciences de la vie* 317: 1151-1157.
- Chabanet P., H. Ralambondrainy, M. Amanieu, G. Faure and R. Galzin 1997. Relationship between coral reef substrata and fish. *Coral Reefs* 16(2): 93-102.
- Chapman C.J., A.D.F. Johnstone, J.R. Dunn and D.J. Creasey 1974. Reactions of fish to sound generated by divers' open-circuit underwater breathing apparatus. *Marine Biology* 27(4): 357-366.
- Chapman M.G., A.J. Underwood and G.A. Skilleter 1995. Variability at different spatial scales between a subtidal assemblage exposed to the discharge of sewage and two control assemblages. *Journal of Experimental Marine Biology and Ecology* 189(1-2): 103-122.
- Charuchinda M. and J. Hylleberg 1984. Skeletal extension of *Acropora formosa* at a fringing reef in the Andaman Sea. *Coral Reefs* 3(4): 215-219.

- Chatfield C. and A.J. Collins 1980. Introduction to multivariate analysis. Chapman and Hall, London, UK. 246 pp.
- Chittaro P.M. 2004. Fish-habitat associations across multiple spatial scales. *Coral Reefs* 23(2): 235-244.
- Chittaro P.M. and P.F. Sale 2003. Structure of patch-reef fish assemblages at St. Croix, U.S. Virgin Islands, and One Tree Reef, Australia. *Marine Ecology Progress Series* 249: 277-287.
- Choat J.H. and D.R. Bellwood 1991. Reef fishes: their history and evolution. In: Sale P.F. (ed.) 1991. *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego and London: 39-66.
- Clark S. 2002. Coral reefs. In: Perrow M.R. and A.J. Davy (eds.) 2002. *Handbook of Ecological Restoration. Volume 2. Restoration in Practice*. University Press, Cambridge, UK: 171-196.
- Clark S. and A.J. Edwards 1994. Use of artificial reef structures to rehabilitate reef flats degraded by coral mining in the Maldives. *Bulletin of Marine Science* 55(2-3): 724-744.
- Clark S. and A.J. Edwards 1995. Coral transplantation as an aid to reef rehabilitation: evaluation of a case study in the Maldives. *Coral Reefs* 14(4): 201-213.
- Clark T. 1997. Tissue regeneration rate of coral transplants in a wave exposed environment, Cape D'Aguilar, Hong Kong. *Proceedings of the 8<sup>th</sup> International Coral Reef Symposium* 2:2069-2074.
- Clarke K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18(1): 117-143.
- Clarke K.R. and R.H. Green 1988. Statistical design and analysis for a 'biological effects' study. *Marine Ecology Progress Series* 46: 213-226.
- Clarke K.R. and M. Ainsworth 1993. A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series* 92: 205-219.
- Clarke K.R. and R.M. Warwick 1994. Change in marine communities: an approach to statistical analysis and interpretation. Natural Environmental Research Council, UK. 144 pp.
- Clarke K.R. and R.N. Gorley 2001. PRIMER v5: User Manual/Tutorial. PRIMER-E Ltd., Plymouth, UK. 91 pp.
- Clarke K.R., R.M. Warwick and B.E. Brown 1993. An index showing breakdown of seriation, related to disturbance, in a coral-reef assemblage. *Marine Ecology Progress Series* 102: 153-160.
- Clarke K.R., P.J. Somerfield and M.G. Chapman 2006. On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. *Journal of Experimental Marine Biology and Ecology* 330(1): 55-80.
- Clarke R.D. 1977. Habitat distribution and species diversity of Chaetodontid and Pomacentrid fishes near Bimini, Bahamas. *Marine Biology* 40(3): 277-289.
- Clarke R.D. 1988. Chance and order in determining fish-species composition on small coral patches. *Journal of Experimental Marine Biology and Ecology* 115(3): 197-212.
- Colton D.E. and W.S. Alevizon 1981. Diurnal variability in a fish assemblage of a Bahamian coral reef. *Environmental Biology of Fishes* 6(3/4): 341-345.
- Connell J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.
- Cormack R.M. 1971. A review of classification. *Journal of the Royal Statistical Society. Series B (General)* 134(3): 321-367.
- Costanza R., R. d'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R.V. O'Neill, J. Paruelo, R.G. Raskin, P. Sutton and M. van den Belt 1997. The value of the world's ecosystem services and natural capital. *Nature* 387: 253-260.

- Cox D.R. 1972. Regression Models And Life-tables. *Journal Of The Royal Statistical Society Series B-statistical Methodology*. 34 (2): 187–220.
- Cox E.F. 1994. Resource use by corallivorous butterflyfishes (family Chaetodontidae) in Hawaii. *Bulletin of Marine Science* 54(2): 535-545.
- Custodio H.M. III and H.T. Yap 1997. Skeletal extension rates of *Porites cylindrica* and *Porites (Synaracea) rus* after transplantation to two depths. *Coral Reefs* 16(4): 267-268.
- Dawson Shepherd A.R., R.M. Warwick, K.R. Clarke and B.E. Brown 1992. An analysis of fish community responses to coral mining in the Maldives. *Environmental Biology of Fishes* 33(4): 367-380.
- Delbeek, C. 2001. Coral farming: past, present and future trends. *Aquarium Sciences and Conservation* 3: 171-181.
- DeVantier L.M. and E. Turak 2004. Managing Marine Tourism in Bunaken National Park and Adjacent Waters, North Sulawesi, Indonesia. Technical Report, Natural Resources Management Program, Jakarta, Indonesia. 157 pp.
- Dixon J.A. 1998. Economic values of coral reefs: what are the issues? In: Hatziolos M.E., M. Fodor and A.J. Hooten (eds.) 1998. *Coral Reefs: Challenges and Opportunities for Sustainable Management*. World Bank Publications, Washington D.C., USA: 157-162.
- Dizon R.T. and H.T. Yap 2006. Effects of coral transplantation in sites of varying distances and environmental conditions. *Marine Biology* 148(5): 933-943.
- Doherty P.J. 1991. Spatial and temporal patterns in recruitment. In: Sale P.F. (ed.) 1991. *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego and London: 261–293.
- Doherty P.F. and D.McB. Williams 1988a. The replenishment of coral reef fish populations. *Oceanography and Marine Biology Annual Review* 26: 487-551.
- Doherty P.F. and D.McB. Williams 1988b. Are local populations of coral reef fishes equilibrial assemblages? The empirical data base. *Proceedings of the 6<sup>th</sup> International Coral Reef Symposium* 1: 131-139.
- Dominici-Arosemena A. and M. Wolff 2005. Reef fish community structure in Bocas del Toro (Caribbean, Panama): Gradients in habitat complexity and exposure. *Caribbean Journal of Science* 41(3): 613-637.
- Dominici-Arosemena A. and M. Wolff 2006. Reef fish community structure in the Tropical Eastern Pacific (Panamá): living on a relatively stable rocky reef environment. *Helgoland Marine Research* 60(4): 287-305.
- Done T.J. 1995. Ecological criteria for evaluating coral reefs and their implications for managers and researchers. *Coral Reefs* 14(4): 183-192.
- Ebeling A.W. and M.A. Hixon 1991. Tropical and temperate reef fishes: comparison of community structures. In: Sale P.F. (ed.) 1991. *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego and London: 509-563.
- Ebersole J.P. 2001. Recovery of fish assemblages from ship groundings on coral reefs in the Florida Keys National Marine Sanctuary. *Bulletin of Marine Science* 69(2): 655-571.
- Eckert G.J. 1985. Settlement of coral reef fishes to different natural substrata and at different depths. *Proceedings of the 5<sup>th</sup> International Coral Reef Congress* 5: 385-390.
- Edgar G.J., N.S. Barrett and A.J. Morton 2004. Biases associated with the use of underwater visual census techniques to quantify the density and size-structure of fish populations. *Journal of Experimental Marine Biology and Ecology* 308(2): 269-290.
- Edmondson C.H. 1929. Growth of Hawaiian corals. *Bulletin of the Bernice P. Bishop Museum Honolulu* 58: 1-38.

- Edwards A.J. and S. Clark 1993. Re-establishment of reef fish populations on a reef flat degraded by coral quarrying in the Maldives. *Proceedings of the 7<sup>th</sup> International Coral Reef Symposium* 1: 593-600.
- Edwards A.J. and S. Clark 1998. Coral Transplantation: A Useful Management Tool or Misguided Meddling? *Marine Pollution Bulletin* 37(8-12): 474-487.
- Edwards A.J. and E. Gomez (eds.) 2007. Reef Restoration Concepts and Guidelines: making sensible management choices in the face of uncertainty. Coral Reef Targeted Research & Capacity Building for Management Programme, St Lucia, Australia. iv + 38 pp.
- Eisinger M., P. van Treck, M. Paster and H. Schuhmacher 2006. Coral transplantation and natural recruitment on electrochemically formed reef structures. Abstract. ISRS European Meeting, 19-22 September 2006, Bremen. Programme and Abstracts: 143.
- Eklund A.-M. 1997. The importance of post-settlement predation and reef resource limitation on the structure of reef fish assemblages. *Proceedings of the 8<sup>th</sup> International Coral Reef Symposium* 2: 1139-1142.
- Ellis S. and E. Ellis 2002. Recent Advances in Lagoon-based Farming Practices for Eight Species of Commercially Valuable Hard and Soft Corals – A Technical Report. CTSA Publication No. 147, Center for Tropical and Subtropical Aquaculture (CTSA), The Oceanic Institute, Waimanalo, Hawaii, USA. 59 pp.
- Emery A.R. 1978. The basis of fish community structure: marine and freshwater comparisons. *Environmental Biology of Fishes* 3(1): 33-47.
- English C., C. Wilkinson and V. Baker 1997. Survey manual for tropical marine resources. 2<sup>nd</sup> edition. Australian Institute of Marine Science, Townsville. 390 pp.
- Epstein N., R.P.M. Bak and B. Rinkevich 2001. Strategies for Gardening Denuded Coral Reef Areas: The Applicability of Using Different Types of Coral Material for Reef Restoration. *Restoration Ecology* 9(4): 432-442.
- Erdmann M.V. 1998. Destructive fishing practices in the Pulau Seribu archipelago. In: Soemodihardjo S. (ed.) 1998. *Proceedings of the Coral Reef Evaluation Workshop, Pulau Seribu, Jakarta, Indonesia, October 1998*. UNESCO, Indonesian Institute of Sciences (LIPI), Research and Development Center for Oceanology: 84-89.
- Erdmann M.V. 2002. Perspective: the WAR on destructive fishing practices. *SPC Live Reef Fish Information Bulletin* 10: 17-18.
- Everitt B. 1978. Graphical techniques for multivariate data. Heinemann, London, UK. 117 pp.
- Everitt B. 1980. Cluster analysis, 2<sup>nd</sup> edition. Heinemann, London, UK. 136 pp.
- Fadlallah Y.H. 1983. Sexual Reproduction, Development and Larval Biology in Scleractinian Corals. A Review. *Coral Reefs* 2(3): 129-150.
- Faith D.P., P.R. Minchin and L. Belbin 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69(1-3): 57-68.
- FAO 2006. Yearbook of Fishery Statistics – Capture Production 2004. FAO, Rome, Vol. 98/1. 560 pp.
- Feeley D.A., G.R. Almany, G.P. Jones and M.I. McCormick 2007. Coral degradation and the structure of tropical reef fish communities. *Marine Ecology Progress Series* 333: 243-248.
- Feely R.A., C.L. Sabine, K. Lee, W. Berelson, J. Kleypas, V.J. Fabry and F.J. Millero 2004. Impact of anthropogenic CO<sub>2</sub> on the CaCO<sub>3</sub> system in the oceans. *Science* 305: 362-366.
- Ferreira C.E.L., J.E.A. Gonçalves and R. Coutinho 2001. Community structure of fishes and habitat complexity on a tropical rocky shore. *Environmental Biology of Fishes* 61(4): 353-369.

- Ferse S.C.A. 2004. Growing corals in an ocean-based nursery: The use of cages. MSc Thesis, Zentrum für Marine Tropenökologie (ZMT), University of Bremen. 64 pp.
- Ferse S.C.A. and S.B.C. Romatzki 2006. Effects of an electric field on the growth and survival of two *Acropora* species. Abstract. ISRS European Meeting, 19-22 September 2006, Bremen. Programme and Abstracts: 279.
- Field J.G., K.R. Clarke and R.M. Warwick 1982. A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series* 8: 37-52.
- Fitzhardinge R.C. 1985. Spatial and temporal variability in coral recruitment in Kaneohe Bay (Oahu, Hawaii). *Proceedings of the 5<sup>th</sup> International Coral Reef Congress* 4: 373-378.
- Fitzhardinge R.C. and J.H. Bailey-Brock 1989. Colonization of artificial reef materials by corals and other sessile organisms. *Bulletin of Marine Science* 44: 567-579.
- Fonseca C.R. and G. Ganade 2001. Species functional redundancy, random extinction and the stability of ecosystems. *Journal of Ecology* 89(1): 118-125.
- Fowler A.J. 1990. Spatial and temporal patterns of distribution and abundance of chaetodontid fishes at One Tree Reef, southern GBR. *Marine Ecology Progress Series* 64: 39-53.
- Fox H.E. 2004. Coral recruitment in blasted and unblasted sites in Indonesia: assessing rehabilitation potential. *Marine Ecology Progress Series* 269: 131-139.
- Fox H.E., J.S. Pet and R. Dahuri 2001. Enhanced Coral Reef Recovery After Destructive Fishing Practices: Initial Results in Komodo National Park. *Indonesian Journal of Coastal and Marine Resources (Jurnal Pesisir dan Lautan)* 3: 36-44.
- Fox H.E., P.J. Mous, J.S. Pet, A.H. Muljadi and R.L. Caldwell 2005. Experimental assessment of coral reef rehabilitation following blast fishing. *Conservation Biology* 19(1): 98-107.
- Franklin H., C.A. Muando and U. Lindahl 1998. Coral culturing and temporal recruitment patterns in Zanzibar, Tanzania. *Ambio* 27(8): 651-655.
- Freytag I. 2001. Growth and mortality of *Acropora nobilis* (Anthozoa: Scleractinia) fragments in shallow waters of the Seribu Islands, Indonesia, using different attachment methods. MSc Thesis, Zentrum für Marine Tropenökologie (ZMT), University of Bremen. 81 pp.
- Friedlander A.M. and J.D. Parrish 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology* 224: 1-30.
- Friedlander A.M., E.K. Brown, P.L. Jokiel, W.R. Smith and K.S. Rodgers 2003. Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs* 22(3): 291-305.
- Froese, R. and D. Pauly (eds.) 2007. FishBase. World Wide Web electronic publication. <http://www.fishbase.org>, version (08/2007).
- Gabrie C., M. Porcher and M. Masson 1985. Dredging in French Polynesian coral reefs: towards a general policy of resource exploitation and site development. *Proceedings of the 5<sup>th</sup> International Coral Reef Congress* 4: 271-277.
- Galzin R., S. Planes, V. Dufour and B. Salvat 1994. Variation in diversity of coral reef fish between French Polynesian atolls. *Coral Reefs* 13(3): 175-180.
- Garpe K.C. and M.C. Öhman 2003. Coral and fish distribution patterns in Mafia Island Marine Park, Tanzania: fish-habitat interactions. *Hydrobiologia* 498(1-3): 191-211.
- Gattuso J.-P. and R.W. Buddemeier 2000. Calcification and CO<sub>2</sub>. *Nature* 407: 311-312.

