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EFFECTS OF LAND-BASED POLLUTION ON INDONESIAN CORAL REEFS: BIODIVERSITY, GROWTH RATES, BIOEROSION, AND APPLICATIONS TO THE FOSSIL RECORD.

By

EVAN NATHANIEL EDINGER, B.A., M.SC.

A Thesis

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POLLUTION AND INDONESIAN CORAL REEFS

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Abstract.

Land-based pollution has dramatic effects on coral species diversity, live coral cover, morphological composition of the coral fauna, coral growth rates, coral bioerosion intensity, and reef carbonate budgets. Pollution damage is measured in surveys of eight Java Sea reefs and eight reefs in Ambon and Sulawesi, Indonesia.

Reefs subject to land-based pollution show are 30-50% less diverse at 3m, and 40-60% less diverse at 10m depth, than unpolluted reefs in the same region. Polluted reefs are dominated by massive and submassive corals, and have almost no Acropora corals. Unpolluted reefs are dominated by Acropora at 3m, and by branching or foliose corals at 10m. Morphological composition ternary diagrams estimate reef conservation value.

Eutrophication has a two-faced effect on corals and coral reefs called the Janus Effect. Coral growth rates on polluted reefs are as high or higher than on unpolluted reefs. Coral growth rates in Java are positively correlated with eutrophication and sedimentation. Live coral cover and coral skeletal density are lower on polluted reefs than on unpolluted reefs, and bioerosion in highest on polluted reefs. The most eutrophic Java Sea reef has a negative carbonate budget, while an unpolluted fringing reef and coral cay both have positive carbonate budgets.

Bioeroding organism frequency in branching coral rubble follows trends in massive coral bioerosion on Java Sea reefs, and can be used as a non-destructive indicator of eutrophication on reefs. Individual sponge boring size accurately reflects total bioerosion in modern corals on the Great Barrier Reef. Sponge borehole size varies with both facies and nutrient level in Puerto Rican fossil reefs, and can be used to estimate paleoproductivity. Geography and oceanography of the Java Sea are similar to the reef-bearing Middle Devonian Onondaga Formation. Java Sea reefs can be used to develop facies models for eperic sea fossil reefs.

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A number of Canadian and American students and volunteers contributed to field work for various parts of this thesis. Hal Lescinsky helped design and establish experiments; Bill Mallchok helped document the coral mass spawning in 1995, and free-dove when necessary; Dave Luxford and Gina Lemieux helped measure transects in 1995, lead a free advanced diving course, and maintained all the gear; Dave Browne assisted with diving field work, sample collection, and interviews in Jepara and Karimunjawa; Kate Holmes helped design and implement the bioerosion study; Chris Boerboom helped section corals for the bioerosion study, and Jim and Ruth Campbell assisted with student histology projects and helped with field observations in Jepara. Ikra and Kay Ikranagara hosted me on my various visits to Jakarta.

Various friends in North America helped with research and/or critiqued proposals and various chapters, including Mairi Best, Farrell Boyce, Dave Browne, Paul Copper, Jeff Heikoop, Hal Lescinsky, John Pandolfi, Jennifer Rendell, and Nigel Waltho, and Steve Westrop. In addition, Richard Bromley, Rachel Wood, Stephen Bengtson, Paul Sammarco and an anonymous reviewer made helpful comments on chapter 7. Paul Sammarco and Robert Richmond made useful comments on the thesis as a whole. Marilyn Kereliuk (Radiology, McMaster Hospital) did X-rays of corals in Canada. Jeff Heikoop assisted in growth rate measurements from X-rays, and Jack Whorwood developed X-ray negatives into positives and psuedoreliefs. Erin Fitzgerald assisted with fossil borehole measurements, and Anu Rao assisted with computerizing maps and with the intensely frustrating but ultimately fruitless task of digitizing modern boreholes from X-rays using Arc-Info. Jim Garrett (Brockhouse Institute of Materials Science) designed and made the pycnometer for coral skeletal density measurements. Dave Browne, Jurek Kolasa, and Nigel Waltho assisted with statistics. The office staff at McMaster, including Edna Cutler, Medi Espiritu, Lynn Falkiner, Angela Oppermann, and Kathy Schowkenik, and at UNDIP, were always kind and helpful. Gary Vermeij, my former advisor at UC Davis, provided encouragement and useful suggestions. My parents, as ever, were supportive, and were there when I needed them.

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Preface.

A brief description of the UNDIP-McMaster project

Since 1990, McMaster University has been linked with Diponegoro University (UNDIP) in Semarang, Central Java, Indonesia, in a cooperative research, education, and training project sponsored by CIDA and (since 1995) the Association of Universities and Colleges of Canada (AUCC). When I first worked in Indonesia in 1991, it was as ESL teacher and research supervisor for 5 UNDIP lecturers who were chosen for M.Sc. studies in Canada as part of this same project. I began my post as On-Site Advisor in late 1994, and initiated research at that time. In 1995, CIDA renewed funding for the UNDIP-McMaster cooperation, and I returned to Indonesia for two more 6-month terms as On-Site advisor in 1995 and 1996.

The UNDIP-McMaster project does four basic things. It funds Ph.D. studies for 4 UNDIP lecturers at Indonesian universities. It funds several UNDIP staff and student research projects each year. It sponsors Canadian student research in Indonesia, in collaboration with Indonesian colleagues. And it arranges for publication of the results of this research in student theses, international journals and Indonesian magazines, and through conferences. My role as On-Site advisor included assisting all of these activities, and conducting research in conjunction with UNDIP staff and students. As such, most of my Indonesian research as presented in my dissertation is co-authored with one or several Indonesian colleagues. Individual Contributions to the various chapters are outlined below.

Contributions to co-authored chapters of this thesis.

Chapter 2: Reef Degradation and Coral Biodiversity in Indonesia: effects of land-based sources of pollution, destructive fishing practices, and changes over time. E.N. Edinger, J. Jompa, G.V. Limmon, W. Widjatmoko, M.J. Risk. In Press, Marine Pollution Bulletin. I conducted all the research in the Java Sea, along with various Indonesian students and with Wisnu Widjatmoko. Jamal Jompa and Gino Limmon collected environmental and life form transect data for Sulawesi and Ambon, while I collected species diversity data with them for those sites. I conducted all data tabulation and analysis, and wrote the paper.

Chapter 5: Bioerosion of massive corals and branching coral rubble on Indonesian coral reefs. E.N. Edinger, K.E. Holmes, Hariyadi, G.V. Limmon, M.J. Risk. To be submitted to Marine Ecology Progress Series. I designed and conducted the massive coral bioerosion sampling and analysis in the Java Sea, along with UNDIP students Badrus Zaman and H. Zahidin. Kate Holmes and I designed the coral rubble bioerosion sampling method and conducted this sampling together in the Java Sea, along with UNDIP lecturer Hariyadi. Kate Holmes continued both massive and branching coral bioerosion sampling in Ambon with Gino Limmon. Kate Holmes and I performed data tabulation and analysis, and I wrote the paper.

Chapter 6: The Janus Effect: do rapid coral growth rates mean healthy coral reefs? E.N. Edinger, G.V. Limmon, J. Jompa, W. Widjatmoko, M.J. Risk. Submitted to Coral Reefs. I conducted all the research in the Java Sea, along with various Indonesian students and with UNDIP lecturers Wisnu Widjatmoko and Hariyadi. Jamal Jompa and Gino Limmon collected environmental and life form transect data for Sulawesi and Ambon. I conducted all data tabulation and analysis, and wrote the paper.

Chapter 7: Sponge borehole size as a relative measure of bioerosion and paleoproductivity. E.N. Edinger, M.J. Risk, 1997. Lethaia 29: 275-286, 1997. This paper arose from re-analysis of data from my Masters research, combined with data from two papers on bioerosion from the Great Barrier Reef: Sammarco & Risk, 1990 (massive Porites bioerosion) and Risk, Sammarco, & Edinger, 1995 (branching Acropora bioerosion). I did the sample and data analysis and wrote the first draft of the Risk et al. (1995) paper. I re-measured fossil material from my M.Sc. research in 1995, analysed all the data together, and wrote the paper.

Chapter 1: Indonesian Coral Reefs and Land-Based Pollution.

1.1 Introduction

The coral reefs of Indonesia have attracted attention from naturalists and reef scientists for over 150 years; many of the initial descriptions of Indonesian coral reefs were written by Dutch explorers and researchers in the late 19th and early 20th centuries (Snellius Expedition, Umbgrove 1947, and many more). Indonesia harbours roughly one third of the world's coral reef area (Wells 1988), and lies close to the centre of diversity of scleractinian corals (Veron 1993; Wallace 1997) and other coral reef organisms (Veron 1995).

At the same time, Indonesian coral reefs are among the most threatened in the world. Anthropogenic threats to coral reefs are varied and numerous; the most publicised threats are blast fishing (e.g. CANORA1997) and poison fishing, chiefly with cyanide (Johannes & Reipen 1995), coral mining (Brown & Dunne 1988; Dulvy et al. 1995), and oil spills (Guzman, et al. 1993) along with general overexploitation of finfish (Roberts 1995) and coral reef invertebrate fisheries (McClanahan 1994). While some attention has been paid to the role of general land-based non-point source pollution to coral reefs (e.g. McManus 1988; Rasmussen et al. 1992), in general, the threat posed to Indonesian coral reefs by sewage pollution has not received much attention. Ranking such threats is dependent on the criteria in question: I have chosen to focus on biodiversity conservation, given Indonesia's recent addition to the 1994

UN biodiversity convention (COPD). Despite a population of nearly 200m people, nowhere in Indonesia is sewage treated; untreated sewage discharge from Jakarta and Ujung Pandang undoubtedly affect the health of coral reefs in the nearshore islands of the Pulau Seribu (Harger 1992) and the Spermonde Archipelago (Jompa 1996; Erdmann and Caldwell 1997), respectively . In one of the papers included in this thesis, I argue that land-based sources of pollution, especially the common and widespread dumping of untreated sewage into coastal waters, may present the greatest threat currently facing Indonesian coral reefs.

Any discussion of the effects of sewage on coral reefs must include a general discussion of the effects of nutrient excess, or eutrophication, on coral reefs. While researchers in Australia have been pursuing the ENCORE experimental research program (e.g. Larkum and Koop 1997; Tentori, et al. 1997; and others), I have chosen to focus on comparative and survey-based approaches, which are more appropriate to an Indonesian context where scientific and laboratory infrastructure is limited, and it is difficult to perform field or lab experiments requiring carefully controlled conditions.

Indonesia's coral reefs form an exemplary natural laboratory, with a wide range of reef geomorphologies and oceanographic environments. As such, Indonesia provides a good source of modern analogues for fossil coral reefs. I have focused in particular on the Java Sea, a modern tropical epicontinental sea, as an analogue for Paleozoic epeiric sea coral reefs, such as the patch reefs of the Middle Devonian Onondaga formation of Ontario and New York State.

This thesis, then, has three purposes. First, it examines the health of Indonesian reefs, and threats to their health, particularly from the standpoint of biodiversity conservation, but also looking at the effects of sewage pollution on coral and coral reef growth. Second, it explores the roles of nutrients, and nutrient pollution, on modern coral reefs of Indonesia, and discusses applications of insights from Indonesia to the fossil record. Third, it draws initial comparisons between modern coral reefs of the Java Sea, a modern epicontinental sea, and Paleozoic coral reefs from epeiric sea paleoenvironments, in terms of reef zonation, onshore - offshore facies patterns, and biogeographic differences between epeiric sea coral reefs and the open ocean counterparts. These three foci together are a tall order, and the treatment of each of them is necessarily incomplete. Certain parts of this thesis, particularly the Paleozoic comparison, are not intended as exhaustive treatments, but rather as starting points, to get ideas into the literature for various researchers to follow up on at a later time. Nor is this work intended to stand alone; much of my work has relied upon co-operative efforts with colleagues in Indonesia, Canada, and the U.S., and several papers resulting from our collective efforts will be published elsewhere.

1.2 Species Diversity and Morphology of Indonesian coral reefs.

The biodiversity and reef degradation paper (chapter 2) quantifies the effects of land-based pollution, especially the combination of sewage and sedimentation, on species diversity of scleractinian corals. This research is based on surveys in Sulawesi (Jompa 1996) and Ambon

(Limmon 1996) and in the Java Sea. Biogeographic distributions of corals and other marine invertebrates with planktonic larvae tend to be widespread, but not generally pandemic (Scheltema 1986; Veron 1993; Edinger & Risk 1995).

The biodiversity data collected in three parts of Indonesia for the biodiversity and reef degradation paper (chapter 2) also provide a useful dataset for examining biogeographic differences between Java Sea coral reefs and their Eastern Indonesian counterparts (chapter 3). These biogeographic differences are of interest for several reasons. First, Indonesian waters are tremendously important in global marine biodiversity, yet there has been little study on biogeographic variation within Indonesia (Wallace 1997). Second, similarity analysis of species records may help to separate the effects of overfishing in the Java Sea from inherent biogeographic differences between eastern Indonesia and the Java Sea.

In chapter 4, I compare the morphological life form composition of onshore and offshore coral reefs of the Java Sea, and with their counterparts in Sulawesi, using the same dataset from chapter 2. The morphological composition of the reef-building corals at a given site can be likened to biofacies patterns within fossil reefs, and will eventually be compared with such biofacies patterns from Paleozoic epeiric sea reefs. In chapter 4, I show that depth- and exposure-related biofacies changes are much less extreme than the onshore-offshore facies changes. I further present a method for estimating the conservation value of reefs based on ternary diagram plots of their morphological composition. Such a method is particularly appropriate in Indonesia, where few researchers have training or experience in coral taxonomy, and nearly all reef survey and monitoring data is collected using stardardized morphological categories (English and Wilkinson 1993). This method for estimating conservation value of reefs can update earlier efforts at defining guidelines of coral reef reserve design and zonation (e.g. Salm 1984; Johannes and Hatcher 1986).

1.3 Nutrients and Coral Reefs.

The roles of nutrients in coral metabolism and coral reef health are imperfectly understood at best. Systems ecologists have modelled nitrogen and phosphorus cycling on coral reefs, and isotope geochemists and biochemists have further elucidated nutrient dynamics and some of the effects of nutrient loading on corals (e.g. Muscatine & Kaplan 1994; Mendes et al. 1996; Heikoop et al., in press). Geologists have focused on the roles of nutrients in reef growth, in particular, on limiting reef growth (e.g. Hallock & Schlager 1986). The effects of nutrients are often confounded with effects of sedimentation and/or turbidity, both for direct effects of sediment on corals (Rogers 1990) and for light limitation (Heikoop 1997). This thesis includes two chapters on the effects of nutrient loading on coral reefs: one on coral growth rates and coral reef health (chapter 6) and one on bioerosion of corals, and the influence of nutrient loading on bioerosion (chapter 5).

One way that nutrients affect corals is on their growth rates. The Janus Effect paper (chapter 6) documents a paradoxical pattern of enhanced coral growth, but retarded coral reef growth, on reefs subject to eutrophication. I invented the term "Janus effect" as part of my M.Sc. research, to help explain the absence of large shelf-edge reef build-ups in the Caribbean Miocene, a time and place of greatly enhanced upwelling (Edinger 1991; Edinger & Risk 1994). This chapter documents the Janus effect on modern reefs of Indonesia, the first time that the Janus effect has been described for modern reefs. Specifically, the Janus Effect predicts rapid coral growth rates coupled with low live coral cover and high bioerosion under eutrophic conditions, resulting in negative carbonate budgets, low or negative reef accretion rates, and ultimately, drowned reefs. The Janus Effect thus also illustrates the decoupling of coral growth and reef growth (Potts 1997) on an ecological timescale.

The mechanisms by which eutrophication can stimulate growth of individual corals are not completely clear. The Java Sea data suggest a combination of morphological and metabolic effects. Whether the metabolic effects reflect increased heterotrophy (Risk et al. 1994) or fertilized autotrophy (Steven and Broadbent 1997) cannot be determined from the data available here. From the geological perspective, however, this is less important than the end result: negative carbonate budgets, negative reef accretion rates, and drowned reefs resulting from eutrophication.

An interesting parallel pattern has been previously documented in Barbados, where juvenile corals are larger, but fewer, and have lower survivorship rates, on eutrophied reefs than on their less eutrophic counterparts (Wittenberg & Hunte 1992). Again, this chapter draws partly on the work of Jamalluddin Jompa and Gino Limmon for the Sulawesi and Ambon portions of the dataset.

Another effect of nutrients on coral reefs is to enhance bioerosion rates and intensities; this pattern has been extensively documented elsewhere (Risk & MacGeachy 1978; Highsmith 1980; Rose & Risk 1985; Sammarco & Risk 1990; Keine & Hutchings 1994; Chazottes et al. 1995; Risk et al. 1995); its effects on fossil reefs have also received considerable attention (Hallock & Schlager 1986; Hallock 1988; Wood 1993). As part of my general research program in the Java Sea, I wanted to include some research on bioerosion and carbonate budgets, but something that would be relatively non-destructive, given the already tattered condition of nearshore reefs in the Java Sea. Katherine Holmes' M.Sc. thesis research (Holmes 1996) provided a new, easy, non-destructive bioindicator for measuring bioerosion and monitoring effects of eutrophication on coral reefs, looking at the abundance of boring sponges in branching coral rubble. In the bioerosion paper (chapter 5), Kate Holmes, Hariyadi, Gino Limmon and I test her rubble method on 9 Indonesian coral reefs, comparing it with bioerosion measured in massive corals using X-rays of slabs (method follows Sammarco & Risk 1990). Our results show that the coral rubble provides an inexpensive, easy, and accurate rapid assessment tool for bioerosion, and for indicating eutrophication stress on coral reefs, which is even more sensitive to eutrophication than is massive coral bioerosion.

1.4 Nutrients and Coral Reefs in the Geologic Record.

The eutrophication gradient along the west coast of Barbados has provided fertile waters for a number of studies on the effects of eutrophication on corals and coral reefs (Scoffin, et al. 1980; Tomascik & Sander 1985, 1987; Tomascik 1991; Wittenberg & Hunte 1992; Holmes 1997, and many more). These various studies have demonstrated reduced live coral cover (Tomascik & Sander 1985), reduced coral growth rates (Tomascik & Sander 1987), decreased coral recruitment (Tomascik 1991), increased size of coral recruits (Wittenberg & Hunte 1992), increased algal cover (Wittenberg & Hunte 1992), increased bioerosion (Holmes 1997), and other patterns along this coast in response to a combined gradient of increasing dissolved nutrient concentrations, biotic pigment concentrations, sedimentation rates, and turbidity. Hallock & Schlager (1986) examined the coral reefs of Barbados as part of their overview of the effects of nutrient excess on coral reefs.

Hallock et al. (1988) attributed the lack of reef development on the Nicaraguan Rise to a doubling of water column biotic pigment (chlorophyll A + phaeopigments) concentrations relative to pigment concentrations off the north coast of Jamaica, where coral reef growth was quite vigourous until recently (Hughes 1994). The increased nutrient availability on the Nicaraguan Rise comes from terrigenous runoff and from wind-driven topographic upwelling, raising chlorophyll A concentrations to 0.25 μg/l, a level similar to ambient levels in the Karimunjawa islands (see chapters 2, 4). While the nutrient levels on the Nicaraguan rise are not extreme, they are apparently just enough, combined with minimal fish grazing, to push the Rise beyond the limits of reef growth. While corals are present on the banks of the Nicaraguan Rise, they usually are not abundant enough, nor large enough, to build framework deposits (Hallock, et al. 1988).

Nutrients levels are one of the primary factors controlling development of coral reefs in the fossil record, along with temperature, turbidity, and siliciclastic sedimentation (Hallock & Schlager 1986; Wood 1993; Kauffman and Fagerstrom 1993; Wood 1995). Eutrophic, oligotaxic periods in pelagic waters (Fischer & Arthur 1977) favour the development of mixotrophy among reef-building invertebrates (Wood 1995), in turn favouring development of large barrier reef complexes, which are the exception, rather than the rule, in the Phanerozoic history of reefs (Wood 1993). Fluctuations in the relative importance of various guilds on Phanerozoic reefs also appears to respond to nutrient availability (Fagerstrom 1987; Kauffman and Fagerstrom 1993). This trend is particularly strong for the bioeroder guild, but also affects reef binders (encrusting algae) and various reef-resident taxa.

The Late Devonian mass extinction has long been the anomaly among mass extinctions, in that the usual mechanisms invoked to explain mass extinctions (e.g. glaciation, regression, climatic cooling, bolide impact, reduction of faunal provinces, continental mergers) all lack sufficient evidence to convince most researchers. The Late Devonian extinction also coincides with the development of widespread terrestrial forests, and Tappan (1982) suggested that forest expansion is frequently correlated with extinction of marine invertebrates as forests reduce the runoff of terrestrial nutrients into continental seas. This idea coincides with Fischer and Arthur's idea that mass extinctions occur during short oligotaxic periods characterised by enhanced upwelling and lack of extensive black shales. Similarly, Vermeij (1995) has proposed that biological innovations among molluscs and other heterotrophic groups primarily occur during times of increasing nutrient availability, often in association with massive submarine volcanism. Similarly, within-community species diversity has a typical hump-shaped curve along nutrient gradients, both in modern and fossil ecosystems (Rosenzweig and Abramsky, 1993)

Nutrients, then, played a crucial role in the development of Phanerozoic reefs: their scarcity favoured mixotrophy and the growth of large shelf-edge barrier reef complexes, while their abundance favoured bioerosion, mound-bank facies, and relatively smaller, though often more extensive, reef building. Nutrients may have encouraged expansion of other guilds of reef-dwelling organisms, but may not have been important in favouring taxonomic radiation among the reef-building taxa themselves.

1.5 Applications of modern research to the fossil record.

Two further chapters focus on research on modern corals and coral reefs, but can be applied to questions in paleoecology, specifically paleoproductivity, taphonomy, and epeiric sea reef facies models. In Chapter 7, I use the size of unicamerate sponge borings to decipher patterns of paleoproductivity and taphonomy on fossil reefs in Puerto Rico. This chapter draws heavily on previous bioerosion studies of bioerosion in modern massive (Sammarco & Risk 1990) and branching corals (Risk et al. 1995) across the continental shelf of the Great Barrier Reef. These results are then compared with bioerosion data from an earlier investigation of the roles of turbidity, temperature, and nutrients in contributing to a regional extinction and geographic restriction of Caribbean corals in the early Miocene (Edinger & Risk 1994). I re-measured fossil boreholes from Oligocene and Miocene corals (Edinger 1991), and re-analysed data from the two Australian bioerosion papers, to evaluate the performance of sponge borehole size as an indicator of paleo-bioerosion and paleo-productivity.

Chapter 7 then documents how the differences in borehole size are also controlled by host coral-related (e.g. McKenna 1997) and facies-related taphonomic factors (e.g. Pandolfi and Greenstein 1997), which complicate interpretation of sponge borehole size as a strict indicator of paleoproductivity. Various researchers have used abundance or size of fossil borings to interpret paleoproductivity, but patterns of productivity are muddied by patterns of burial or reworking, or in general, the length of time shells or corals remain in the taphonomically active zone. For example, Pandolfi and Greenstein (1997) found that bioerosion of dead corals was less intense on the exposed side of Orpheus Island, on the Great Barrier Reef of Australia, than on the protected side. Likewise, bioerosion was less intense at shallow sites than at deep sites. They interpreted these patterns as results of differences in exposure level, where greater wave energy at the exposed site either buries corals or transports them away, hence making them unavailable to bioeroding organisms.

Finally, chapter 8 compares the oceanography and sedimentology of the Java Sea and the Appalachian Basin, and puts them both in the context of circulation models for epeiric seas. Epeiric seas were broad shallow epicontinental seas, often with restricted circulation, that covered much of North America during the Paleozoic, and are the source of much of the Paleozoic invertebrate fossil record (Boucot 1988). The Java Sea is one of the very few modern epicontinental seas, along with Hudson Bay, the Baltic Sea, the North Sea, and the Arafura Sea - Torres Straits region between Australia and New Guinea (Woodroffe 1993) that can be used as mondern analogues for Paleozoic epeiric seas. Chapter 8 discusses oceanographic models for epeiric seas and establishes the validity of the Java Sea as a modern analogue for the Middle Devonian Onondaga Formation, which lies at the base of the Middle Devonian series in the Appalachian Basin.

The Sunda Shelf, comprising the Java Sea and southern portion of the South China Sea, is surrounded by land on most sides, is less than 70m deep throughout its extent, and has mixed carbonate and clastic depositional environments (Wyrtki 1961; Tjia 1980; Dewi 1993; Cecil et al. 1993), making it the best modern analogue for epicontinental sea environments that covered much of North America during the Paleozoic. Cecil et al. (1993) have compared nearshore siliciclastic dominated mangrove environments of the South China Sea to Pennsylvanian coal-bearing rocks in the Appalachian basin.

The faunal differences between the Java Sea and Eastern Indonesia (chapter 3, chapter 4) are important for using the Java Sea as a modern analogue to Paleozoic epeiric seas of North America and elsewhere (chapter 8). Recent and past work on Devonian corals of North America has shown considerable biogeographic differences between the coral faunas of epeiric seas in the Eastern Americas realm vs. open-ocean regions in north-western North America and elsewhere in the Old World realm (Oliver 1977; Oliver 1980; Boucot 1988).These and other factors are considered in chapter 8, as a prelude to future papers comparing species diversity, morphological, and taphonomic patterns of Java Sea reefs with Onondaga Fmn. and other Paleozoic epeiric sea reefs (Lescinsky and Edinger 1997; Edinger, in preparation).

1.6 Geography and Oceanography of the Java Sea.

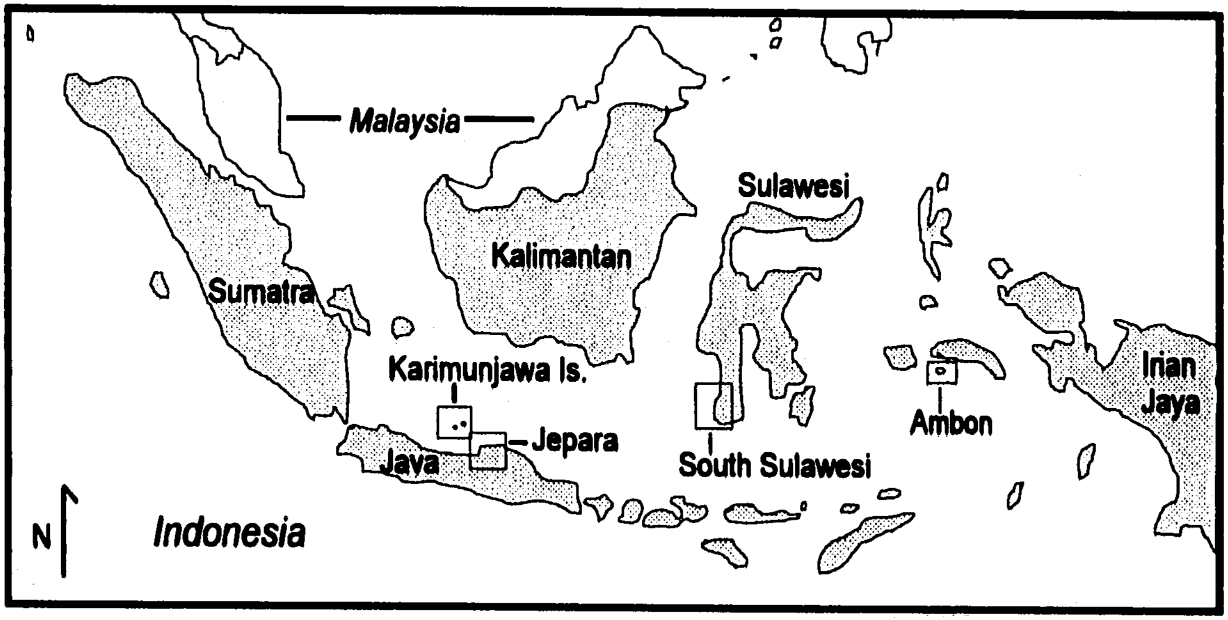
Because the core dataset for this thesis derives from the Java Sea, it is important to discuss the geography and oceanography of the Java Sea before describing individual study areas (section 1.7). The Java Sea is about 300 km wide and 1000 km long, and is bounded by Java and Sumatra to the South and West, Borneo to the North, and the much deeper waters of the Makassar Strait and Bali Sea to the East. The Java Sea is quite muddy, particularly in the rainy season, with significant fluvial sedimentation and nutrient flux from major rivers in Java, Borneo, and southern Sumatra (Wyrtki 1961; Dewi 1993). At no point is the Java Sea deeper than 70m, and the entire Sunda Shelf was exposed during the Pleistocene glaciations. An extensive network of submerged river canyons cuts the sediments of the Sunda Shelf, draining east to the Bali Sea or north into the China Sea (Wyrtki 1961). These channels are visible in side scan sonar, and may still act as sediment conduits (Dewi 1993)

Monsoonal current systems dominate the Java Sea, flowing westward in the dry season (April to October) and eastward in the wet season (November to March). Salinity usually varies between 30-32 ppt, with up to 5 ppt seasonal variation in some coastal areas, particularly along the south coast of Borneo (Wyrtki 1961). Water temperature in the Java Sea areas in this study varied less than 2°C between the wet season and the dry season.

Abundant terrigenous nutrients and warm shallow water favour photosynthesis, but the biological oxygen demand is quite high, leading to anoxic conditions in some nearshore muddy sediments (Dewi 1993; EE, unpublished data). The Java Sea is too shallow, however, to develop a true oxygen minimum zone in the water column, such as develops in deeper basins of the South China Sea (Wyrtki 1961). Cool, nutrient-rich water upwells from the Makassar strait onto the eastern edge of the Sunda shelf, and may be in part responsible for the extensive development of Halimeda bioherms on the edge of the shelf, and on the Kalukalukuang Platform, immediately east of the Java Sea (Roberts et al. 1987, 1988). During the rainy season (west monsoon), wind-driven circulation generates waves frequently exceeding 3-4m in height; these waves are capable of mixing Java Sea waters for much of their depth, and may move bottom sediments in coastal portions of the Java Sea floor (Dewi 1993). The extent to which coral reefs affect the oceanography and sedimentology of surrounding waters in the Java Sea is unclear, but is thought to be extensive, as illustrated by sediment composition and by ostracod faunal composition near Bawean Island, approximately 150 km east of Karimunjawa (Dewi 1993).

Coral reefs are found in various parts of the Java Sea, including scattered fringing reefs and coral cays along the north coast of Java, shallow carbonate platform reefs in the Pulau Seribu area north of Jakarta, several archipelagos running along a structural arch trending east-west through the Java Sea, and near the eastern shelf edge. The Karimunjawa islands, 100 km north of Jepara, in central Java, represent the largest and most easily accessible group of relatively unaffected Java Sea coral reefs. While the Pulau Seribu are more easily accessible and have received much more study than any other group of Java Sea coral reefs (e.g. Brown 1985; Brown & Suharsono 1990), many of the reefs close to Jakarta are dying or dead, due to pollution from Jakarta (Brown & Suharsono 1990; Harger 1992; Uneputty and Evans 1997), and they do not make an ideal study area for natural effects. Recent reports indicate that many of the reefs in the northern end of the Pulau Seribu have been damaged by oil pollution from oil fields to the Northeast of the archipelago (Willoughby, pers comm., 1996; Uneputty and Evans 1997).

Figure 1.1. Map of Indonesia showing study regions.



1.7 Study areas.

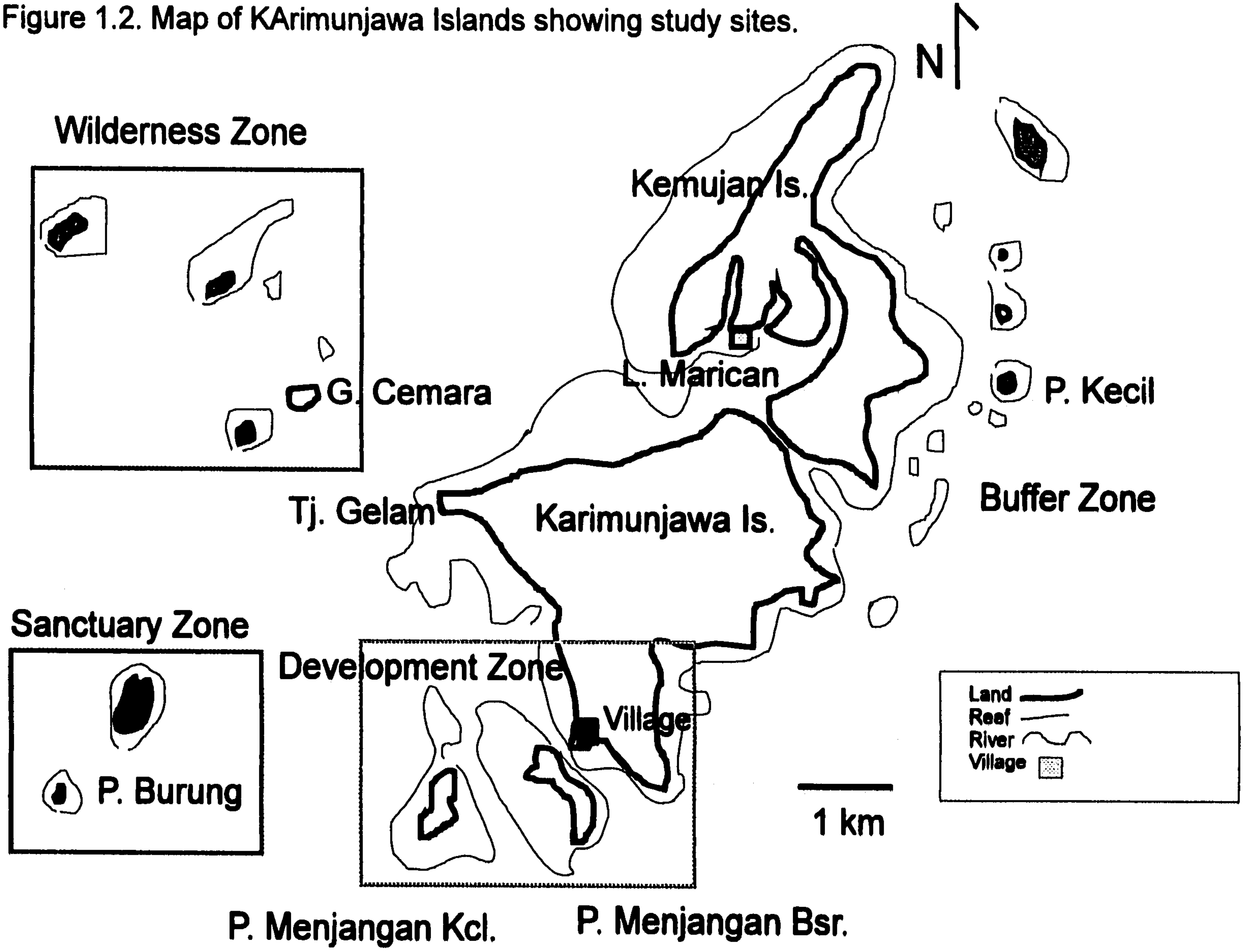
In the remainder of this introduction, I describe the study areas in the Java Sea, and to a lesser extent, those in Ambon and Sulawesi, which have already received some discussion elsewhere (Jompa 1996; Limmon 1996). Maps of the areas sampled in this thesis are shown in figures 1.1 to 1.5. The research in this thesis was mainly conducted in three parts of Indonesia (fig 1.1): Central Java, South Sulawesi, and Ambon (Moluccas). The reefs in the eastern Indonesian regions (Sulawesi and Ambon) were each the subject of M.Sc. theses (Jompa 1996; Limmon 1996), and are discussed more fully in those works. The Java Sea sites consisted of offshore reefs in the Karimunjawa islands and nearshore reefs in the Jepara region. Indonesian researchers, principally at Diponegoro University, have conducted extensive research on the coral reefs of Karimunjawa (e.g. Susanto 1994) and Jepara (e.g. Bachtiar 1994), but virtually none of this is published in English.

1.7.1 Java Sea study sites.

Karimunjawa National Marine Park (fig 1.2) lies about 100 km north of Jepara, in one of the deepest parts of the Java Sea (maximum depth surrounding the islands is 52m). The 27 islands of the Karimunjawa archipelago are a mix of five high islands composed of Cretaceous arkosic sandstone to feldspathic quartzite and Miocene Pliocene volcanic bedrock, and a larger number of small coral cays scattered around the high islands (Nayoan 1975; Sidarto, et al. 1993). Water depth surrounding some of the reefs of Karimunjawa descends to 52m, and most reefs rise from a sandstone bedrock basement in about 40m of water. Maximum depth of coral growth ranges from 15m to 35m in the various sites observed in the archipelago (pers.obs). Given their distance from the island of Java, the reefs of Karimunjawa may have among the lowest rates of clastic sedimentation and terrigenous input of any reefs in the Java Sea (Dewi 1993; Edinger, unpublished data), save those at the eastern edge of the Sunda shelf (Roberts et al. 1987).

Nearshore reefs in the Jepara area (fig. 1.3) include both fringing reefs and a few platform reefs rising from 10-12m water depth, such as P. Panjang and P. Bokor. Fringing reefs line small promontories along the coast; most of the bays are composed of mixed carbonate-clastic sand and mud. Coral and seagrass biostromes are found close to the shore in many areas, and are much more widespread than are wave resistant reefs (Kamiludin et al. 1991). Rapid coastal erosion is common in the Jepara area; coastline retreat rates as high as 500m in 50 years have been reported (Kamiludin et al. 1991), although erosion rates are probably much lower in most cases. Coral reef coastlines are eroding at a slower, but still measurable rate, on the order of 10-20m/100 yrs. (Kamiludin et al. 1991). Subaerially exposed Holocene reefs on P. Panjang are being eroded on al sides, and the island has decreased in size by about 10-15% since 1944 (Kamiludin et al. 1991).

Figure 1.2. Map of KArimunjawa Islands showing study sites.



Seven reefs were sampled intensively in the Karimunjawa and Jepara areas, representing a range of habitats. These reefs were sampled for coral species diversity, coral life form and cover classes, coral growth rates, and bioerosion. Molluscan taphonomy experiments (Lescinsky and Edinger 1997) were conducted at two of the reefs (G. Cemara, Karimunjawa; P. Panjang, Jepara), with settling plates for an artificial reef experiment deployed in five locations at three reefs (Edinger et al. 1996; Widjatmoko et al. 1996).

Chlorophyll A concentration, suspended particulate matter concentration (SPM), sediment resuspension into sediment traps, sediment composition and light intensity were measured at most of these reefs; in some cases, sediment traps were not deployed, due to time constraints. Two McMaster theses examined stable carbon (Lazier 1997) and nitrogen (Dunn 1995; Lazier 1997) isotope ratios in corals from the Jepara sites. While some minimal discussion of the isotope data are included here, the data themselves are not reported in this thesis.

_1.7.2 Karimunjawa.

Five reefs were sampled in the Karimunjawa islands national marine park. Two of the Karimunjawa reefs represent the unaffected reef condition for the Java Sea, except that all the reefs in Karimunjawa are subject to intense fishing pressure (Susanto 1994; see chapter 3). Coral mining is common on Karimunjawa reefs closest to villages, with effects similar to those described from the Maldives (Brown and Dunne 1988) and Zanzibar (Dulvy et al. 1995). In all but the fringing reef, both the windward and leeward sides, at both 3m and 10m depth, were sampled, yielding four transect datasets for each reef, plus one for L. Marican.

Two Karimunjawa reefs, Pulau Kecil and Gosong Cemara, show no obvious signs of mechanical damage, and are well isolated from mainland anthropogenic sources of terrigenous nutrients and sedimentation, but they are subject to intense fishing by conventional non-destructive means. These represent the unaffected reefs for the Java Sea. P. Kecil is an uninhabited vegetated coral cay, approximately 250m x 250m, and lies to the east of the high island of Karimunjawa; G. Cemara is a submerged, unvegetated sand cay, about 200m x 100m, and lies to the west of Karimunjawa island. Maximum depth of reef growth is 25m at P. Kecil and 20m at G. Cemara. Chlorophyll A and SPM values were both higher at G. Cemara than at P. Kecil (table 2.2), probably reflecting slight influence of the high islands P. Karimunjawa and P. Kemujan, which lie upwind from G. Cemara during the dry season.

Three other reefs in Karimunjawa affected by various natural factors were sampled for this study: Pulau Burung, Pp. Menjangan, and Lagun Marican. Pulau Burung, an uninhabited vegetated coral cay, is the southernmost island in the archipelago. Local residents of Karimunjawa island say that P. Burung was hit by a major storm in 1992 that left a large rubble rampart (Scoffin 1993) on the windward (S) reef flat. There is little or no evidence of storm damage on the leeward (N) side of the island. SPM values are among the lowest we measured in Karimunjawa, and were lower on the windward than the leeward side. Chlorophyll A values were somewhat higher than at the other open water reefs in Karimunjawa (table 2.2), but do not indicate eutrophic conditions. Maximum depth of reef growth was 25m on both sides of the island. The windward side of P. Burung represents storm damage of a similar intensity to the anchor and bombing damaged reefs sampled in Sulawesi.

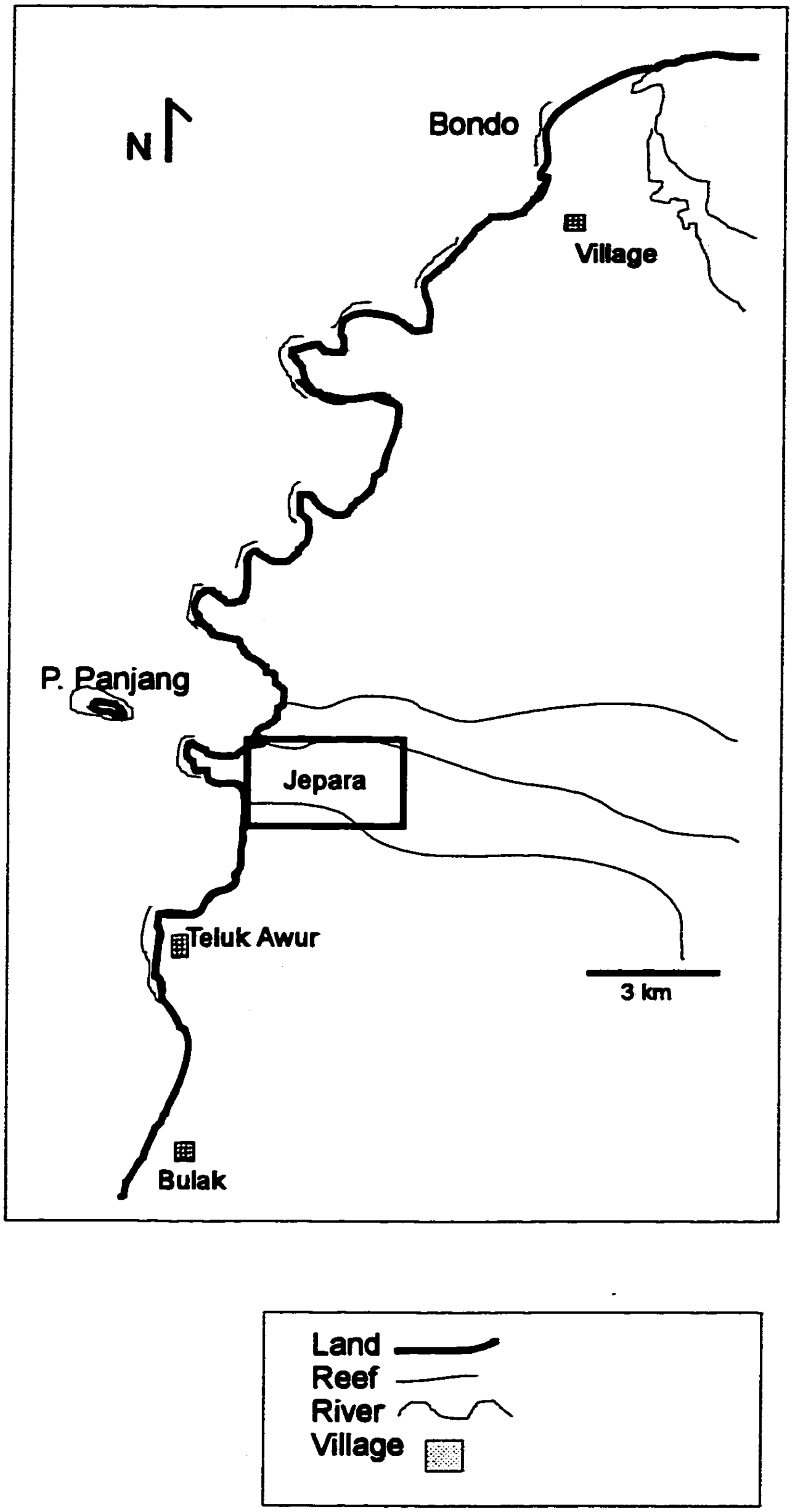
Pulau Menjangan Besar and P. Menjangan Kecil are two inhabited coral cays immediately across the harbour from Karimunjawa village, which have been zoned for tourism development. P. Menjangan Besar has a small quartzite hill at its southern (windward) end, although the reef extends considerably south of the island. These reefs were primarily sampled in December 1994, at a time when heavy surf precluded sampling on the most exposed windward (S-facing) reefs of the two islands. The windward portions of these reefs sampled, then, are in the channel between the two islands, close to the S end of the reef, but in a location somewhat more protected than the most exposed windward reef. Subsequent snorkel surveys (Sept., Nov. 1996) suggested that the coral community sampled in the channel is not much different from the coral community on the more exposed windward reef front. Because only four transects were sampled at each exposure on each island (rather than the usual 6), I pooled the data from P. Menjangan Besar and P. Menjangan Kecil into a single sample set, Pp. Menjangan, segregated into windward and leeward, 3m and 10m.

The reefs at Pp. Menjangan are dominated by large monospecific stands of branching corals (Porites cylindrica) and foliose corals (Pavona cactus, Echinopora lamellosa, Montipora foliosa), and appear typical of low diversity reefs at a late successional stage (Loya 1976; Connell 1978;

Aronson and Precht 1995). Unfortunately, at the original time of sampling, some of the taxonomic data was collected by students and volunteers without my supervision, and is unreliable, although the morphology data in the transects is quite accurate. I resampled some portions of P. Menjangan Kecil, verifying that the initial patterns observed do reflect the reef as a whole, but I was not able to repeat sampling on the whole reef. Therefore, the Pp. Menjangan data is used in morphological composition analyses, but not in species diversity analyses.

Lagun Marican is a mangrove-lined inlet between Karimunjawa island and Kemujan island. The bottom sediment is carbonate mud in the outer portions of the lagoon, and siliciclastic mud in the inner areas of the lagoon. We sampled a fringing reef adjacent to healthy mangroves in the outer, carbonate mud, portion. Chlorophyll A and SPM values at this site were higher than elsewhere in Karimunjawa, and comparable to those on the nearshore reefs in Jepara. Maximum depth of coral growth is 4m, and we sampled at 3m only. The Lagun Marican reef, adjacent to mangroves, has high sediment and high nutrient conditions similar to those experienced by nearshore reefs in Jepara, but without toxins and pathogens from sewage and other pollution, and represents a natural comparison for anthropogenically stressed reefs like those in Jepara.

Figure 1.3 Map of Jepara region showing reefs studied.



1.7.3 Jepara.

The nearshore reefs in Jepara are the most degraded that we sampled during this study, and were rated among the most degraded reefs in Indonesia by a LIPI survey based on live coral cover (Moosa and Suharsono 1996). Two reefs were sampled: Pulau Panjang, a coral cay close to the town of Jepara (population ca. 50,000), and Bondo, a fringing reef about 20km Northwest of the town of Jepara. Preliminary analyses suggest significant Zn and Cu contamination in Jepara bay (Dunn 1995).

Pulau Panjang is a coral cay approximately 4km from the town of Jepara, a rapidly expanding centre in the furniture and wood carving industry, but which also has extensive development of shrimp aquaculture ponds (tambaks). The island receives large inputs of sewage pollution and siliciclastic sediment from coastal rivers emptying into Jepara Bay and nearby Awur Bay, as evidenced by high chlorophyll A and SPM concentrations (table 2.2), and by $\delta^{15}N$ values in corals (Bachtiar 1994; Dunn 1995; Lazier 1997).

Sediment resuspension rates are up to 10x higher than in the Karimunjawa sites. Maximum depth of reef growth on both the windward and leeward sides of Pulau Panjang is 7-8m; we sampled both windward and leeward at 3m and 6m depth. The reefs in Jepara represent reef growth under highly eutrophic, high sedimentation conditions, resulting from sewage pollution, sedimentation, and aquaculture effluent.

Bondo reef is a fringing reef adjacent to a raised Holocene beach which is mined for coral gravel. The site receives large inputs of siliciclastic muds further up the coast, as well as carbonate sand from the adjacent beach. There is a small fishing village just south of the reef, and another about 5km further north. Coastal population density is considerably lower than in Jepara. We sampled Bondo reef as an example of a nearshore reef subject to high sedimentation loads, but without sewage pollution. Chlorophyll A concentrations are slightly lower than in Jepara (table 2.2), but $\delta^{15}N$ values in corals are higher than at P. Panjang (Lazier 1997), suggesting agricultural runoff, rather than sewage, as the source of nutrients. Light intensity and SPM values are similar to those in at Pulau Panjang (see table 6.2). Sediment resuspension data for Bondo are poorly constrained, because the 3m sediment trap (see section 2.2) was repeatedly lost. Sediment resuspension rates reported for Bondo are 1m resuspension rates x 0.39, the coefficient relating 1m and 3m sediment resuspension rates at Pulau Panjang.

1.7.4 Eastern Indonesian study areas.

Eight reefs were sampled in regions of Eastern Indonesia (Ambon, fig 1.4, Limmon 1996; South Sulawesi, fig. 1.5. Jompa 1996). I assisted each of those students with field work in August - Sept. 1995, particularly for measuring coral species diversity at each reef. They collected environmental data (chlorophyll A concentration, nitrate, phosphate concentrations, suspended particulate matter, sediment resuspension, and water clarity) which are summarised here. More complete discussion of these study sites and their environmental data are presented in Limmon (1996) and Jompa (1996). The four Ambon reefs studied here were also sampled for beach litter and biological indicators of organotin contamination in 1993 (Evans et al. 1995).

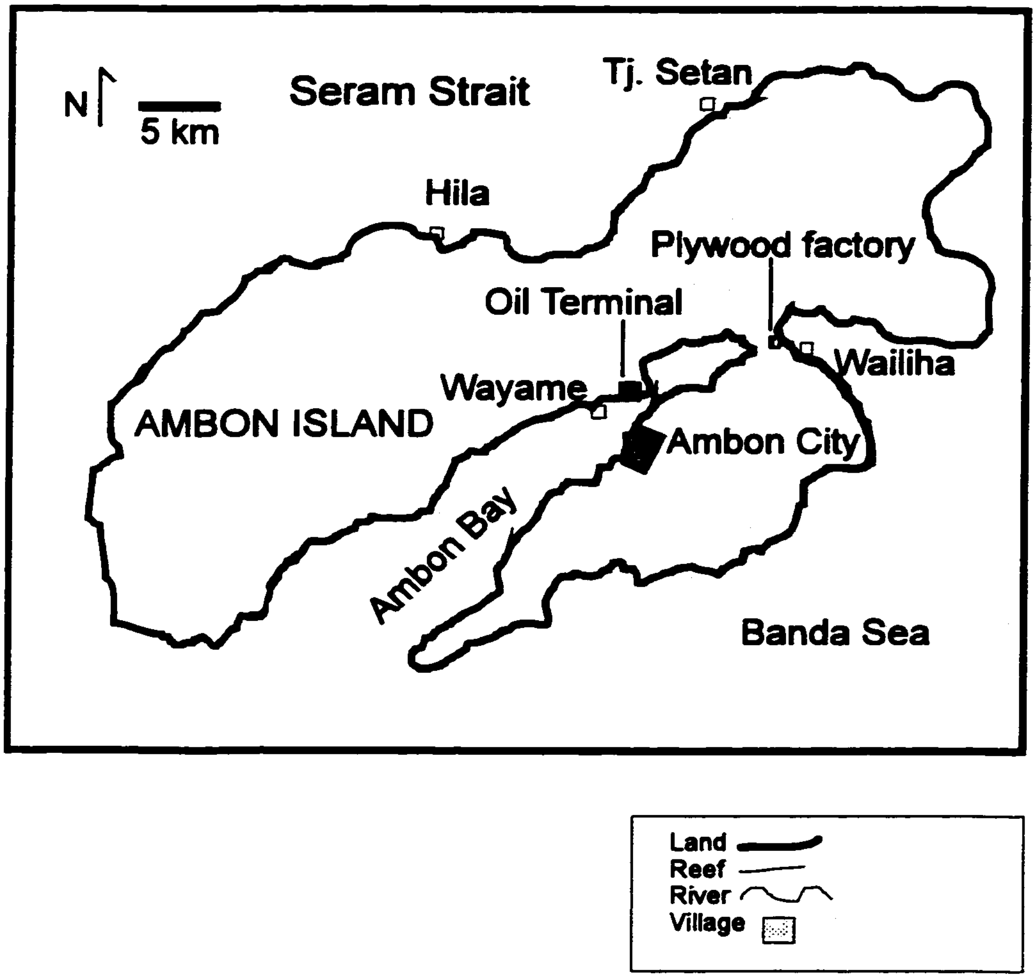
In each region, four reefs were sampled: one relatively pristine reef, and three reefs subject to different types and intensities of anthropogenic impact, which are broadly separable into chronic land-based pollution stresses and acute mechanical damage.

1.7.5 Ambon sites.

Tanjung Setan. A fringing reef built on Pliocene lahars and Pleistocene carbonates on the north side of Ambon island, Tanjung Setan is located in a densely forested region with no roads. We found fish traps and gill nets deployed from canoes, but no motorised fishing craft at this site. There were no bomb craters, nor other evidence of mechanical damage to this site. Tanjung Setan means "Satan's Point" in Indonesian, and the mythology surrounding the site may contribute to its relatively unaffected nature.

Hila. The reef at Hila, also on the north coast of Ambon island, is built on a rubble bottom, composed of rounded basalt and andesite cobbles plus coral fragments. Local residents frequently overturn corals on the reef flat and other shallow portions of the reef searching for invertebrates. Construction of the pier for the UNPATTI marine lab caused mechanical damage to the reef down to 10m depth. Several fresh bomb craters were observed during sampling. Runoff from local small villages discharges untreated sewage onto the reef.

Figure 1.4: Map of Ambon sites.



Nitrate, phosphate and SPM concentrations (table 2.2), and $\delta^{15}N$ values (Limmon 1996), are marginally higher than at Tanjung Setan. Hila, growing on a rubble bottom, represents a natural comparison for the effects of mechanical damage on reef cover, diversity, and coral morphology.

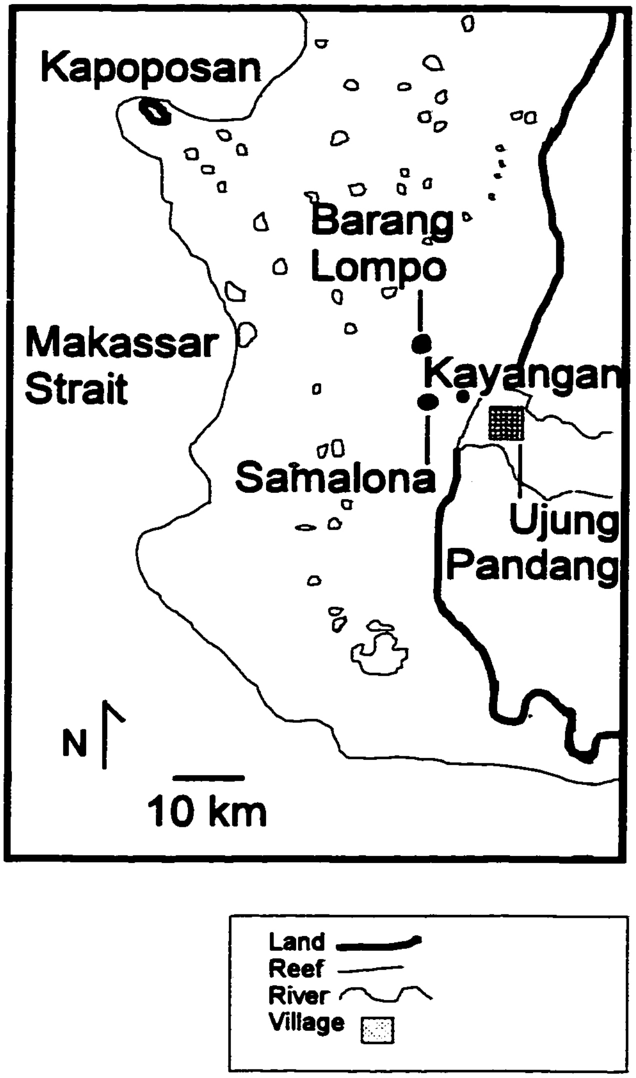
Wayame. Wayame lies in the Northeast portion of outer Ambon Bay, close to the new Pertamina oil tanker terminal for Ambon City, and is likely affected by domestic waste, industrial discharge, and possibly shipping activities (Evans et al. 1995). Nutrient levels, SPM and sediment resuspension values (table 2.2), and $\delta^{15}N$ values (Limmon 1996) in Wayame corals are much higher than on the north coast sites. We saw no bomb craters, nor did we document construction damage to the reef from the nearby Pertamina pier.

Wailiha. Wailiha reef is in Baguala Bay, on the south coast of Ambon island, and is subject to heavier surf than the other Ambon sites during the rainy season (May to October). Baguala Bay is one of the principal fishing harbours along the south coast of Ambon island. The reef we sampled is about 250m from a new plywood factory. Nitrate and phosphate levels are marginally higher than on the north coast sites, but SPM and sediment resuspension rates are the highest we documented in Ambon (table 2.2), and Porites lobata at Wailiha have higher concentrations of acid insoluble materials in their skeletons than do corals at the other Ambon sites (Limmon 1996). As maximum depth at which live coral occur at Wailiha is 6m, we sampled only at 3m depth.

1.7.6 Sulawesi.

Kapoposan. Kapoposan serves as the relatively unaffected comparison site for Sulawesi. Kapoposan island is a coral cay at the western edge of the Spermonde archipelago, bordering on the deep waters of the Makassar Strait. We observed fresh bomb craters at 3m on several parts of Kapoposan, including the portion we sampled, and we heard bombs detonating while we were in the water. We also documented several barren hardground areas, possibly resulting from a major storm that local residents say hit Kapoposan reef in 1993. At 10m depth, we saw no bomb craters; the 10m site is on the reef wall, while bomb fishermen typically detonate bombs in water shallow enough for them to retrieve fish that sink to the bottom (Erdmann 1995). At the edge of the Spermonde shelf, Kapoposan is far removed from mainland land-based pollution sources, and less than 500 people live on the island. Nitrate and phosphate concentrations and $\delta^{15}N$ levels at Kapoposan were the lowest we measured in Ambon and Sulawesi (table 2.2, Jompa 1996), and chlorophyll A levels were the lowest among the Sulawesi sites. SPM concentrations were comparable to the north coast of Ambon sites (table 2.2).

Figure 1.5. Map of South Sulawesi sites.



Barang Lompo. Barang Lompo island, approximately 12 km from Ujung Pandang city, is home to approximately 2000 people and the UNHAS marine lab. The reef receives untreated sewage from local residents and may receive long distance transport of pollutants from Ujung Pandang (Erdmann and Caldwell 1997). Nitrate and phosphate concentrations (table 2.2) and $\delta^{15}N$ levels (Jompa 1996) suggest a moderate degree of eutrophication. SPM and sediment resuspension rates are also moderate (table 2.2). We observed numerous fresh bomb craters on portions of the reef, including the NW (leeward) portion where we sampled; most of these craters were in less than 5m deep water. Local residents include a number of known blast and cyanide fishermen (Aspari Rachmann, UNHAS marine lab director, pers. comm. 1995).

Samalona. Samalona reef, 8 km from Ujung Pandang, has a very small local population, but receives many domestic and foreign tourists for day and overnight visits. SPM and sediment resuspension rates are nearly identical to those at Barang Lompo. We observed numerous areas of boat and anchor damage primarily on the reef flat, but continuing down to approximately 5m depth. The reef receives pollutants from Ujung Pandang, as evidenced by nitrate, phosphate, and $\delta^{15}N$ values (table 2.2; Jompa 1996).

Kayangan. Kayangan reef lies at the entrance to Ujung Pandang harbour; the shipping channel marker stands at the S end of the reef itself, less than 100m from where we sampled. This site receives untreated sewage pollution from Ujung Pandang city, as well as oil and other chemical pollution from ships and the nearby oil and LNG terminal

(Erdmann and Caldwell 1997). Chlorophyll A, nitrate, phosphate (table 2.2), and $\delta^{15}N$ (Jompa 1996) concentrations are all considerably higher than at any other site in Sulawesi; the nitrate and phosphate concentrations are similar to Wailiha in Ambon. SPM and sediment resuspension rates are the highest recorded in all the Ambon and Sulawesi sites. There were no live corals on the NW (leeward) portion of the reef, so we sampled on the SE (windward) side, where coral growth continues to approximately 11m depth.

1.8 Silent Spring for Indonesian coral reefs?

One of the principal modern anthropogenic effects on reefs in coastal regions is increased dissolved nutrient levels, usually accompanied by increased phytoplankton productivity and suspended sediment levels (Pastorak and Bilyard 1985; Birkland 1996). This land-based pollution may push environmental conditions on coastal reefs past the empirically defined nutrient tolerance limits for reef growth (Kleypas and McManus 1997). Eutrophication, combined with other anthropogenic pollution sources, may thus be one of the key agents of demise for modern coastal reefs. The modern anthropogenic mass extinction in the making threatens to equal mass extinctions in the fossil record in scale, but dwarf them in speed (Sepkoski 1997). The research in this thesis documents the local effects of pollution on some of the world's most diverse coral reefs, and may help to serve as a warning of things to come.