- GBRMPA 1978. Workshop on reef fish assessment and monitoring. GBRMPA Workshop Series 2. Great Barrier Reef Marine Park Authority, Townsville, Australia. 64 pp.
- Gittings S.R., T.J. Bright, A. Choi and R.R. Barnett 1988. The recovery process in a mechanically damaged coral reef community: recruitment and growth. *Proceedings of the 6<sup>th</sup> International Coral Reef Symposium* 2: 225-230.
- Gladfelter W.B. and E.H. Gladfelter 1978. Fish community structure as a function of habitat structure on West Indian patch reefs. *Revista de Biología Tropical* 26, Supplement 1: 65-84.
- Gladfelter W.B., J.C. Ogden and E.H. Gladfelter 1980. Similarity and diversity among coral reef fish communities: a comparison between Tropical Western Atlantic (Virgin Islands) and Tropical Central Pacific (Marshall Islands) patch reefs. *Ecology* 61(5): 1156-1168.
- Glassom D. and N.E. Chadwick 2006. Recruitment, growth and mortality of juvenile corals at Eilat, northern Red Sea. *Marine Ecology Progress Series* 318: 111-122.
- Glynn P.W. 1990. Feeding ecology of selected coral-reef macroconsumers: patterns and effects on coral community structure. In: Dubinsky Z. (ed.) 1990. *Ecosystems of the World, Volume 25 — Coral Reefs*. Elsevier Science, New York and Amsterdam: 365-400.
- Goldman B. and F.H. Talbot 1976. Aspects of the ecology of coral reef fishes. In: Jones O.A. and R. Endean (eds.) 1976. *Biology and Geology of Coral Reefs. Volume III: Biology* 2. Academic Press, New York and London: 125-154.
- Gomez E.D., W.Y. Licuanan and V.V. Hilomen 1988. Reef fish-benthos correlations in the northwestern Philippines. *Proceedings of the 6<sup>th</sup> International Coral Reef Symposium* 3: 245-249.
- Goreau T.J., W. Hilbertz and A.A.A. Hakeem 2000. Increased coral and fish survival on mineral accretion reef structures in the Maldives after the 1998 bleaching event. *Abstracts, 9<sup>th</sup> International Coral Reef Symposium, 23-27 October 2000, Bali*: 264.
- Gottfried M. and M.R. Roman 1983. Ingestion and incorporation of coral-mucus detritus by reef zooplankton. *Marine Biology* 72(3): 211-218.
- Gratwicke B. and M.R. Speight 2005a. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology* 66(3): 650-667.
- Gratwicke B. and M.R. Speight 2005b. Effects of habitat complexity on Caribbean marine fish assemblages. *Marine Ecology Progress Series* 292: 301-310.
- Green A.L. 1996. Spatial, temporal and ontogenetic patterns of habitat use by coral reef fishes (family Labridae). *Marine Ecology Progress Series* 133: 1-11.
- Green E. 2003. International trade in marine aquarium species: using the Global Marine Aquarium Database. In: Cato J.C. and C.L. Brown (eds.) 2003. *Marine Ornamental Species: collection, culture, and conservation*. Iowa State Press, Ames, Iowa, USA: 31-47.
- Green E.P. and F. Shirley 1999. The global trade in coral. World Conservation Monitoring Center, World Conservation Press, Cambridge, UK. 70 pp.
- Greene L.E. and J.M. Shenker 1993. The effects of human activity on the temporal variability of coral reef fish assemblages in the Key Largo National Marine Sanctuary. *Aquatic Conservation: Marine and Freshwater Ecosystems* 3(3): 189-205.
- Grigg R.W. 1994. Effects of sewage discharge, fishing pressure and habitat complexity on coral ecosystems and reef fishes in Hawaii. *Marine Ecology Progress Series* 103: 25-34.
- Grossman G.D., G.P. Jones and W.J. Seaman, Jr. 1997. Do artificial reefs increase regional fish production? A review of existing data. *Fisheries* 22(4): 17-23.

- Grottoli-Everett A.G. and G.M. Wellington 1997. Fish predation on the scleractinian coral *Madracis mirabilis* controls its depth distribution in the Florida Keys, USA. *Marine Ecology Progress Series* 160: 291-293.
- Grove R.S. and C.J. Sonu 1985. Fishing reef planning in Japan. In: D'Itri F.M. (ed.) 1985. *Artificial reefs: marine and freshwater applications*. Lewis Publishing Inc., Chelsea, Michigan, USA: 187-251.
- Guest J.R., L.M. Chou, A.H. Baird and B.P.L. Goh 2002. Multispecific, synchronous coral spawning in Singapore. *Coral Reefs* 21(4): 422-423.
- Guzmán H.M. 1991. Restoration of coral reefs in Pacific Costa Rica. *Conservation Biology* 5(2): 189-195.
- Harii S., H. Kayanne, H. Takigawa, T. Hayashibara and M. Yamamoto 2002. Larval survivorship, competency periods and settlement of two brooding corals, *Heliopora coerulea* and *Pocillopora damicornis*. *Marine Biology* 141(1): 39-46.
- Harriott V.J. 1999. Coral growth in subtropical eastern Australia. *Coral Reefs* 18(3): 281-291.
- Harriott V.J. and D.A. Fisk 1987. A comparison of settlement plate types for experiments on the recruitment of scleractinian corals. *Marine Ecology Progress Series* 37: 201-208.
- Harriott V.J. and D. A. Fisk 1988a. Accelerated Regeneration of Hard Corals: A Manual for Coral Reef Users and Managers. Technical Memorandum 16, Great Barrier Reef Marine Park Authority, Townsville, Australia. 42 pp.
- Harriott V.J. and D.A. Fisk 1988b. Coral Transplantation as a reef management option. *Proceedings of the 6<sup>th</sup> International Coral Reef Symposium* 2: 375-379.
- Harrison P.L. and C.C. Wallace 1990. Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky Z. (ed.) 1990. *Ecosystems of the World, Volume 25 — Coral Reefs*. Elsevier Science, New York and Amsterdam: 133-207.
- Harrison P.L., R.C. Babcock, G.D. Bull, J.K. Oliver, C.C. Wallace and B.L. Willis 1984. Mass spawning in tropical reef corals. *Science* 223: 1186-1189.
- Hart A.M., D.W. Klumpp and G.R. Russ 1996. Response of herbivorous fishes to crown-of-thorns starfish *Acanthaster planci* outbreaks. II. Density and biomass of selected species of herbivorous fish and fish-habitat correlations. *Marine Ecology Progress Series* 132: 21-30.
- Harvell C.D., C.E. Mitchell, J.R. Ward, S. Altizer, A.P. Dobson, R.S. Ostfeld and M.D. Samuel 2002. Climate warming and disease risks for terrestrial and marine biota. *Science* 296: 2158-2162.
- Harvey E., D. Fletcher and M. Shortis 2001. A comparison of the precision and accuracy of estimates of reef-fish length determined visually by divers with estimates produced by a stereo-video system. *Fishery Bulletin* 99(1): 63-71.
- Hatcher B.G., R.E. Johannes and A.I. Robertson 1989. Review of research relevant to the conservation of shallow tropical marine ecosystems. *Oceanography and Marine Biology Annual Review* 27: 337-414.
- Heeger T. and F. Sotto (eds.) 2000a. *Coral Farming: A Tool for Reef Rehabilitation and Community Ecotourism*. German Ministry of Environment (BMU) and German Technical Cooperation, Tropical Ecology Program (GTZ-TÖB), Manila, Philippines. 94 pp.
- Heeger T. and F. Sotto 2000b. Coral farming: inexpensive rehabilitation tool and a livelihood option for fisherfolk. *Reef Encounter* 27: 18-19.
- Heeger T.M., M. Cashman and F. Sotto 1999. Coral farming as alternative livelihood, sustainable natural resource management and coral reef rehabilitation. *Proceedings of Oceanology International 99 Pacific Rim, Spearhead Exhibitions Ltd., New Malden, Surrey, UK*: 171-185.
- Helfman G.S. 1978. Patterns of community structure in fishes: summary and overview. *Environmental Biology of Fishes* 3(1): 129-148.

- Heyward A.J. and J.D. Collins 1985. Fragmentation in *Montipora ramosa*: the genet and ramet concept applied to a reef coral. *Coral Reefs* 4(1): 35-40.
- Hiatt R.W., D.W. Strasburg 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecological Monographs* 30(1): 65-127.
- Highsmith R.C. 1982. Reproduction by Fragmentation in Corals. *Marine Ecology Progress Series* 7: 207-226.
- Hilbertz W.H. 1992. Solar generated building material from seawater as a sink for carbon. *Ambio* 21: 126-129.
- Hilbertz W.H., D. Fletcher and C. Krausse 1977. Mineral accretion technology: applications for architecture and aquaculture. *Industrial Forum* 8: 75-84.
- Hixon M.A. 1991. Predation as a process structuring coral reef fish communities. In: Sale P.F. (ed.) 1991. *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego and London: 475-508.
- Hixon M.A. 1998. Population dynamics of coral-reef fishes: controversial concepts and hypotheses. *Australian Journal of Ecology* 23(3): 192-201.
- Hixon M.A. and J.P. Beets 1989. Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. *Bulletin of Marine Science* 44(2): 666-680.
- Hoegh-Guldberg O., P.J. Mumby, A.J. Hooten, R.S. Steneck, P. Greenfield, E. Gomez, C.D. Harvell, P.F. Sale, A.J. Edwards, K. Caldeira, N. Knowlton, C.M. Eakin, R. Iglesias-Prieto, N. Muthiga, R.H. Bradbury, A. Dubi and M.E. Hatziolos 2007. Coral reefs under rapid climate change and ocean acidification. *Science* 318: 1737-1742.
- Hoeksema B.W. 2007. Delineation of the Indo-Malayan centre of maximum marine biodiversity: the coral triangle. In: Renema W. (ed.) 2007. *Biogeography, Time, and Place: Distributions, Barriers, and Islands*. Springer, Dordrecht, Netherlands: 117-178.
- Holbrook S.J., G.E. Forrester and R.J. Schmitt 2000. Spatial patterns in abundance of a damselfish reflect availability of suitable habitat. *Oecologia* 122(1): 109-120.
- Holling C.S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4: 1-23.
- Hope A.C.A. 1968. A simplified Monte Carlo significance test procedure. *Journal of the Royal Statistical Society. Series B (Methodological)* 30(3): 582-598.
- Hourigan T.F., T.C. Tricas and E.S. Reese 1988. Coral reef fishes as indicators of environmental stress in coral reefs. In: Soule D.F. and G.S. Kleppel (eds.) 1988. *Marine Organisms as Indicators*. Springer Verlag, New York: 107-135.
- Hudson J.H. and R. Diaz 1988. Damage survey and restoration of M/V Wellwood grounding site, Molasses Reef, Key Largo National Marine Sanctuary, Florida. *Proceedings of the 6<sup>th</sup> International Coral Reef Symposium* 2: 231-236.
- Hudson J.H. and W.B. Goodwin 1997. Restoration and growth rate of hurricane pillar coral (*Dendrogyra cylindricus*) in the Key Largo National Marine Sanctuary, Florida. *Proceedings of the 8<sup>th</sup> International Coral Reef Symposium* 1: 567-570.
- Hudson J.H. and W.B. Goodwin 2001. Assessment of vessel grounding injury to coral reef and seagrass habitats in the Florida Keys National Marine Sanctuary, Florida: protocols and methods. *Bulletin of Marine Science* 69(2): 509-516.
- Hudson J.H., D.M. Robin, J.T. Tilmant and J.W. Wheaton 1990. Building a coral reef in SE Florida: combining technology with aesthetics. *Bulletin of Marine Science* 44(2): 1067.
- Hughes T.P. 1985. Life histories and population dynamics of early successional corals. *Proceedings of the 5<sup>th</sup> International Coral Reef Congress* 4: 101-105.

IFM Geomar 2007. Online Map Creation, World Wide Web electronic resource. <http://www.aquarius.ifm-geomar.de/omc> (10/2007).

Ino T. 1974. Historical review of artificial reef activities in Japan. In: Colunga L. and R. Stone (eds.) 1974. *Proceedings: Artificial Reef Conference*. Texas A&M University, TAMU-SG-74-103: 21-23.

Jaap W.C. 2000. Coral reef restoration. *Ecological Engineering* 15(3-4): 345-364.

Jennings S. and N.V.C. Polunin 1997. Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities. *Coral Reefs* 16(2): 71-82.

Jennings S., D.P. Boullé and N.V.C. Polunin 1996. Habitat correlatives of the distribution and biomass of Seychelles' reef fishes. *Environmental Biology of Fishes* 46(1): 15-25.

Johnson D.W. 2007. Habitat complexity modifies post-settlement mortality and recruitment dynamics of a marine fish. *Ecology* 88(7): 1716-1725.

Jokiel P.L., S.P. Kolinski, J. Naughton and J.E. Maragos 2006. Review of coral reef restoration and mitigation in Hawaii and the U.S.-affiliated Pacific Islands. In: Precht W.F. 2006. *Coral Reef Restoration Handbook*. CRC Press/Taylor and Francis, Boca Raton, Florida, USA: 271-290.

Jones G.P. 1991. Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. In: Sale P.F. (ed.) 1991. *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego and London: 295-328.

Jones G.P. and U.L. Kaly 1996. Criteria for selecting marine organisms in biomonitoring studies. In: Schmitt R.J. and C.W. Osenberg (eds.) 1996. *Detecting Ecological Impacts. Concepts and Applications in Coastal Habitats*. Academic Press, San Diego and London: 29-48.

Jones G.P., M.I. McCormick, M. Srinivasan and J.V. Eagle 2004. Coral decline threatens fish diversity in marine reserves. *Proceedings of the National Academy of Science USA* 101(21): 8251-8253.

Kalbfleisch J.D. and R.L. Prentice 1980. The Statistical Analysis of Failure Time Data. John Wiley and Sons, New York, USA. 321 pp.

Kaufman L.S. 1983. Effects of Hurricane Allen on reef fish assemblages near Discovery Bay, Jamaica. *Coral Reefs* 2(1): 43-47.

Kaufman L.S. 2006. If you build it, will they come? Toward a concrete basis for coral reef gardening. In: Precht W.F. 2006. *Coral Reef Restoration Handbook*. CRC Press/Taylor and Francis, Boca Raton, Florida, USA: 119-142.

Kawasaki H., M. Sano and T. Shibuno 2003. The relationship between habitat physical complexity and recruitment of the coral reef damselfish, *Pomacentrus amboinensis*: an experimental study using small-scale artificial reefs. *Ichthyological Research* 50(1): 73-77.

Kendall M.G. 1970. Rank correlation methods, 4<sup>th</sup> edition. Griffin, London, UK. 202 pp.

Keough M.J. and P.T. Raimondi 1995. Responses of settling invertebrate larvae to bioorganic films: effects of different types of films. *Journal of Experimental Marine Biology and Ecology* 185(2): 235-253.

Khalaf M.A. and M. Kochzius 2002. Community structure and biogeography of shore fishes in the Gulf of Aqaba, Red Sea. *Helgoland Marine Research* 55(4): 252-284.

Kingsford M.J. and A.B. MacDiarmid 1988. Interrelations between planktivorous reef fish and zooplankton in temperate waters. *Marine Ecology Progress Series* 48: 103-117.

Kinzie R.A. III and R.H. Snider 1978. A simulation study of coral reef survey methods. In: Stoddart D.R. and R.E. Johannes (eds.) 1978. *Coral Reefs: Research Methods*. UNESCO Monographs on Oceanographic Methodology 5: 231-250.

- Kleypas J.A., R.W. Buddemeier, D. Archer, J.-P. Gattuso, C. Langdon and B.N. Opdyke 1999. Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* 284: 118-120.
- Knop D. 2003. Korallenfarmen – Riffsschutz der Zukunft? In: Knop D. 2003. *Riffaquaristik für Einsteiger. Preiswerte Technik – pflegeleichte Tiere*. 3. überarbeitete und ergänzte Auflage. Dähne Verlag, Ettlingen, Germany: 188-193.
- Kojis B.L. and N.J. Quinn 1981. Factors to consider when transplanting hermatypic corals to accelerate regeneration of damaged coral reefs. *Proceedings of the Conference on Environmental Engineering, Townsville 8-10 July 1981*. Institution of Engineers, Barton, Australia: 183-187.
- Kojis B.L. and N.J. Quinn 2001. The importance of regional differences in hard coral recruitment rates for determining the need for coral restoration. *Bulletin of Marine Science* 69(2): 967-974.
- Kruskal J.B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29: 1-27.
- Kuiter R.H. and T. Tonozuka 2004. Pictorial guide to: Indonesian Reef Fishes. Parts 1-3. PT Dive & Dive's, Sanur, Bali, Indonesia. 893 pp.
- Kulbicki M. 1998. How the acquired behaviour of commercial reef fishes may influence the results obtained from visual censuses. *Journal of Experimental Marine Biology and Ecology* 222(1-2): 11-30.
- Ladd H.S. 1977. Types of coral reefs and their distribution. In: Jones O.A. and R. Endean (eds.) 1977. *Biology and Geology of Coral Reefs. Volume IV: Geology 2*. Academic Press, New York and London: 1-19.
- Lam K.K.Y. 2003. Coral recruitment onto an experimental pulverized fuel ash-concrete artificial reef. *Marine Pollution Bulletin* 46(5): 642-653.
- Lassig B.R. 1977. Socioecological strategies adopted by obligate coral dwelling fishes. *Proceedings of the Third International Coral Reef Symposium* 1: 565-570.
- Lecchini D., M. Adjeroud, M.S. Pratchett, L. Cadoret and R. Galzin 2003. Spatial structure of coral reef fish communities in the Ryukyu Islands, southern Japan. *Oceanologica Acta* 26(5-6): 537-547.
- Leis J.M. and M.I. McCormick 2006. The biology, behaviour and ecology of the pelagic, larval stage of coral reef fishes. In: Sale P.F. (ed) 2006 *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, New York, USA: 171-200.
- Leis J.M., B.M. Carson-Ewart, A.C. Hay and D.H. Cato 2003. Coral-reef sounds enable nocturnal navigation by some reef-fish larvae in some places and at some times. *Journal of Fish Biology* 63(3): 724-737.
- Letourneau Y. 1996a. Dynamics of fish communities on Reunion fringing reefs, Indian Ocean. I. Patterns of spatial distribution. *Journal of Experimental Marine Biology and Ecology* 195(1): 1-30.
- Letourneau Y. 1996b. Dynamics of fish communities on Reunion fringing reefs, Indian Ocean. II. Patterns of temporal fluctuations. *Journal of Experimental Marine Biology and Ecology* 195(1): 31-52.
- Lewis A.R. 1997a. Recruitment and post-recruitment immigration affect the local population size of coral reef fishes. *Coral Reefs* 16(3): 139-149.
- Lewis A.R. 1997b. Effects of experimental coral disturbance on the structure of fish communities on large patch reefs. *Marine Ecology Progress Series* 161: 37-50.
- Lewontin R.C. 1969. The meaning of stability. *Brookhaven Symposium in Biology* 22: 13-24.
- Liddell W.D. and S.L. Ohlhorst 1987. Patterns of reef community structure, north Jamaica. *Bulletin of Marine Science* 40: 311-329.
- Lindahl U. 1998. Low-tech rehabilitation of degraded coral reefs through transplantation of staghorn corals. *Ambio* 27(8): 645-650.