Chapter 2: Reef Degradation and Coral Biodiversity in Indonesia: Effects of Land-Based Sources of Pollution, Destructive Fishing Practices, and Changes over Time.

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2.1 Introduction

Indonesia's coral reef resources are the richest and most diverse in the world. Eastern Indonesia lies at the centre of diversity for corals (Veron 1993), molluscs, reef fishes (Montgomery 1990), and other reef organisms, along with the Philippines (McManus 1985) and the north coast of Papua New Guinea (Pandolfi 1992). This wealth in biodiversity emphasises Indonesia's importance in global efforts to conserve marine resources and preserve biodiversity (BAPPENAS 1993).

Threats to Indonesia's coral reef resources can be divided into two main types: acute threats and chronic stresses. Acute threats cause dramatic damage in a short period of time. Examples include destructive fishing practices, such as blast fishing, as well as other forms of mechanical damage, like anchor damage, ship groundings, cyclones, or Acanthaster outbreaks. Acute threats cause significant damage, but do not persist; the reef can, and usually will, recover if protected from further assaults (Pearson 1981). Chronic stresses, on the other hand, alter the physical or biological environment on a long term basis, and cause long term damage to coral reefs. Examples in Indonesia include sewage pollution, increased sedimentation, nearshore eutrophication and industrial pollution (Tomascik, et al. 1993). Non-point source pollution, such as sewage and agricultural/aquacultural runoff, is an increasingly important type of stressor in Indonesia (McManus 1988; Cesar 1996). Reefs normally will not recover from chronic stresses until the stressor is removed, i.e. the pollution is cleaned up (Richmond 1993; Grigg 1995).

This study quantitatively evaluates several threats to Indonesian coral reefs with respect to their impact on coral reef biodiversity. The implications of this study for coral reef biodiversity conservation and management are simple: to understand what threats to reefs deserve most attention, we should evaluate which threats have the greatest impact on biodiversity. Our results suggest that the severity of the threats are greater than previously thought, and that many of these problems will be difficult to address.

2.2 Methods.

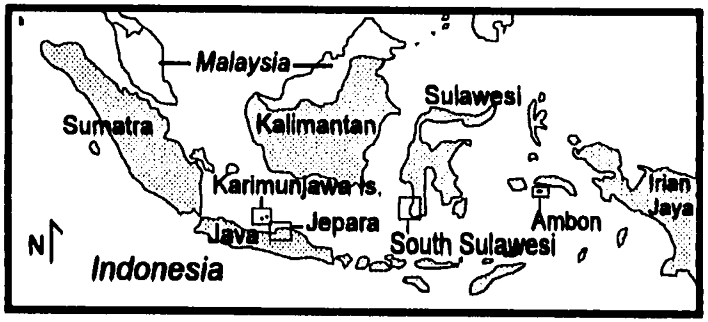
2.2.1 Study Areas

This study was conducted in three areas within Indonesia (Fig. 2.1A): Ambon (Moluccas; Fig. 2.1E), the Spermonde Archipelago (South

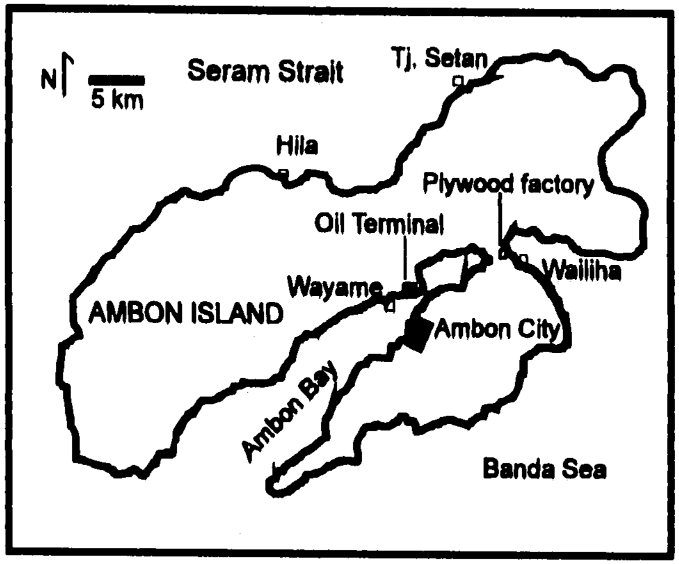
Sulawesi; Fig. 2.1D), and Central Java (Fig. 2.1B, 2.1C). In eastern Indonesia, we sampled four reefs in each region, one relatively unaffected site, and three sites subjected to varying forms of degradation. Comparison sites are operationally defined - they are the reefs within each region showing the least evidence of anthropogenic stress, usually by virtue of being located away from centres of habitation. The degraded sites included three subject to land-based pollution (Wailiha, Wayame, Kayangan) and three subject to various forms of mechanical damage (Hila, Samalona, Barang Lompo). Further details on the Eastern Indonesian sites are presented in Jompa (1996) and Limmon (1996).

The Java Sea sites include two comparison reefs in the Karimunjawa islands national marine park (P. Kecil, G. Cemara; Fig. 1C), one reef affected by storm damage (P. Burung, windward), one fringing reef adjacent to mangroves, and nearshore reefs in Jepara (P. Panjang, Bondo (Fig. 1D)), both subject to high levels of land-based pollution. The comparison reefs in the Karimunjawa islands are far from pristine; they are subject to intense fishing activity by non-destructive means, with attendant effects (Roberts 1995). Nonetheless, they provide the best local comparison for degraded Java Sea reefs. The reef names, morphological types, maximum depth of coral growth, and primary stresses are listed in Table 2.1. Environmental data characterising each site are listed in Table 2.2; methods for measuring environmental data are discussed below.

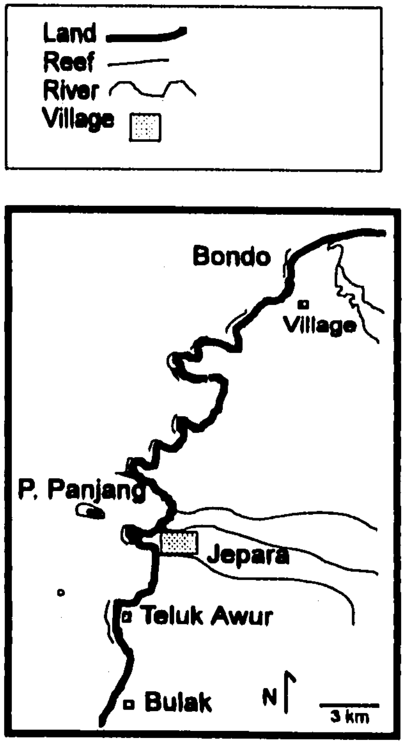
Fig. 2.1 Map of all study regions in Indonesia. A; All Indonesia base map. B: Jepara region. C. Karimunjawa. D. South Sulawesi. E. Ambon. See chapter 1 for details on study sites.



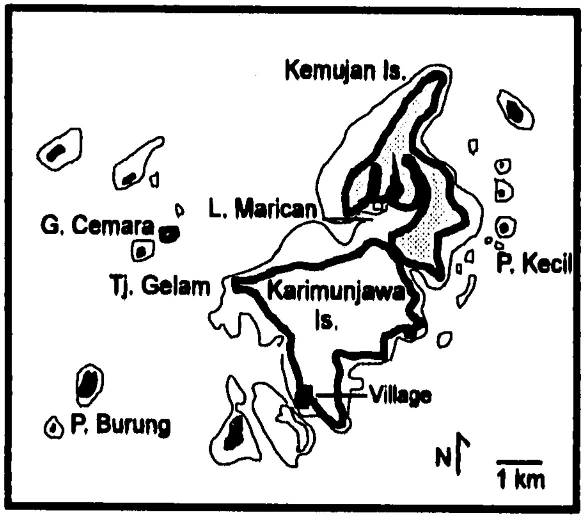
A. Map of Indonesia, showing regions studied.



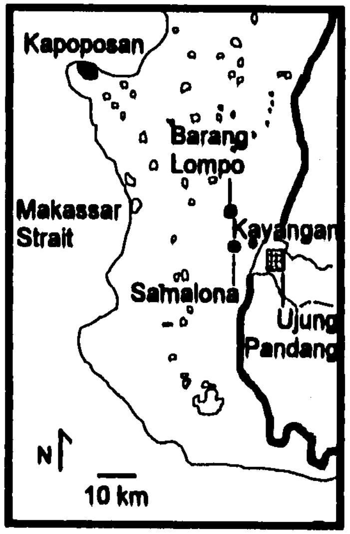
E. Ambon



B. Jepara region.



C. Karimunjawa Islands



D. South Sulawesi

Table 2.1 Study Site regions, names, morphologies, and summaries of stresses. Max. depth: maximum depth of coral growth. Water Clarity: water clarity as measured by average secchi disk extinction depth. Source of stresses summarizes impacts on each reef. More detailed descriptions of each reef can be found in Limmon (1996), Jompa (1996), and Edinger et al. (in review).

Region	Reef Name	reef morphology	max. depth	source of stresses
Ambon	Tanjung Setan	fringing reef /wall	40m	unaffected sites (10m, 3m)
	Hila	fringing reef	20m	bombing, construction, rubble bottom
	Wayame	fringing reef	15m	harbour, sewage, sedimentation
	Wailiha	fringing reef	6m	sediment, plywood factory
So. Sulawesi	Kapoposan	coral cay/wall	50m	unaffected (10m), bombed (3m)
	Barang Lompo	coral cay island	25m	bombing, local sewage pollution
	Samalona	coral cay island	25m	anchor damage, pollution from city
	Kayangan	coral cay island	11m	harbour, industry, sewage, sedimentation
Karimunjawa	Pulau Kecil	coral cay island	25m	Java unaffected, overfishing
(Central Java)	Gosong Cemara	coral cay, submerged	20m	Java unaffected, overfishing
	Pulau Burung	coral cay island	25m	storm damage (windward only)
	Lagun Marican	mangrove fringe	4m	carbonate sedimentation
Jepara	Pulau Panjang	coral cay island	8m	sewage, sediment, aquaculture
(Central Java)	Bondo	fringing reef	5m	sedimentation, agricultural runoff

2.2.2 Environmental Data: methods

The nature of the stresses at each site were determined by qualitative observations, (notes on bomb craters, etc.) and by a series of environmental measurements including chlorophyll A, suspended particulate matter (SPM) concentrations, and sediment resuspension rates, and water clarity or light penetration, measured by secchi disk extinction depth. All measurements were repeated on at least three occasions for each reef; averages and standard deviations are reported in Table 2. Ambon and Sulawesi sampling was conducted in May - August 1995; sampling in the Java Sea was conducted in Nov - Dec. 1994, July - Nov. 1995, and Aug. - Nov. 1996.

chlorophyll A, dissolved nutrient concentrations.

At all reefs in South Sulawesi and Central Java, chlorophyll A levels were measured using standard filter methodology (Parsons et al. 1984). Filters were frozen and transported on ice to Canada, where they were analysed using the method of Burnison et al. (1980).

Suspended Particulate Matter (SPM).

Suspended particulate matter (SPM) was measured at all reefs by filtering 1 litre of seawater onto a pre-weighed glass fibre filter, which was subsequently oven-dried and weighed (Cortes and Risk 1985).

Table 2.2 Environmental parameters measured for each reef in the study. All values are averages of a series of measurements. Ambon measurements are wet season, while Sulawesi and Java measurements are mostly dry season or transitional (November). Methods are described in text.

Region	Reef Name	depth m	chloro. A mg/m3	SPM mg/l	resuspension mg/cm2/day	water clarity m
Ambon	Tanjung Setan	all	0.39 (0.18)	4.49 (1.40)	0.08 (0.02)	>20m
	Hila	all	0.44 (0.21)	4.91 (2.66)	0.19 (0.14)	20m
	Wayame	all	0.38 (0.06)	11.15 (3.40)	0.55 (0.23)	10m
	Wailiha	all	0.46 (0.14)	15.3 (10.21)	3.08 (3.13)	<4m
So. Sulawesi	Kapoposan	all	0.47 (0.05)	5.26 (1.24)		>20m
	Barang Lompo	all	.075 (0.07)	8.62 (1.60)	0.7 (0.2)	17m
	Samalona	all	0.82 (0.05)	8.22 (1.30)	0.6 (0.1)	18m
	Kayangan	all	1.52 (0.53)	19.25 (4.61)	2.8 (0.2)	<5m
Karimunjawa	Pulau Kecil W/W	3	0.33 (0.08)	9.75 (6.71)	2.03 (0.55)	20m
(Central Java)	Pulau Kecil L/W	3	0.29 (0.17)	19.69(18.27)	1.63 (1.31)	18m
	G. Cemara W/W	3	0.40 (0.21)	22.98 (2.98)	4.21 (3.31)	20m
	G. Cemara L/W	3	0.25 (0.14)	22.26 (7.56)	2.80 (3.62)	16m
	P. Burung W/W	all	0.40 (0.01)	4.45		22m
	P. Burung L/W	all	0.22 (0.01)	19.69		18m
	Lagun Marican	3	1.24 (0.90)	26.39(11.58)		<3m
Jepara	P. Panjang W/W	3	1.23 (0.54)	21.83 (8.40)	26.19(24.42)	<4m
(Central Java)	P. Panjang L/W	3	1.09 (0.62)	28.91(17.86)	31.69(38.74)	<2m
	Bondo	3	1.22 (0.52)	21.04 (4.60)	38.5 (25.7)	<2m

sediment resuspension.

Sediment resuspension was measured using sediment traps, consisting of 30cm long PVC tubes, 5cm in diametre. In Ambon and Sulawesi, these were deployed in arrays 25 cm, 50cm, and 75cm above the bottom, at 3m depth on each reef (Cortes and Risk 1985). In Central Java, these were deployed on the reef surface at 3 depths: 3m, 10m, and at the base of the reef (Karimunjawa), or 1m, 3m, and base of the reef (nearshore reefs). Sediment traps were collected weekly in Ambon and Sulawesi, and twice monthly or monthly in Central Java. Accumulated sediment was oven dried, weighed, and subsampled for carbonate content and constituent analysis, for use in other studies.

Water clarity.

Water clarity was estimated using standard secchi disk extinction depth measurements. These were repeated on at least three occasions at each reef, noting weather and sea conditions. Because these data are highly variable, bounding conditions, rather than mean and standard deviation, are reported in table 2.2.

2.2.3 Sampling methods.

In Ambon, all reefs sampled were fringing reefs. In Sulawesi, all coral cays were sampled on the leeward side, which generally had the most luxuriant coral growth, except at Kayangan, where the leeward reef is dead, and we sampled the windward reef. In Java, all reefs were sampled on both windward and leeward sides, except the fringing reef at

Bondo and the reef fringing the mangroves at Lagun Marican. Transect locations were non-adjacent, non-overlapping and dispersed over at least 200m laterally along each reef, such that the reef areas sampled would incorporate variation on each reef. Windward vs. leeward replication in the Java Sea, and replication of disturbance on nearby reefs in Sulawesi ensured that kilometre scale heterogeneity (Edmunds & Bruno 1996) was accounted for, while replication of degradation type within and between regions helped to account for larger scale biogeographic variation.

Coral morphology and reef cover classes.

At least six replicate 20m line intercept transects (Risk 1972; Loya 1978) were measured at 3m and at 10m depth at each of the sites, totalling a minimum of twelve transects, or 240m cumulative transect length, per reef in most cases. For three reefs on which coral growth did not continue beyond 6m depth (Wailiha, Bondo, L. Marican), transects were measured at 3m only. Ambon and Sulawesi sampling took place in May - Aug. 1995; Java Sea transect sampling took place in July - Nov. 1995 and Aug. - Nov. 1996. Life form transects were measured for cover of live corals, separated by morphological life forms, and cover of dead coral, algae, other invertebrates, and abiotic substrates (e.g. sand and rubble), and mortality index (Gomez 1994) was calculated as MI = live coral cover/ (live coral cover + dead coral cover).

Coral Species Diversity

Of a total 146 transects measured, 94 were recorded with coral species identifications, and were used for compiling a total of 32 species-area curves (Loya 1978). During intensive sampling in August - November 1995, all coral species occurring on each 20m transect were noted, as were the positions of the first occurrence of each species along each transect. In nearly all cases, species-area curves asymptotically approached saturation within a cumulative sampling distance of 40m; the exceptions were the highly diverse reefs in Ambon (fig. 2.2), which approached saturation by 60m cumulative transect length.

All corals except Acropora were identified using Veron (1986). Field parties did not have sufficient experience in Acropora taxonomy to allow species identifications underwater, and due to the impoverished nature of many of the stressed reefs, we were reluctant to collect large suites of specimens for later identification. Rather, Acropora corals were identified to species group (Veron and Wallace 1984) in the field, and representatives of each species group were collected for provisional identifications and subsequent verification by Dr. C.C. Wallace.

2.2.4 Data Analysis.

Line intercept transect data were pooled for each reef to compute average percent covers of seven basic categories: Acroporid corals, non-Acroporid corals, total live corals, dead corals, algae, other invertebrates, and abiotic substrates. Morphology data are discussed in chapter 4.

Coral species-area curves were compared statistically using two methods. First, because nearly all species-area curves were observed to asymptotically approach horizontal slope (no increase in diversity) by 40m cumulative length (fig. 2.2, 2.3, 2.4), coral diversity was compared among reefs by counting the number of coral species sampled in the first 40m of each species-area curve. Next, the distance axis of species-area curves from each reef were $\log_{10}$ transformed, converting the curves to lines, N spp. vs. $\log_{10}$ (distance), passing through the origin. The slopes of these lines were calculated using linear regression ($r^2>0.90$ in all but 1 case, where $r^2=0.83$)), and were compared using 1-way ANOVA (Sokal and Rohlf 1973). Slopes of these diversity lines were also used in regression analyses of diversity vs. cover (Aronson and Precht 1995) and vs. environmental parametres (Fraser and Currie 1990).

These two methods yielded nearly identical results, and were very highly significantly correlated with one another ($r^2=0.95$, $p<0.0001$, $n=32$). Species-area curves are presented in figures 2.2 - 2.7); these are more intuitively understandable than the $\log_{10}$ transformed slopes (fig. 2.8, fig. 2.9), which are used in statistical analyses.

Figure 2.2: Ambon Species-Area curves. Location codes follow Table 2.1. Distance sampled in metres.

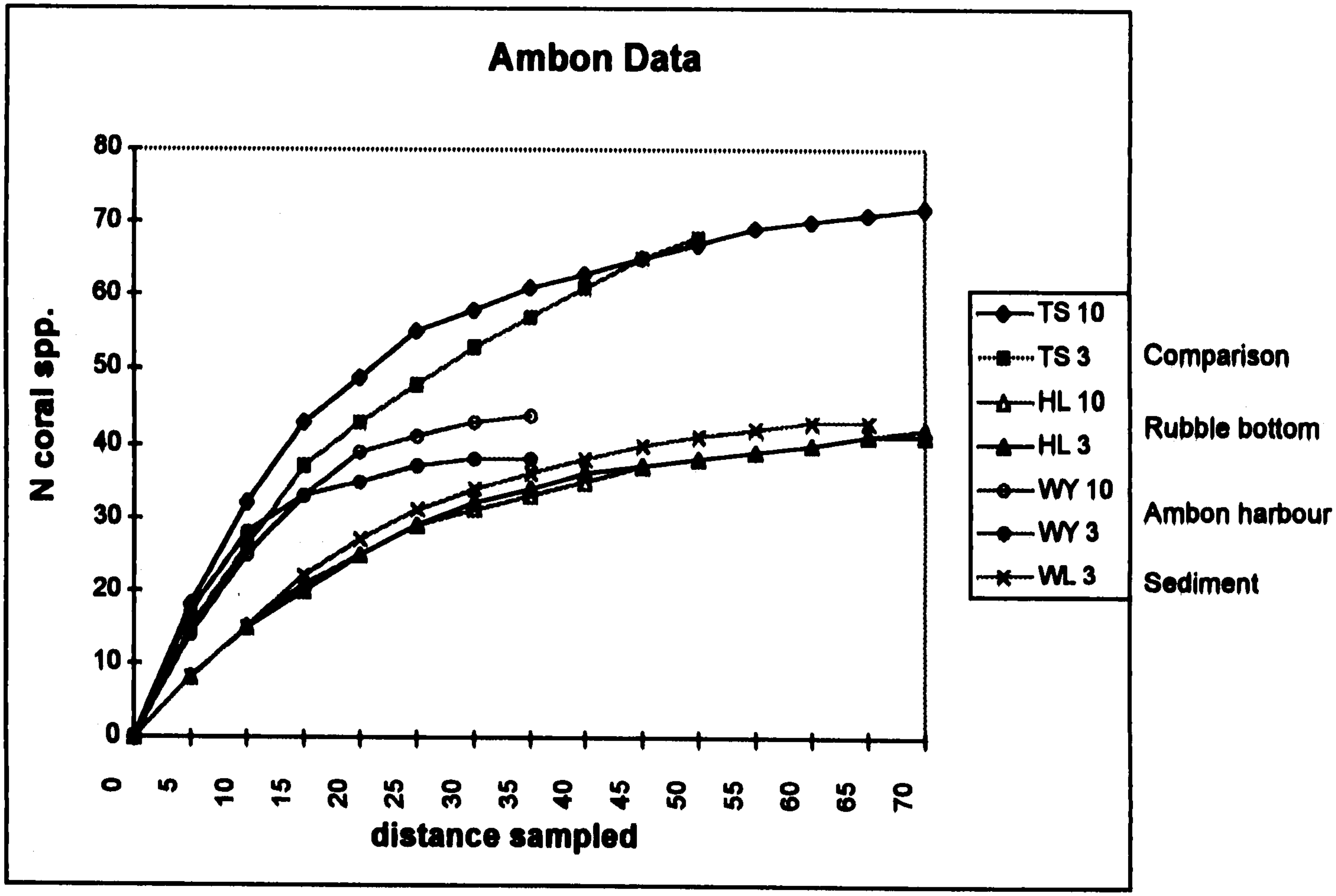


Figure 2.3: Sulawesi species-area curves. Location codes follow Table 2.1. Distance sampled in metres.

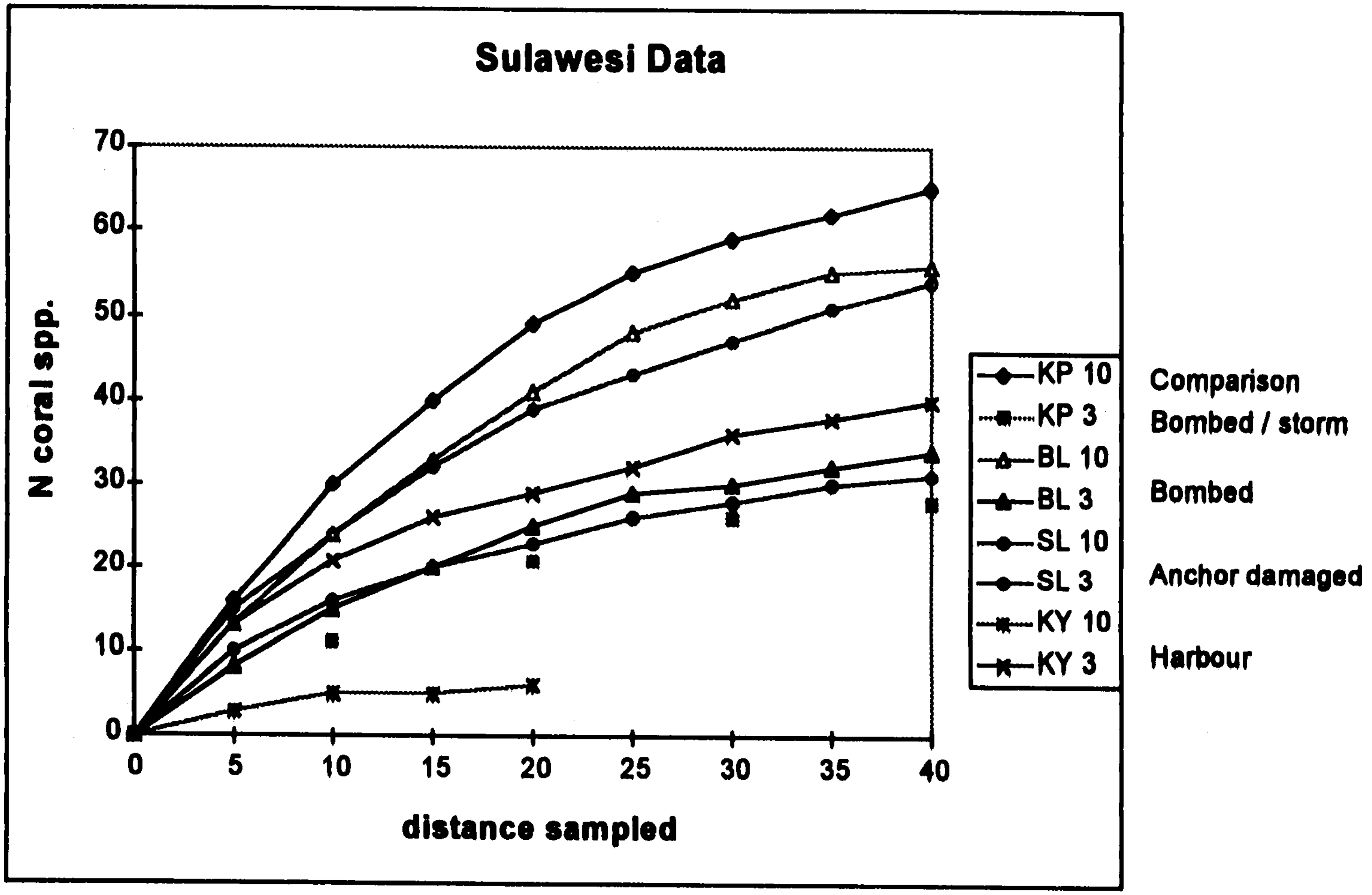
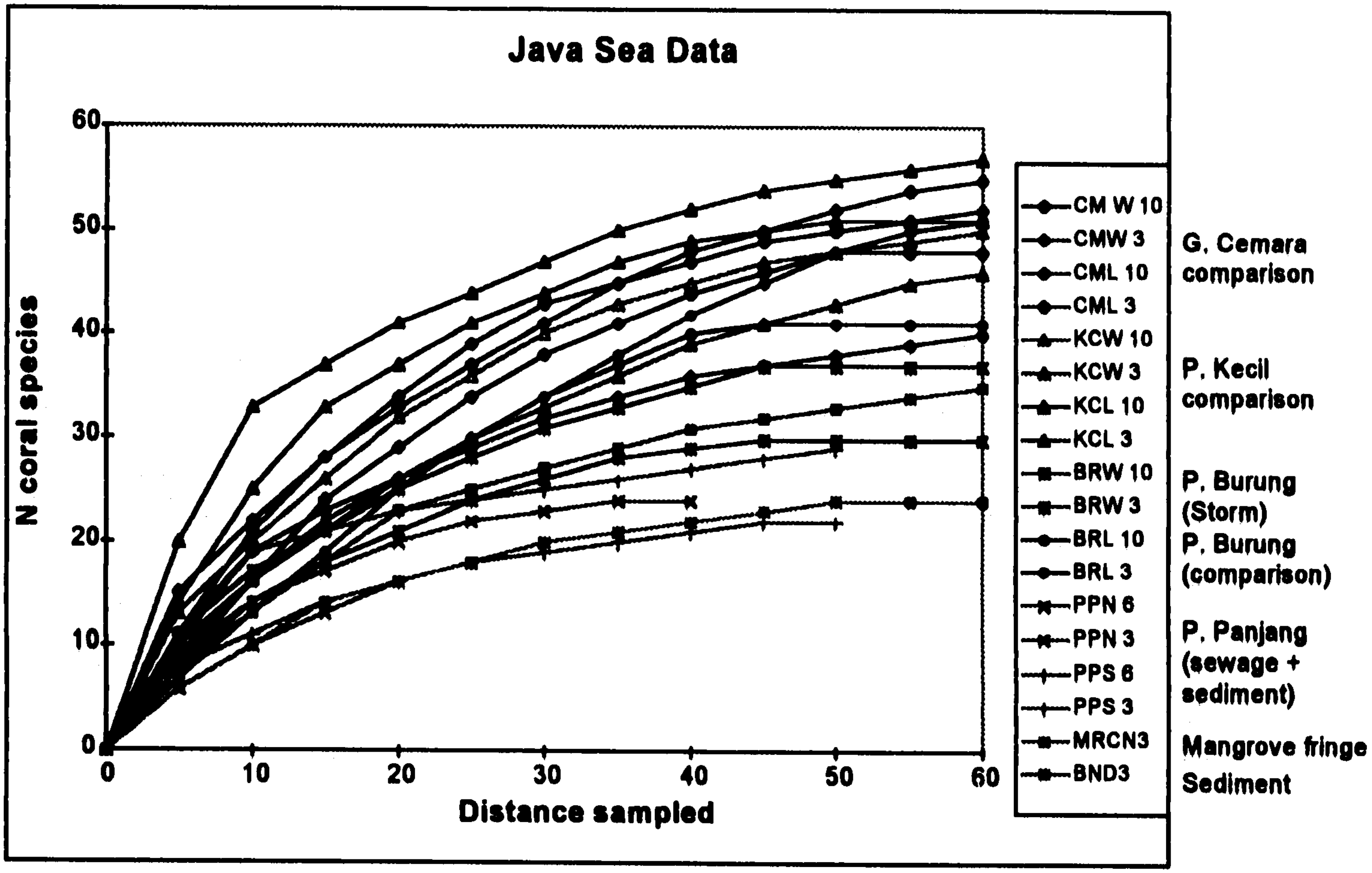


Figure 2.4: Java Sea species-area curves. Location codes follow Table 2.1. Distance sampled in metres.



2.3 Results

2.3.1 Species-area curves.

Within biogeographic regions, species-area curves clearly show reduced species diversity on reefs subjected to various forms of degradation (Ambon, fig. 2.2; Sulawesi, fig. 2.3; Central Java, fig. 2.4). Figures 2.5 to 2.7 show the effects of different kinds of reef degradation, pooled among the various regions.

Comparison / comparison reefs.

The comparison reefs in Ambon (Tanjung Setan 3m and 10m) and Sulawesi (Kapoposan 10m) all show approximately equivalent diversity (fig. 2.5). The most diverse comparison Central Java reefs at P. Kecil and G. Cemara, Karimunjawa are about 20% less diverse than their Eastern Indonesian counterparts. The differences between Eastern Indonesian diversity and Java Sea diversity probably reflect both biogeographic differences (Cornell and Karlson 1996; Fraser and Currie 1996; Wallace 1997) and more intense overfishing in the Java Sea (Roberts 1995); this question is briefly addressed in chapter 3.

Coral cover and species diversity are approximately equivalent at P. Kecil, G. Cemara and P. Burung (leeward side), and the coral faunas at P. Kecil and G. Cemara are >77% similar (Jaccard similarity index, S=63.5). The leeward sides of these reefs are generally 15-20% more diverse than the windward sides (Table 3)

Fig. 2.5: Species-area curves: comparison sites, overfishing.

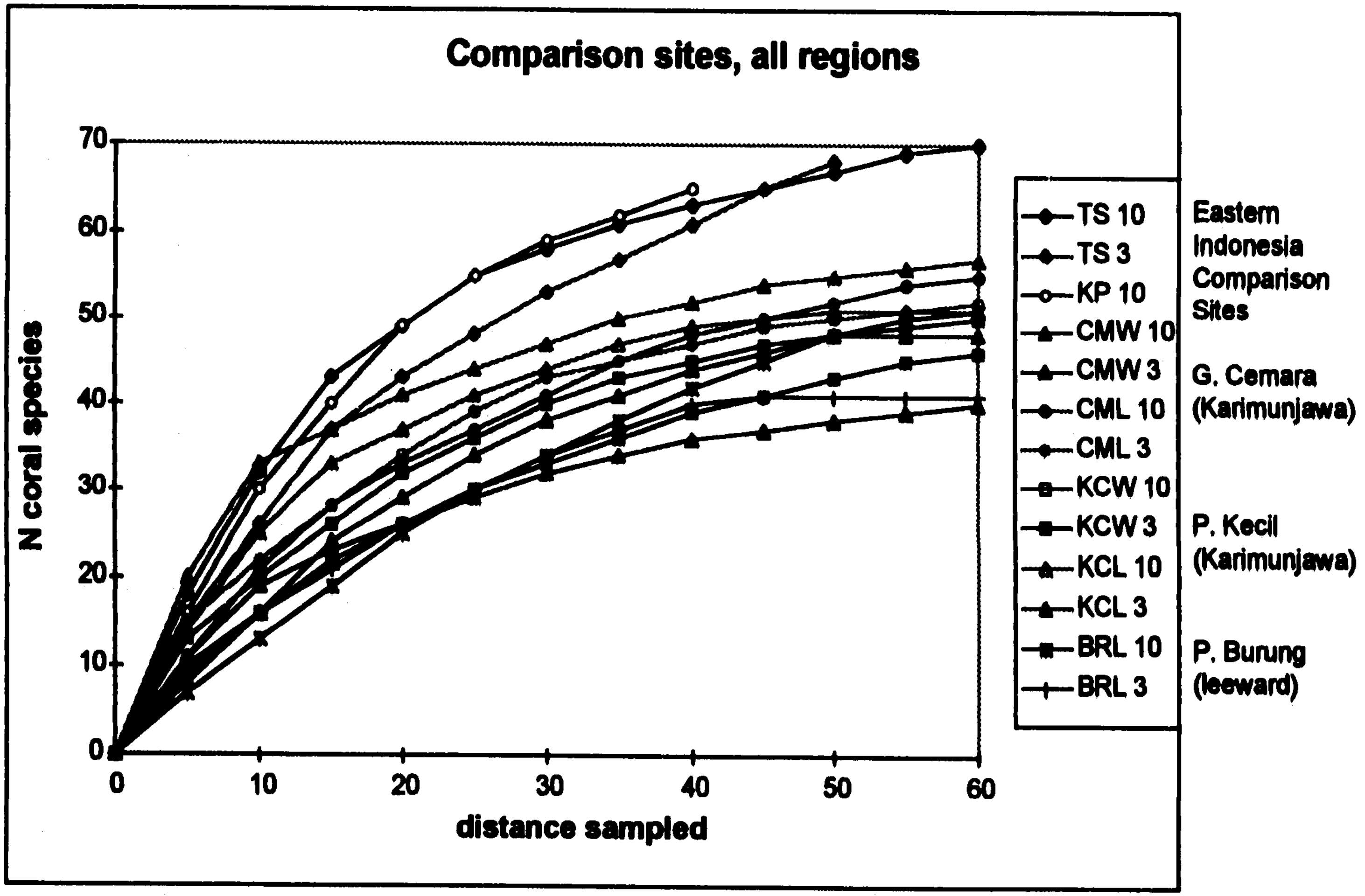
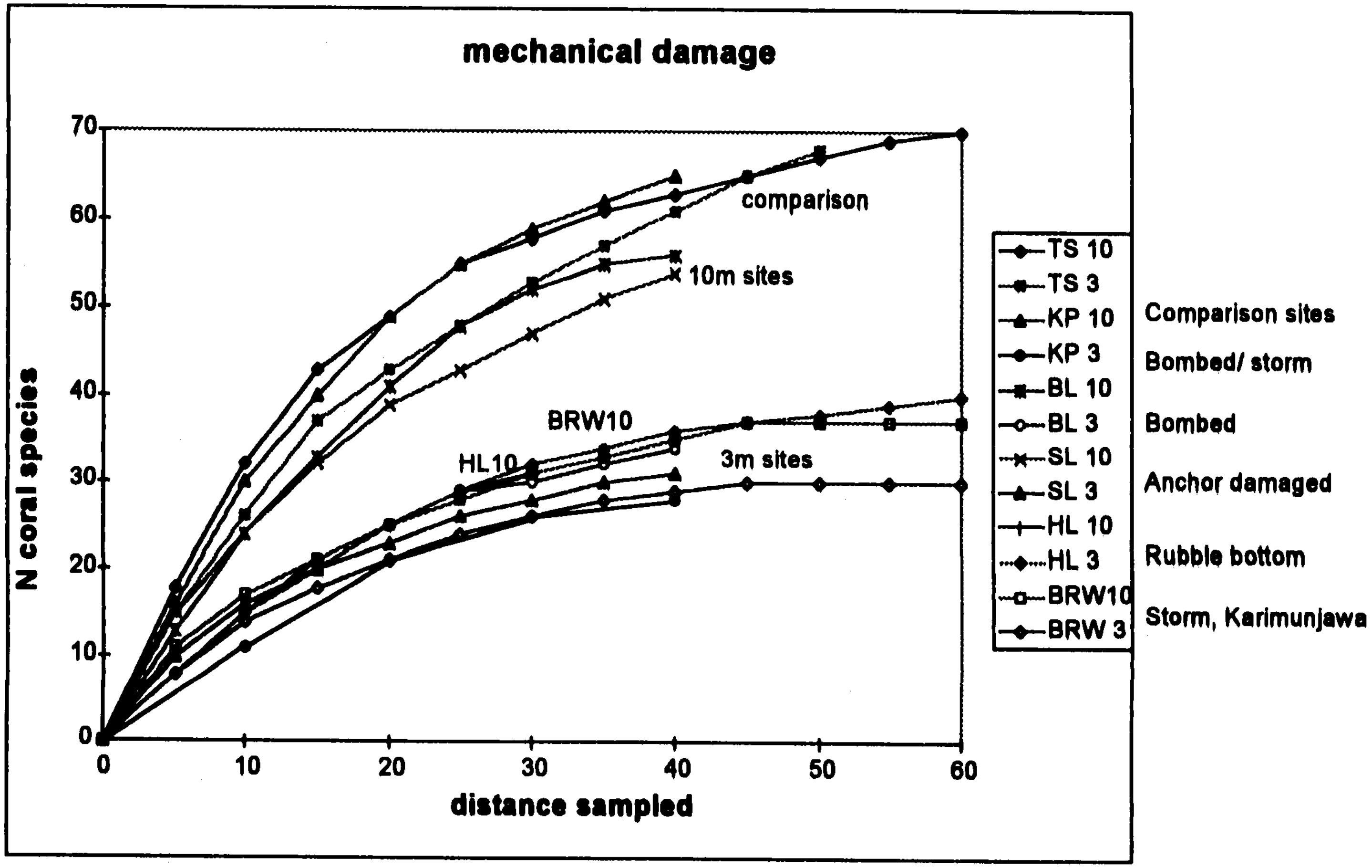


Fig 2.6: species-area curves: mechanical damage. Hila and BRW10 curves almost exactly override each other.



Mechanical damage.

Two reefs subject to anthropogenic mechanical damage, such as anchor damage (Samalona) or bombing (Barang Lompo), show dramatically reduced diversity at 3m, approximately 50% of diversity on comparison reefs in the region. Diversity at 10m on these reefs is only slightly reduced below the level on comparison reefs (fig. 2.6). By contrast, a reef damaged by storms (P. Burung, Karimunjawa, windward side) had 30% reduced diversity at 3m, and 15% reduced diversity at 10m, relative to the average diversity on the windward sides of P. Kecil and G. Cemara. The reef at Hila, growing on a rubble bottom, and affected by bombing, construction damage, and villagers overturning corals in shallow water, had 50% reduced diversity at both 3m and 10m depth.

Eutrophication stresses.

Five reefs subject to various forms of land-based pollution were sampled (fig. 2.7). In most cases, these reefs suffered from a combination of stresses, and it is difficult to separate clearly the effects of sewage, agricultural and aquacultural runoff, sedimentation, and industrial effluent. Reefs subject to these stresses had approximately equivalent reductions in coral diversity, about 30-60%, with diversity reductions at 10m greater than or equal to those at 3m, except at Wayame (Ambon). Sites subjected to sedimentation and agricultural runoff (e.g. Bondo) had greater diversity than those subjected to combined sewage and sedimentation (e.g. P. Panjang). The lowest diversity sites in Jepara had equivalent diversity to fringing reefs bordering intact mangroves in Karimunjawa (L. Marican).

2.3.2 Statistical comparisons.

The slopes of the $\log_{10}$-transformed species-area curves were used for calculating statistical analyses of diversity. Figure 2.8A shows the mean diversity ± 95% confidence limits of reefs sampled in each degradation type and depth, summed over all three regions. Although variance is particularly high for mechanical damage at 10m depth, where two sites (anchor damage and bombing) had much higher diversity than the other two (construction/rubble bottom, and storm damage), and for the harbour sites (Wayame, Kayangan), average slopes are significantly different among the various groups (ANOVA, F=6.98, $p<0.0002$, d.f.=36). There is a biogeographic bias to these groupings, however, where Eastern Indonesian sites of all degradation types appear to be more diverse than Java Sea counterparts of the same degradation types. Biogeographic differences in diversity are discussed in chapter 3.

Fig 2.7: species-area curves: land-based pollution.

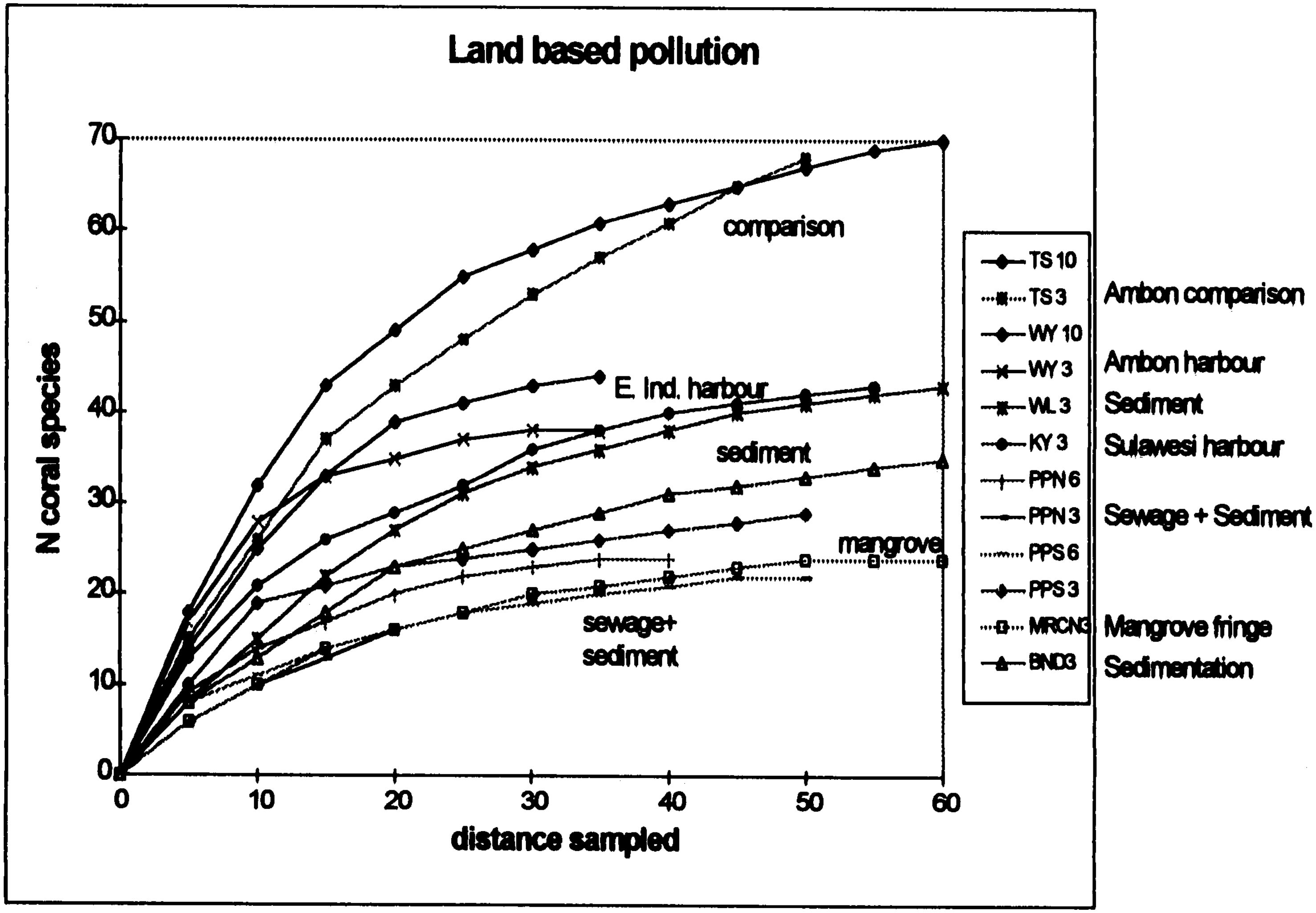
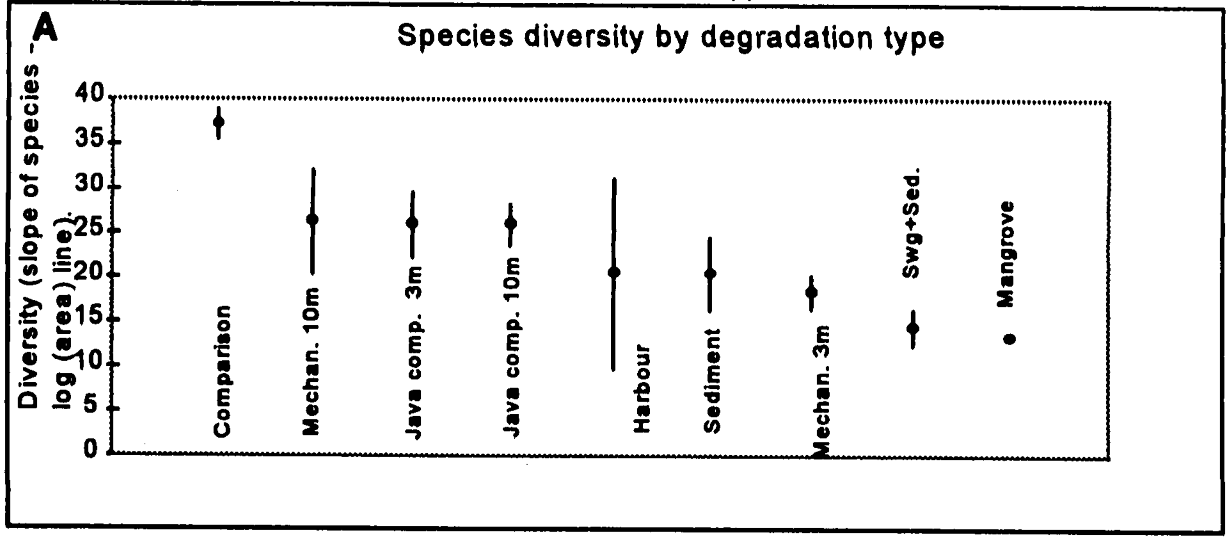


Fig. 2.8A. Coral species diversity by degradation type. Mean ± 95% confidence limits.



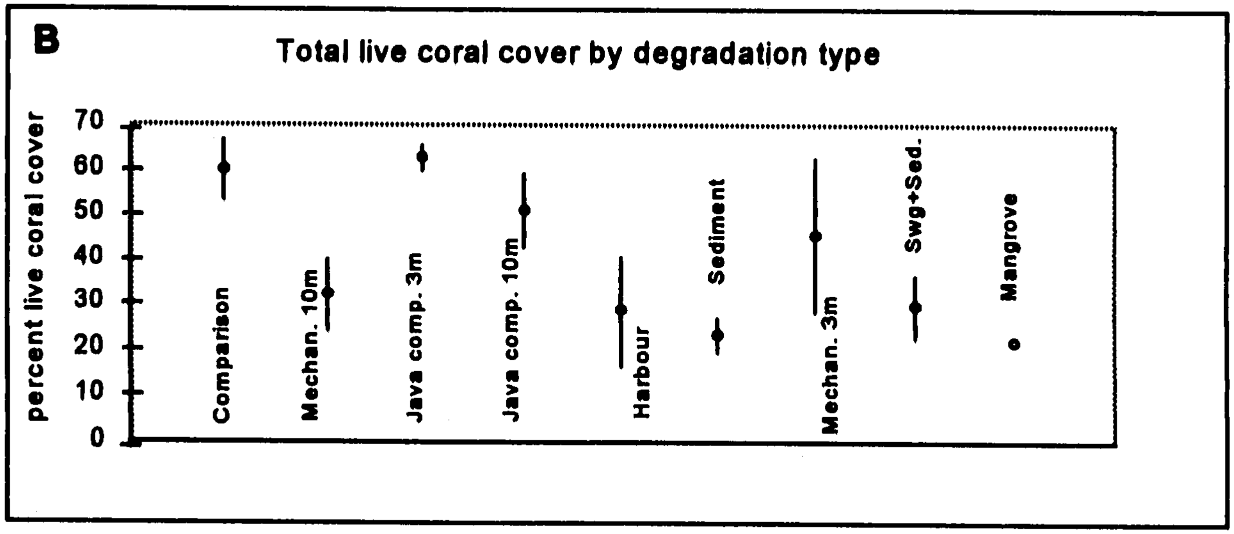


Fig 2.8B. Total live coral cover by degradation type. Mean ± 95% confidence limits.

Table 2.3. Diversity and Cover Summaries for all Reefs. W, L, 3, or 10 at ends of codes indicate aspect (windward/leeward) and depth.

Reef	stress	site	depth	S /40m	Slope	Acropora (%)	% non-Acropora	% live coral	% dead coral	% algae	% other fauna	%abiotic	mortality index
Wailiha	sediment	WL 3	3	38	22.66	5,98	15,75	21.73	22,31	4.44	21.10	30,41	0,51
Wayame	harbour	WM 10	10	44	28,25	10,51	22.18	32,69	20,59	3.44	16,54	26.76	0,39
		WM 3	3	38	28,25	14,95	24.36	39,31	25,94	1,22	17,15	16,39	0,40
Hila	rubble	HL 10	10	35	21,83	0.71	22.25	22,96	30,33	0.02	9,32	37,37	0,57
		HL 3	3	36	21,47	4,11	27,26	31,37	26,46	0,94	9,78	31.45	0,46
Tjg. Setan	control	TJS 10	10	63	38,58	21,56	38,80	60,36	19,41	0,87	11,42	7,96	0,24
		TJS 3	3	61	35,81	23,82	44,19	68,01	16,19	1,78	10,81	3,23	0,19
Kayangan	harbour	KY 10	10	6	4,55	0,00	9,83	9,83	11,23	1,99	15,71	61.08	0,59
		KY 3	3	40	23,90	3,52	14,67	18,18	25,67	12,63	9,13	33,16	0,59
Samalona	offshore	SM 10	10	54	30,59	4,91	36,64	41,55	16,85	0.05	14,57	26,98	0,29
	anchor	SM 3	3	31	18,32	14,18	32,86	47,04	14,66	0,55	5,35	32.30	0,24
B. Lompo	local sewage	BL 10	10	56	32,51	6,92	33,34	40,26	18,81	2,01	6,41	32,51	0,30
	bombed	BL 3	3	34	19,44	24,15	30,01	54,16	16,85	1,29	7,07	20,64	0,23
Kapoposan	control	KP 10	10	65	37,79	7,47	47,02	54,49	6,80	7,28	22,42	3,42	0,18
	bom/strm	KP 3	3	28	16.10	28,80	45,59	74,39	13,67	1,33	8,24	2,25	0,14
Cemara	control/	CMW 10	10	44	25.59	18,15	37,65	55,80	24,35	0,00	0,75	16,85	0,30
	overfish	CMW 3	3	36	21,61	47,35	15,58	62,93	16,69	6,01	3,95	7,81	0,21
		CML 10	10	48	28,51	8,57	36,98	45,55	20,27	0.17	4,57	29,28	0,31
		CML 3	3	47	28,26	41,32	27,18	68,50	19,83	1,02	9,09	1,55	0,22
Kecil	control/	KCW 10	10	39	23,24	6,72	34,70	41,42	24,54	4,92	5,35	17,80	0,37
	overfish	KCW 3	3	45	26,81	27,37	33,53	60,90	20,70	4,47	5,32	6,75	0,25
		KCL 10	10	49	29,22	2,40	62,10	64,50	25,88	5,53	0,33	3,61	0,29
		KCL 3	3	52	29,22	25,84	35,90	61,74	13,61	5,85	4,23	14,58	0,18
Burung	storm	BRW 10	10	35	20,74	8,82	23,67	32,48	12,17	7,50	13,10	34,75	0,27
	storm	BRW 3	3	29	17,12	10,32	17,90	28,22	4,40	46,97	6,33	14,08	0,13
	control/	BRL 10	10	42	24,53	22,23	33,58	55,82	9,80	13,47	11,05	9,87	0,15
	overfish	BRL 3	3	40	22,65	37,57	28,82	66,38	8,00	6,62	12,50	6,50	0,11
Marican	mangrove	MRCN 3	3	22	13.24	1,85	21,92	23,77	5,38	37,10	17,10	16,65	0,18
Jepara	sewg+sed	PPN 6	6	24	15,13	0,00	34,75	34,75	18,63	0,00	7,88	38,75	0,35
		PPN 3	3	22	12,65	0,63	31,89	32,51	15,35	3,24	26,39	22,51	0,32
		PPS 6	6	21	12,73	0,00	35,77	35,77	37,47	0,00	3,55	22,32	0,51
		PPS 3	3	27	17,13	0,50	20,68	21,18	58,93	0,00	0,80	18,63	0,74
Bondo	sediment	Bondo	3	31	18,43	0,55	27,48	28,03	21,22	3,85	10,10	36,80	0,43

Analysis of the slopes of the log-transformed species-area curves showed that relative diversity among the degradation types studied may be ranked as follows:

1. Eastern Indonesian comparison reefs.
2. Java Sea comparison reefs.
3. mechanically damaged reefs at 10m depth.
4. Eastern Indonesian polluted reefs.
5. mechanically damaged reefs at 3m depth.
6. Java Sea polluted reefs.

These differences are highly significantly different (ANOVA, F=23.96, p<0.0001, d.f.=29). Further analysis b post-hoc Tukey test (table 2.4) shows the same ranking. Additionally, our site data may be grouped into six major categories: the three site types (comparison, mechanical damage, and land-based pollution) times 3m and 10m depth, which have very highly significant differences in diversity (1-way ANOVA, F=9.26, p<.0001)..

Table 2.4. Results of Tukey HSD post-hoc test on coral species diversity, measured as the slope of log-transformed species-area curves. Means listed in a given column are statistically equivalent.

Site type	N sites	subset 1	subset 2	subset 3
Java Sea eutrophic	4	14.35		
High sedimentation	3	18.11	18.11	
E. Indonesia Mechanical, 3m	5	18.49	18.49	
Java Sea Mechanical Damage	2		26.21	
Eastern Indonesian Eutrophic	4		26.28	
Java Sea Comparison (overfishing)	8		26.42	
E. Indonesian Mechanical 10m	3		27.21	27.24
Eastern Indonesian Comparison	3			37.39

2.3.3 Live coral cover.

Total percent live coral cover was highest on the Eastern Indonesian comparison reefs, but was not significantly different among the Eastern Indonesian control sites and the Karimunjawa comparison reefs. Total live coral cover was intermediate on reefs subject to mechanical damage, and lowest on reefs subject to eutrophication stresses, such as sedimentation, or combined sewage and sedimentation (fig. 2.8B; 1-way ANOVA, F=10.28, P<.0001). Table 2.3 shows the diversity and major cover class data for all the sites. Mortality index was higher on reefs subject to land-based pollution ($\bar{x}$= 0.44) than on comparison reefs ($\bar{x}$= 0.22) or mechanically damaged reefs ($\bar{x}$= 0.31; ANOVA, F=10.13, p<0.0005, d.f.=32).

2.3.4 Relationships between diversity and live coral cover.

Coral species richness and live coral cover are positively correlated in coral communities that are undersaturated, that is, where diversity is not limited by interspecific competition (Aronson and Precht 1995; Cornell and Karlson 1996). There is a highly significant positive correlation between cover and diversity (log-transformed slope) for reefs affected by land-based pollution and comparison sites (fig 2.9; r^2=0.47, n=24, p<0.001), but not for reefs subject to mechanical damage (r^2=0.14, n=11, p>0.25; 3 comparison sites included in regression). Coral species diversity on polluted and comparison sites is negatively correlated with cholorphyll A concentration (r^2=0.73, p<0.0001, n=33) and SPM (r^2=0.58, p<0.0001, n=33), both of which are indicative of land-based pollution. On mechanically damaged sites, diversity is not significantly correlated with any environmental variables.

Diversity and total live coral cover are positively correlated among all the sites (r^2=0.18, n=32, p<.0.015), but there is considerable scatter to the data. This relation appears to be driven primarily by the non-Acropora corals (r^2=0.17, n=32, p<0.02). Most of the eutrophied or high sediment sites have little or no Acropora cover, particularly in the Java Sea (Table 3). Average Acropora cover on reefs subject to land-based pollution was 3.5%; compared to 8.8% on mechanically damaged reefs, and 22.8% on comparison reefs.

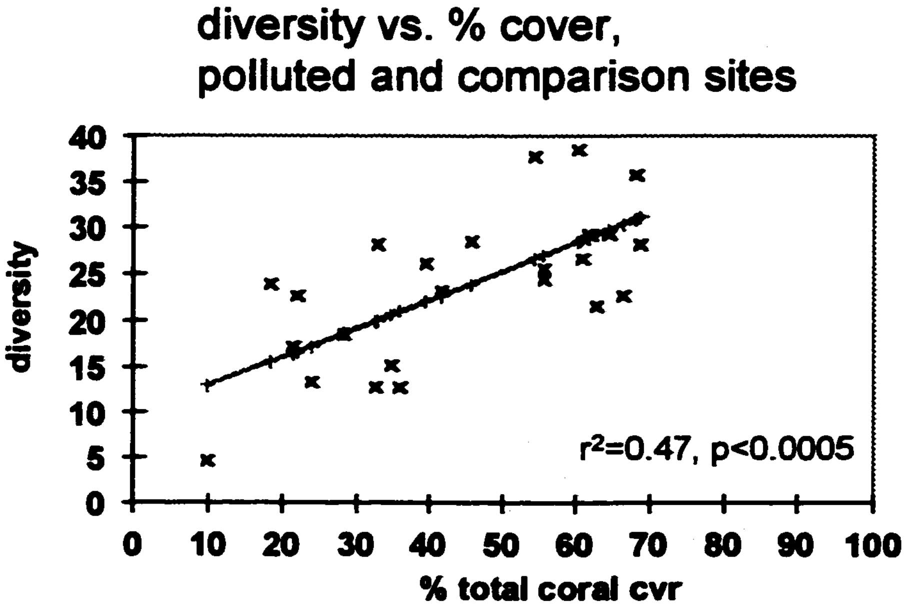


Figure 2.9. Relationship between diversity and percent live coral cover, pollution-affected reefs. Diversity measured as slope of log10-transformed species-area curves.

2.3.5 Change in diversity over time.

There are very few regional scale quantitative studies of coral species diversity in Indonesia. Most records consist of species-lists, but do not record how much area was searched (e.g. Randall and Eldredge 1983), and cannot readily be compared to examine within-habitat diversity changes resulting from reef degradation. It is extremely difficult to perform comparisons with previous reef studies. Not only does the taxonomic expertise of the two sets of researchers have to be equivalent, and the methodologies comparable, but site locations must be precisely specified.

The best known previous work quantifying coral species diversity in the areas we sampled was Moll's (1983) Ph.D. research, conducted mainly during 1980 across the Spermonde archipelago of S. Sulawesi, using similar methods and sampling intensity: repeated line intercept transects at 3m depth and 10m depth. These estimates of within-habitat species diversity from species-area curves yielded results very similar to ours (Moll 1983). Moll also listed the genera occurring on each of the 8 reefs he sampled. We resampled two of the same reefs in 1995: Samalona and Barang Lompo, and recorded approximately 25% fewer genera on each reef (table 2.5).

Table 2.5. Number of coral genera on two Sulawesi reefs, 1980 and 1995.

Reef	N genera	N genera	% change
year	1980	1995	
Samalona	37	28	-25%
Barang Lompo	39	29	-26%

The total number of coral genera recorded on each of these reefs decreased by approximately 25% over the last 15 years. Moll's total genus count was compiled from the reef flat, reef edge, and reef slope, while our 1995 data were collected only in the reef edge and reef slope zones. The reef flat, however, was the least diverse zone Moll sampled, accounting for less than 10% of the total species he sampled across the archipelago, such that even adding 10% to our genus counts would still yield a 20% reduction in genus numbers. A 20-25% reduction in generic diversity over 15 years is shocking; a similar level of extinction in the fossil record would be considered a minor mass extinction (Jablonski 1986).

2.6 Discussion.

2.6.1 Effects of Reef degradation types on coral biodiversity:

This study compares land-based pollution stress versus mechanical damage, or chronic vs. acute stress, in terms of their effects on coral biodiversity. At this time we cannot separate statistically the effects of different kinds of land-based pollution, such as sedimentation, sewage pollution, and industrial pollution on Indonesian coral biodiversity. Land based pollution is associated with greater reductions in diversity at all depths than is mechanical damage.

On reefs subject to anthropogenic mechanical damage (Samalona, Barang Lompo, Kapoposan 3m), coral species diversity is reduced by 50% at shallow depths (3m), but not at 10m (reef slope). This contrasts with the reef damaged by storms (P. Burung), where diversity is reduced by 30% at 3m and 15% at 10m. The pattern of diversity and cover reduction at P. Burung is typical of storm impacted reefs (Karlson and Hurd 1993; Rogers 1993). Reefs affected by mechanical damage can recover from that damage, if two conditions are met: (1) they are protected from further damage, and (2) some reefs in the area are undamaged (Pearson 1981; Done 1995).