- Lindahl U. 2003. Coral reef rehabilitation through transplantation of staghorn corals: effects of artificial stabilization and mechanical damages. *Coral Reefs* 22(3): 217-223.
- Lindahl U., M.C. Öhman and C.K. Schelten 2001. The 1997/1998 mass mortality of corals: effects on fish communities on a Tanzanian coral reef. *Marine Pollution Bulletin* 42(2): 127-131.
- Lindberg W.J. 1997. Can science resolve the attraction-production issue? *Fisheries* 22(4): 10-13.
- Lingo M.E. and S.T. Szedlmayer 2006. The influence of habitat complexity on reef fish communities in the northeastern Gulf of Mexico. *Environmental Biology of Fishes* 76(1): 71-80.
- Lirman D. 1999. Reef fish communities associated with *Acropora palmata*: relationships to benthic attributes. *Bulletin of Marine Science* 65(1): 235-252.
- Lucas H.A. and G.A.F. Seber 1977. Estimating coverage and particle density using the line intercept method. *Biometrika* 64: 618-622.
- Luckhurst B.E. and K. Luckhurst 1978. Analysis of the influence of substrate variables on coral reef fish communities. *Marine Biology* 49(4): 317-323.
- MacArthur R.H. and E.O. Wilson 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA. 203 pp.
- Magurran A.E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey, USA. 179 pp.
- Mantel N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research* 27: 209-220.
- Maragos J.E. 1974. Coral transplantation: a method to create, preserve and manage coral reefs. *Sea Grant Advising Report SEA-GRANT-AR.74-03-COR-MAR-14*. University of Hawaii, Honolulu. 30 pp.
- Maragos J.E. 1992. Restoring Coral Reefs with Emphasis on Pacific Reefs. In: Thayer G.W. (ed.) 1992. *Restoring the Nation's Marine Environment*. National Oceanic and Atmospheric Administration. College Park, Maryland: 141-221.
- Marsh L.M. 1993. The occurrence and growth of *Acropora* in extra-tropical waters off Perth, Western Australia. *Proceedings of the 7<sup>th</sup> International Coral Reef Symposium* 2: 1233-1238.
- Mayor A.G. 1924. Growth-rate of Samoan corals. *Papers of the Department of marine Biology, Carnegie Institution Washington* 340(19): 51-72.
- MBA International 1993. Coral transplantation, Palau Pacific Resort, a pilot-demonstration project PODCO No. 2156. Final report prepared for the U.S. Army Corps of Engineers, Honolulu Engineer District, Fort Shafter, HI, USA. No page numbers available.
- McClanahan T.R., N.A.J. Graham, J. Maina, P. Chabane, J.H. Bruggemann and N.V.C. Polunin 2007. Influence of instantaneous variation on estimates of coral reef fish populations and communities. *Marine Ecology Progress Series* 340: 221-234.
- McCormick M.I. 1994. Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. *Marine Ecology Progress Series* 112: 87-96.
- McManus J.W. 1985. Marine speciation, tectonics and sea-level changes in Southeast Asia. *Proceedings of the 5<sup>th</sup> International Coral Reef Congress* 4: 133-138.
- McManus J.W. 1997. Tropical marine fisheries and the future of coral reefs: A brief review with emphasis on Southeast Asia. *Coral Reefs* 16, Supplement: 121-127.
- McManus J.W., R.I. Miclat and V.P. Palaganas 1982. Coral and fish community structure of Sombrero Island, Batangas, Philippines. *Proceedings of the 4<sup>th</sup> International Coral Reef Symposium* 2: 271-280.

- Miller M.W. 2002. Using ecological processes to advance artificial reef goals. *ICES Journal of Marine Science* 59: S27-S31.
- Miller M.W. and J. Barimo 2001. Assessment of juvenile coral populations at two reef restoration sites in the Florida Keys National Marine Sanctuary: indicators of success? *Bulletin of Marine Science* 69(2): 395-405.
- Miller S.L., G.B. McFall and A.W. Hulbert (eds.) 1993. Guidelines and recommendations for coral reef restoration in the Florida Keys National Marine Sanctuary. Workshop Report. National Undersea Research Center, University of North Carolina, Wilmington, USA. 38 pp.
- Molles M.C., Jr. 1978. Fish species diversity on model and natural reef patches: experimental insular biogeography. *Ecological Monographs* 48(3): 289-305.
- Montgomery J.C., N. Tolimieri and O.S. Haine 2001. Active habitat selection by pre-settlement reef fishes. *Fish and Fisheries* 2(3): 261-277.
- Montgomery W.L. 1990. Zoogeography, behavior and ecology of coral-reef fishes. In: Dubinsky Z. (ed.) 1990. *Ecosystems of the World, Volume 25 — Coral Reefs*. Elsevier Science, New York and Amsterdam: 329-364.
- Moore M. and M. Erdmann 2002. EcoReefs: a new tool for coral reef restoration. *Conservation in Practice* 3: 41-44.
- Morse D.E., N. Hooker, A.N.C. Morse and R.A. Jensen 1988. Control of larval metamorphosis and recruitment in sympatric agariciid corals. *Journal of Experimental Marine Biology and Ecology* 116(3): 193-217.
- Mottet M.G. 1985. Enhancement of the marine environment for fisheries and aquaculture in Japan. In: D'Itri F.M. (ed.) 1985. *Artificial reefs: marine and freshwater applications*. Lewis Publishing Inc., Chelsea, Michigan, USA: 13-112.
- MSN 2008. Monthly averages of air temperatures at Dr. Sam Ratulangi Airport, Manado. [http://weather.msn.com/monthly\\_averages.aspx?&wealocations=wc%3aIDXX0031&setunit=C](http://weather.msn.com/monthly_averages.aspx?&wealocations=wc%3aIDXX0031&setunit=C) (03/2008).
- Mundy C.N. and R.C. Babcock 1998. Role of light intensity and spectral quality in coral settlement: implications for depth-dependent settlement? *Journal of Experimental Marine Biology and Ecology* 223(2): 235-255.
- Mundy C. and R. Babcock 2000. Are vertical distribution patterns of scleractinian corals maintained by pre- or post-settlement processes? A case study of three contrasting species. *Marine Ecology Progress Series* 198: 109-119.
- Muñoz-Chagín R.F. 1997. Coral transplantation program in the Paraiso coral reef, Cozumel Island, Mexico. *Proceedings of the 8<sup>th</sup> International Coral Reef Symposium* 2: 2075-2078.
- Munro J.L. 1984. Yields from coral reef fisheries. *Fishbyte* 2: 13-15.
- Munro J.L. and D.McB. Williams 1985. Assessment and management of coral reef fisheries: biological, environmental and socio-economical aspects. *Proceedings of the 5<sup>th</sup> International Coral Reef Congress* 4: 545-581.
- Myers R.F. 1999. Micronesian Reef Fishes: A practical guide to the identification of the inshore marine fishes of the tropical Central and Western Pacific, 3<sup>rd</sup> revised and expanded edition. Coral Graphics, Barrigada, Guam. 331 pp.
- Myrberg A.A. and L.A. Fuiman 2006. The sensory world of coral reef fishes. In: Sale P.F. (ed) 2006. *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, New York, USA: 123-148.
- Nagelkerken I., S. Bouma, S. van den Akker and R.P.M. Bak 2000. Growth and survival of unattached *Madracis mirabilis* fragments transplanted to different reef sites, and the implication for reef rehabilitation. *Bulletin of Marine Science* 66(2): 497-505.

- Nanami A., M. Nishihira, T. Suzuki and H. Yokochi 2005. Species-specific habitat distribution of coral reef fish assemblages in relation to habitat characteristics in an Okinawan coral reef. *Environmental Biology of Fishes* 72(1): 55-65.
- Neudecker S. 1977. Transplant experiments to test the effect of fish grazing on coral distribution. *Proceedings of the Third International Coral Reef Symposium*: 317-323.
- Neudecker S. 1979. Effects of grazing and browsing fishes on the zonation of corals in Guam. *Ecology* 60(4): 666-672.
- Neudecker S. 1982. Growth and survival of scleractinian corals exposed to thermal effluents at Guam. *Proceedings of the 4<sup>th</sup> International Coral Reef Symposium* 1: 173-180.
- Newman H. and C.S. Chuan 1994. Transplanting a reef: a Singapore community project. *Coastal Management in Tropical Asia* 3: 11-14.
- O'Brien Shoup C. and A. Gaski 1995. Trade in CITES-listed hard corals, 1989-1993: a preliminary report. TRAFFIC USA, Washington, D.C. 14 pp.
- Öhman M.C. and A. Rajasuriya 1998. Relationships between habitat structure and fish communities on coral and sandstone reefs. *Environmental Biology of Fishes* 53(1): 19-31.
- Öhman M.C., A. Rajasuriya and E. Ólafsson 1997. Reef fish assemblages in north-western Sri Lanka: distribution patterns and influences of fishing practices. *Environmental Biology of Fishes* 49(1): 45-61.
- Ogden J.C. and J.P. Ebersole 1981. Scale and community structure of coral reef fishes: a long-term study of a large artificial reef. *Marine Ecology Progress Series* 4: 97-103.
- Ohlhorst S.L., W.D. Liddell, R.J. Taylor and J.M. Taylor 1988. Evaluation of reef census techniques. *Proceedings of the 6<sup>th</sup> International Coral Reef Symposium* 2: 319-324.
- Okubo N., T. Motokawa and M. Omori 2007. When fragmented coral spawn? Effect of size and timing on survivorship and fecundity of fragmentation in *Acropora formosa*. *Marine Biology* 151(1): 353-363.
- Oliver J.K., B.E. Chalker and W.C. Dunlap 1983. Bathymetric adaptations of reef-building corals at Davies Reef, Great Barrier Reef, Australia. I. Long-term growth responses of *Acropora formosa* (Dana 1846). *Journal of Experimental Marine Biology and Ecology* 73(1): 11-35.
- Omori M. and S. Fujiwara (eds.) 2004. Manual for restoration and remediation of coral reefs. Nature Conservation Bureau. Ministry of the Environment, Japan. 84 pp.
- Ortiz-Prosper A.L., A. Bowden-Kerby, H. Ruiz, O. Tirado, A. Cabán, G. Sanchez and J.C. Crespo 2001. Planting small massive corals on small artificial concrete reefs or dead coral heads. *Bulletin of Marine Science* 69(2): 1047-1051.
- Pamintuan I.S. 1994. Successional trends of artificial reef communities in Bolinao, Northwestern Pangasinan. MSc Thesis, University of the Philippines.
- Pamintuan I.S., P.M. Aliño and E.D. Gomez 1994a. Enhancement of fish recruitment through coral transplantation. Abstract. In: Sudara S., C.R. Wilkinson and L.M. Chou (eds.) 1994. *Proceedings of the Third ASEAN-Australia Symposium on Living Coastal Resources, Volume 2: Research Papers*. Chulalongkorn University, Bangkok, Thailand: 235.
- Pamintuan I.S., P.M. Aliño, E.D. Gomez and R.N. Rollon 1994b. Early successional patterns of invertebrates in artificial reefs established at clear and silty areas in Bolinao, Pangasinan, Northern Philippines. *Bulletin of Marine Science* 55(2-3): 867-877.
- Patton W.K. 1976. Animal associates of living reef corals. In: Jones O.A. and R. Endean (eds.) 1976. *Biology and Geology of Coral Reefs. Volume III: Biology* 2. Academic Press, New York and London: 1-36.
- Paxton J.R. 1995. Habitats and adaptations. In: Paxton J.R. and W.N. Eschmeyer (eds) 1995. *Encyclopedia of Fishes*. Academic Press, New York, USA: 32-41.

- Pet-Soede C., H.S.J. Cesar and J.S. Pet 1999. An economic analysis of blast fishing on Indonesian coral reefs. *Environmental Conservation* 26(2): 83-93.
- Pet-Soede C., W.L.T. van Densen, J.S. Pet and M.A.M. Machiels 2001. Impact of Indonesian coral reef fisheries on fish community structure and the resultant catch composition. *Fisheries Research* 51(1): 35-51.
- Pet-Soede L., H.S.J. Cesar and J.S. Pet 2000. Blasting away: the economics of blast fishing on Indonesian coral reefs. In: Cesar H.S.J. (ed.) 2000. *Collected Essays on the Economics of Coral Reefs*. CORDIO, Kalmar University, Kalmar, Sweden: 77-84.
- Pickering H., D. Whitmarsh and A. Jensen 1998. Artificial Reefs as a Tool to Aid Rehabilitation of Coastal Ecosystems: Investigating the Potential. *Marine Pollution Bulletin* 37(8-12): 505-514.
- Pielou E.C. 1975. Ecological Diversity. John Wiley & Sons, Inc., New York, USA. 165 pp.
- Plucer-Rosario G.P. and R.H. Randall 1987. Preservation of rare coral species by transplantation: an examination of their recruitment and growth. *Bulletin of Marine Science* 41: 585-593.
- Poernomo A., S. Mardlijah, M.L. Linting, E.M. Amin and Widjopriono 2003. Ikan hias laut Indonesia. Penebar Swadaya, Depok, Jakarta, Indonesia. 182 pp.
- Porter J.W. and K.G. Porter 1977. Quantitative sampling of demersal plankton migrating from different coral reef substrates. *Limnology and Oceanography* 22(3): 553-556.
- Precht W.F. 2006. Coral Reef Restoration Handbook. CRC Press/Taylor and Francis, Boca Raton, Florida, USA. 363 pp.
- Putra S. and A. Cottrell 2000. Conflicts of coastal management in North Sulawesi. *Proceedings of the 9<sup>th</sup> International Coral Reefs Symposium* 2: 791-795.
- Randall J.E. 1963. An analysis of fish populations of artificial and natural reefs in the Virgin Islands. *Caribbean Journal of Science* 3: 31-47.
- Randall J.E. 1974. The effect of fishes on coral reefs. *Proceedings of the Second International Coral Reef Symposium* 1: 159-166.
- Ray R.D., G.D. Egbert and S.Y. Erofeeva 2005. A brief overview of tides in the Indonesian Seas. *Oceanography* 18(4): 74-79.
- Raymakers C. 1998. Imports of Indonesian Marine Products into the European Union 1990-1995. TRAFFIC Europe and WWF-NL. 91 pp.
- Raymundo L.J.H., A.P. Maypa and M.M. Luchavez 1999. Coral seeding as a technology for recovering degraded coral reefs in the Philippines. *Phuket Marine Biology Center Special Publication* 20: 81-92.
- Reef Ball Foundation 2007. <http://www.reefball.org> (02/2008).
- Reese E.S. 1977. Coevolution of corals and coral feeding fishes of the family Chaetodontidae. *Proceedings of the Third International Coral Reef Symposium*: 267-274.
- Reyes M.Z. and H.T. Yap 2001. Effect of artificial substratum material and resident adults on coral settlement patterns at Danjugan Island, Philippines. *Bulletin of Marine Science* 69(2): 559-566.
- Richman S., Y. Loya and L.B. Slobodkin 1975. The rate of mucus production by corals and its assimilation by the coral reef copepod *Acartia negligens*. *Limnology and Oceanography* 20(6): 918-923.
- Riegl B. 2001. Degradation of reef structure, coral and fish communities in the Red Sea by ship groundings and dynamite fisheries. *Bulletin of Marine Science* 69(2): 595-611.
- Rilov G. and Y. Benayahu 2000. Fish assemblage on natural versus vertical artificial reefs: the rehabilitation perspective. *Marine Biology* 136(5): 931-942.