On reefs subject to land-based pollution stress, coral species diversity is reduced 40-60% at shallow depths, and an equal or greater amount at 10m. Those reefs subject to the greatest combined sediment and nutrient loads often have little (Kayangan) or no (Wailiha, P. Panjang, Bondo) coral growth at 10m depth. Coral species diversity at 6m at Pulau Panjang, subject to sewage, sedimentation, and effluent from shrimp ponds, is reduced by approximately 50-60% relative to comparison reefs in Karimunjawa. Diversity on reefs subject to high sediment and nutrient loads (P. Panjang) is similar to coral diversity on fringing reefs adjacent to healthy mangroves (Lagun Marican). The highly significant correlation between species richness and coral cover among pollution-affected indicates that local species diversity has not reached saturation on these reefs, and that extrinsic factors (i.e. pollution) restrict species diversity on these sites, rather than intrinsic factors like spatial competition (Aronson and Precht 1995; Cornell and Karlson 1996).

Land-based pollution stresses, such as sewage, sedimentation, and industrial pollution, alter the physical and biological environment on a long term basis (Pastorok and Bilyard 1985; Tomascik and Sander 1987; Rogers 1990; Montaggioni et al. 1993). It is extremely difficult for reefs to recover from such chronic stresses (Pearson 1981; Pastorok and Bilyard 1985; Richmond 1993;Grigg 1995). As chronic stresses on reefs, pollution effects endure until the source of the pollution is shut off; recovery from eutrophication damage to reefs appears to require at least 10 years (Maragos et al. 1985; Grigg 1995). Pathogenic bacteria in untreated sewage attack and can kill corals (Mitchell and Chet 1975). Bioerosion increases with nutrient availability (Rose and Risk 1985; Hallock 1988; Sammarco and Risk 1990; see chapter 5), reducing accretion of carbonate material into the reef system (Hallock and Schlager 1986; see chapter 6).

Regional patterns

There are no accurate estimates available for the amount of reef area throughout Indonesia subject to the various forms of reef degradation we have outlined. All national-scale reef surveys published to date in Indonesia have focused on coral cover only (e.g. Moosa and Suharsono 1996; Chou 1997), not including coral species diversity, and have quantified condition based on a linear scale of live coral cover only (Gomez and Yap 1988). More important, they do not quantitatively classify the types of degradation occurring.

In general, chronic pollution stresses are localised along heavily populated shorelines (e.g. the north coast of Java, coast of S. Sulawesi), or near major cities (e.g. Jakarta, Surabaya, Ujung Pandang; Willoughby 1986; Tomascik et al. 1993), and are a more serious threat to reefs in western Indonesia than in the relatively underpopulated east (Chou

1997). Blast fishing and cyanide fishing appear to be most prevalent in Eastern Indonesia (Erdmann and Pet-Soede 1996), although the west coast of Sumatra has also suffered considerable bomb and cyanide damage in the last 5-10 years (Kunzmann, pers. comm. 1996; Molis 1997). Blast and cyanide fishing appear to be a greater threat to Indonesia reefs that are far from major populations centres.

2.6.2 Land-based sources of pollution and threats to biodiversity.

Land-based pollution on Indonesian reefs comes from 3 primary sources: untreated human sewage, agricultural runoff (including increased sedimentation from deforestation and aquacultural runoff), and industrial effluent (Brown 1985; McManus 1988; Yap 1992; BAPPENAS 1993). The aquaculture industry, particularly the shallow brackish water shrimp ponds (tambaks) prevalent in much of Indonesia, are a considerable source of nutrient and sediment effluent into coastal waters, including reefs (Chua et al. 1989; Tomascik et al. 1993). Widespread clearing of mangroves for shrimp ponds further exacerbates their effects (Yap 1996).

Sewage

There is no sewage treatment system in place for any major coastal city in Indonesia. $\delta^{15}N$ data suggest that sewage pollution from the city of Ujung Pandang reaches many of the nearshore reefs of the Spermonde archipelago (Jompa 1996). The decline and death of the remaining reefs in Jakarta Bay, and in the southern islands of the Pulau

Seribu attest to the long distance effects of urban effluent on Indonesian reefs (Tomascik et al. 1993; Willoughby et al. 1997).

Industrial Effluent.

Industrial effluent was a factor in three of the sites we studied. Wailiha (Ambon) reef is about 200m from a new plywood factory, and corals there have elevated lignin concentrations in their skeletons (Limmon 1996). Wayame reef (Ambon Bay) is adjacent to the oil delivery terminal for Ambon City, and slight oil slicks have been observed in Ambon Bay (Evans et al. 1995). Kayangan reef (Sulawesi) is in the mouth of Ujung Pandang harbour, and receives oil from shipping activities and other industrial wastes dumped into the Ujung Pandang harbour. The reefs of Jakarta Bay, however, show the clearest effects of combined industrial waste and sewage on reefs. These reefs are now entirely dead (Tomascik et al. 1993; Willoughby et al. 1997). While most kinds of litter and chemical pollution decrease away from the shoreline, oil pollution in the Jakarta Bay and Thousand Islands region increases offshore, with most of this oil apparently coming from South China Sea oilfields (Uneputty and Evans 1997).

1985 surveys in the Pulau Seribu islands north of Jakarta showed that the amount of plastic garbage per linear metre of strand line was the best single measure of pollution from Jakarta, and the best single correlate of reef health, in 38 islands in the chain (Willoughby 1986). Repeat surveys in 1994 (Uneputty and Evans 1997) and 1995 (Willoughby et al. 1997) showed that the amount of garbage per length of strand line had doubled, that the relationships with reef health still applied, and that many of the reefs in Jakarta Bay that were in serious decline in 1985 are now entirely dead (Uneputty and Evans1997).

2.6.3 Reduction in diversity over time.

Following time trends in diversity on coral reefs can be done by comparing present studies with ones done in the past, but in fact it is extraordinarily difficult to relocate and replicate previous coral reef surveys. Locations of the original surveys must be given with a precision that allows re-occupying the same site, with an error of only a few metres. In addition, the original reference must give sufficient details of the methodology that similar techniques may be employed in the re-survey. This is rarely the case in coral reef science. Even when sample sites are "permanenty" marked, by stakes, nails, etc., there needs to be regular checking of the site. In our work in Maldives, for example, we found that one-third of our markers (large nails in corals or hardground, pieces of pipe driven into the sediment, etc.) disappeared each year, either through vandalism or coral head dislodgement. There are very few coral reef surveys more than a decade old that are published with enough detail to allow proper resurvey. In our area, the only published survey results we felt were sufficiently precise for our purposes came from Moll's PhD research (Moll 1983).

Comparing sites that were sampled by Moll and ourselves, we show that there has been a 25% decrease in coral generic diversity over the past 15 years. Nonetheless, we hasten to point out that we have established only two reefs from the Spermonde Archipelago where this decrease has been demonstrated, and while we suspect that this decrease is anthropogenic, we cannot prove that to be so. It is not clear whether similar decreases have occurred on all the reefs of Indonesia, especially as the baseline diversity for corals in Indonesia is very poorly known.

On the other hand, both the reefs surveyed by Moll (1983) and ourselves are well offshore Ujung Pandang. They are subjected to the same sorts of stresses that affect most, if not all, Indonesian reefs. The comparison between Moll's results and ours, therefore, may well serve as a general guide to the situation in the entire country.

2.6.4 Implications for coral reef fisheries in Indonesia.

Coral reef fisheries depend heavily on the quality and quantity of coral reef habitat. Fish diversity and abundance on coral reefs is positively correlated with live coral cover (Bell and Galzin 1984; Sukarno et al. 1986), and with habitat complexity (Risk 1972; Luckhurst & Luckhurst 1978; Roberts and Ormond 1987; Dulvy et al. 1995; Jennings et al. 1996). The loss of Acropora in polluted nearshore habitats as documented in this study causes a dramatic reduction in habitat complexity (Done 1996; chapter 4). Thus, coral cover in the Pulau Seribu islands is positively correlated with distance from Jakarta, and fish diversity is positively correlated with live coral cover (r^2=0.67), resulting in the loss of most reef fish species on nearshore reefs of the Pulau Seribu (Harger 1992). Likewise, fisheries yields on bombed Philippine reefs were approximately five times lower than on reefs in good to excellent condition (McAllister 1988; Rubec 1988).

Cesar (1996) has modelled the economic effects of reef degradation in Indonesia, and estimates losses to the Indonesian fishery sector resulting from reef degradation and overfishing at \$410,000 per km^2, assuming a 10% discount rate, summed over 25 years. Assuming that these economic models are correct, and assuming that our figures are representative of the overall situation of Indonesian reefs, then Indonesia has already lost 40% of its reef fisheries resources. Given approximately 75,000 km^2 total reef area in Indonesia, this yields an estimated \$30 billion loss to the Indonesian economy over 25 years.

2.7 Limitations to this study

There are several important limitations to this study:

1. There are no pristine coral reefs in our data set. There may be none in Indonesia - Jackson (1997) argues that any discussion of pristine coral reefs world-wide is ludicrous, given the intensity of reef resource exploitation. Even the Tanjung Setan reefs in Ambon, the closest we could find to reefs protected from anthropogenic impacts, are subject to artisanal fishing.

2. Most of the impacted sites are subject to more than one type of anthropogenic stressor. For example, Barang Lompo, which has been bombed along with many of the reefs of the Spermonde archipelago, also suffers impacts from locally generated sewage pollution (Jompa 1996),

and may be affected by oil and other chemical pollution from Ujung Pandang (Erdmann and Caldwell 1997).

3. Anthropogenic effects are not completely separated from the effects of substrate type (Hila, Wailiha), successional stage (possibly some shallow sites in the Spermonde shelf), and biogeographic effects (Java Sea vs. Eastern Indonesia).

Nonetheless, the consistent and highly significant inverse correlations between coral species diversity and environmental variables indicative of land-based pollution on the polluted and comparison reefs provide sufficient evidence that pollution reduces coral biodiversity to make environmental policy decisions (cf. Sindermann 1997).

2.8 Conclusions

1. Stresses from land-based sources of pollution are associated with 40-70% reductions in coral species diversity at all depths, with greater impact at 10m depth than at 3m depth.

2. Mechanical damage to coral reefs is generally associated with up to 50% reduced coral species diversity in shallow water (3m), with relatively minor effects at 10m depth. The reduced diversity in 3m is approximately equivalent to the reductions associated with natural mechanical damage such as storms or growth on an unstable bottom, but these natural forms of mechanical damage also reduce diversity at 10m depth.

3. Coral species diversity and live coral cover are positively correlated. Diversity and cover are both reduced most on reefs subject to combined sewage and siltation, while reefs subject to mechanical damage show more variation.

4. Efforts at coral reef and marine biodiversity conservation that do not include controlling land-based pollution sources will fail to address the major threats to Indonesian coral reefs.

Chapter 3: Biogeographic comparisons.

Within-site coral species diversity on reefs in three regions of Indonesia.

3.1 Introduction.

Chapter 2 examined differences in within-site coral species richness attributable to different types and intensities of reef degradation and noted an approximately 20% difference in species diversity between the relatively comparison sites in the Java Sea and their counterparts in eastern Indonesia. This difference in diversity is probably attributable to a combination of biogeographic and geomorphological differences and to anthropogenic factors, particularly differences in fishing intensity, given the intense fishing pressure on the Karimunjawa islands. Here, I present similarity indices for the reefs sampled in the three regions, and discuss factors that could be responsible for regional differences in within-site species diversity and regional species richness.

3.2 Methods.

Species lists derived from transect data for each site were compiled to form composite regional species lists (Appendix 1). These composite species lists contain many fewer species than lists compiled only by searching for species. The number and proportion of species in each region which were apparent endemics or apparent pandemics was then calculated. Several of the apparent eastern Indonesian endemics were recorded elsewhere in the Karimunjawa islands (but not included in the quantitative species diversity dataset); these observations are included in the "adjusted endemism" calculations.

Jaccard similarity indices and Bray-Curtis dissimilarity indices were computed among four pairwise combinations, Ambon-Sulawesi, Ambon-Java, Sulawesi-Java, and internally within Karimunjawa, to define more quantitatively the extent to which diversity differences between the regions are biogeographic in origin. The internal comparison within Karimunjawa was designed to assess the contribution of sampling error to apparent biogeographic difference, and was computed by comparing the combined species lists of 12 transects at Pulau Kecil vs. 12 transects at Gosong Cemara.

3.3 Results.

3.3.1 Species numbers and apparent endemicity.

One hundred ninety-six (196) coral species were recorded in quantitative surveys. Regional totals of 150 species were recorded in Ambon, 133 in Sulawesi, and 114 in the Java Sea sites (table 3.1; appendix 1). Of these, 109 were apparent pandemics, occurring both in the Java Sea and in the Eastern Indonesian sites. Of the remainder, 12 (6%) were recorded in the Java Sea only, and 75 (38%) were recorded in Eastern Indonesia only.

Table 3.1 Total eastern and western Indonesian endemic species. All Acropora species counted for endemic species, but only Acropora species groups counted for adjusted endemism.

	Endemic	species		
region	western	eastern	pandemic	all
N spp.	12	75	109	196
% spp.	6	38.3	55.6	100
	adjusted	endemism		
region	western	eastern	pandemic	all
N spp.	12	45	122	179
% spp.	7	25	68	100

Of these apparent endemics, however, 18 were Acropora species, belonging to Acropora species groups of which all but one are pandemic. Of the remaining coral species recorded in Eastern Indonesia, but not in Central Java, 13 were observed elsewhere in Central Java, but were not sampled in this study. Thus, of 75 apparent eastern endemics, 17 are eliminated and 13 are considered pandemics, leaving a total of 45 apparent eastern endemics out of 179 total species records, where acroporids were recorded to the species group level only (adjusted endemism, table 3.1). Species endemic to Eastern Indonesia, then, are 45 of 179, or 25% of the total species pool sampled. Of these remaining eastern endemics, the other most abundant genus of apparent endemics was Fungia; 12 fungiid corals sampled in eastern Indonesia were not recorded in Karimunjawa. The abundant records of fungiids in Eastern Indonesia came mainly (5/12) from Hila, the site on a rubble bottom, where fungiids were particularly common and diverse.

3.3.2 Similarity analysis.

Similarity analyses among three regional faunas (Ambon, Sulawesi, and Karimunjawa) using Acropora species groups revealed overall fairly similar faunas, with basic similarities among all three groups greater than 70% (table 3.2). Interestingly, internal similarity among two reefs (24 transects) in Karimunjawa is 78%, only 3% greater than similarity between Ambon and Karimunjawa, suggesting that sampling artifacts account for a large portion of the the dissimilarity observed among regional faunas. Future work using cluster analysis followed by ANOVA will help resolve the separate biogeographic variation from sampling artifact variation.

Table 3.2 Similarity analyses of Ambon, Sulawesi, and Karimunjawa corals. Basic similarity is defined as 2(common spp.)/(A+B), with a maximum value of 1. Jaccard similarity is computed as S(a,b)=common spp*10/(A+B-common), with no maximum value. Bray-Curtis dissimilarity is computed as BC=(A=B)/(2*common spp. + B + total spp.), with a maximum dissimilarity of 1.

Comparison	Ambon-Sulawesi	Ambon -Java	Sulawesi-Java	Java internal
N spp. A	150	150	133	88
N spp. B	133	114	114	100
common spp.	100	99	89	73
N spp. A only	48	60	46	15
N spp. B only	34	16	24	27
total N spp.	183	175	159	114
basic Similarity	0.707	0.75	0.72	0.777
Jaccard	54.65	60.00	56.33	63.48
Bray-Curtis	0.568	0.571	0.581	0.563

3.3.3 Diversity and cover relationships revisited.

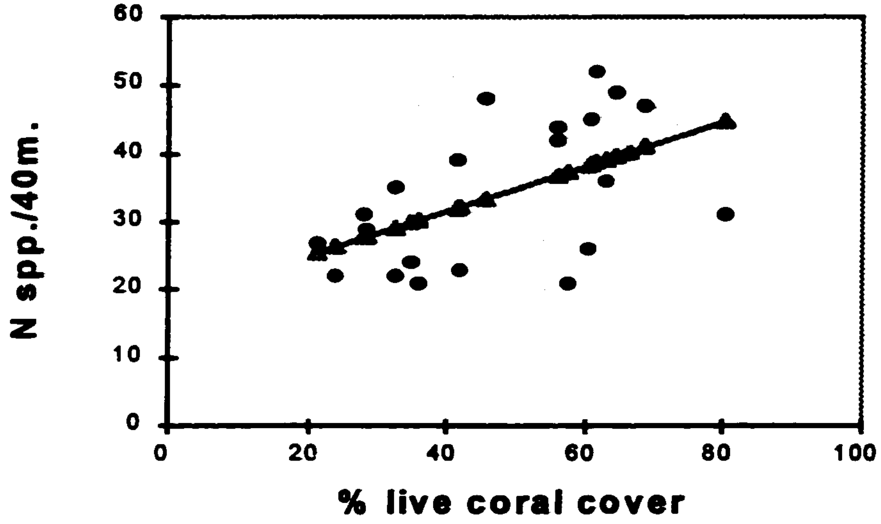
Coral species diversity (N spp./40m curve) is positively correlated with total live coral cover when all sites are considered (r^2=0.31, $p<0.001$), and when the Java Sea sites (fig 3.1A, r^2=0.65, $p<0.0001$, n=22) and eastern Indonesian sites (fig 3.1B, r^2=0.23, $p<0.07$, n=15) are treated separately. The slopes of the lines relating cover and diversity in the Java Sea and the eastern Indonesian sites are nearly parallel (β=0.51, Java Sea; β=0.40, E. Indonesia), but the y-intercept, indicative of "baseline diversity" is higher in the eastern Indonesian sites (y=13.2, Java Sea, y=25.3, E. Indonesia; fig. 3.1). Because the eastern Indonesia regression is not significant, it is not possible to test the difference in slopes between the two lines.

3.4 Discussion.

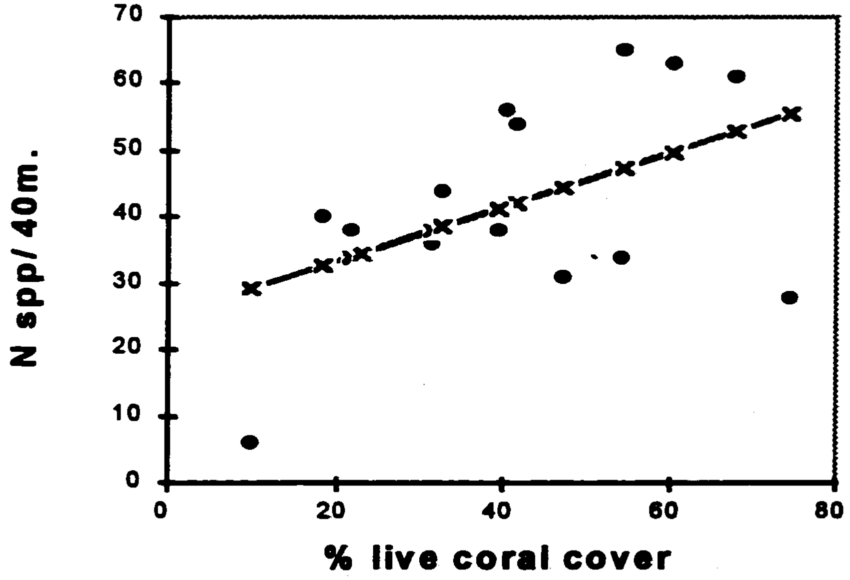
The biogeographic results presented here, using Acropora species groups, and species of all other corals, are broadly similar to previous maps of Indo-Pacific coral species distributions (Veron 1993) and to recent findings on biogeography and diversity of Indonesian Acropora corals (Wallace 1997). The southwest region (Sumatra and Java) was the least diverse of five regions, with 28 Acropora species, and no endemics. The other regions (all parts of eastern Indonesia) all had more than 50 Acropora species, including one or more endemic Acropora species. Wallace (1997) cautions, however, that the reefs of Sumatra

Figure 3.1. Diversity and cover relationships in eastern and western Indonesia. A. Relationship between diversity and cover on all Java Sea Reefs. B. Relationship between diversity and cover on all Eastern Indonesian reefs.

A. Java Sea Diversity (S/40m) vs. cover



B. Easterm Indonesia Diversity (S/40m) vs. cover



and Java are relatively poorly sampled. More Acropora were recorded from all parts of Sulawesi than from the Moluccas, in contrast to the diversity pattern presented here.

Three possible explanations may account for the greater within-site and total coral species diversity in eastern Indonesia than in the Java Sea: (1) a smaller species pool in the Java Sea due to regional biogeographic differences (Veron 1993; Wallace 1997), (2) geomorphological differences related to reef growth in an epeiric sea, and (3) more intense fishing pressure in the Java Sea than in eastern Indonesia. The first two of these are consequences of Pleistocene sea-level fluctuations, during which the Sunda Shelf was drained and exposed (Wyrtki 1961).

3.4.1 Species pool effects

The total species occurrence data (table 3.1) suggest that eastern Indonesia is inherently more diverse than the Java Sea, corroborating the patterns seen in other datasets (Wallace 1997). Just as western Indonesia contains no reported endemic Acropora species, it also contains Acropora species that are either all pan-Indo-Pacific or of Indian Ocean origin. All parts of eastern Indonesia contain some mix of pandemics, Indian Ocean species, Pacific Ocean species, and endemic Acropora species. Their greater diversity is attributed to this mixing (Wallace 1997)

The similarity analysis, however, suggests that biogeographic differentiation of regional faunas is only slightly above differentiation associated with sampling error (table 3.2). While regional species richness may contribute to lower within-site diversity (Cornell and Karlson 1996) on Java Sea reefs, such innate biogeographic differences in diversity probably do not account for all of the 20% reduced diversity in the Java Sea.

3.4.2 Geomorphology

The most diverse sites in the dataset are the eastern Indonesian wall reefs, Tanjung Setan 3m and 10m and Kapoposan 10m. Most of the new endemic Acropora species reported from Indonesia are from reef slopes between 10 and 30m depth (Wallace 1997). Geomorphological differences in reefs, principally the absence of wall reefs bordering open ocean in the Java Sea, may contribute to lower average diversity on Java Sea reefs, although most of the species occurring on the wall reefs in Ambon and Sulawesi also occur on Karimunjawa reefs (appendix 1). Furthermore, the prevalence of free-living fungiids among the eastern Indonesian endemics does not support the importance of wall reefs in maintaining species diversity.

Growth on a recently exposed continental shelf may, however, restrict occurrence of endemic coral species. Morphological features of newly described endemic Acropora species from eastern Indonesia suggest that these species are not newly evolved (Wallace 1997); endemic Acropora (and presumably other) coral species would not be expected on a broad continental shelf that was frequently exposed during

Pleistocene sea-level lowstands, and that was only re-flooded within the past 10,000 years (Tjia 1980).

3.4.3 Fishing Intensity

The Karimunjawa islands are one of the principal fishing grounds in the Java Sea for peri-reefal pelagic fish, and increasingly, reef fish. In the course of more than 80 dives in the Karimunjawa islands, I never saw any large fish, but I did see abundant fish traps, and fishing boats operating in all zones of the marine park, regardless of protection status. Blast fishing and cyanide fishing appear to be less intense than in the Spermonde archipelago, but cyanide fishing for the highly lucrative live fish trade is apparently on the rise. Fishing pressure by traditional (non-destructive) means appears to be more intense in the Java Sea than in eastern Indonesia, but Indonesian fisheries statistics are notoriously unreliable, making quantitative assessment of this hypothesis difficult.

Numerous studies have documented the impact of overfishing on coral reef community structure (reviewed by Roberts 1995) and species diversity (e.g. McClanahan 1994). Overfishing, first of large predatory species, then of large herbivorous fishes, contributed to the shift to macroalgal dominance on Jamaican coral reefs in the wake of 2 hurricanes and the Diadema antillarum die-off (Hughes 1994). Intense fishing activity in the Java Sea undoubtedly affects the species diversity and composition of Java Sea coral reefs, but separating this effect from inherent biogeographic differences is not possible from the current dataset alone.

3.5 Conclusions.

1. The eastern Indonesian coral fauna sampled in this study is considerably more diverse than the Java Sea coral fauna, matching the results of other studies of regional variation in Indonesian coral species diversity.

2. Nearly two thirds of the coral species occurring on transects in the three regions are pandemics. Approximately 25% of the species occurring on eastern Indonesian transects are apparent endemics, while only 7% of Java Sea species are apparent endemics.

3. Similarity analysis suggests that dissimilarity between the Java Sea fauna and its eastern Indonesian counterparts is only 3-5% greater than apparent dissimilarity due to sampling artifacts.

4. A combination of a smaller total species pool, reduced variation in reef geomorphology, resulting from Pleistocene sea-level fluctuations and the recent re-flooding of the Sunda shelf, probably accounts for most of the reduced species diversity in the Java Sea.

5. More intense fishing pressure in the Java Sea than in eastern Indonesia may enhance the biogeographic differences in diversity between the two regions.

Chapter 4. Morphological composition of Java Sea reefs.

4.1 Introduction.

The goal of this chapter is to characterise the morphological composition of the corals on the various reef facies sampled in the Java Sea, where morphological composition refers to the relative abundance of coral morphology categories (English and Wilkinson 1993) on a given reef. These data are useful for examining changes in coral community structure resulting from land-based pollution effects on nearshore reefs and for describing changes in community composition related to aspect and depth in relatively unaffected reefs of the Karimunjawa islands.

The morphological composition of the corals on a reef can be used to classify the reef and to estimate its conservation value in a manner not dependent on taxonomic expertise. Such taxonomy-independent methods are particularly appropriate in Indonesia, where most researchers and reef monitoring personnel have little or no training or expertise in coral taxonomy. Morphological comparisions can be used to develop morpho-facies models of modern epeiric sea coral reefs applicable to the fossil record (see chapter 8).

4.2 Methods.

4.2.1 Study Sites.

A total of 7 reefs were sampled in the Java Sea: four coral cays in the Karimunjawa islands, a fringing reef bordering mangroves in Karimunjawa (Lagun Marican), nearshore coral cay in Jepara (Pulau Panjang), and a nearshore fringing reef near Jepara (Bondo). All coral cays were sampled at both 3m and 10m, both windward and leeward sides, except P. Panjang, which was sampled at 3m and 6m. Fringing reefs were sampled at 3m only, because in both cases, coral growth did not extend beyond 5m depth.

Of the four Karimunjawa coral cays, P. Kecil, G. Cemara, P. Burung and Pp. Menjangan Besar+Kecil, Pulau Menjangan Besar+Kecil was treated separately as a climax community, where "climax" is defined as a reef with very high cover of a few long-lived, slow-growing species, mainly in large monospecific stands (Aronson and Precht 1995), and typically an end product of successional change (Connell 1978; Huston 1994). The high percentage of live coral cover and species composition at Pp. Menjangan appeared very different from the other reefs sampled. The species composition data from Pp. Menjangan are suspect, as the taxonomic knowledge of the transect recorders is limited, and I was unable to check the species data on all the transects myself; this species richness data is not used in chapter 2. The windward side of Pulau Burung was severely damaged by a storm in 1993, and was also treated separately.

Table 4.1. Categories and reefs sampled for morphological comparison, Java Sea and Sulawesi.

Category	Reefs in group	Depth	Aspect	Reefs	Transects
Karimunjawa 3m	Kecil, Cemara, Burung (l/w)	3m	w/w + l/w	3	15
Karimunjawa 10	Kecil, Cemara, Burung (l/w)	10	w/w + l/w	3	15
Karimunjawa w	Kecil, Cemara	all	windward	2	12
Karimunjawa l/w	Kecil, Cemara, Burung	all	leeward	3	18
Karimun climax	Pp. Menjangan	all	w/w + l/w	1	12
Karimunjawa storm	P. Burung w/w	all	windward	1	6
Sulawesi 3m	Samalona, B Lompo, Kapoposan	3m	leeward	3	18
Sulawesi 10m	Samalona, B. Lompo, Kapoposan	10m	leeward	3	18
Nearshore reefs	P. Panjang, L. Marican, Bondo, Kayangan	all	w/w only, w/w+l/w at P. Pjg.	4	32

Table 4.2. Coral morphology categories used in reef surveys. The last column, rKS, indicates the assignment of adaptive strategy for conservation value ternary diagram analyses.

Morphology	Code	Description	rKS group
Acropora, branching	ACB	staghorn corals, long thin branches	r
Acropora, bottlebrush	ACBB	mainly A. echinata group	r
Acropora, corymbose	ACC	stout branches, low bushy shape	r
Acropora, digitate	ACD	digitate stubby, mainly A. humilis group	r
Acropora, tabular	ACT	tables, mainly A. hyacinthus group	r
Acropora, submassive	ACS	columns + blades, very stout, mainly A. palifera and A. cuneata (subgenus Isopora)	r
branching coral	CB	branching non-Acropora corals; esp. Porites cylindrica, some other spp.	K
encrusting coral	CE	low relief, often small colonies.	K
massive-platy coral	CMP	plate-like corals forming large massive colonies, esp. Euphyllia, Lobophyllia spp., very often with large fleshy polyps	S
massive coral	CM	massive or domelike corals of all sizes.	S
foliose coral	CF	foliose, either horizontal or vertical, non-Acropora, esp. Montipora, Echinopora, and Pavona spp.	K
tabular coral (non-Acorpora)	CT	tabular non-Acropora, esp. Montipora	r
submassive coral	CSM	multilobate or "lumpy" corals, sometimes columnar or mixed massive-columnar.	S
mushroom coral	CMR	free-living fungiid corals.	Not classified
Millepora	CME	various species of Millepora. (hydrocoral)	r
Heliopora	CHL	blue coral (a hydrocoral)	not classified

4.2.2. Coral morphologies.

Reefs were sampled using the standard line-intercept transect surveys (Loya 1978) used by the Indonesian institute of science (English and Wilkinson 1993). These include a set of 15 basic coral morphologies, to which I added four more morphological categories to the Java Sea sampling to reflect locally abundant morphologies that were not clearly represented in the AIMS standard methodology. Morpologies, codes, and descriptions are listed in table 4.2, along with r-K-S adaptive strategy groups (section 4.3.7).

4.2.3 Data analysis.

Transect data from the seven reefs sampled in the Java Sea and the four reefs sampled in Sulawesi were pooled to calculate averages and standard deviations. Reefs were grouped into the following categories: Karimunjawa 3m, Karimunjawa 10m, Karimunjawa windward, Karimunjawa leeward, Karimunjawa storm damaged (P. Burung w/w), Karimunjawa climax community (P. Menjangan Besar + P. Menjangan Kecil) nearshore reefs (PPN, PPS, Bondo, LM, Kayangan), Sulawesi offshore 3m, and Sulawesi offshore 10m. Composition of each reef was calculated before calculating averages for each category, ensuring that all reefs within each category were equally represented.

Conservation value ternary diagrams (section 4.3.7) were constructed by summing the total cover of the various morphologies in each of the three adaptive strategy groups defined by Grime (1979): r-strategists, K-strategists, and Stress-tolerators, where r-strategists are rapidly growing early successional organisms, K-strategists are slower-growing competitive dominants, often forming large monospecific stands, and stress-tolerators are slow-growing organisms present in all environments, but which can tolerate harsh environments and become the dominant groups only under such harsh conditions. These strategies can be applied to corals, and can be used to estiimate the conservation value of reefs (fig. 4.5A). Assignment of morphologies to groups, as shown in table 4.2, was based on field observations, primarily in Karimunjawa. Percent cover values for each adaptive strategy group were normalised to total live coral cover on each site on all 15 reefs sampled in Ambon, Sulawesi, and the Java Sea, yielding 36 points plotted in r-K-S space, such that the three categories always sum to 100%. These points were plotted on a ternary diagram using the Rockware software package.

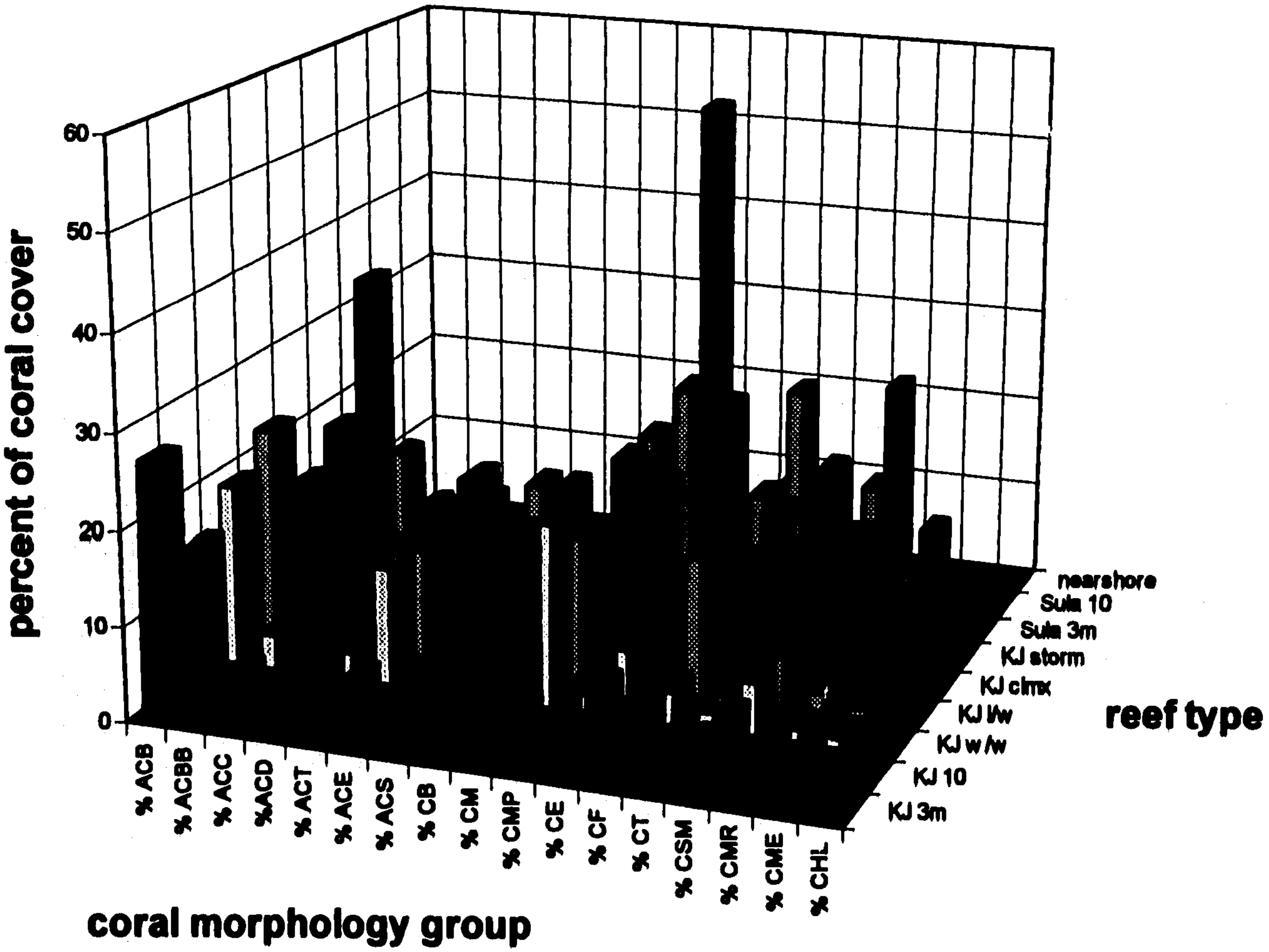
4.3 Results and Discussion

Several important comparisons of morphological composition emerge from the data: onshore-offshore differences, depth related differences, windward-leeward differences, and regional differences between platform reefs in Karimunjawa and Sulawesi.

Table 4.3. Morphological composition summaries for 9 categories of reefs sampled in the Java Sea and Sulawesi.. Group labels follow table 4.1. Morphological categories are described in table 4.2. All data presented as percentage of total live coral cover.

Group	ACB	ACBB	ACC	ACD	ACT	ACE	ACS	CB	CE	CMP	CM	CF	CT	CSM	CMR	CME
nearshore	1.04	0	0.25	0.04	1.25	0.13	1.38	3.63	7.75	2.38	51.88	3.75	0	21.29	5.20	0
KJ 3m	27.00	1.26	3.20	3.80	20.80	0.20	0	11.20	3.20	1.20	13.00	7.00	1.40	5.80	1.00	0.52
KJ 10m	15.20	2.40	1.00	0.26	3.46	0	0	26.00	6.40	2.80	20.80	13.40	0	5.00	2.40	1.12
KJ w/w	19.00	3.50	4.50	2.83	12.58	0	0	16.50	7.25	2.00	19.25	3.50	1.75	5.75	1.25	0.90
KJ l/w	22.50	0.72	0.50	1.50	11.83	0.17	0	20.00	3.17	2.00	15.33	14.67	0	5.17	2.00	0.77
KJ climax	14.25	4.00	2.50	3.75	5.00	0	1.25	17.25	5.50	1.75	8.50	28.00	0	5.50	2.75	0.08
KJ storm	18.00	0.50	0	2.00	11.50	0	0	7.50	4.50	2.00	17.50	8.50	0	19.50	7.50	1.00
Sula 3m	32.67	N/a	0	0.20	1.10	0.77	6.67	15.33	5.33	n/a	12.67	11.33	n/a	9.33	3.00	1.67
Sula10m	10.00	n/a	0	0.43	1.00	0.30	3.00	15.33	10.0	n/a	21.33	22.33	n/a	12.33	3.00	1.00

Figure 4.1: Morphological composition summary. Reef types follow table 4.1, morphologies follow table 4.2.



4.3.1 Onshore vs. Offshore morphological composition.

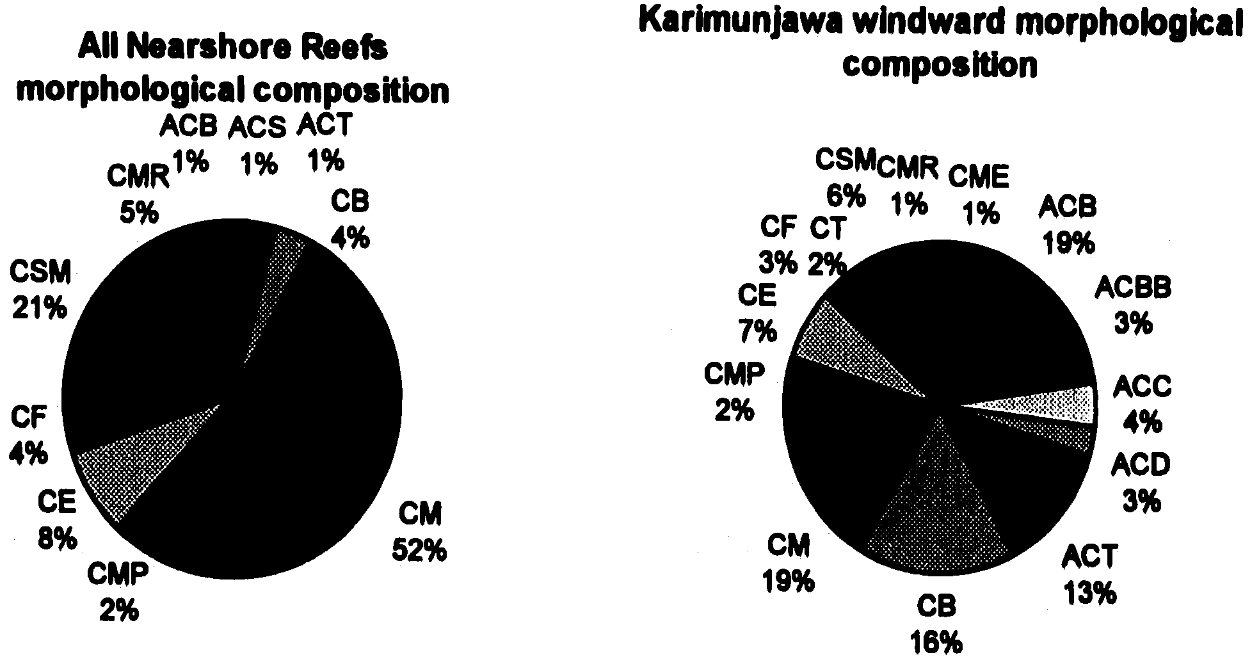
By far, the most dramatic differences are seen comparing onshore and offshore reefs. The first, most obvious, difference is the almost complete lack of Acropora corals on inshore reefs. No Acropora morphology accounts for more than 1% of the coral fauna on any of the nearshore Java Sea reefs, and the decreased Acropora cover on nearshore reefs (t-test, $p<0.0001$) is largely responsible for the decrease in total live coral cover on nearshore reefs (t-test, $p<0.0001$). Next, branching and foliose corals, common on nearly all the offshore reefs, both drop to less than 5% of the fauna. The dominant morphologies on nearshore reefs are massive (50.2%) and submassive (27.3%) corals (2-way ANOVA; interactions $F=4.97$, $p<0.0001$). The apparent prominence of fungiid corals on nearshore reefs is attributable to Kayangan reef at 10m depth, where fungiids make up a large proportion of the low live coral cover . The relative uniformity of the morphological composition of the corals suggests that the morphology responds more to sedimentation than to sewage contamination and eutrophication alone.

4.3.2 Karimunjawa reefs at 3m vs. 10m.

The morphological composition of reefs at 3m and 10m is significantly different (2-way ANOVA, interactions $F=3.61$, $p<0.0001$). Nearly half the coral cover (47.8%) on the 3m reefs in Karimunjawa is composed of branching and table Acroporas; the two next common

Figure 4.2: Morphological composition of nearshore reefs (left) and offshore reefs (right).

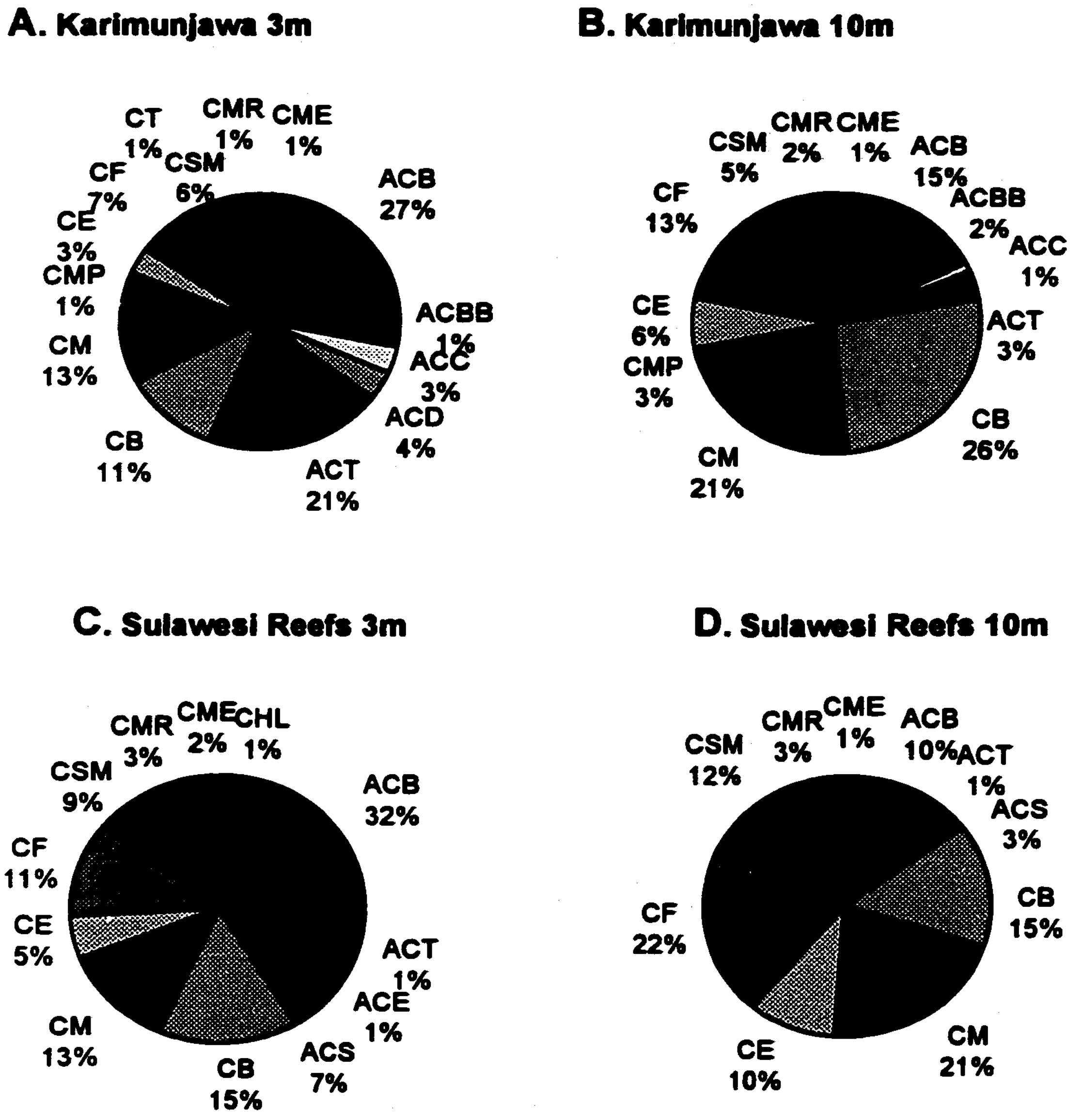
Karimunjawa windward reefs are typical of offshore reefs in the islands. Morphology codes follow table 4.2.



All Nearshore Reefs morphological composition

Karimunjawa windward morphological composition

Figure 4.3. Morphological composition changes with depth.
A: Karimunjawa 3m. B: Karimunjawa 10m. C: Sulawesi 3m. D. Sulawesi 10m.
Morphology codes follow table 4.2.


A. Karimunjawa 3m

B. Karimunjawa 10m

C. Sulawesi Reefs 3m

D. Sulawesi Reefs 10m

groups are massive and branching corals. Tabular non-Acropora corals occur on 3m windward reefs only, and mainly consist of large platy-tabular Montipora. Likewise, corymbose and digitate Acropora are most common on the 3m windward reefs. At 10m, branching non-Acropora corals are the most abundant morphology, principally Porites cylindrica, followed by massive corals of all species. The next two common groups are branching Acroporas and foliose corals (principally Pavona cactus and Echinopora lamellosa). The only Acropora morphology more abundant at 10m than at 3m is bottlebrush Acropora (ACBB, Acropora echinata group).

The differences in coral morphological composition between 3m and 10m appear to respond primarily to wave energy, as the 3m reefs are dominated by robust morphologies, while more delicate morphologies are much more abundant at 10m. These differences imply the competitive domination of 3m reefs by rapidly growing branching and tabular Acropora corals, while the 10m reefs are frequently dominated by monospecific stands of branching Porites cylindrica, which is not as strong as the Acroporas and does not commonly form large stands in shallow waters, except in protected reef flats (EE, pers. obs.).

4.3.3 Effects of exposure on morphological composition, Karimunjawa.

There are no significant differences in morphological composition between windward and leeward reefs (2-way ANOVA, interactions F=0.91, p>0.55). Stout growth forms like corymbose, digitate, and tabular Acropora are all more abundant on windward reefs than leeward reefs.

Branching non-Acropora and foliose corals are much more abundant on leeward reefs than on windward reefs. The minimal morphological differentiation between windward and leeward reefs may reflect the monsoonal climate system of the Java Sea, with predominant wind and wave directions shifting almost 180 degrees between the wet season and dry season (Wyrtki 1961).

It is intriguing that within-site coral species diversity is consistently higher on the leeward sides than on the windward sides of Karimunjawa reefs (fig 2.3; t-test, $p<0.05$, d.f.=9), including at storm-damaged P. Burung. This difference remains unexplained; there are no significant differences in total live coral cover between windward and leeward reefs (t-test, $p<0.10$, d.f.=9).

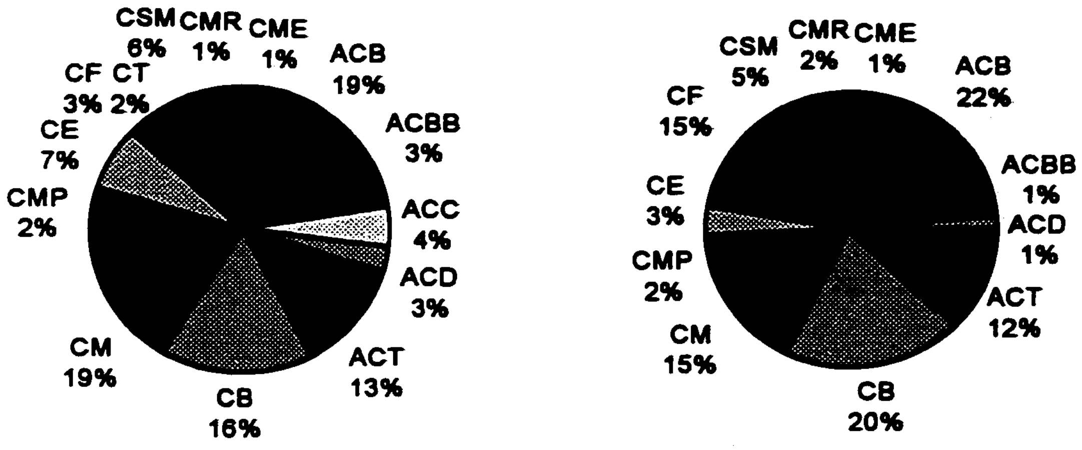
4.3.4 Disturbance: Storm-damaged and Successional Climax reefs.

The storm affected reef (P. Burung w/w) has virtually the same morphological composition as the other windward reefs in Karimunjawa, with the exception of a very high abundance of submassive corals (principally the weedy species Galaxea fascicularis). Branching Acropora are nearly as abundant as on other windward reefs, but other branching corals are much less abundant. This probably reflects the rapid re-growth of branching Acropora following the storm, compared to slower regrowth of other branching corals like Porites cylindrica.

Figure 4.4. Exposure and disturbance effects on morphological composition, Karimunjawa. A. Windward reefs. B. Leeward reefs. C. Successional climax reefs. D. Storm damaged reefs. Morphology codes follow table 4.2. See table 4.1 for reef names.

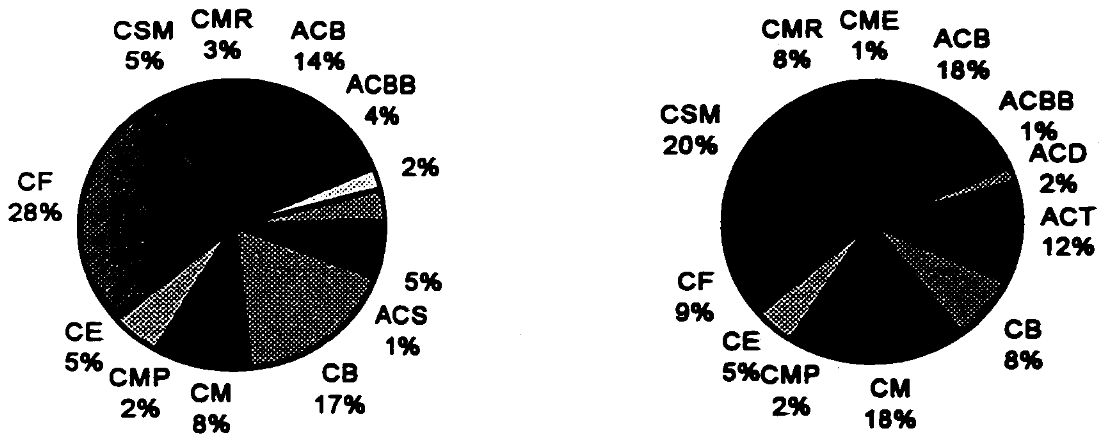
A. Karimunjawa windward

B. Karimunjawa Leeward



C. Successional Climax Reefs

D. Storm Damaged Reefs



The successional climax reef (Pp. Menjangan Besar and Kecil) has very high live coral cover values (all transects have >75% live coral cover), and is dominated by large monospecific stands of branching and foliose corals, which together account for 45% of the coral cover. It has about triple the abundance of foliose corals (principally *Pavona cactus*, *Echinopora lamellosa*, and *Montipora foliosa*) of the other Karimunjawa reefs, and about half the abundance of massive corals and platy *Acropora* corals of other Karimunjawa reefs. Otherwise, the morphological composition differs very little from Karimunjawa reefs in general; the composition of Karimunjawa leeward reefs and Menjangan reefs is not statistically distinguishable (ANOVA, F=.01, p<0.50).

4.3.5 Sulawesi vs. Karimunjawa

Comparing the morphological composition of the offshore reefs in Sulawesi with the Karimunjawa coral cays can help to establish regional patterns, and can help to indicate the extent to which differences in species richness are a result of disturbance regime or successional change. The relative morphological composition of the coral fauna at 3m is almost identical in Sulawesi and Karimunjawa (fig. 4.3 A,C; ANOVA, F=1.35, p<0.10): only the much greater abundance of tabular and digitate *Acropora* in Karimunjawa, and of submassive *Acropora* (primarily *Acropora palifera* and *A. cuneata*) in Sulawesi distinguishes the two. Branching corals (ACB and CB) are both slightly more abundant in Sulawesi than in Karimunjawa. At 10m depth, branching corals, both *Acropora* and non-*Acropora* are about half as abundant in Sulawesi as in

Karimunjawa, while foliose corals are almost twice as abundant in Sulawesi as in Karimunjawa (fig 4.3B, D). The composition of the fauna when 3m and 10m reefs are combined is nearly identical, except for the greater abundance of ACS, CSM, and CMR in Sulawesi, and of ACT in Karimunjawa.

Compared to the storm damaged reef at P. Burung, the Sulawesi reefs have slightly more branching corals (ACB and CB), about double the abundance of foliose corals, and half the abundance of CSM and CMR as on the storm damaged reef in Karimunjawa. Compared to the climax reef at Karimunjawa (Pp. Menjangan), the composition is nearly identical, except for the greater abundance of foliose corals at the climax reef in Karimunjawa than in Sulawesi, and the greater abundance of CSM on Sulawesi reefs than on the climax reef in Karimunjawa.

These comparisons all suggest that there is some signal of disturbance left in the morphological composition of the Sulawesi reefs, indicating that anthropogenic mechanical damage has influenced the diversity of the coral fauna. But there is an equally strong signal of successional dominance by branching Acropora and other corals. These data on the whole suggest that it would be incorrect to attribute the reduced diversity on the shallow Sulawesi reefs (see chapter 2) entirely to mechanical damage, as these reefs seem to display a strong signal of advanced succession as well.

4.3.6 Overall patterns.

Morphological composition of the fauna responds to several physical and biological factors. The primary physical factor is sedimentary environment - onshore vs offshore, including related changes in sedimentation rate and nutrient influx. Among the offshore reefs, depth affects the morphological composition of the coral fauna much more than aspect does. Biogeographic differences between open ocean (Sulawesi) and epeiric sea (Karimunjawa) are virtually nil. Biological factors such as monospecific stands of successional dominant species, and natural mechanical damage (storms) cause minor alterations in the morphological composition of the fauna, much less dramatic than those observed between onshore and offshore reefs.

4.3.7. Ternary conservation value diagrams.

These broad shifts in morphological composition of the corals on reefs, viewed in the context of ternary diagrams of organism adaptive strategies (Grime 1979), can form a useful management tool for determining the conservation value of a given site. Such a tool would be particularly useful to the Indonesian marine parks authorities in choosing sites for levels of protection, given the large volume of life-form transect data already collected by Indonesian government and university surveys (Moosa and Suharsono 1996; Chou 1997).

Based on the morphological patterns evident among Java Sea reefs, all the <u>Acropora</u> corals, plus <u>Millepora</u>, can be considered r-strategists (table 4.2), due to their rapid recruitment and growth rates and mechanical fragility. Foliose (CF) and non-Acropora branching corals (CB), which recruit and grow more slowly than Acroporas, but frequently form large monospecific stands on protected reefs, can be considered K-strategists. Massive (CM), submassive (CSM), and massive-platy (CMP) corals such as Lobophyllia and Euphyllia tend to dominate the most polluted environments, and can be considered Stress-Tolerators.

The position of a given reef on the ternary diagram reflects its conservation value (fig 4.5; table 4.4). Highest morphological and species diversity of both structural and interstitial fauna (*sensu* Huston 1994) is found on reefs plotting near the centre of the ternary diagram; these reefs also have the greatest morphological complexity, and would support the greatest abundance and diversity of fish (Roberts 1995; Jennings et al 1996; Polunin and Roberts 1996; Waltho 1997). These various factors combine to give the reefs in the centre of the diagram the highest conservation value.

Reefs composed almost exclusively (>65%) of stress-tolerators (PPN, PPS, LM, BND, KY) typically have low live coral cover and low species diversity, and are frequently degraded by pollution and/or sedimentation (see chapter 2). These reefs have low conservation value, because they harbour low coral and fish abundance and diversity, and because their prospects for recovery are limited unless pollution sources are cleaned up. According to the triage approach to reef conservation planning (Risk 1994), the low conservation value of such reefs does not generally warrant the high cost and low success rate of restoration efforts.

Table 4.4. Relative composition of r-strategists, K-strategists, and Stress-tolerators on 36 reef sites in conservation value ternary diagram. Diversity, live coral cover, and mortality index data repeated from chapter 2 for clarity. Reef/site codes follow table 2.3.

region	reef/site	S/40m	diversity (slope)	% live coral	mortality index	% r-strategists	% K-strategists	% stress tolerators	conservation value
ambon	HL 10	35	21.83	22.96	0.57	4.86	55.12	40.01	moderate
ambon	HL 3	36	21.47	31.37	0.46	19.54	48.17	32.29	med-high
ambon	TJS 10	63	35.58	60.36	0.24	36.40	31.85	31.75	high
ambon	TJS 3	61	35.81	68.01	0.19	36.27	46.01	17.71	high
ambon	WL 3	38	22.66	21.73	0.51	37.97	24.26	37.78	moderate
ambon	WM 10	44	28.25	32.69	0.39	35.18	22.20	42.62	moderate
ambon	WM3	38	28.25	39.31	0.40	43.09	19.60	37.31	moderate
jepara	PPN 3	44	25.59	32.51	0.32	1.93	2.28	95.78	low
jepara	PPN 6	36	21.61	34.75	0.35	0	5.04	94.96	low
jepara	PPS 3	48	28.51	21.18	0.74	2.36	8.18	89.46	low
jepara	PPS 6	47	28.26	35.77	0.51	0	17.51	82.49	low
jepara	Bondo 3	31	18.43	28.03	0.43	2.00	5.63	92.37	low
karimunjawa	BRL 10	42	24.53	55.82	0.15	42.55	19.33	38.12	med-high
karimunjawa	BRL 3	40	22.65	66.38	0.11	58.22	4.02	37.76	moderate
karimunjawa	BRW 10	35	20.74	32.48	0.27	30.53	29.94	39.54	med-high
karimunjawa	BRW 3	29	17.12	28.22	0.13	41.13	5.18	53.69	moderate
karimunjawa	CML10	52	32.08	45.55	0.31	21.16	43.00	35.83	high
karimunjawa	CML3	49	29.22	68.50	0.22	62.09	26.20	11.71	moderate
karimunjawa	CMW 10	45	26.81	55.80	0.30	35.69	25.98	38.33	high
karimunjawa	CMW3	39	29.22	62.93	0.21	77.46	9.86	12.68	moderate
karimunjawa	MRCN 3	21	12.73	23.77	0.18	7.81	11.26	80.93	low

Table 4.4, continued.

region	reef/site	S/40m	diversity (slope)	% live coral	mortality index	% r-strategists	% K-strategists	% stress tolerators	conservation value
karimunjawa	MBKL 10	26	15.32	60.34	0.34	5.86	69.88	24.26	moderate
karimunjawa	MBKL 3	31	18.8	80.18	0.20	24.28	50.51	25.21	moderate
karimunjawa	MBKW 10	21	12.73	57.55	0.37	27.28	56.29	16.43	moderate
karimunjawa	MBKW 3	23	14.4	41.83	0.62	68.76	11.36	19.88	moderate
karimunjawa	PKL 10	27	17.13	64.50	0.29	3.78	82.24	13.97	moderate
karimunjawa	PKL 3	24	15.13	61.74	0.18	42.34	36.60	21.06	med-high
karimunjawa	PKW 10	22	12.65	41.42	0.37	16.93	29.13	53.95	med-high
karimunjawa	PKW 3	22	13.24	60.90	0.25	47.68	17.55	34.78	med-high
sulawesi	BL 10	56	32.51	38.37	0.30	17.74	41.04	41.22	med-high
sulawesi	BL 3	34	19.44	53.60	0.23	47.94	25.58	26.48	med-high
sulawesi	KP 10	65	37.79	56.52	0.18	16.58	31.47	51.96	high
sulawesi	KP 3	28	16.1	76.76	0.14	51.37	23.00	25.63	med-high
sulawesi	KY 10	6	4.5	9.83	0.53	0	2.84	97.16	low
sulawesi	KY 3	40	23.9	18.18	0.59	20.62	11.05	68.33	low
sulawesi	SL 10	54	30.59	41.55	0.29	13.11	44.59	42.30	med-high
sulawesi	SL 3	31	18.32	47.04	0.24	32.18	34.82	33.00	med-high

Figure 4.5. A: Ternary diagram of reef conservation value determined by morphological composition of the fauna. See text for details.