- Rinkevich B. 1995. Restoration strategies for coral reefs damaged by recreational activities: The use of sexual and asexual recruits. *Restoration Ecology* 3(4): 241-251.
- Rinkevich B. 2005. Conservation of coral reefs through active restoration measures: recent approaches and last decade progress. *Environmental Science and Technology* 39(12): 4333-4342.
- Risk M.J. 1972. Fish diversity on a coral reef in the Virgin Islands. *Atoll Research Bulletin* 153: 1-6.
- Roberts C.M. and R.F.G. Ormond 1987. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Marine Ecology Progress Series* 41: 1-8.
- Roberts C.M., R.F.G. Ormond and A.R. Dawson Shepherd 1988. The usefulness of butterflyfishes as environmental indicators on coral reefs. *Proceedings of the 6<sup>th</sup> International Coral Reef Symposium* 2: 331-336.
- Roberts C.M., C.J. McClean, J.E.N. Veron, J.P. Hawkins, G.R. Allen, D.E. McAllister, C.G. Mittermeier, F.W. Schueler, M. Spalding, F. Wells, C. Vynne and T.B. Werner 2002. Marine Biodiversity Hotspots and Conservation Priorities for Tropical Reefs. *Science* 295: 1280-1284.
- Robertson D.R. 1998. Do coral-reef fish faunas have a distinctive taxonomic structure? *Coral Reefs* 17(2): 179-186.
- Rogers C.S. 1990. Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series* 62: 185-202.
- Russ G.R. 1991. Coral reef fisheries: effects and yields. In: Sale P.F. (ed.) 1991. *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego and London: 601-635.
- Russell B.C. 1975. The development and dynamics of a small artificial reef community. *Helgoländer wissenschaftliche Meeresuntersuchungen* 27(3): 298-312.
- Russel B.C., F.H. Talbot and S. Domm 1974. Patterns of colonization of artificial reefs by coral reef fishes. *Proceedings of the Second International Coral Reef Symposium* 1: 207-215.
- Russel B.C., F.N. Talbot, G.R.V. Anderson and B. Goldman 1978. Collection and sampling of reef fishes. In: Stoddart D.R. and R.E. Johannes (eds.) 1978. *Coral Reefs: Research Methods*. UNESCO Monographs on Oceanographic Methodology 5: 329-345.
- Sabater M.H. and H.T. Yap 2002. Growth and survival of coral transplants with and without electrochemical deposition of CaCO<sub>3</sub>. *Journal of Experimental Marine Biology and Ecology* 272(2): 131-146.
- Sabater M.G. and H.T. Yap 2004. Long-term effects of induced mineral accretion on growth, survival and corallite properties of *Porites cylindrica* Dana. *Journal of Experimental Marine Biology and Ecology* 311(2): 355-374.
- Sale P.F. 1977. Maintenance of high diversity in coral reef fish communities. *The American Naturalist* 111(978): 337-359.
- Sale P.F. 1978. Chance patterns of demographic change in population of territorial fish in coral rubble patches on Heron Reef. *Journal of Experimental Marine Biology and Ecology* 34(3): 233-244.
- Sale P.F. 1980a. The ecology of fishes on coral reefs. *Oceanography and Marine Biology Annual Review* 18: 367-421.
- Sale P.F. 1980b. Assemblages of fish on patch reefs – predictable or unpredictable? *Environmental Biology of Fishes* 5(3): 243-249.
- Sale P.F. 1991a. Reef fish communities: open nonequilibrium systems. In: Sale P.F. (ed.) 1991. *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego and London: 564-598.

- Sale P.F. 1991b. Habitat structure and recruitment in coral reef fishes. In: Bell S.S., E.D. McCoy and H.R. Mushinsky (eds.) 1991. *Habitat Structure: the physical arrangement of objects in space*. Chapman and Hall, London, UK: 197-210.
- Sale P.F. 1997. Visual census of fishes: how well do we see what is there? *Proceedings of the 8<sup>th</sup> International Coral Reef Symposium* 2: 1435-1440.
- Sale P.F. and R. Dybdahl 1975. Determinants of community structure for coral reef fishes in an experimental habitat. *Ecology* 56(6): 1343-1355.
- Sale P.F. and W.A. Douglas 1981. Precision and accuracy of visual census technique for fish assemblages on coral patch reefs. *Environmental Biology of Fishes* 6(3-4): 333-339.
- Sale P.F. and D.McB. Williams 1982. Community structure of coral reef fishes: are the patterns more than those expected by chance? *The American Naturalist* 120(1): 121-127.
- Sall J., L. Creighton and A. Lehman 2005. JMP Start Statistics. A Guide to Statistics and Data Analysis Using JMP and JMP IN Software. 3<sup>rd</sup> Edition. SAS Institute Inc. Thomson Learning, Belmont, Canada. 560 pp.
- Sammarco P.W. and J.H. Carleton 1982. Damselfish territoriality and coral community structure: reduced grazing, coral recruitment and effects on coral spat. *Proceedings of the 4<sup>th</sup> International Coral Reef Symposium* 2: 525-535.
- Samoilys M.A. and G. Carlos 2000. Determining methods of underwater visual census for estimating the abundance of coral reef fishes. *Environmental Biology of Fishes* 57(3): 289-304.
- Sanders H.L. 1968. Marine benthic diversity: a comparative study. *The American Naturalist* 102(925): 243-282.
- Sanderson S.L. and A.C. Solonksy 1986. Comparison of a rapid visual and a strip transect technique for censusing reef fish assemblages. *Bulletin of Marine Science* 39(1): 119-129.
- Sano M., M. Shimizu and Y. Nose 1984. Changes in structure of coral reef fish communities by destruction of hermatypic corals: observational and experimental views. *Pacific Science* 38: 51-79.
- Sano M., M. Shimizu and Y. Nose 1987. Long-term effects of destruction of hermatypic corals by *Acanthaster planci* infestation on reef fish communities at Iriomote Island, Japan. *Marine Ecology Progress Series* 37: 191-199.
- SAS Institute 2007. JMP Statistics and Graphics Guide, Release 7. SAS Institute Inc., Cary, North Carolina, USA. 1048 pp.
- Schmahl G.P., D. Deis and S.K. Shutler 2006. Cooperative natural resource damage assessment and coral reef restoration at the countainer ship *Houston* grounding in the Florida Keys National Marine Sanctuary. In: Precht W.F. 2006. *Coral Reef Restoration Handbook*. CRC Press/Taylor and Francis, Boca Raton, Florida, USA: 235-256.
- Schmidt S. 2007. In-Situ-Observation von Korallenrecruitment via Fluoreszensfotografie in Indonesien. Diplomarbeit, Carl von Ossietzky Universität Oldenburg. 68 pp.
- Schuhmacher H. 1973. Die lichtabhängige Besiedlung von Hafenstützpfählen durch sessile Tiere und Algen aus dem Korallenriff bei Eilat (Rotes Meer). *Helgoländer wissenschaftliche Meeresuntersuchungen* 24(1-4): 307-326.
- Schuhmacher H. 1977. Initial phases in reef development, studied at artificial reef types off Eilat (Red Sea). *Helgoländer wissenschaftliche Meeresuntersuchungen* 30(1-4): 400-411.
- Seaman W., Jr. and L.M. Sprague 1991. Artificial Habitats for Marine and Freshwater Fisheries. Academic Press, London, UK. 285 pp.
- Shannon C.E. and W. Weaver 1949. The Mathematical Theory of Communication. University of Illinois Press, Urbana, Illinois, USA. 117 pp.

- Shapiro S.S. and M.B. Wilk 1965. An analysis of variance test for normality (complete samples). *Biometrika* 52: 591-611.
- Shepard R.N. 1962. The analysis of proximities: multidimensional scaling with an unknown distance function. I. *Psychometrika* 27: 125-140.
- Sherman R.L., D.S. Gilliam and R.E. Spieler 2001. Site-dependent differences in artificial reef function: implications for coral reef restoration. *Bulletin of Marine Science* 69(2): 1053-1056.
- Sherman R.L., D.S. Gilliam and R.E. Spieler 2002. Artificial reef design: void space, complexity, and attractants. *ICES Journal of Marine Science* 59: S196-S200.
- Shinn E.A. 1976. Coral reef recovery in Florida and the Persian Gulf. *Environmental Geology* 1(4): 241-254.
- Shulman M.J. 1984. Resource limitation and recruitment patterns in a coral reef fish assemblage. *Journal of Experimental Marine Biology and Ecology* 74(1): 85-109.
- Shutler S.K., S. Gittings, T. Penn and J. Schittone 2006. Compensatory restoration: how much is enough? Legal, economic, and ecological considerations. In: Precht W.F. 2006. *Coral Reef Restoration Handbook*. CRC Press/Taylor and Francis, Boca Raton, Florida, USA: 77-93.
- Sier, C.J. and P.J.W. Olive 1994. Reproduction and reproductive variability in the coral *Pocillopora verrucosa* from the Republic of Maldives. *Marine Biology* 118(4): 713-722.
- Smith C.L. 1973. Small rotenone stations: a tool for studying coral reef fish communities. *American Museum Novitates* 2512: 1-21.
- Smith C.L. and J.C. Tyler 1975. Succession and stability in fish communities of dome-shaped patch reefs in the West Indies. *American Museum Novitates* 2572: 1-18.
- Smith G.B. 1979. Relationship of eastern Gulf of Mexico reef-fish communities to the species equilibrium theory of insular biogeography. *Journal of Biogeography* 6: 49-61.
- Smith L.D. and T.P. Hughes 1999. An experimental assessment of survival, re-attachment and fecundity of coral fragments. *Journal of Experimental Marine Biology and Ecology* 235(1): 147-164.
- Smith S.R. 1992. Patterns of coral recruitment and post-settlement mortality on Bermuda's reefs: comparisons to Caribbean and Pacific reefs. *American Zoologist* 32: 663-673.
- Smith S.R. 1997. Patterns of coral settlement, recruitment and juvenile mortality with depth at Conch Reef, Florida. *Proceedings of the 8<sup>th</sup> International Coral Reef Symposium* 2: 1197-1202.
- Smith S.V. 1978. Coral-reef area and the contributions of reefs to processes and resources of the world's oceans. *Nature* 273: 225-226.
- Spalding M.D., C. Ravilious and E.P. Green 2001. World atlas of coral reefs. UNEP World Conservation Monitoring Centre, University of California Press, Berkeley, USA. 424 pp.
- Spurgeon J.P.G. 1992. The economic valuation of coral reefs. *Marine Pollution Bulletin* 24(11): 529-536.
- Spurgeon J.P.G. and U. Lindahl 2000. Economics of Coral Reef Restoration. In: Cesar H.S.J. (ed.) 2000. *Collected Essays on the Economics of Coral Reefs*. CORDIO, Kalmar University, Kalmar, Sweden: 125-135.
- Steele M.A. 1999. Effects of shelter and predators on reef fishes. *Journal of Experimental Marine Biology and Ecology* 233(1): 65-79.
- Stimson, J.S. 1978. Mode and timing of reproduction in some common hermatypic corals of Hawaii and Enewetak. *Marine Biology* 48(2): 173-184.

- Stone R.B. 1985. History of artificial reef use in the United States. In: D'Itri F.M. (ed.) 1985. *Artificial reefs: marine and freshwater applications*. Lewis Publishing Inc., Chelsea, Michigan, USA: 3-11.
- Stone R.B., H.L. Pratt, R.O. Parker, Jr. and G.E. Davis 1979. A comparison of fish populations on an artificial and natural reef in the Florida Keys. *Marine Fisheries Review* 41(9): 1-11.
- Sweatman H.P.A. 1983. Influence of conspecifics on choice of settlement sites by larvae of two pomacentrid fishes (*Dascyllus aruanus* and *D. reticulatus*) on coral reefs. *Marine Biology* 75(2-3): 225-229.
- Syms C. and G.P. Jones 2000. Disturbance, habitat structure, and the dynamics of a coral-reef fish community. *Ecology* 81(10): 2714-2729.
- Syms C. and G.P. Jones 2001. Soft corals exert no direct effects on coral reef fish assemblages. *Oecologia* 127(4): 560-571.
- Talbot F.H. and B. Goldman 1972. A preliminary report on the diversity and feeding relationships of the reef fishes of One Tree Island, Great Barrier Reef system. *Proceedings of the First International Symposium on Corals and Coral Reefs*: 425-443.
- Talbot F.H., B.C. Russell and G.R.V. Anderson 1978. Coral reef fish communities: unstable, high-diversity systems? *Ecological Monographs* 48(4): 425-440.
- Thanner S.E., T.L. McIntosh and S.M. Blair 2006. Development of benthic and fish assemblages on artificial reef materials compared to adjacent natural reef assemblages in Miami-Dade County, Florida. *Bulletin of Marine Science* 78(1): 57-70.
- Thomas J.D. (ed.) 2001. Proceedings of the International Conference on Scientific Aspects of Coral Reef Assessment, Monitoring, and Restoration, 14-16 April 1999, National Coral Reef Institute, Fort Lauderdale, Florida. *Bulletin of Marine Science* 69(2): 289-1056.
- Thompson A.A. and B.D. Mapstone 2002. Intra- versus inter-annual variation in counts of reef fishes and interpretations of long-term monitoring studies. *Marine Ecology Progress Series* 232: 247-257.
- Thongtham N. and H. Chansaang 1999. Influence of surface complexity on coral recruitment at Maiton Island, Phuket, Thailand. *Phuket Marine Biology Center Special Publication* 20: 93-100.
- Tilman D. 1996. Biodiversity: population versus ecosystem stability. *Ecology* 77(2): 350-363.
- Tilman D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80(5): 1455-1474.
- Tilmant J., L. Canzanelli, R. Clark, R. Curry, B. Graham, M. Mayr, A. Moulding, R. Mulcahy, S. Viehman and T. Whittington 2003. Restoration of coral reef habitats within the National Park System. *Conference Proceedings, "Protecting Our Diverse Heritage: The Role of Parks, Protected Areas, and Cultural Sites."*, The George Wright Society Biennial Conference - CR2003 - A conference for the National Park Service and its partners, April 14-18, 2003, San Diego: 234-239.
- Tioho H., M. Tokeshi and S. Nojima 2001. Experimental analysis of recruitment in a scleractinian coral at high latitude. *Marine Ecology Progress Series* 213: 79-86.
- Tomascik T., A.J. Mah, A. Nontji and M.K. Moosa (eds.) 1997. The Ecology of the Indonesian Seas. Part One. Periplus Editions (HK) Ltd., Singapore. 642 pp.
- Tupper M. and W. Hunte 1998. Predictability of fish assemblages on artificial and natural reefs in Barbados. *Bulletin of Marine Science* 62(3): 919-935.
- Turak E. and L. DeVantier 2003. Reef-building corals of Bunaken National Park, North Sulawesi, Indonesia: Rapid ecological assessment of biodiversity and status. Final Report to the International Ocean Institute Regional Centre for Australia & the Western Pacific. 65 pp.

- Unsworth R.K.F., E. Wylie, D.J. Smith and J.J. Bell 2007. Diel trophic structuring of seagrass bed fish assemblages in the Wakatobi Marine National Park, Indonesia. *Estuarine, Coastal and Shelf Science* 72(1-2): 81-88.
- Van Treck P. and H. Schuhmacher 1997. Initial survival of coral nubbins transplanted by a new coral transplantation technology – options for reef rehabilitation. *Marine Ecology Progress Series* 150: 287-292.
- Van Treck P. and H. Schuhmacher 1998. Mass Diving Tourism – A New Dimension Calls for New Management Approaches. *Marine Pollution Bulletin* 37(8-12): 499-504.
- Vaughan T.W. 1911. The Madreporia and marine bottom deposits of southern Florida. *Yearbook of the Carnegie Institution of Washington* 10: 147-156.
- Vaughan T.W. 1915. On recent Madreporaria of Florida, the Bahamas, and the West Indies, and on Collections from Murray Island, Australia. *Yearbook of the Carnegie Institution of Washington* 14: 221-231.
- Vaughan T.W. 1919. Corals and the formation of coral reefs. *Annual Report of the Smithsonian Institution for the year 1917*: 189-238.
- Veron J.E.N. 2000. Corals of the world. Vol. 1-3. Australian Institute of Marine Science, Townsville, Australia. 1382 pp.
- Victor B.C. 1986. Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. *Ecological Monographs* 56(2): 145-160.
- Wabnitz C., M. Taylor, E. Green und T. Razak 2003. From Ocean to Aquarium. The global trade in marine ornamental species. UNEP World Conservation Monitoring Centre, Cambridge, UK. 64 pp.
- Walker B.H. 1992. Biodiversity and ecological redundancy. *Conservation Biology* 6(1): 18-23.
- Wallace C.C. 1985. Seasonal peaks and annual fluctuations in recruitment of juvenile scleractinian corals. *Marine Ecology Progress Series* 21: 289-298.
- Wallace C.C. and G.D. Bull 1982. Patterns of juvenile coral recruitment on a reef front during a spring summer spawning period. *Proceedings of the 4<sup>th</sup> International Coral Reef Symposium* 2: 345-350.
- Walsh W.J. 1983. Stability of a coral reef fish community following a catastrophic storm. *Coral Reefs* 2(1): 49-63.
- Walsh W.J. 1985. Reef fish community dynamics on small artificial reefs: the influence of isolation, habitat structure, and biogeography. *Bulletin of Marine Science* 36(2): 357-376.
- Walter R.P. and J.M. Haynes 2006. Fish and coral community structure are related on shallow water patch reefs near San Salvador, Bahamas. *Bulletin of Marine Science* 79(2): 365-374.
- Walther N.D. and J. Kolasa 1996. Stochastic determinants of assemblage patterns in coral reef fishes: a quantification by means of two models. *Environmental Biology of Fishes* 47(3): 255-267.
- Warwick R.M. and K.R. Clarke 1993. Increased variability as a symptom of stress in marine communities. *Journal of Experimental Marine Biology and Ecology* 172(1-2): 215-226.
- Warwick R.M., K.R. Clarke and Suharsono 1990. A statistical analysis of coral community responses to the 1982-83 El Niño in the Thousand Islands, Indonesia. *Coral Reefs* 8(4): 171-179.
- Wass R.C. 1987. Influence of *Acanthaster*-induced coral kills on fish communities at Fagatele Bay and at Cape Larsen. In: Birkeland C., R.H. Randall, R.C. Wass, B.D. Smith and S. Wilkins (eds.) 1987. *Biological resource assessment of the Fagatele Bay National Marine Sanctuary*. NOAA Technical Memorandum NOS MEMD 3, United States Department of Commerce: 193-209.
- Weibull W. 1951. A statistical distribution function of wide applicability. *Journal of Applied Mechanics* 18(3): 293-297.

- Wellington G.M. 1982a. An experimental analysis of the effects of light and zooplankton on coral zonation. *Oecologia* 52(3): 311-320.
- Wellington G.M. 1982b. Depth zonation of corals in the Gulf of Panama: control and facilitation by resident reef fishes. *Ecological Monographs* 52(3): 223-241.
- Wellington G.M. and B.C. Victor 1985. El Niño mass coral mortality: a test of resource limitation in a coral reef damselfish population. *Oecologia* 68(1): 15-19.
- Wells J.W. 1957. Coral reefs. In: Hedgpeth J.W. (ed.) 1957. *Treatise on Marine Ecology and Paleoecology. I. Ecology*. Geological Society of America Memoir 67(1): 609-631.
- White A.T., L.M. Chou, M.W.R.N. De Silva and F.Y. Guarin 1990. Artificial Reefs for Marine Habitat Enhancement in Southeast Asia. *ICLARM Education Series* 11. International Centre for Living Aquatic Resources Management (ICLARM), Manila, Philippines. 45 pp.
- White A.T. and A. Cruz-Trinidad 1998. The Values of Philippine Coastal Resources: Why Protection and Management are Critical. Coastal Resource Management Project, Cebu City, Philippines. 96 pp.
- Whitten T., M. Mustafa and G.S. Henderson 2002. The Ecology of Sulawesi. The Ecology of Indonesia Series, Volume IV. Periplus Editions Ltd., Singapore. 754 pp.
- Wild C., M. Huettel, A. Klueter, S.G. Kremb, M.Y.M. Rasheed and B.B. Jørgensen 2004. Coral mucus functions as an energy carrier and particle trap in the reef ecosystem. *Nature* 428: 66-70.
- Wilkinson C.R. (ed.) 2004. Status of coral reefs of the world: 2004. Global Coral Reef Monitoring Network (GCRMN), Australian Institute of Marine Science, Townsville, Queensland, Australia. 557 pp.
- Williams D.McB. 1991. Patterns and processes in the distribution of coral reef fishes. In: Sale P.F. (ed.) 1991. *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego and London: 437-474.
- Williams I.D., W.J. Walsh, B.N. Tissot and L.E. Hallacher 2006. Impact of observers' experience level on counts of fishes in underwater visual surveys. *Marine Ecology Progress Series* 310: 185-191.
- Willis B.L., R.C. Babcock, P.L. Harrison, J.K. Oliver and C.C. Wallace 1985. Patterns in the mass spawning of corals on the Great Barrier Reef from 1981 to 1984. *Proceedings of the 5<sup>th</sup> International Coral Reef Congress* 4: 343-348.
- Willis T.J. and M.J. Anderson 2003. Structure of cryptic reef fish assemblages: relationships with habitat characteristics and predator density. *Marine Ecology Progress Series* 257: 209-221.
- Willis T.J., F. Badalamenti and M. Milazzo 2006. Dial variability in counts of reef fishes and its implications for monitoring. *Journal of Experimental Marine Biology and Ecology* 331(1): 108-120.
- Wilson S.K., N.A.J. Graham and N.V.C. Polunin 2007. Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Marine Biology* 151(3): 1069-1076.
- Wittenberg M. and W. Hunte 1992. Effects of eutrophication and sedimentation on juvenile corals. I. Abundance, mortality and community structure. *Marine Biology* 112(1): 131-138.
- Wolff M. and E. Alarcon 1993. Structure of a scallop *Argopecten purpuratus* (Lamarck, 1819) dominated subtidal macro-invertebrate assemblage in northern Chile. *Journal of Shellfish Research* 12(2): 295-304.
- Yap H.T. 2000. The case for restoration of tropical coastal ecosystems. *Ocean & Coastal Management* 43(8-9): 841-851.
- Yap H.T. 2004. Differential survival of coral transplants on various substrates under elevated water temperatures. *Marine Pollution Bulletin* 49(4): 306-312.
- Yap H.T. and E.D. Gomez 1982. Growth of *Acropora pulchra* (Brook) in Bolinao, Pangasinan, Philippines. *Proceedings of the 4<sup>th</sup> International Coral Reef Symposium* 2: 207-213.

- Yap H.T. and E.D. Gomez 1984. Growth of *Acropora pulchra*. II. Responses of natural and transplanted colonies to temperature and day length. *Marine Biology* 81(2): 209-215.
- Yap H.T. and E.D. Gomez 1985. Growth of *Acropora pulchra*. III. Preliminary observations on the effects of transplantation and sediment on the growth and survival of transplants. *Marine Biology* 87(2): 203-209.
- Yap H.T. and R.A. Molina 2003. Comparison of coral growth and survival under enclosed, semi-natural conditions and in the field. *Marine Pollution Bulletin* 46(7): 858-864.
- Yap H.T., P.M. Aliño and E.D. Gomez 1992. Trends in growth and mortality of three coral species (Anthozoa: Scleractinia), including effects of transplantation. *Marine Ecology Progress Series* 83: 91-101.
- Yap H.T., R. Alvarez Molina, H.M. Custodio III and R.M. Dizon 1998. Physiological and ecological aspects of coral transplantation. *Journal of Experimental Marine Biology and Ecology* 229(1): 69-84.
- Zar J.H. 1999. Biostatistical Analysis, 4<sup>th</sup> edition. Prentice-Hall, Upper Saddle River, NJ, USA. 929 pp.
- Zimmer B. 2006. Coral reef restoration: an overview. In: Precht W.F. 2006. *Coral Reef Restoration Handbook*. CRC Press/Taylor and Francis, Boca Raton, Florida, USA: 39-59.

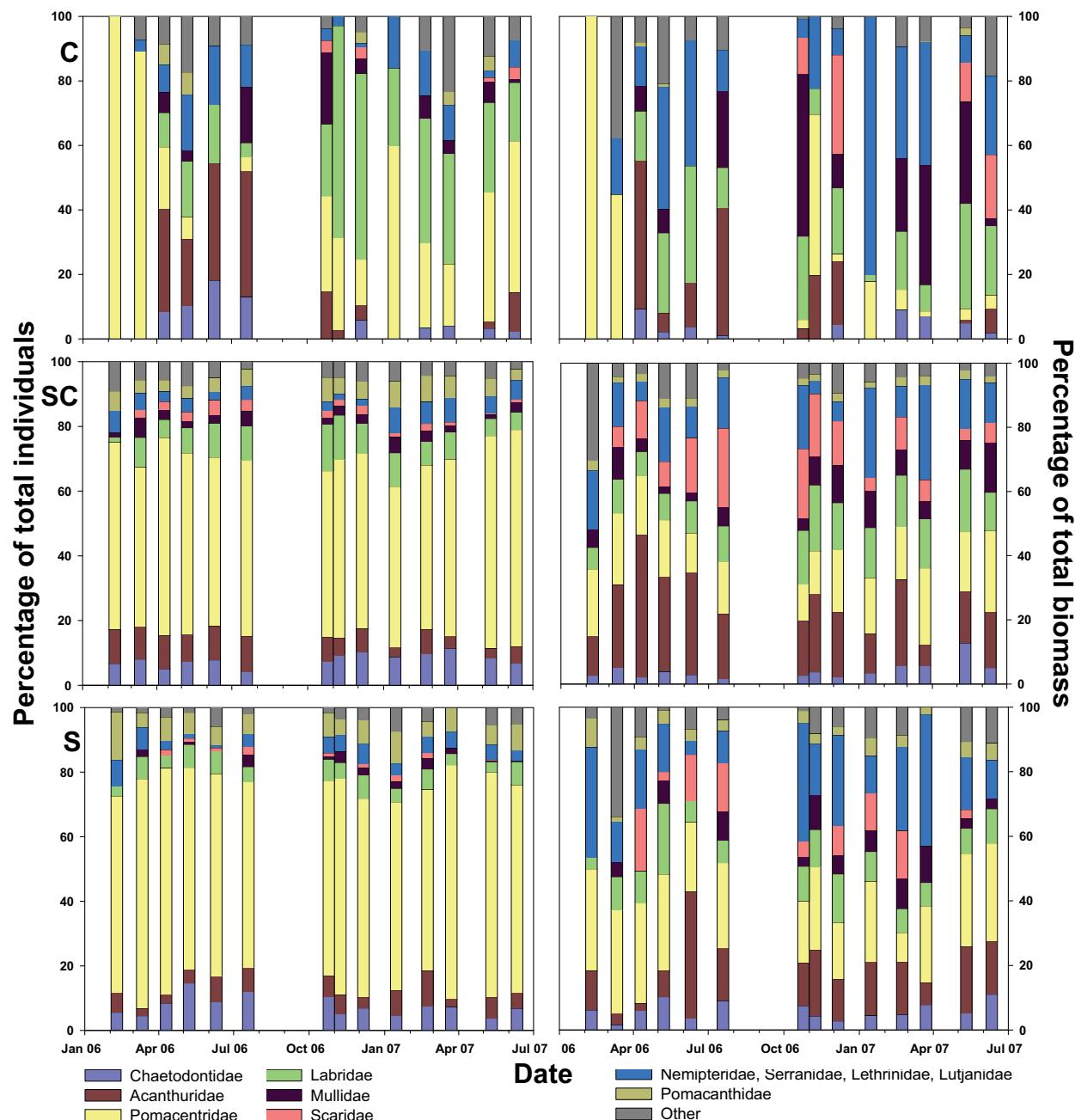
## 6. Appendix

**Table A 1:** Prices used to calculate the approximate average value of all fishes present in one plot at one sampling time.

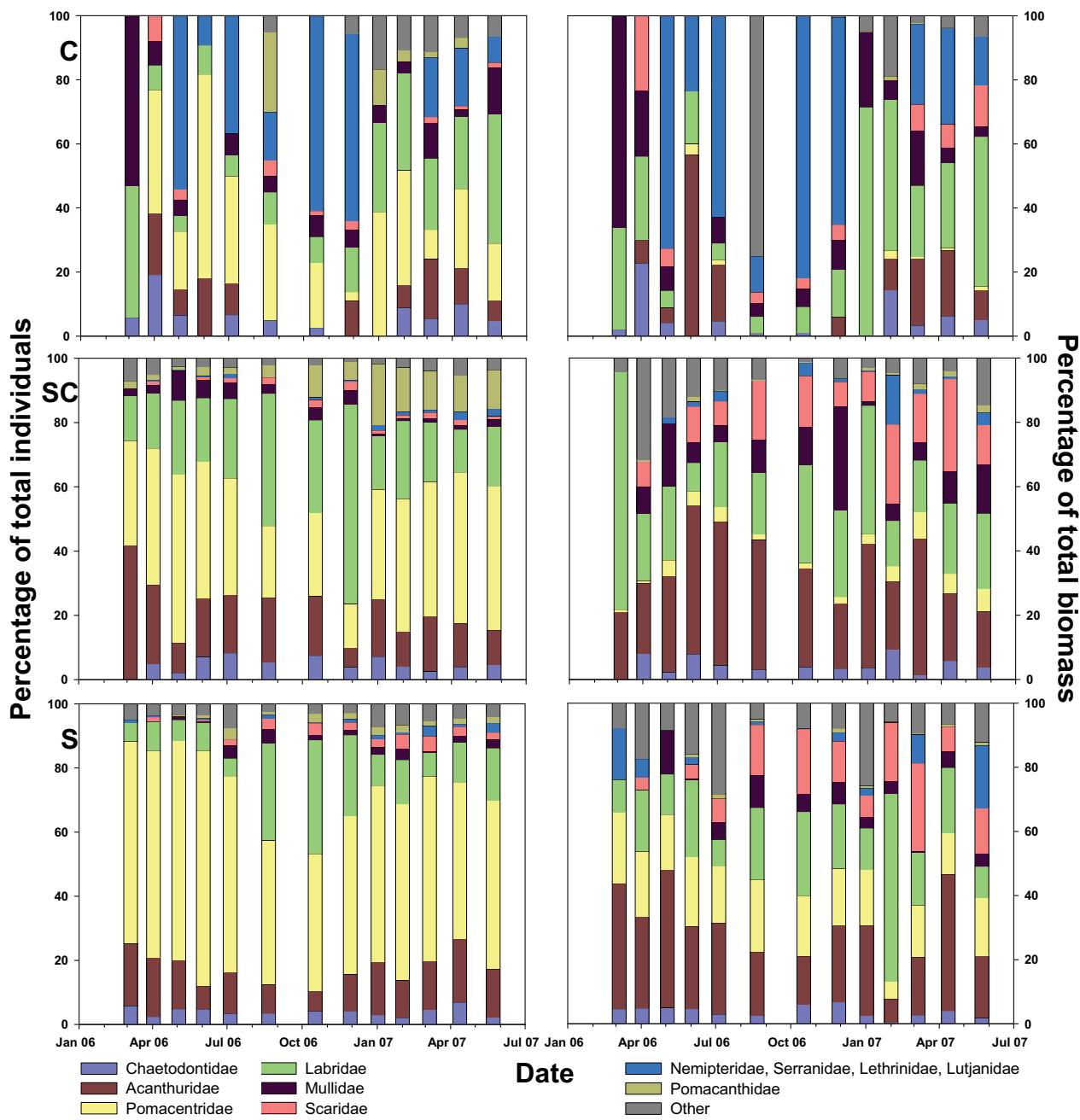
Family	Species	Price per fish [IDR]	Price per kg [IDR]
Acanthuridae	<i>Acanthurus auranticavus</i>		20,000
	<i>Acanthurus bariene</i>		20,000
	<i>Acanthurus nigricauda</i>		20,000
	<i>Acanthurus nigrofasciatus</i>		15,000
	<i>Acanthurus olivaceus</i>		15,000
	<i>Acanthurus pyroferus</i>		15,000
	<i>Acanthurus thompsoni</i>		15,000
	<i>Ctenochaetus binotatus</i>		15,000
	<i>Ctenochaetus striatus</i>		15,000
	<i>Naso hexacanthus</i>		10,000
Balistidae	<i>Zebrasoma scopas</i>	1500	
	<i>Zebrasoma veliferum</i>	5000	
	<i>Balistapus undulatus</i>	2000	
Centriscidae	<i>Rhineacanthus verrucosus</i>	1500	
	<i>Aeoliscus strigatus</i>	500	
Chaetodontidae	<i>Chaetodon auriga</i>	2000	
	<i>Chaetodon bennetti</i>	3500	
	<i>Chaetodon citrinellus</i>	2500	
	<i>Chaetodon ephippium</i>	6000	
	<i>Chaetodon kleinii</i>	1000	
	<i>Chaetodon lunula</i>	4000	
	<i>Chaetodon melannotus</i>	1000	
	<i>Chaetodon meyeri</i>	6000	
	<i>Chaetodon ornatus</i>	5000	
	<i>Chaetodon punctatofasciatus</i>	2000	
	<i>Chaetodon rafflesii</i>	1500	
	<i>Chaetodon ulietensis</i>	6000	
	<i>Chaetodon unimaculatus</i>	2000	
	<i>Chaetodon vagabundus</i>	1000	
	<i>Forcipiger flavissimus</i>	6000	
	<i>Forcipiger longirostris</i>	6000	
	<i>Heniochus varius</i>	2000	
	<i>Plectorhinchus chaetodonoides</i>	3000	
Haemulidae	<i>Bodianus mesothorax</i>	2000	
	<i>Cheilinus chlorourus</i>	1500	
	<i>Cheilinus fasciatus</i>		20,000
	<i>Coris gaimard</i>	2000	
	<i>Gomphosus varius</i>	2000	
	<i>Halichoeres hortulanus</i>	1000	
	<i>Hemigymnus melapterus</i>		15,000
	<i>Labroides bicolor</i>	3000	
	<i>Labroides dimidiatus</i>	500	
	<i>Novaculichthys taenioura</i>	2000	
Lethrinidae	<i>Pseudocheilinus hexataenia</i>	2000	
	<i>Thalassoma amblycephalum</i>	1000	
	<i>Lethrinus ornatus</i>		20,000
Lutjanidae	<i>Monotaxis grandoculis</i>		25,000
	<i>Macolor macularis</i>		15,000