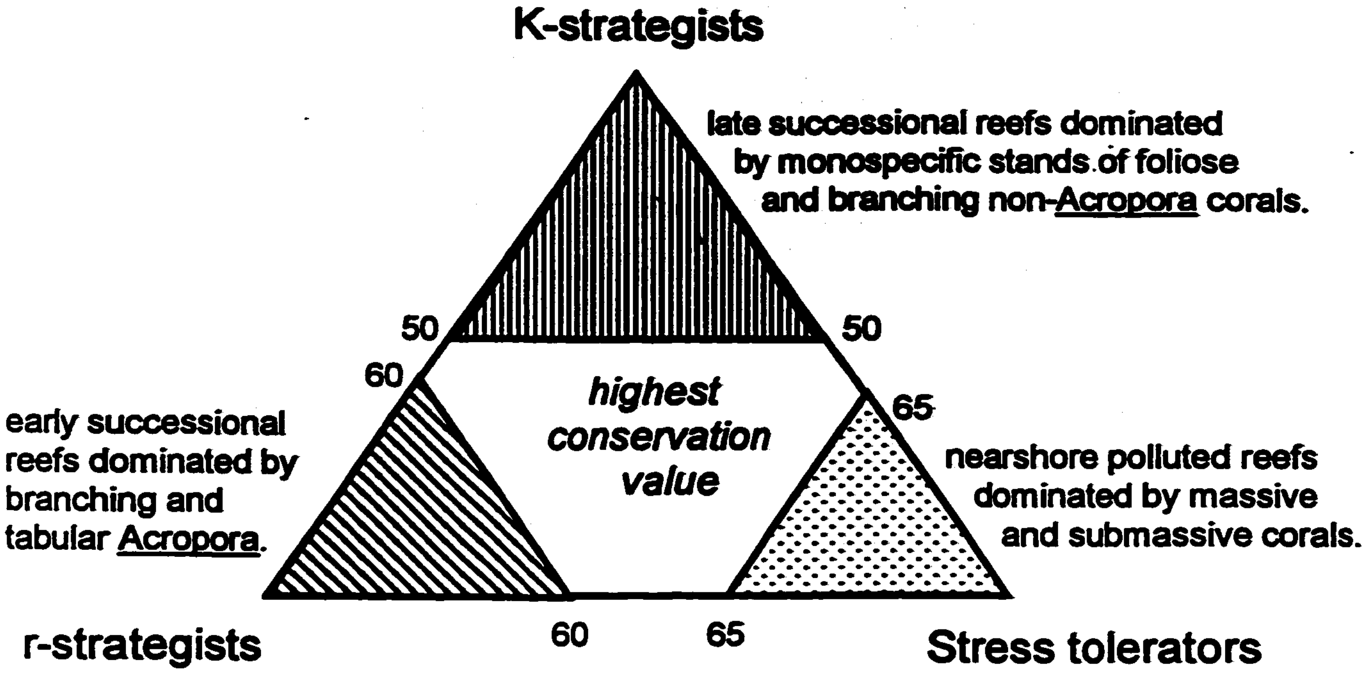
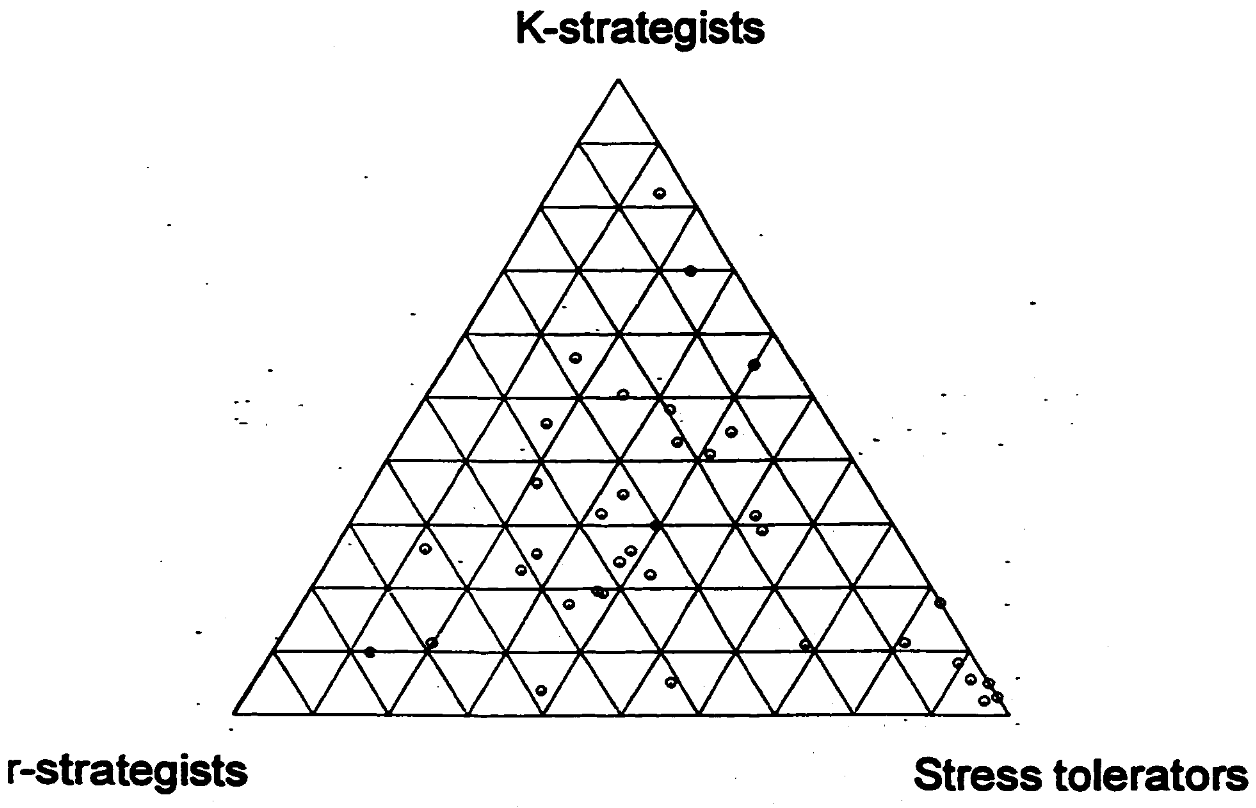


figure 4.5. B: Reef sities in this study plotted on ternary diagram by morphological composition of the coral fauna. See text for details.



Reefs dominated (>60%) by r-strategists (mainly Acropora corals; BRL3, CMW3, CML3, MBKW3) tend to be early successional reefs recovering from physical disturbance, and often have low to moderate cover and diversity. These have moderate conservation value, since their biodiversity and fish habitat potential are likely to increase, if protected from anthropogenic disturbance.

Reefs dominated (>50%) by K-strategists are composed mainly of monospecific stands of foliose corals and branching non-Acropora corals (HL, MBKL, MBKW10, PKL10) and tend to have very high live coral cover, but low coral species diversity, and probably provide less than optimal fish habitat, since their morphological complexity is less than that provided by reefs with more mixed morphologies. These K-strategist dominated reefs also have moderate conservation value, since their coral biodiversity is low, but live coral cover is high, indicating favourable conditions for coral growth overall. Highest morphological and coral species diversity is found on reefs in the centre of the ternary diagram (<60% r-strategists, < 50% K-strategists, <65% Stress-tolerators; TJS, KP, SL, BL, PKW, PKL3). These reefs provide the best fish habitat and have the highest conservation value.

Ternary morphograms can be used to help design and zone marine protected areas, updating earlier guidelines on marine reserve design for biodiversity conservation (e.g. Salm 1984; Johannes and Hatcher 1986).

Average morphology for whole reefs should be plotted on the same ternary diagrams, and highest conservation value assigned to those reefs with less than 50% of r-strategists, K-strategists, or Stress-tolerators. Ternary morphograms can help conservation planners view coral reefs as dynamic ecosystems that undergo successional change. Conservation planners should aim to include a sampling of both moderate and high conservation value sites, to allow for adequate representation of alternate community types and multiple stable states (*sensu* Sutherland 1976) within a given marine protected area.

4.4 Conclusions

1. Onshore-offshore differences in the morphological composition of the coral fauna are dramatic. Acropora corals are virtually eliminated from nearshore polluted reefs, which are dominated by stress-tolerant massive and submassive growth forms.

2. Morphological composition of windward and leeward reefs in Karimunjawa are nearly identical, reflecting the seasonally changing wave exposure patterns on these reefs. Windward reefs tend to have lower diversity, and have a higher proportion of high turbulence adapted growth forms, such as digitate and corymbose Acropora.

3. Depth exerts a strong influence on morphological composition of the coral fauna, with greater dominance of shallow (3m) reefs by branching and tabular Acropora, and greater dominance of deeper (10m) reefs by weaker branching Porites and foliose corals. These differences probably result from differences in wave exposure more than differences in light intensity.

4. Storm disturbance or advanced successional stages do not cause major changes to the morphological composition of the affected reefs, but seem to accentuate prevailing patterns.

5. Morphological composition of coral faunas on platform reefs in the Spermonde archipelago, Sulawesi and the Karimunjawa islands are nearly identical. The growth of Karimunjawa reefs within a recently re-flooded epeiric sea appears to have had virtually no effect on their morphological composition.

6. Ternary diagrams of r-K-S adaptive strategies of coral morphologies can be used to classify reef successional status and conservation value. Reefs of highest conservation value plot in the centre of the diagram, and have less than 50% r- or K-selected morphologies, and less than 65% stress-tolerant morphologies.

Chapter 5: Bioerosion of massive corals and branching coral rubble on Indonesian coral reefs.

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5.1 Introduction.

Bioerosion is one of several processes that regulate rates and patterns of coral reef growth (Scoffin et al. 1980; Hutchings 1986; Hubbard et al. 1990; Conand et al. 1997), and increased bioerosion in response to nutrient availability limits reef accretion, contributing to reefs drowning during sea level rise (Neuman and MacIntyre 1985; Hallock 1988; Hallock et al. 1988). Measuring rates and patterns of bioerosion, however, can be difficult (Hutchings and Bamber 1985; Hutchings 1986; Keine and Hutchings 1994; Chazottes et al. 1995; Risk et al. 1995). Perhaps the most common method of assessing levels (but not rates) of bioerosion intensity on modern corals is to measure the area removed from cross-sections of corals, either in X-ray (e.g. Sammarco and Risk 1990) or photograph (e.g. Risk et al. 1995). These techniques are costly and time-consuming, frequently require computer image analysis equipment that is not readily available in the developing world (e.g Chazottes et al. 1995), and most important, require killing live corals. One of our goals in this paper is to present a new, non-destructive method of assessing bioerosion intensity on coral reefs.

Previous work along a well-documented eutrophication gradient in Barbados has shown a variety of responses to eutrophication by corals (Tomascik & Sander 1985, 1987; Hunte & Wittenburg 1992) and by bioeroding organisms (Holmes 1996 and references therein). Among those responses is an increase in bioerosion of corals and of coral rubble, and an increased abundance of clionid sponges within coral rubble in more eutrophic environments (Holmes 1997). In this paper, we apply measurements of boring sponge frequency in rubble to assessing intensity of bioerosion on Indonesian reefs along eutrophication gradients and as a bioindicator of eutrophication on coral reefs. We combine these data with measurements of massive head coral bioerosion from X-rays of coral slabs. These combined data sets provide us a comprehensive view of bioerosion processes on some of the world's most imperilled coral reefs, and test our new method of assessing bioerosion from coral rubble.

Eutrophication and other land-based sources of pollution pose among the greatest threats to coral reefs world-wide, especially in Indonesia, home to one third of the world's coral reefs (Chou 1997), and close to the centre of world coral species diversity (Veron 1993, 1995). One of the principle ways in which nutrient pollution threatens coral reefs is by increasing bioerosion intensity (Hallock 1988; Hallock et al. 1988).

Our technique for measuring coral rubble bioerosion is non-destructive, and can serve as a rapid assessment tool for indicating the degree of eutrophication stress on a coral reef. We designed the rubble bioerosion sampling to be easy and low-technology, as appropriate for application in remote areas of the developing world, and for community based management and monitoring of coral reefs.

In this paper, we measure bioerosion on nine reefs in two parts of Indonesia, using two methods, and compare the results to environmental variables, as well as to reef health parameters derived from line transect reef surveys (chapter 2). We test hypotheses (1) that rubble bioerosion is correlated with chlorophyll concentration and other environmental variables, (2) that coral rubble bioerosion is correlated with reef health parameters derived from transect data, and (3) that measuring bioerosion levels in coral rubble can be a reliable measure of overall bioerosion intensity. These analyses help establish this non-destructive technique as a useful rapid assessment tool for measuring coral reef health.

5.2 Methods

5.2.1 Study Sites.

We measured bioerosion on five reefs in the Java Sea and on four reefs in Ambon, Moluccas. In the Java Sea, two offshore reefs and a fringing reef adjacent to mangroves were sampled in the Karimunjawa National Marine Park (see map, fig. 1.2), and two more nearshore reefs were sampled in the Jepara area, along the north coast of Central Java (see map, fig. 1.3). In Ambon, we sampled four reefs (see map, fig. 1.4), two relatively unpolluted reefs on the north coast of Ambon, facing the Seram strait, one reef in Ambon Bay, subject to harbour pollution and urban runoff, and one reef on the south coast of Ambon, subject to high sedimentation and immediately adjacent to a plywood factory. All of these reefs had been previously sampled in comprehensive coral reef surveys, including environmental variables, line intercept transects for cover data, coral growth rates, and in some cases, stable carbon and nitrogen isotopes. Table 5.1 lists the reefs sampled in this study; figure 2.1 shows the locations of all the study reefs. The range of pollution, eutrophication, and reef health differences are much greater among the Java Sea sites than among the Ambon sites.

5.2.2 Massive Coral Bioerosion.

Massive coral bioerosion sampling followed a balanced nested ANOVA design. Bioerosion of massive Porites lobata heads was measured from X-rays of three parallel but non-adjacent slabs through each of five live coral heads collected at 1m depth from each site, yielding a total of 15 cross-sections per site (method follows Sammarco and Risk 1990; sample X-ray in fig. 5.1). Cross sectional area of each slab and the borings in it was measured using a hand-held planimeter (method follows Edinger and Risk 1997). Bioerosion intensity is reported as percentage of cross-sectional area removed by boring organisms.

Table 5.1. Study Site regions, names, morphologies, and summaries of stresses. Max. depth: maximum depth of coral growth. Water Clarity was measured as average secchi disk extinction depth. Source of stresses summarizes impacts on each reef. More detailed descriptions of each reef can be found in Limmon (1996) and in chapter 1.

Region	Reef Name	reef morphology	max. depth	water clarity	source of stresses
Ambon	Tanjung Setan	fringing reef /wall	40m	>20m	unaffected sites (10m, 3m)
	Hila	fringing reef	20m	20m	bombing, construction, rubble btm.
	Wayame	fringing reef	15m	10m	harbour, sewage, sedimentation
	Wailiha	fringing reef	6m	<5m	harbour, sediment, plywood factory
Karimunjawa	Pulau Kecil	coral cay island	25m	20m	Java unaffected, overfishing
(Central Java)	Gosong Cemara	coral cay, submerged	25m	20m	Java unaffected, overfishing
	Lagun Marican	mangrove fringe	4m	<3m	carbonate sedimentation
Jepara	Pulau Panjang	coral cay island	8m	<3m	sewage, sediment, aquaculture
(Central Java)	Bondo	fringing reef	5m	<2m	sedimentation, agricultural runoff

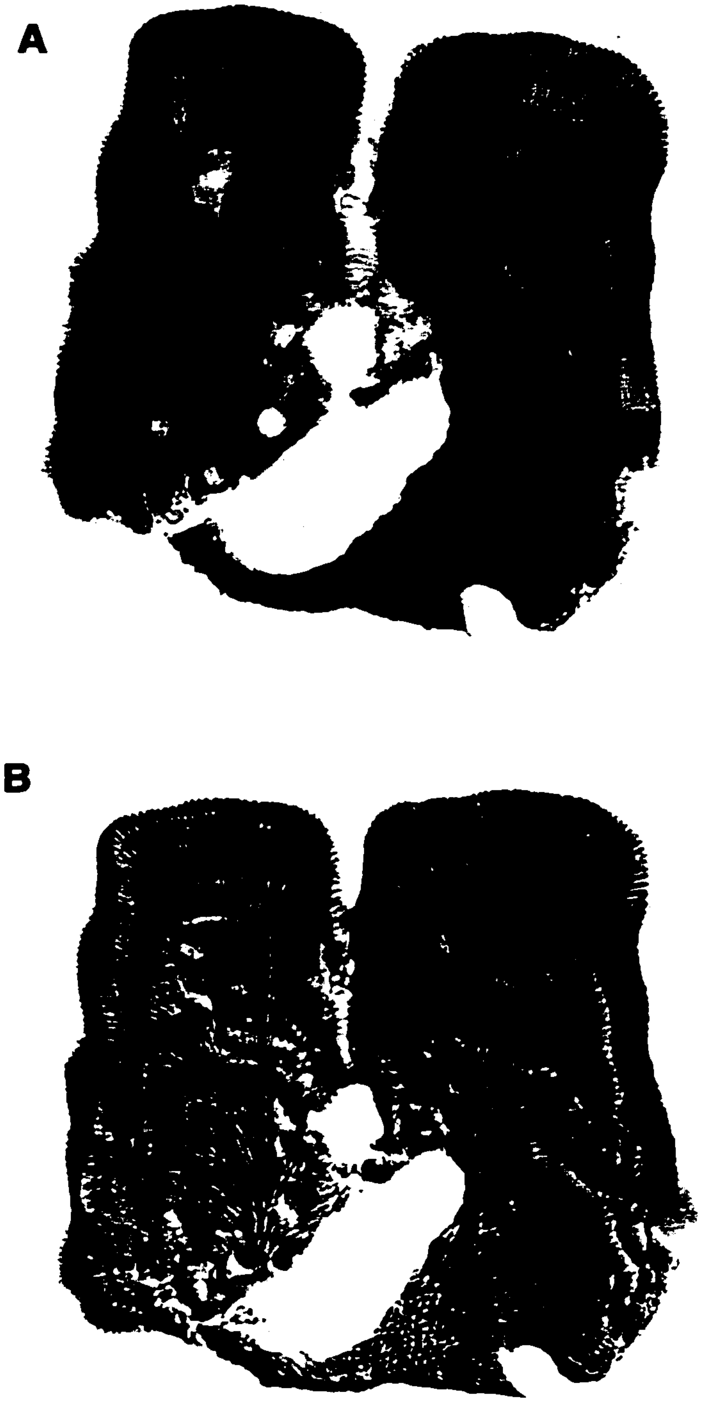


Figure 5.1: X-radiograph of heavily bioeroded coral, Pulau Panjang, Jepara. □A: X-ray positive. □B: X-ray pseudorelief, in which positive and negative are overlaid and offset by <1mm, enhancing details including growth lines. Large oblong borehole is gall shrimp Upogebia; smaller round borehole at lower right is Lithophaga; other irregular boreholes are various boring sponges.

5.2.3 Coral Rubble Bioerosion.

Acropora branching corals are in low abundance on nearshore reefs subject to sewage pollution and sedimentation (fig. 4.2; table 4.3), particularly in the Java Sea. In order to standardise for species composition of the rubble, Acropora rubble was excluded from the Java Sea collections. In Ambon, where Acropora were more common at all sites, two separate rubble collections were made, one for non-Acropora branching coral rubble, and one for branching Acropora rubble only. The Acropora and non-Acropora collections were analysed separately.

Coral rubble bioerosion sampling also followed a balanced nested ANOVA design. Ten pieces of branching coral rubble were collected from 3m depth along each of 10 x 1m transects spaced 10m apart along a 100m transect along each reef, for a total of 100 pieces of rubble per reef. Each piece of rubble was cut five times with a dry-cut rock saw, and each cut was scored for presence or absence of bioeroding organisms, including boring sponges, worms, bivalves, gall shrimps and others. This yielded a bioerosion score of zero-5 for each piece of rubble. Bioerosion intensity is reported as the average bioerosion score of the 10 pieces of rubble per sample. Rubble bioerosion was not measured at Bondo, the high sedimentation Java Sea site, because it was not accessible by land or by boat during the wet season.

5.2.4 Environmental Data.

One goal of this paper is to demonstrate the relationship between coral or rubble bioerosion and environmental variables indicative of eutrophication stress on reefs. A variety of environmental variables were measured at each reef, including chlorophyll A concentration, nitrate and phosphate concentration, suspended particulate matter, concentration, sediment resuspension, and water clarity (secchi disk extinction depth; see table 5.2). These variables all indicate eutrophication, and tend to covary, making it difficult to separate the effects of eutrophication from those of sedimentation. All environmental variables were measured on at least 3 separate dates; Ambon data were collected in May - Aug. 1995; Java Sea data were collected in Nov. 1994 - Jan. 1995, July - Dec. 1995, and Aug. - Dec. 1996. Chlorophyll sampling in Ambon was repeated in June - Sept., 1997. Full environmental data for Ambon sites are reported in Limmon (1996).

Chlorophyll sampling and analysis followed Parsons et al. (1984). Suspended particulate matter (SPM) was measured by filtering 1 litre of seawater onto a pre-weighed glass fibre filter, which was subsequently oven-dried and weighed (Cortes and Risk 1985). Sediment resuspension was measured using sediment traps consisting of 30 cm long, 5cm diametre PVC tubes. In Java, traps were deployed on the reef surface at 3m depth and changed monthly or bimonthly in Karimunjawa, and biweekly in Jepara. Sediment traps at the Ambon sites were deployed 25cm above the reef surface at 3m depth and were changed weekly.

5.2.5 Reef Health Parameters.

Reef health was estimated using line intercept transects to measure % live coral cover, coral mortality index, coral species diversity, and other parameters. At each reef, we measured 12 replicate 20m line intercept transects, 6 at 3m depth, and 6 at 10m depth for cover of live corals, dead coral, algae, other fauna, and abiotic substrates (e.g. sand and rubble). Other fauna included sessile invertebrates such as sponges, gorgonians, alcyonarian soft corals, zooanthids, and ascidians. On 3 reefs where coral depth did not extend beyond 5m (Wailiha, L. Marican, Bondo; see table 1), we measured transects at 3m only, and at P. Panjang, Jepara, we measured transects at 3m and 6m. Coral mortality index (Gomez 1994) was computed as MI= dead coral cover/(live coral cover + dead coral cover), with values ranging from 0 (all corals live) to 1 (all corals dead). Complete transect data are reported in chapter 2 and 6, and only summaries of transect data are used here.

5.2.6 Data Analysis.

Massive coral and branching coral rubble bioerosion were analysed separately. Bioerosion intensity was compared among reefs using 1-way ANOVA, with separate analyses for Java and Ambon. Bioerosion intensity was correlated with environmental variables and reef health parameters using linear regression analysis, again with separate analyses for Java and Ambon. Massive and branching bioerosion were compared using correlation and linear regression. Linear regression analysis was chosen because it provides a first-order approximation of relationships among environmental variables, bioerosion, and reef health, and because it is possible to calculate significance and estimate the amount of variance attributable to a given environmental variable.

Table 5.2. Environmental parameters measured for each reef in the study. All values are averages of at least 3 measurements, followed by standard deviations (in brackets). Ambon measurements are wet season, while Sulawesi and Java measurements are mostly dry season or transitional. W/W: windward. L/W: leeward. Methods described in text. Bondo sediment resuspension data are poorly constrained.

Reef Name	chl. A	NO3	PO4	SPM	resuspension
	mg/m^3	µM	µM	mg/l	mg/cm^2/day
Tanjung Setan	0.39 (0.19)	0.76 (0.40)	0.28 (0.19)	4.49 (1.40)	0.077 (0.018)
Hila	0.44 (0.21)	0.77 (0.44)	0.38 (0.20)	4.91 (2.66)	0.19 (0.14)
Wayame	0.38 (0.06)	1.46 (1.01)	0.46 (0.18)	11.15 (3.40)	0.55 (0.23)
Wailiha	0.46 (0.14)	0.82 (0.32)	0.30 (0.17)	15.3 (10.21)	3.08 (3.13)
P. Kecil W/W	0.33 (0.08)			9.75 (6.71)	2.03 (0.55)
Pulau Kecil L/W	0.29 (0.17)			19.69 (18.27)	1.63 (1.31)
G. Cemara W/W	0.40 (0.21)			22.98 (2.46)	4.21 (3.31)
G. Cemara L/W	0.25 (0.14)			22.26 (7.56)	2.80 (3.62)
Lagun Marican	1.24 (0.90)			26.39 (11.58)	
P. Panjang North	1.23 (0.54)			21.83 (8.40)	26.19 (24.42)
P. Panjang South	1.09 (0.62)			28.91 (17.86)	31.69 (38.74)
Bondo	1.22 (0.52)			21.04 (4.60)	38.45 (25.7)

5.3 Results.

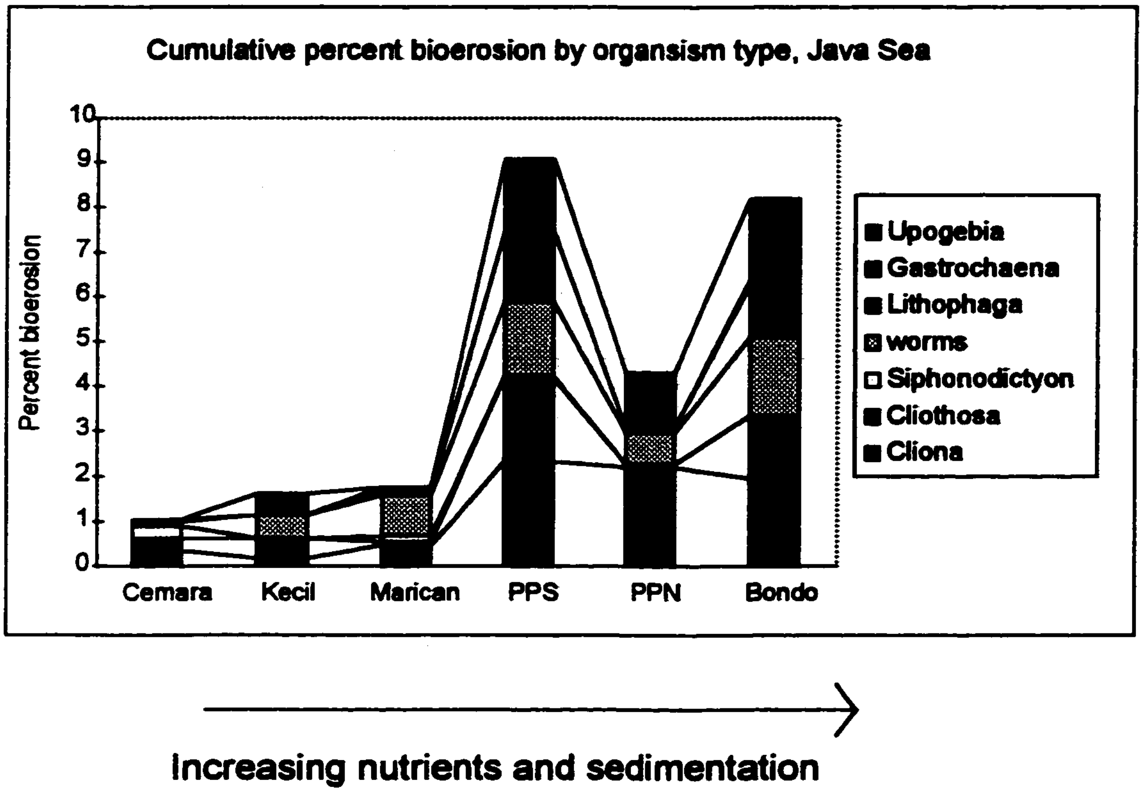
5.3.1 Java Sea massive coral bioerosion.

Total bioerosion, and bioerosion by all of the individual bioeroding taxa, was higher on nearshore polluted reefs than on offshore reefs or the mangrove fringing reef (fig. 5.2). Total bioerosion, and bioerosion by almost all of the individual bioeroding taxa was highest at Pulau Panjang South (PPS), the nearshore site with the greatest influx of domestic sewage and aquacultural runoff. Boring worms were slightly more abundant at Bondo, the site with primarily agricultural runoff, than at Pulau Panjang.

Total bioerosion of massive corals was significantly higher on nearshore reefs than on offshore reefs (1-way ANOVA, $F=9.18$, $p<0.0001$, d.f.=77). This pattern also held true for total boring sponges ($F=5.24$, $p<0.0005$), for Cliona and Cliothosa individually, and for boring worms ($F=3.06$, $p<0.02$), but not for Lithophaga ($F=1.27$, $p>0.28$). In all cases except worms, bioerosion was most intense at Pulau Panjang.

Total bioerosion was positively correlated with chlorophyll A concentration ($r^2=0.245$, $p<0.012$, $n=25$), as was total sponge bioerosion ($r^2=0.177$, $p<0.03$) and Cliona bioerosion ($r^2=0.24$, $p<0.013$). Cliothosa, worm, and Lithophaga bioerosion were not significantly correlated with chlorophyll A concentration. Total bioerosion was positively correlated with coral mortality index ($r^2=0.46$, $p<0.0002$, $n=25$) and with abiotic substrate cover ($r^2=0.25$, $p<0.012$), and was negatively correlated with live coral cover ($r^2=0.23$, $p<0.014$).

Figure 5.2.: Cumulative bioerosion by organism type in massive corals, Java Sea.



5.3.2 Java Sea Coral Rubble Bioerosion.

The bioerosion score of rubble pieces from onshore eutrophic reefs was significantly greater than that for offshore unpolluted reefs (fig. 5.3A; 1-way ANOVA, F=14.82, $p<0.0001$), and was positively correlated with chlorophyll A concentration ($r^2=0.17$, $p<0.005$, n=50). The average frequency of boring sponge occurrence (fig 5.3B) was also positively correlated with chlorophyll A concentration ($r^2=0.09$, $p<0.03$, n=50), but there were no significant trends in the frequency of boring bivalves or worms.

For the Java Sea data, the bioerosion score of rubble pieces on each reef was positively correlated with average percent bioerosion of massive corals on that reef (table 5.3; $r^2=0.14$, $p<0.01$, n=50). Rubble bioerosion score was inversely correlated with live coral cover on each reef (r^2=0.137, p<0.01, n=50).

Figure 5.3: Branching coral rubble bioerosion, Java Sea. A: Total bioerosion score. B: boring sponge frequency. Means ± 95% confidence intervals.