<b>Monacanthidae</b>	<i>Oxymonacanthus longirostris</i>	1500	
<b>Mullidae</b>	<i>Parupeneus barberinus</i>		20,000
	<i>Parupeneus cyclostomus</i>		20,000
	<i>Parupeneus indicus</i>		20,000
	<i>Parupeneus multifasciatus</i>		15,000
	<i>Parupeneus trifasciatus</i>		15,000
<b>Ostraciidae</b>	<i>Ostracion cubicus</i>	2000	
<b>Platycephalidae</b>	<i>Cymbacephalus beauforti</i>		15,000
<b>Pomacanthidae</b>	<i>Centropyge bicolor</i>	3000	
	<i>Centropyge bispinosa</i>	5000	
	<i>Centropyge tibicen</i>	3000	
	<i>Centropyge vrolikii</i>	3000	
	<i>Pomacanthus imperator</i>	20,000	
	<i>Pygoplites diacanthus</i>	20,000	
<b>Pomacentridae</b>	<i>Amphiprion clarkii</i>	2500	
	<i>Amphiprion ocellaris</i>	1500	
	<i>Dascyllus aruanus</i>	500	
	<i>Dascyllus reticulatus</i>	500	
	<i>Dascyllus trimaculatus</i>	500	
<b>Pseudochromidae</b>	<i>Pseudochromis paccagnellae</i>	2000	
<b>Scaridae</b>	<i>Cetoscarus bicolor</i>		20,000
	<i>Chlorurus bleekeri</i>		20,000
	<i>Scarus dimidiatus</i>		20,000
	<i>Scarus flavipectoralis</i>		20,000
	<i>Scarus forsteni</i>		20,000
	<i>Scarus niger</i>		20,000
	<i>Scarus oviceps</i>		20,000
	<i>Scarus prasiognathus</i>		20,000
	<i>Scarus tricolor</i>		20,000
	<i>Scarus quoyi</i>		20,000
	<i>Scarus rubroviolaceus</i>		20,000
	<i>Scarus female</i>		15,000
<b>Scorpaenidae</b>	<i>Dendrochirus zebra</i>	2500	
	<i>Pterois antennata</i>	2500	
	<i>Pterois volitans</i>	5000	
<b>Serranidae</b>	<i>Aethaloperca rogaa</i>		35,000
	<i>Cephalopholis leopardus</i>		35,000
	<i>Cephalopholis urodetta</i>		35,000
	<i>Cromileptes altivelis</i>		75,000
	<i>Epinephelus fasciatus</i>		35,000
	<i>Epinephelus merra</i>		35,000
	<i>Variola albimarginata</i>		35,000
	<i>Variola louti</i>		35,000
<b>Siganidae</b>	<i>Siganus argenteus</i>	7000*	
	<i>Siganus corallinus</i>	7000*	
	<i>Siganus guttatus</i>	7000*	
	<i>Siganus puello</i>	7000*	
	<i>Siganus spinus</i>	7000*	
	<i>Siganus vulpinus</i>	3000*	
<b>Syngnathidae</b>	<i>Doryrhamphus dactyliophorus</i>	1500	
<b>Tetraodontidae</b>	<i>Arothron hispidus</i>	1500	
	<i>Arothron nigropunctatus</i>	1500	
	<i>Canthigaster valentini</i>	1500	
<b>Zanclidae</b>	<i>Zanclus cornutus</i>	2000	

\* for siganids, prices on the fish markets were given per individual. These were included with the fishes caught for consumption, not for the aquarium trade.



**Figure A 1:** Relative contribution of selected families to total number of individuals (left) and biomass (right) in the Control (C), Structures + Corals (SC) and Structures (S) treatments (top to bottom) at Meras.



**Table A 2:** Results of the linear model testing for effects of treatment, time and visibility on abundance at the three sites.

Test	Source	df	F	p
<b>Gangga</b>				
ANOVA	Model ( $R^2 = 0.9453$ )	11,117	183.8372	< 0.0001
Effect Test	Treatment	2	646.5159	< 0.0001
	Time	1	458.0275	< 0.0001
	Visibility	1	0.6832	0.4102
	Treatment*Time	2	62.5202	< 0.0001
	Visibility*Time	1	0.5366	0.4653
	Visibility*Treatment	2	8.1588	0.0005
	Vis.*Time*Treatm.	2	2.7934	0.0653
<b>Meras</b>				
ANOVA	Model ( $R^2 = 0.9384$ )	11,110	152.2392	< 0.0001
Effect Test	Treatment	2	640.3060	< 0.0001
	Time	1	89.0283	< 0.0001
	Visibility	1	34.3195	< 0.0001
	Treatment*Time	2	6.4911	0.0022
	Visibility*Time	1	0.8988	0.3452
	Visibility*Treatment	2	2.3478	0.1004
	Vis.*Time*Treatm.	2	10.8679	< 0.0001
<b>Bunaken</b>				
ANOVA	Model ( $R^2 = 0.7883$ )	11,105	35.5389	< 0.0001
Effect Test	Treatment	2	134.5803	< 0.0001
	Time	1	11.9407	0.0008
	Visibility	1	21.1686	< 0.0001
	Treatment*Time	2	1.2505	0.2906
	Visibility*Time	1	0.8033	0.3722
	Visibility*Treatment	2	6.7483	0.0017
	Vis.*Time*Treatm.	2	0.9374	0.3949

**Table A 3:** Results of the linear model testing for effects of treatment, time and visibility on number of species at the three sites.

Test	Source	df	F	p
<b>Gangga</b>				
ANOVA	Model ( $R^2 = 0.9272$ )	11,117	135.6536	< 0.0001
Effect Test	Treatment	2	484.0676	< 0.0001
	Time	1	312.6058	< 0.0001
	Visibility	1	1.4764	0.2268
	Treatment*Time	2	47.5290	< 0.0001
	Visibility*Time	1	0.8303	0.3641
	Visibility*Treatment	2	2.6644	0.0739
	Vis.*Time*Treatm.	2	3.1583	0.0461
<b>Meras</b>				
ANOVA	Model ( $R^2 = 0.8724$ )	14,107	68.3768	< 0.0001
Effect Test	Treatment	2	298.7164	< 0.0001
	Time	1	29.6517	< 0.0001
	Visibility	1	29.0059	< 0.0001
	Treatment*Time	2	0.3643	0.6955
	Visibility*Time	1	4.1513	0.0440
	Visibility*Treatment	2	0.3780	0.6861
	Vis.*Time*Treatm.	2	10.4011	< 0.0001

<b>Bunaken</b>					
ANOVA	Model ( $R^2 = 0.8299$ )	14,102	35.5573	< 0.0001	
Effect Test	Treatment	2	157.1263	< 0.0001	
	Time	1	15.5758	0.0001	
	Visibility	1	1.9218	0.1687	
	Treatment*Time	2	10.0987	< 0.0001	
	Visibility*Time	1	0.6905	0.4079	
	Visibility*Treatment	2	0.4459	0.6415	
	Vis.*Time*Treatm.	2	2.5092	0.0863	
	(Time) <sup>2</sup>	1	5.0973	0.0261	
	Treatment*(Time) <sup>2</sup>	2	8.6990	0.0003	

**Table A 4:** Results of the linear model testing for effects of treatment, time and visibility on fish biomass at the three sites.

Test	Source	df	F	p
<b>Gangga</b>				
ANOVA	Model ( $R^2 = 0.8259$ )	11,117	50.4463	< 0.0001
Effect Test	Treatment	2	202.7812	< 0.0001
	Time	1	65.0128	< 0.0001
	Visibility	1	0.0116	0.9144
	Treatment*Time	2	23.8406	< 0.0001
	Visibility*Time	1	0.0380	0.8457
	Visibility*Treatment	2	1.7182	0.1839
	Vis.*Time*Treatm.	2	0.0268	0.9735
<b>Meras</b>				
ANOVA	Model ( $R^2 = 0.8153$ )	14,107	33.7409	< 0.0001
Effect Test	Treatment	2	115.9942	< 0.0001
	Time	1	2.9664	0.0879
	Visibility	1	21.3672	< 0.0001
	Treatment*Time	2	9.4377	0.0002
	Visibility*Time	1	1.5883	0.2103
	Visibility*Treatment	2	14.5844	< 0.0001
	Vis.*Time*Treatm.	2	2.5849	0.0801
	(Time) <sup>2</sup>	1	1.6558	0.2009
	Treatment*(Time) <sup>2</sup>	2	9.6066	0.0001
<b>Bunaken</b>				
ANOVA	Model ( $R^2 = 0.4745$ )	11,105	8.6202	< 0.0001
Effect Test	Treatment	2	27.9756	< 0.0001
	Time	1	9.1055	0.0032
	Visibility	1	0.9596	0.3295
	Treatment*Time	2	3.5947	0.0309
	Visibility*Time	1	0.8479	0.3593
	Visibility*Treatment	2	1.3396	0.2664
	Vis.*Time*Treatm.	2	1.6486	0.1972

**Table A 5:** Results of the linear model testing for effects of treatment, time and visibility on diversity at the three sites.

Test	Source	df	F	p
<b>Gangga</b>				
ANOVA	Model ( $R^2 = 0.8995$ )	11,117	95.1967	< 0.0001
Effect Test	Treatment	2	361.1281	< 0.0001
	Time	1	216.2119	< 0.0001
	Visibility	1	0.8873	0.3481
	Treatment*Time	2	7.6755	0.0007
	Visibility*Time	1	1.2054	0.2745
	Visibility*Treatment	2	1.6143	0.2034
	Vis.*Time*Treatm.	2	2.1269	0.1238
<b>Meras</b>				
ANOVA	Model ( $R^2 = 0.8749$ )	14,107	69.9439	< 0.0001
Effect Test	Treatment	2	296.0001	< 0.0001
	Time	1	28.9771	< 0.0001
	Visibility	1	32.2217	< 0.0001
	Treatment*Time	2	2.2759	0.1075
	Visibility*Time	1	2.5875	0.1106
	Visibility*Treatment	2	0.5551	0.5756
	Vis.*Time*Treatm.	2	7.4620	0.0009
<b>Bunaken</b>				
ANOVA	Model ( $R^2 = 0.8532$ )	14,102	42.3400	< 0.0001
Effect Test	Treatment	2	197.3488	< 0.0001
	Time	1	11.2053	0.0011
	Visibility	1	2.3328	0.1298
	Treatment*Time	2	12.1997	< 0.0001
	Visibility*Time	1	0.0420	0.8381
	Visibility*Treatment	2	0.3900	0.6781
	Vis.*Time*Treatm.	2	3.2351	0.0434
	(Time) <sup>2</sup>	1	2.6559	0.1062
	Treatment*(Time) <sup>2</sup>	2	12.5631	< 0.0001

**Table A 6:** Results of the linear model testing for effects of treatment, time and visibility on evenness of the samples at the three sites. Note the low fit of the models at all sites.

Test	Source	df	F	p
<b>Gangga</b>				
ANOVA	Model ( $R^2 = 0.3347$ )	14,114	4.0956	< 0.0001
Effect Test	Treatment	2	5.4578	0.0055
	Time	1	0.4871	0.4867
	Visibility	1	0.8461	0.3596
	Treatment*Time	2	4.6063	0.0119
	Visibility*Time	1	0.6639	0.4169
	Visibility*Treatment	2	4.0657	0.0197
	Vis.*Time*Treatm.	2	0.2761	0.7592
	(Time) <sup>2</sup>	1	0.1444	0.7047
	Treatment*(Time) <sup>2</sup>	2	7.3844	0.0010
<b>Meras</b>				
ANOVA	Model ( $R^2 = 0.5356$ )	14,106	8.7339	< 0.0001
Effect Test	Treatment	2	34.4593	< 0.0001
	Time	1	1.8357	0.1783
	Visibility	1	0.2298	0.6327
	Treatment*Time	2	1.3044	0.2757

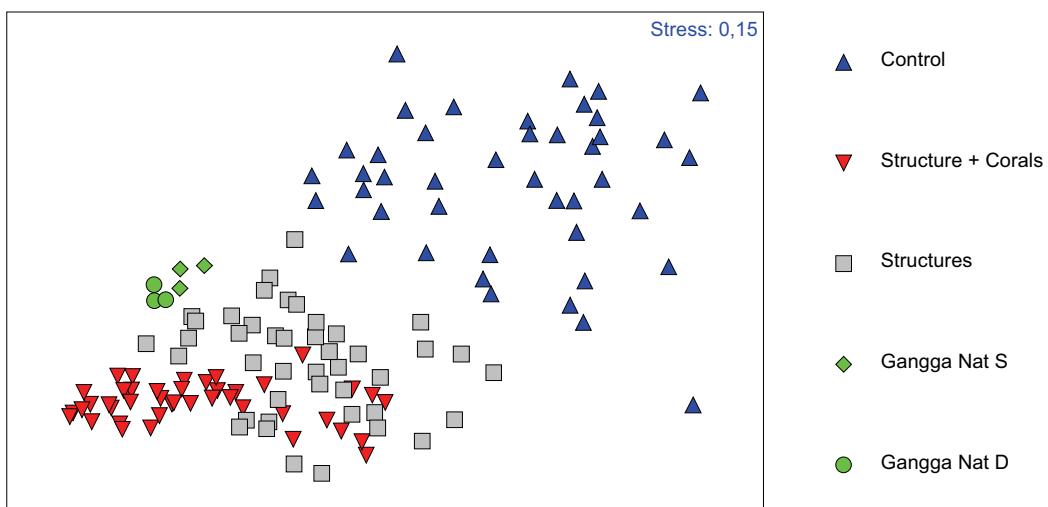
	Visibility*Time	1	0.4460	0.5057
	Visibility*Treatment	2	0.3375	0.7143
	Vis.*Time*Treatm.	2	0.4098	0.6649
	(Time) <sup>2</sup>	1	0.6072	0.4376
	Treatment*(Time) <sup>2</sup>	2	1.4866	0.2308
<b>Bunaken</b>				
ANOVA	Model ( $R^2 = 0.3347$ )	14,114	4.0956	< 0.0001
Effect Test	Treatment	2	5.4578	0.0055
	Time	1	0.4871	0.4867
	Visibility	1	0.8461	0.3596
	Treatment*Time	2	4.6063	0.0119
	Visibility*Time	1	0.6639	0.4169
	Visibility*Treatment	2	4.0657	0.0197
	Vis.*Time*Treatm.	2	0.2761	0.7592
	(Time) <sup>2</sup>	1	0.1444	0.7047
	Treatment*(Time) <sup>2</sup>	2	7.3844	0.0010

**Table A 7:** Results of a crossed two-way ANOSIM for effects of Treatment and Time using all experimental fish census samples from Gangga.

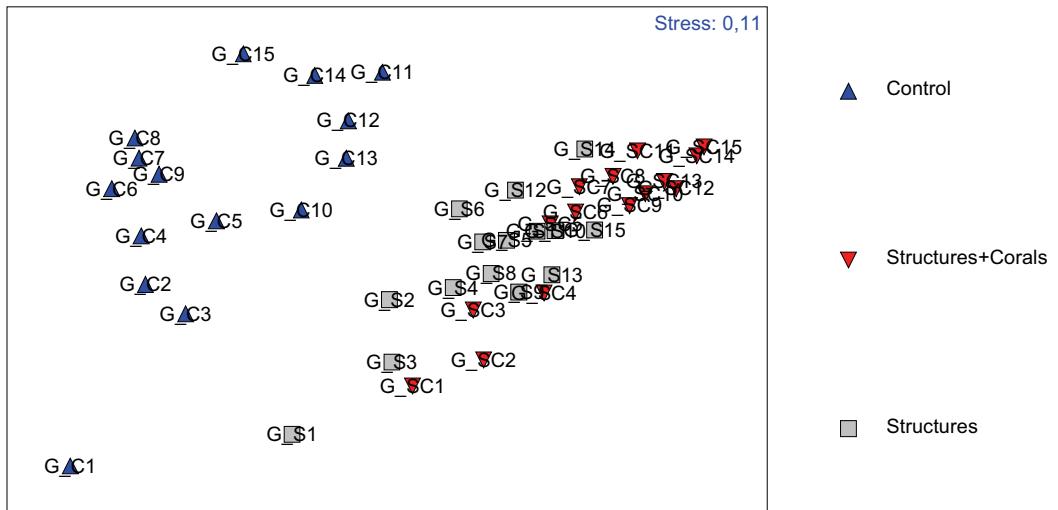
Test	Factor	Test pairs	$\rho$	p
Global pairwise	Treatment		0.924	0.001
		Control, S + C	0.987	0.001
		Control, Structures	0.979	0.001
		S + C, Structures	0.947	0.001
Global	Time		0.832	0.001

**Table A 8:** Results of a crossed two-way ANOSIM for effects of Treatment and Time using all experimental fish census samples from Bunaken.

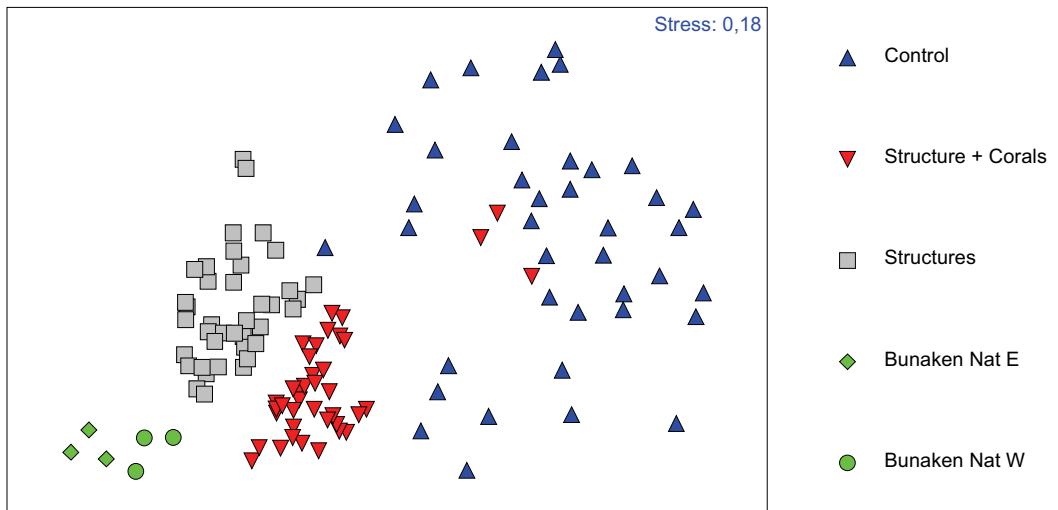
Test	Factor	Test pairs	$\rho$	p
Global pairwise	Treatment		0.869	0.001
		Control, S + C	0.923	0.001
		Control, Structures	0.94	0.001
		S + C, Structures	0.994	0.001
Global	Time		0.747	0.001



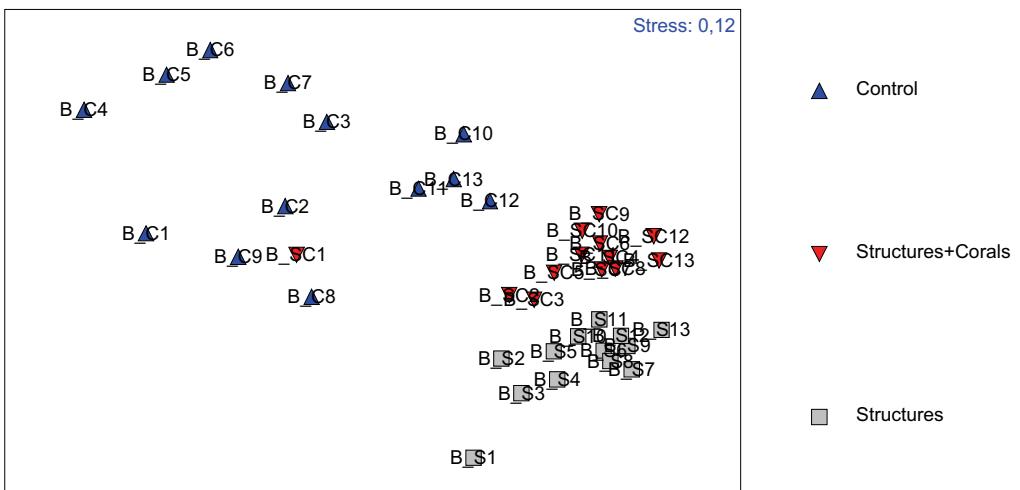
**Figure A 3:** Non-metric Multi Dimensional Scaling (MDS) based on Bray-Curtis similarity of all fish community samples taken at Gangga.



**Figure A 4:** Non-metric Multi Dimensional Scaling (MDS) based on Bray-Curtis similarity of the average census data from the experimental plots for consecutive samplings at Gangga, showing the development of the fish communities over time.



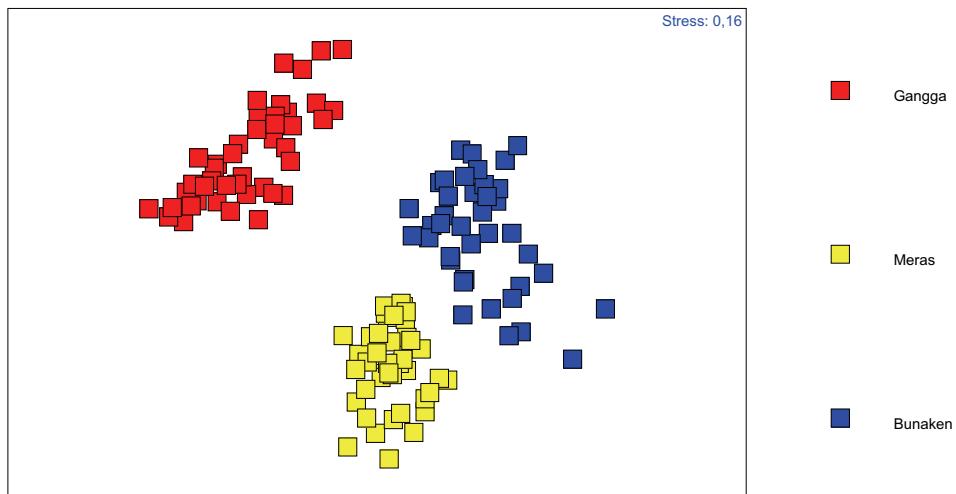
**Figure A 5:** Non-metric Multi Dimensional Scaling (MDS) based on Bray-Curtis similarity of all fish community samples taken at Bunaken.



**Figure A 6:** Non-metric Multi Dimensional Scaling (MDS) based on Bray-Curtis similarity of the average census data from the experimental plots for consecutive samplings at Bunaken, showing the development of the fish communities over time.

**Table A 9:** Results of a crossed two-way ANOSIM for effects of Location and Time using all experimental fish census samples from the Structures treatment.

Using sampling campaign number as time					Using sampling month as time				
Test	Factor	Test pairs	p	p	Test	Factor	Test pairs	p	p
Global pairwise	Location		0.992	0.001	Global pairwise	Location		0.915	0.001
		Gangga, Meras	1.0	0.001			Gangga, Meras	0.997	0.001
		Gangga, Bun.	1.0	0.001			Gangga, Bun.	0.947	0.001
		Meras, Bun.	0.988	0.001			Meras, Bun.	0.8	0.001
Global	Time		0.863	0.001	Global	Time		0.247	0.001



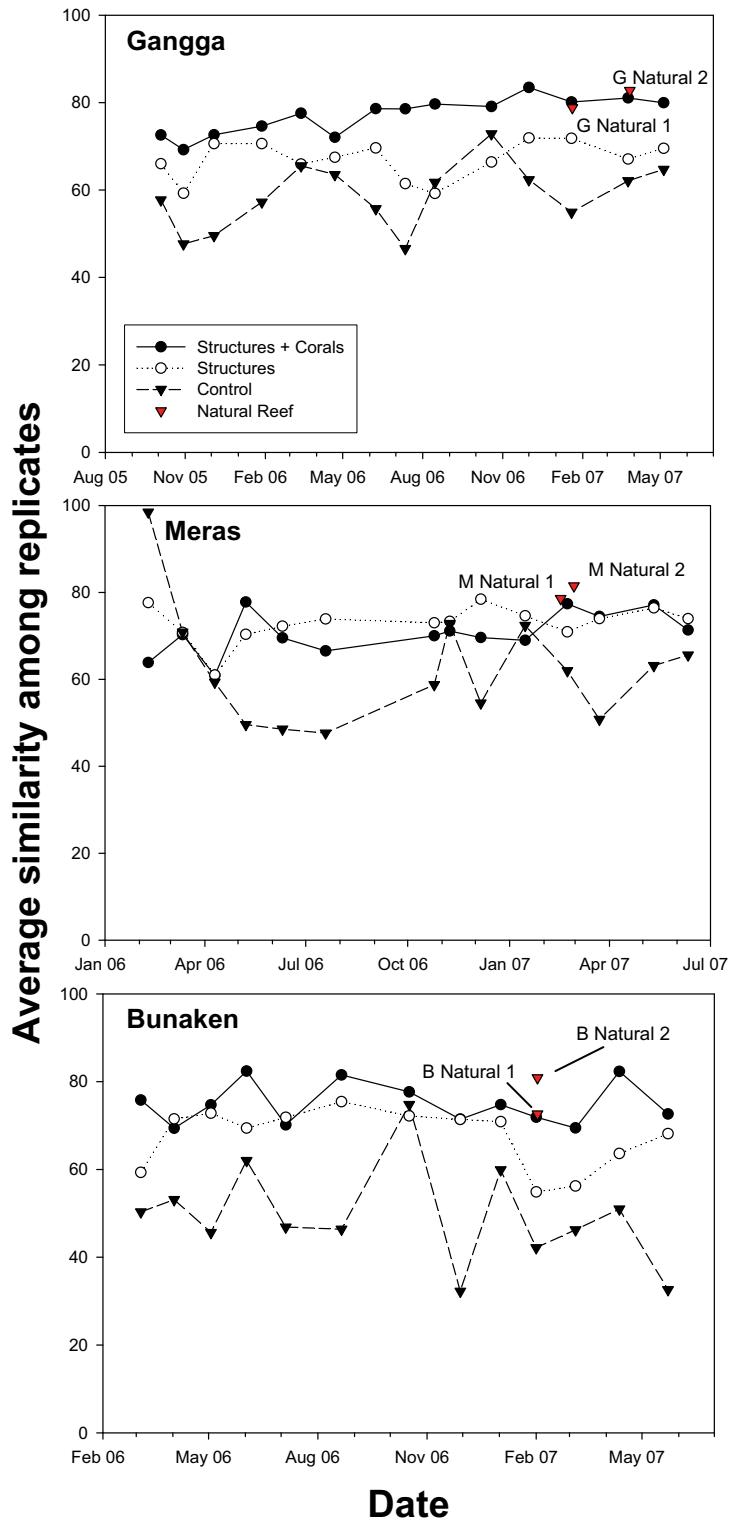
**Figure A 7:** Non-metric Multi Dimensional Scaling (MDS) based on Bray-Curtis similarity of all fish community samples taken from the Structures treatment.

**Table A 10:** Results of the reduced linear model (crossed two-way ANOVA) for effects of Location and Treatment on within-sample similarity.

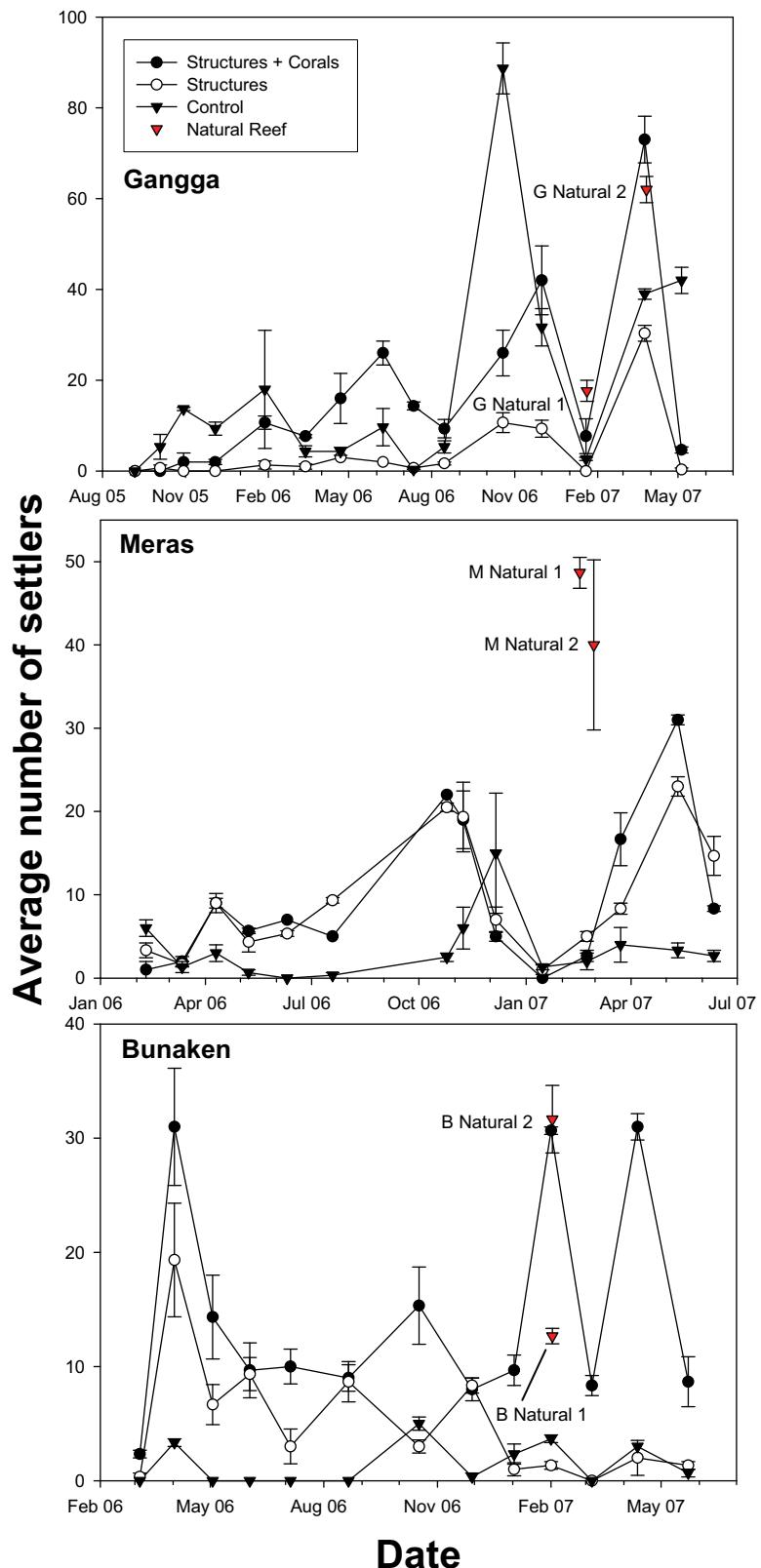
Test	Source	df	F	p
ANOVA	Model ( $R^2 = 0.6154$ )	8,99	19.8009	< 0.0001
Effect Test	Location	2	2.4930	0.0878
	Treatment	2	68.2690	< 0.0001
	Location*Treatment	4	4.2208	0.0034

**Table A 11:** Results of the non-parametric Kruskal-Wallis test and pairwise Mann-Whitney *U* tests for effects of Treatment on within-sample similarity.

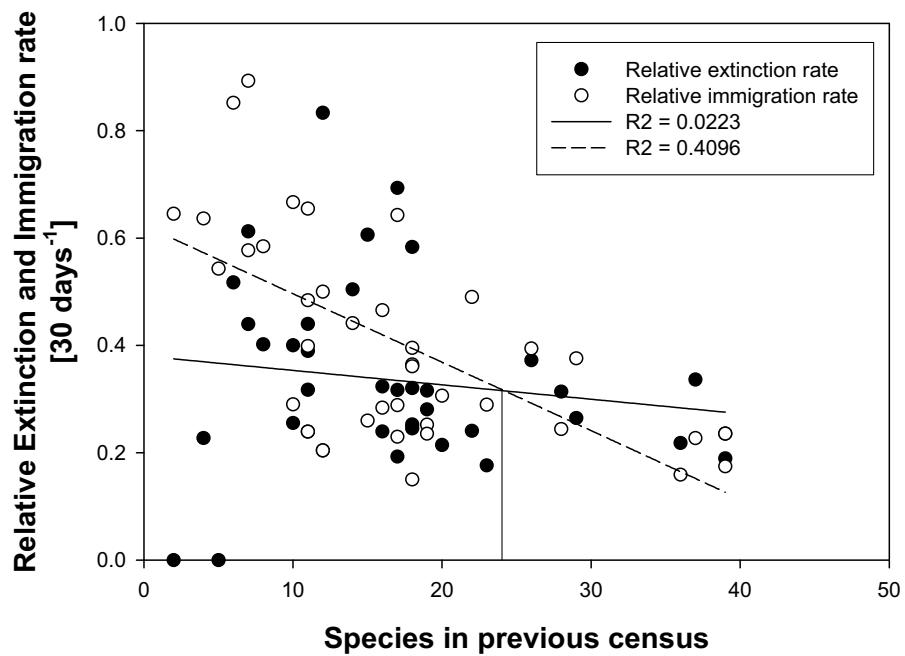
Test	Effect tested	$\chi^2$	p
Kruskal-Wallis	Treatment	49.8931	< 0.0001
pairwise Mann-Whitney	Control vs Structures	26.2589	< 0.0001
	Control vs S+C	39.3517	< 0.0001
	Structures vs S+C	10.3028	0.0013



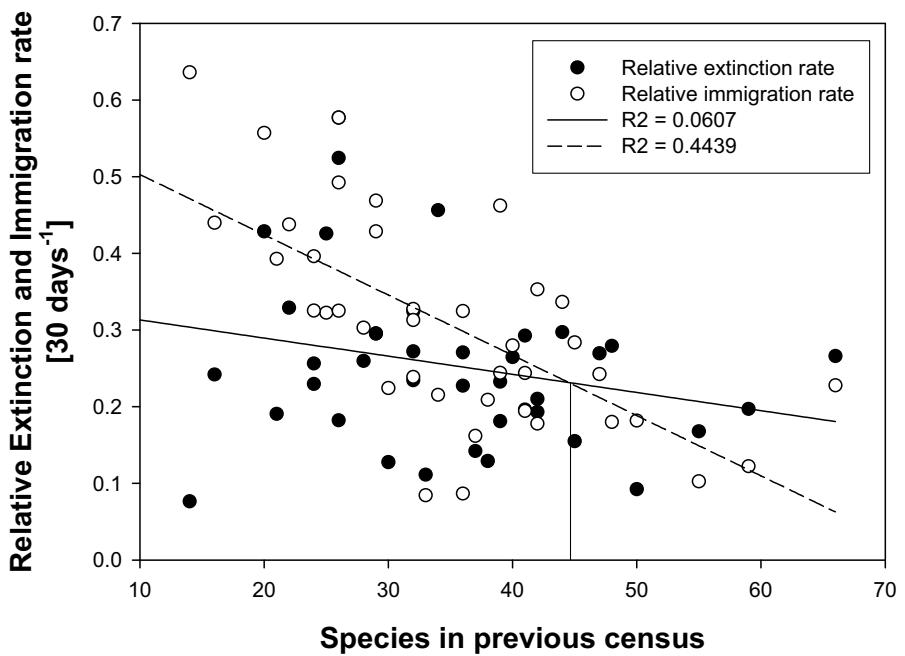
**Figure A 8:** Average among-replicate Bray-Curtis similarity for the experimental treatments at all three locations calculated by the SIMPER routine, with the similarities of the natural reef plots shown for comparison.



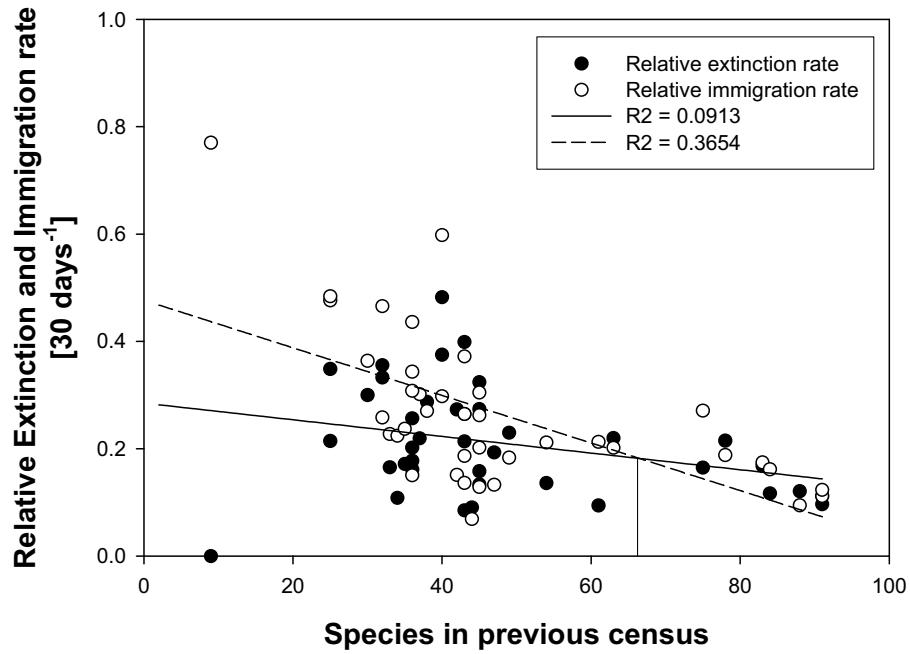
**Figure A 9:** Average number of pomacentrid and labrid fishes  $\leq 2$  cm observed at the three experimental sites in each census, with the number of recruits from the natural reef plots shown for comparison.



**Figure A 10:** Relative extinction  $\left( \frac{E_x}{S_{x-1}} \frac{30}{t} \right)$  and immigration  $\left( \frac{I_x}{S_x} \frac{30}{t} \right)$  rates in the Control plots ( $E_x$  is the number of species lost since the previous sample,  $S_{x-1}$  is the number of species in the previous sample,  $t$  is the time between the samples in days,  $I_x$  denotes the amount of new species in a sample and  $S_x$  is the number of species in the present sample).

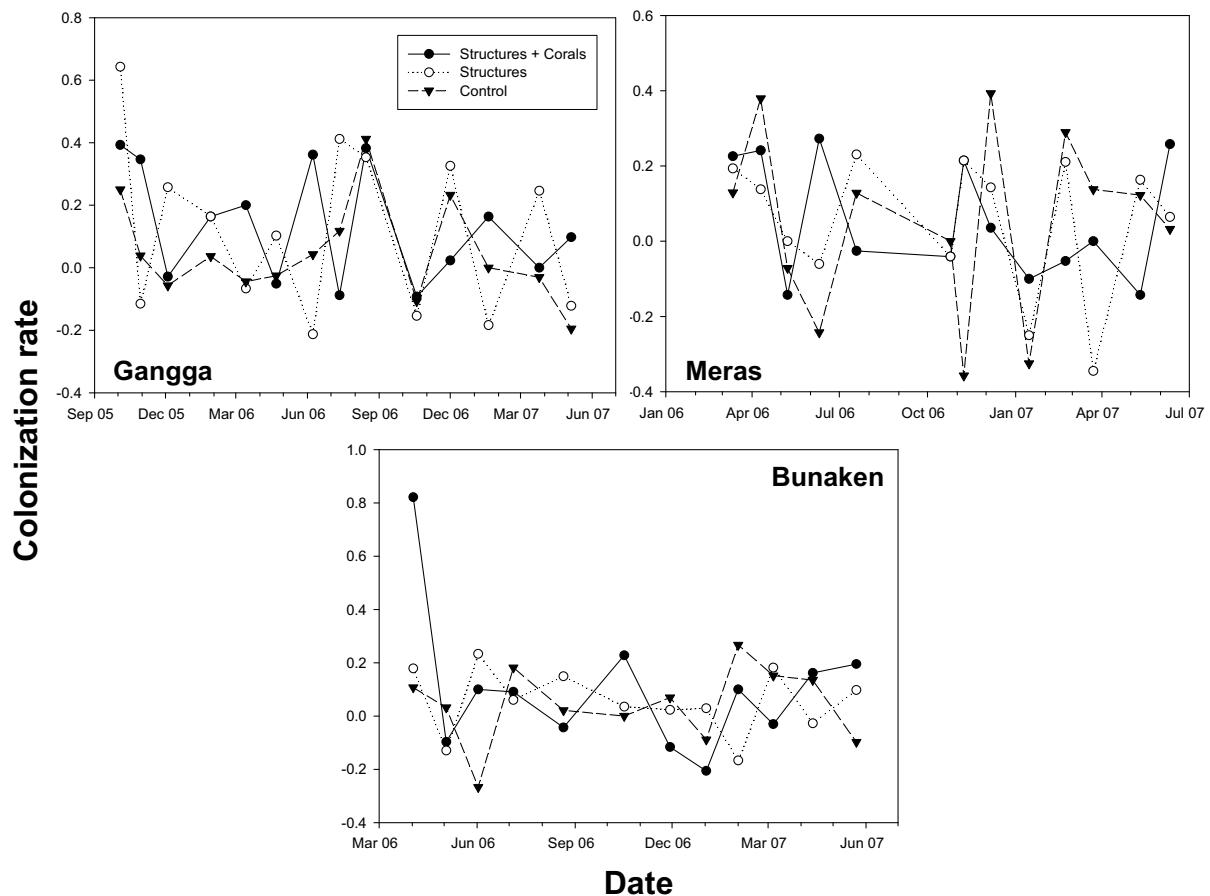


**Figure A 11:** Relative extinction  $\left( \frac{E_x}{S_{x-1}} \frac{30}{t} \right)$  and immigration  $\left( \frac{I_x}{S_x} \frac{30}{t} \right)$  rates in the Structure plots ( $E_x$  is the number of species lost since the previous sample,  $S_{x-1}$  is the number of species in the previous sample,  $t$  is the time between the samples in days,  $I_x$  denotes the amount of new species in a sample and  $S_x$  is the number of species in the present sample).



**Figure A 12:** Relative extinction  $\left( \frac{E_x}{S_{x-1}} \frac{30}{t} \right)$  and immigration  $\left( \frac{I_x}{S_x} \frac{30}{t} \right)$  rates in the Structure + Corals plots

( $E_x$  is the number of species lost since the previous sample,  $S_{x-1}$  is the number of species in the previous sample,  $t$  is the time between the samples in days,  $I_x$  denotes the amount of new species in a sample and  $S_x$  is the number of species in the present sample).



**Figure A 13:** Colonization rates (immigration – extinction rates) in the experimental treatments at each location.

































<i>Variola louti</i>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>0.3</b>	<b>0.0</b>	<b>0.3</b>	<b>0.3</b>	<b>1.0</b>	<b>0.7</b>	<b>0.0</b>	<b>2.0</b>	<b>1.7</b>
<i>Meiacanthus grammistes</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	2.0
<i>Pomacentrus nigromarginatus</i>	0.0	0.0	0.0	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	2.0
<i>Pomacanthus imperator</i>	<b>0.0</b>	<b>0.3</b>	<b>0.3</b>	<b>0.7</b>									
<i>Scarus forsteni</i>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>0.7</b>	<b>1.7</b>	<b>0.0</b>	<b>0.0</b>	<b>0.3</b>	<b>1.0</b>	<b>1.0</b>
<i>Pomacentrus brachialis</i>	0.0	3.7	9.0	7.0	2.3	0.7	1.3	1.0	0.0	0.0	0.3	2.0	4.0
<i>Zebrasoma veliferum</i>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>3.0</b>	<b>1.7</b>	<b>3.0</b>	<b>3.3</b>	<b>2.0</b>	<b>2.7</b>	<b>0.3</b>	<b>1.3</b>	<b>1.3</b>	<b>1.3</b>
<i>Scarus tricolor</i>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>1.0</b>	<b>0.3</b>	<b>1.3</b>	<b>0.7</b>	<b>1.7</b>	<b>0.7</b>	<b>0.7</b>	<b>0.3</b>	<b>1.0</b>	<b>0.7</b>
<i>Centropyge heraldi</i>	<b>0.0</b>	<b>1.0</b>	<b>0.3</b>	<b>0.7</b>	<b>0.7</b>	<b>2.0</b>	<b>0.7</b>						
<i>Thalassoma lunare</i>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>1.3</b>	<b>0.7</b>	<b>1.3</b>	<b>2.3</b>	<b>3.0</b>	<b>0.3</b>	<b>0.7</b>	<b>1.0</b>	<b>1.0</b>	<b>0.3</b>
<i>Chrysiptera bleekeri</i>	0.0	0.0	0.3	1.0	1.0	2.0	2.0	2.7	1.7	1.3	0.7	1.0	1.0
<i>Chaetodon kleinii</i>	0.0	1.0	2.3	7.0	5.3	5.3	8.3	7.7	3.0	1.7	2.0	3.3	6.7
<i>Ctenochaetus binotatus</i>	0.0	4.0	1.3	8.0	1.3	8.3	5.0	3.7	0.3	2.0	1.3	10.7	7.0
<i>Amphiprion clarkii</i>	<b>0.0</b>	<b>1.0</b>	<b>1.0</b>	<b>2.0</b>	<b>2.0</b>	<b>2.0</b>	<b>1.0</b>						
<i>Pomacentrus vaiuli</i>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>1.3</b>	<b>1.3</b>	<b>1.3</b>	<b>1.7</b>	<b>2.7</b>	<b>2.3</b>	<b>5.7</b>	<b>3.7</b>
<i>Acanthurus nigricauda</i>	0.0	4.3	4.0	4.0	2.3	4.3	5.3	2.0	2.3	2.7	3.7	1.3	0.7
<i>Centropyge flavicauda</i>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>1.7</b>	<b>0.3</b>	<b>3.3</b>	<b>4.3</b>	<b>4.0</b>	<b>5.7</b>	<b>6.7</b>
<i>Pomacentrus reidi</i>	0.0	12.7	22.7	17.0	7.0	4.0	4.7	8.0	6.0	13.7	5.3	13.3	25.0
<i>Halichoeres chrysus</i>	0.0	10.3	13.7	15.3	10.7	12.0	15.7	3.7	6.3	14.3	10.0	12.3	12.3
<i>Pomacentrus amboinensis</i>	0.0	6.7	14.0	9.7	6.7	3.7	11.3	6.0	3.7	16.0	17.0	32.3	37.0
<i>Paracheilinus</i> sp.	0.0	0.0	31.3	60.7	66.3	219.7	295.7	397.7	369.3	335.7	284.7	367.7	201.7