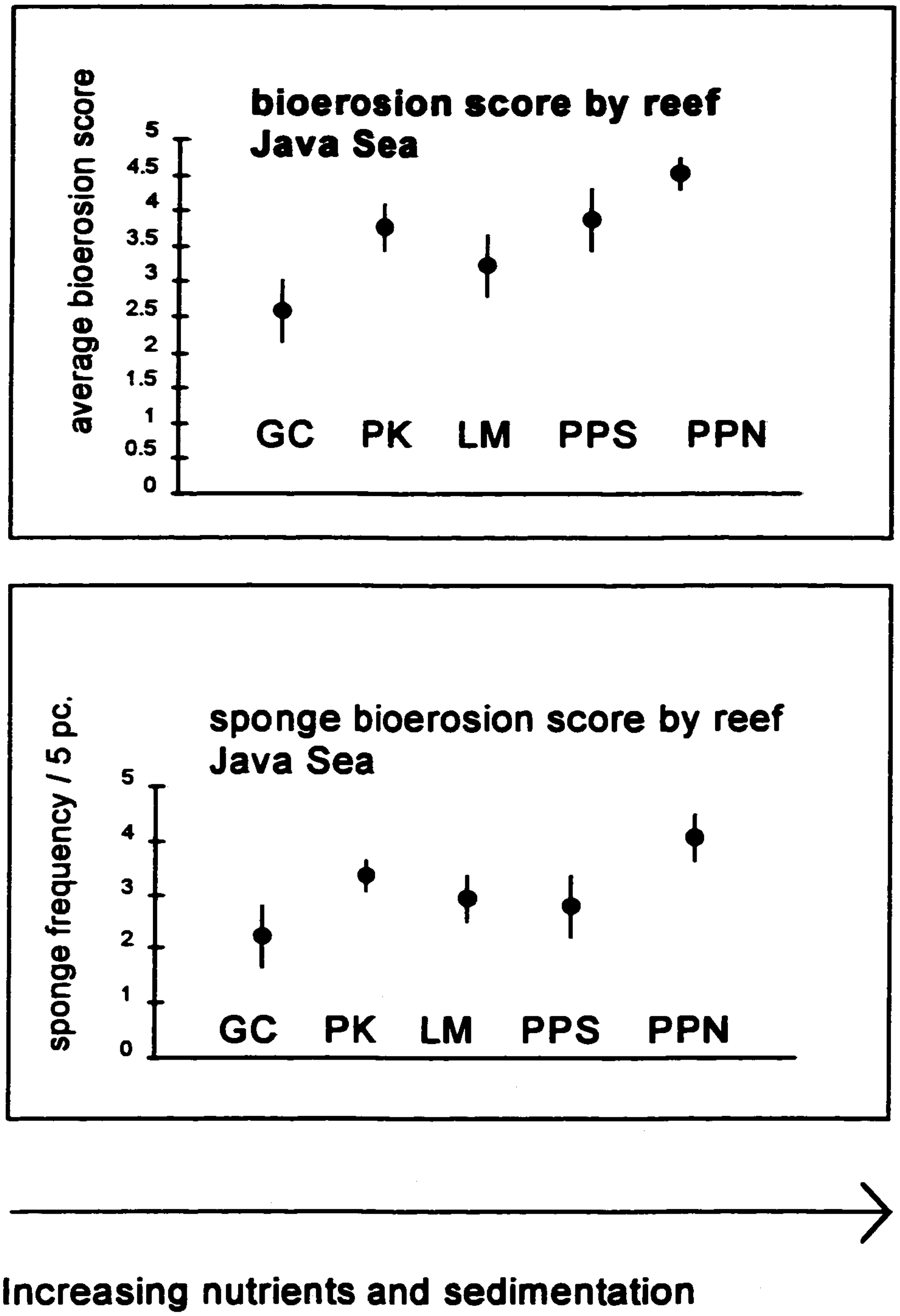


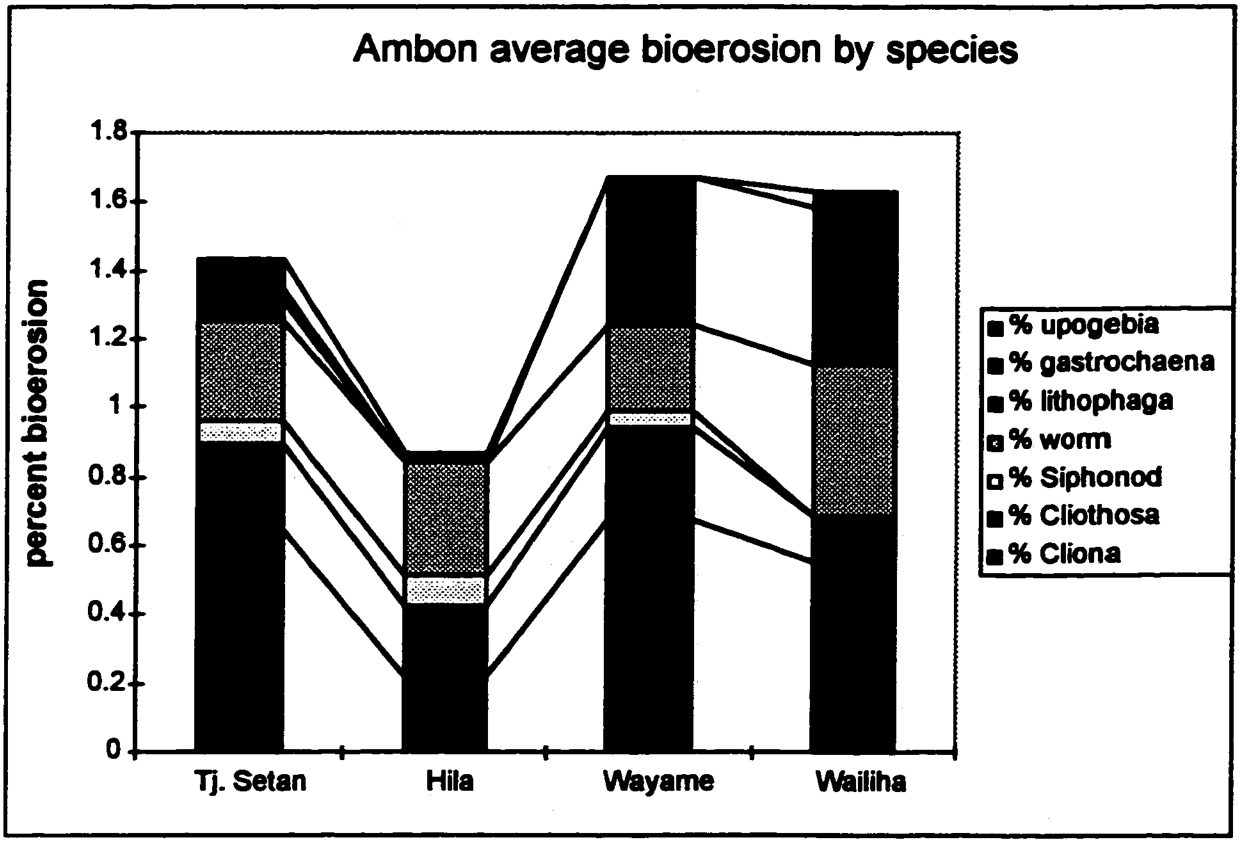
Table 5.3. Java Sea, correlations between bioerosion scores in non-Acropora rubble, environmental parameters, reef health parameters, and massive coral bioerosion.

	average bored n=10	average sponges n=10	average bivalves n=10	average worms n=10	avg msv coral bioerosion	mortality	avg cover	avg chlorophyll	avg SPM	avg resusp.
average bored	1.00									
average sponges	0.82	1.00								
average bivalves	0.36	0.03	1.00							
average worms	0.46	0.22	0.48	1.00						
avg msv coral bioero	0.38	0.09	0.59	0.39	1.00					
mortality	0.16	-0.10	0.42	0.27	0.88	1.00				
avg cover	-0.37	-0.21	-0.26	-0.16	-0.66	-0.81	1.00			
avg chlorophyll	0.41	0.31	0.14	0.02	0.51	0.64	-0.96	1.00		
avg SPM	-0.06	-0.25	0.21	0.09	0.68	0.94	-0.78	0.62	1.00	
avg resusp.	0.50	0.27	0.49	0.24	0.92	0.74	-0.69	0.66	0.53	1.00

5.3.3 Ambon Massive Coral Bioerosion

Total bioerosion at the polluted sites, Wailiha and Wayame, was slightly higher than at the unpolluted sites, Hila and Tanjung Setan, but these differences were not statistically significant (fig. 5.4; 1-way ANOVA, F=0.65, p=0.65, d.f.=59). There were no significant correlations between total massive coral bioerosion in Ambon and any of the environmental variables or reef health parameters measured (table 5.4).

Figure 5.4: Massive coral bioerosion, Ambon.



Increasing nutrients and sedimentation

5.3.4 Ambon Coral Rubble Bioerosion.

The average bioerosion score of non-Acropora rubble pieces (fig 5.5A) from Tanjung Setan, the cleanest water reef, was significantly less than that for the other three Ambon reefs (1-way ANOVA, $F=4.69$, $p<0.01$, d.f.=41). Average boring sponge bioerosion score (fig 5.5B)was highest at Wayame (2.35), followed by Hila (1.84), Wailiha (1.27), and Tanjung Setan (1.26; 1-way ANOVA, $F=6.30$, $p<0.002$, d.f.=41).

The average bioerosion score of non-Acropora rubble was weakly correlated with chlorophyll A concentration (table 5.4; $r^2=0.077$, $p<0.075$, $n=42$), and significantly correlated with SPM ($r^2=0.13$, $p<0.02$, $n=42$). Non-Acropora bioerosion score was positively correlated with coral mortality index ($r^2=0.26$, $p<0.001$, $n=42$). There were no significant correlations between non-Acropora bioerosion score and massive coral bioerosion on the same reefs.

Acropora rubble bioerosion scores (fig 5.5C) were lower at Tanjung Setan than at the other 3 reefs sampled in Ambon, but this pattern was not significant (ANOVA, $F=1.94$, $p<0.15$). The pattern for sponges (fig 5.5D) was quite different from that for total bioerosion: the average sponge bioerosion score of Acropora rubble pieces from Wailiha (highest sedimentation site) was significantly less than that for the other three Ambon reefs (1-way ANOVA, $F=12.80$, $p<0.0001$, d.f.=39). This probably reflects the negative influence of high sedimentation on the boring sponges. Boring sponge bioerosion in Acropora rubble was significantly correlated with sponge bioerosion in massive corals ($r^2=0.10$, $p<0.05$, $n=40$).

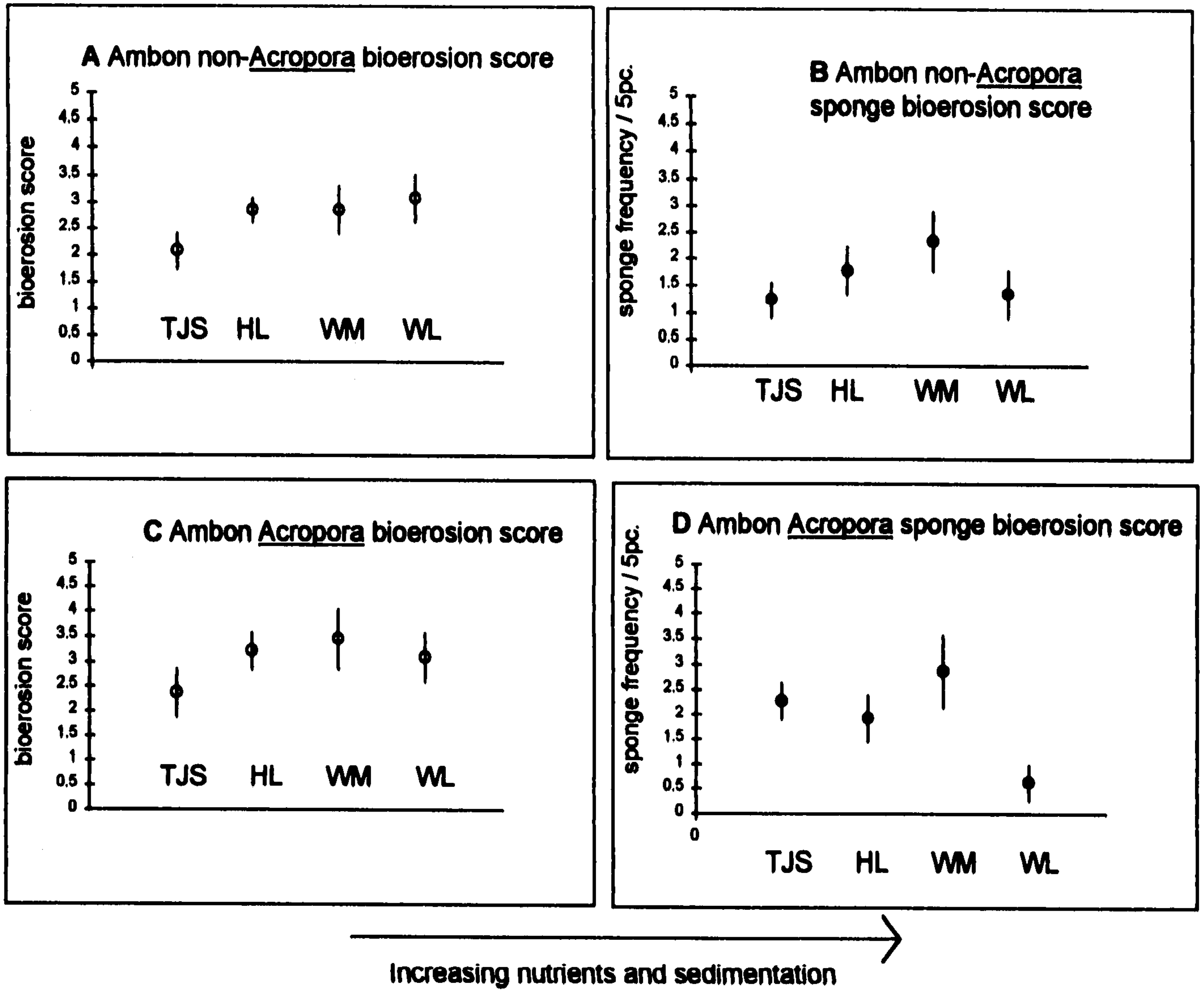


Fig. 5.5: Branching coral rubble bioerosion scores, Ambon. A: Total bioerosion score, non-Acropora rubble. B: boring sponge frequency, non-Acropora rubble. C: Total bioerosion score, Acropora rubble. D: Boring sponge frequency, Acropora rubble. Means ± 95% confidence interval.

Table 5,4. Ambon, correlations between bioerosion scores in non-Acropora rubble, environmental parameters, reef health parameters, and massive coral bioerosion.

	average bored	*average sponges*	*average bivalves*	*average worms*	*average other*	*chl-A*	*NO3*	*PO4*	*SPM*	*resusp.*	*cover*	*mortality*	*massive bioerosion*	*massive total sponge*	*massive bivalves*
average bored	1,00														
average sponges	0,50	1,00													
average bivalves	0,37	-0,29	1,00												
average worms	0,51	-0,32	0,49	1,00											
average other	0,19	-0,52	0,37	0,29	1.00										
chl-A	**0.28**	**-0,30**	**0,48**	**0,40**	**0,40**	1,00									
NO3	**0,08**	0,33	-0,08	-0,10	-0,16	-0,61	1,00								
PO4	**0,18**	0,31	-0,39	-0,06	-0,21	0,10	-0,39	1,00							
SPM	**0.36**	0,00	0,48	0,33	0,28	0,40	0,48	-0,43	1,00						
resusp.	**0,30**	-0,25	0,63	0,41	0,43	0,74	0,03	-0,44	0,87	1,00					
cover	**-0,50**	-0,10	-0,30	-0,36	-0,23	-0,72	0,06	-0,33	-0,68	-0,68	1,00				
mortality	**0,51**	0,12	0,27	0,35	0,21	0,70	-0,07	0,38	0,64	0,63	-1,00	1,00			
massive bioerosion	**0,03**	-0,07	0,35	0,10	0,15	-0,15	0,73	-0,86	0,73	0,54	0,01	-0,05	1,00		
massive ttl sponge	**-0,26**	0,02	-0,02	-0,19	-0,11	-0,70	0,75	-0,77	0,14	-0,11	0,61	-0,63	0,76	1,00	
massive bivalves	**0,27**	0,12	0,32	0,18	0,13	0,00	0,78	-0,53	0,92	0,64	-0,41	0,39	0,87	0,47	1,00

Table 5.5. Ambon, correlations between bioerosion scores in Acropora rubble, environmental parameters, reef health parameters, and massive coral bioerosion.

	average bored	*average sponges*	*average bivalves*	*average worms*	*average other*	*chl-A*	*NO3*	*PO4*	*SPM*	*resusp.*	*cover*	*mortality*	*massive bioerosion*	*massive ttl sponge*	*massive bivalves*
average bored	1,00														
average sponges	0,37	1,00													
average bivalves	0,28	-0,35	1,00												
average worms	0,32	-0,22	0,75	1,00											
average other	0,37	0,07	0,48	0,61	1,00										
chl-A	0,06	-0,67	0,26	0,07	-0,16	1,00									
NO3	0,20	0,34	0,05	0,18	0,33	-0,60	1,00								
PO4	0,17	0,14	-0,11	0,00	0,22	0,13	-0,41	1,00							
SPM	0,26	-0,36	0,34	0,27	0,16	0,39	0,49	-0,41	1,00						
resusp.	0,12	-0,60	0,36	0,19	-0,06	0,73	0,05	-0,43	0,88	1,00					
cover	-0,33	0,42	-0,29	-0,24	-0,22	-0,73	0,06	-0,35	-0,67	-0,67	1,00				
mortality	0,34	-0,39	0,28	0,24	0,24	0,71	-0,07	0,40	0,63	0,62	-1,00	1,00			
massive bioerosion	0,04	-0,07	0,19	0,15	0,03	-0,17	0,74	-0,87	0,73	0,54	0,03	-0,07	1,00		
massive ttl sponge	-0,11	0,31	-0,06	0,00	-0,01	-0,71	0,74	-0,79	0,14	-0,10	0,62	-0,64	0,77	1,00	
massive bivalves	0,25	-0,11	0,26	0,26	0,24	0,00	0,79	-0,52	0,92	0,65	-0,40	0,37	0,87	0,47	1,00

5.3.5 Overall patterns.

Both massive coral bioerosion and coral rubble bioerosion reflect productivity patterns in the Java Sea and Ambon together. When the Java Sea and Ambon datasets are combined, massive coral bioerosion is strongly correlated with chlorophyll A concentration (r^2=0.42, $p<0.0001$, n=42). Likewise, non-*Acropora* bioerosion score is strongly correlated with chlorophyll A concentration (r^2=0.26, $p<0.0001$, n=92), and bioerosion score is strongly correlated with massive coral bioerosion (r^2=0.15, $p<0.0002$, n=92). In all these cases, the strong correlations are driven by the nearshore Java Sea sites, where productivity levels and bioerosion intensity are highest.

5.4 Discussion.

Our data demonstrate four patterns of massive coral and branching coral rubble bioerosion in relation to eutrophication and reef health in two areas of Indonesia:

1. Massive coral bioerosion is positively correlated with environmental variables indicative of eutrophication. This pattern was clearly supported by the Java Sea data, but not by the Ambon data, where levels of contamination are generally low.
2. Branching coral rubble bioerosion is positively correlated with environmental variables indicative of eutrophication. This pattern was clearly supported by the Java Sea data and by the entire combined dataset, but only weakly by the Ambon data alone.
3. Both massive coral bioerosion and branching coral rubble bioerosion score are negatively correlated with transect measurements indicative of

coral reef health. For both (2) and (3), the Ambon Acropora and non-Acropora branching coral rubble datasets showed similar results.

4. Massive coral bioerosion is positively correlated with branching coral rubble bioerosion. This pattern was clearly supported by the Java Sea data and by the entire combined dataset, but not by the Ambon data alone. These patterns have important implications for regional differences in productivity and bioerosion, for effects of coral morphology on bioerosion, for carbonate budgets, and for the use of our technique as a rapid assessment tool in reef health surveys.

5.4.1 Regional Differences in productivity and bioerosion.

The intensity of massive coral bioerosion is much greater on the nearshore Java Sea reefs than on any of the Ambon reefs. Massive coral bioerosion on the Ambon reefs is similar to the offshore clearwater reefs of the Java Sea. Likewise, rubble bioerosion score on the nearshore Java Sea reefs is higher than on any of the Ambon sites. Bioerosion in massive and branching corals were only well correlated among the Java Sea sites where differences in nutrient availability were dramatic, rather than subtle.

These patterns relate to the pattern of productivity differences among the sites in the two regions, and to overall differences in productivity between the Java Sea and Ambon. The environmental gradient among study sites is much more dramatic on the Java Sea than on the Ambon reefs. The Java Sea sites segregate much more clearly into offshore clearwater reefs or nearshore eutrophic reefs, while the Ambon sites are all fringing reefs and all lie closer together along a more continuous gradient. Chlorophyll A concentrations at the nearshore Java Sea reefs are 4-5x those on their offshore counterparts, while chlorophyll A concentrations on contaminated Ambon reefs are about 1.5x those of the cleanest reef, Tanjung Setan.

In the Java Sea, both massive coral bioerosion and branching coral rubble bioerosion were inversely correlated with transect measurements indicative of coral reef health. In Ambon, however, these patterns were only true for branching coral rubble. Rubble bioerosion, then, is apparently a more sensitive proxy measurement for reef health than is massive coral bioerosion. Branching coral rubble bioerosion cannot, however, be used as a reliable proxy for massive coral bioerosion in carbonate budget calculations.

5.4.2 Massive Coral bioerosion vs. Rubble Bioerosion.

Bioerosion intensity was generally greater in branching coral rubble than in live massive corals, although the numbers from the two techniques are not directly comparable. In the Java Sea, where eutrophication stress on nearshore reefs is intense, the two methods of measuring bioerosion intensity broadly agreed. The poor correlation between massive coral bioerosion and branching coral rubble bioerosion on the Ambon reefs is inexplicable. Rubble bioerosion in Ambon was weakly correlated with environmental indicators of eutrophication and negatively correlated with reef health measurements, while massive coral bioerosion in Ambon showed no significant trends whatsoever. Taphonomic processes may help to explain some of the differences.

Coral rubble is dead, so rubble bioerosion is influenced by burial, breakage, and other taphonomic processes (Pandolfi and Greenstein 1997) as well as productivity and burial (Edinger & Risk 1997; Lescinsky & Edinger 1997). Residence time on the surface is a key factor determining the intensity of boring into dead corals (Pandolfi & Greenstein 1997). On average, larger pieces of rubble can be expected to remain on the surface on a reef for a longer period of time, and therefore should be more heavily bored. We found a strong positive correlation between non-Acropora coral rubble size and bioerosion score ($r2=0.24$, $p<0.0001$, $n=92$), with similar relationships in the Ambon and Java Sea separately. This added taphonomic influence on boring frequency in rubble appears to make rubble a more sensitive indicator of eutrophication stress than is massive coral bioerosion.

5.4.3 Application to Carbonate Budgets.

Massive or branching coral bioerosion are important aspects of carbonate budgets for coral reefs, and as such are important variables to measure in assessments of coral reef health. Bioerosion of both branching and massive corals increases with productivity, in agreement with many previous studies (Risk & MacGeachy 1978; Highsmith 1980; Hallock 1988; Sammarco & Risk 1990; Risk et al. 1995). Massive coral bioerosion can be used in calculations of net carbonate production (calcification minus bioerosion; Stearn et al. 1977), while coral rubble bioerosion can be used in determining residence time of coral rubble, hence sediment export rates (Scoffin et al. 1980; Hubbard, et al. 1990). Our technique for measuring branching coral rubble bioerosion cannot substitute for massive coral bioerosion in carbonate budgets, and it does not directly measure rates of rubble bioerosion. Its primary application is as a semi-quantitative detector of eutrophication stress on coral reefs.

5.4.4 Application as a Rapid Assessment Technique.

The frequency of boring organism occurrence in branching coral rubble can be used as a rough indicator of sewage or other eutrophication pollution on coral reefs, but is most useful in concert with other measures of eutrophication and of reef health. Rubble bioerosion was more sensitive to subtle environmental gradients and reef health measurements in Ambon than massive coral bioerosion. On the Java Sea reefs, where eutrophication stress is much more intense, massive and branching coral bioerosion yielded similar results, both reflecting environmental and reef health patterns. Most important, both massive coral bioerosion and raw bioerosion score showed dramatic differences between a reef adjacent to mangroves (Lagun Marican), and subject to natural runoff, and nearshore reefs subject to anthropogenic sewage pollution (Pulau Panjang).

This technique of assessing bioerosion and, by extension, eutrophication stress on reefs is low cost, easy, and relatively simple to execute. It is far less costly, labour intensive, or destructive than measurements of massive coral bioerosion from slabs, or experimental measurements of carbonate bioerosion. Sampling, sample processing, and data reduction for a given reef usually took two experienced operators about 1 day. Students under supervision took slightly longer, as they learned to recognise bioeroding organism types.

5.5 Conclusions.

1. Massive coral bioerosion is positively correlated with environmental variables indicative of eutrophication in the Java Sea. Branching coral rubble bioerosion is also positively correlated with environmental variables indicative of eutrophication in both Ambon and the Java Sea.

2. Massive coral bioerosion is negatively correlated with transect measurements indicative of coral reef health in the Java Sea. Branching coral rubble bioerosion is negatively correlated with transect measurements indicative of coral reef health in both Ambon and the Java Sea.

3. Massive coral bioerosion is positively correlated with branching coral rubble bioerosion in the Java Sea, but not in Ambon. This regional difference results from a much greater degree of eutrophication on nearshore Java Sea reefs than on any of the Ambon reefs.

4. Branching coral rubble bioerosion is more sensitive to low levels of eutrophication and sedimentation stress than is massive coral bioerosion. Branching coral rubble bioerosion can be used as a general indicator of eutrophication stress on coral reefs and as a rough index of bioerosion intensity, but cannot be used as a proxy for massive coral bioerosion in carbonate budget calculations.

Chapter 6: The Janus Effect: Do high coral growth rates mean healthy coral reefs?

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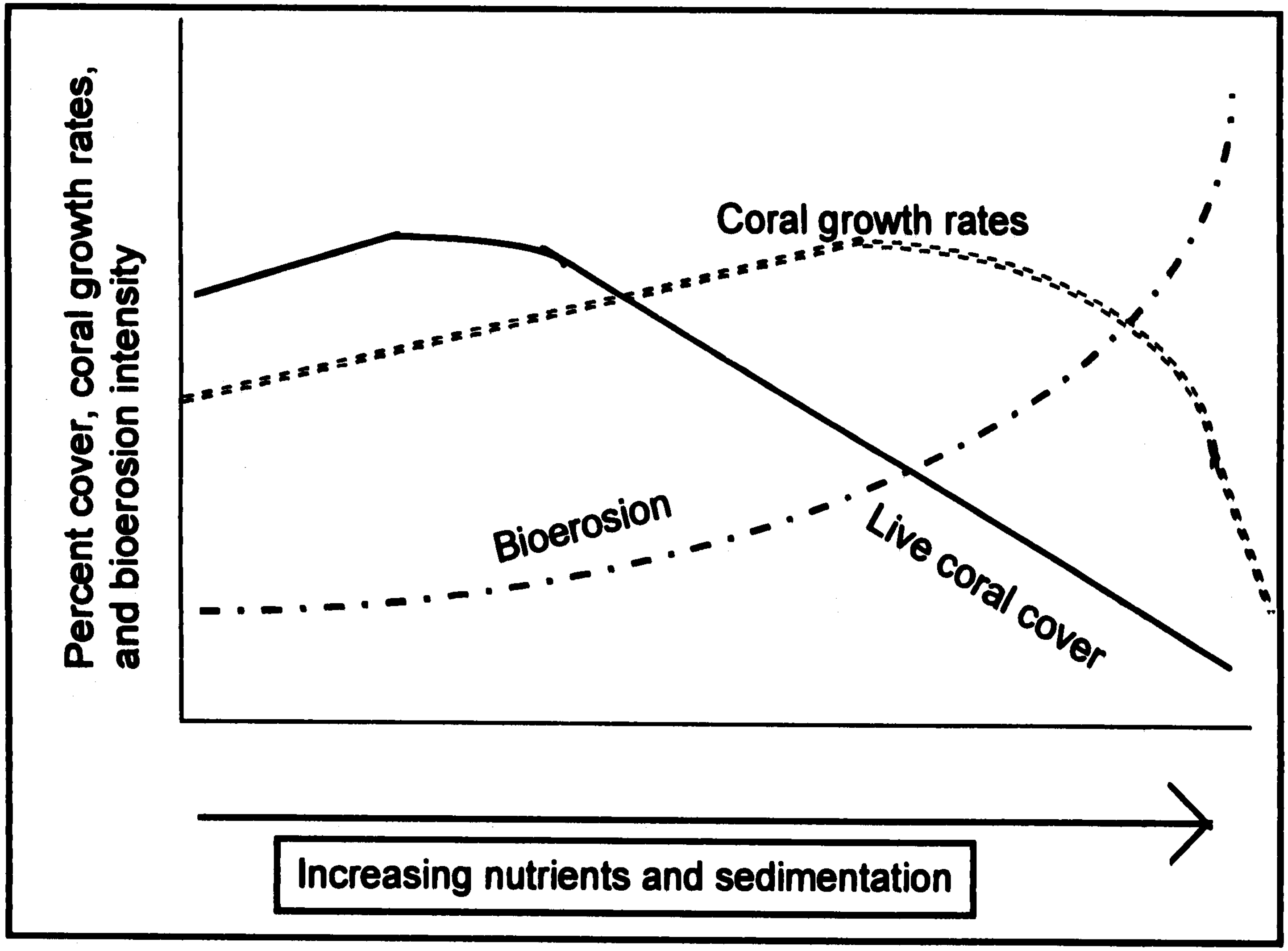
Submitted, Coral Reefs

6.1 Introduction

The Janus Effect is a paradoxical pattern of coral growth and coral reef growth, where individual corals grow fast under eutrophic conditions, but reef growth as a whole is slow, or even negative. Individual corals may grow fast by feeding on dissolved and particulate organic matter, living more heterotrophically than in clear water oligotrophic environments (Risk et al. 1994). Alternatively, nearshore corals may have higher zooxanthellae and chlorophlast densities and grow faster using enhanced zooxanthellar photosynthesis fertilised by increased dissolved inorganic nutrients (Steven and Broadbent 1997; Dubinsky and Jokiel 1994). Corals on reefs and biostromes very close to shore, however, may be subject to extremely high sedimentation and show a decline in growth rates toward shore (e.g. Dodge et al. 1974; Cortes and Risk 1985).

Fig. 6.1: Hypothetical curves of coral growth rates, live coral cover, and total bioerosion with increasing eutrophication and sedimentation. Under eutrophic conditions, low live coral cover and high bioerosion combine to produce negative carbonate budgets and reef accretion rates.



The Janus Effect thus predicts a curve (figure 6.1) in which corals exhibit low growth rates on offshore oligotrophic reefs, high growth rates on nearshore eutrophic reefs, and low growth rates again on reefs subject to extremely high eutrophication and sedimentation.

Highly productive waters, however, also favour growth of fleshy algae and non-calcified invertebrates (Birkland 1977; Wood 1993; but see also Larkum and Koop 1997), and enhance the growth of bioeroding organisms (Rose and Risk 1985; Hallock 1988). These factors combine to limit reef growth in nutrient-rich waters (Hallock and Schlager 1986). We developed the Janus Effect concept for fossil reefs, to help explain the absence of large offshore reef build-ups in the Caribbean Miocene during a time of enhanced upwelling (Edinger and Risk 1994), but the pattern has not previously been documented on modern reefs.

The Janus Effect yields three specific hypotheses about modern coral reefs growing in nearshore eutrophic environments:

1. individual corals grow faster than on offshore clearwater reefs in the same region,
2. total coral cover and coral species diversity on nearshore reefs are lower than on offshore reefs, while cover of fleshy algae and invertebrates are higher than on offshore reefs.
3. intensity of bioerosion is higher on nearshore reefs than on offshore reefs.

The combination of low live coral cover, high algal and non-calcified invertebrate cover, and high bioerosion pushes carbonate budgets toward negative accretion rates (Scoffin, et al. 1980).

In this paper, we document increased growth rates of Porites lobata in some eutrophic reef environments. We also document decreased live coral cover and increased cover of non-calcified invertebrates and increased bioerosion on those reefs, relative to unpolluted reefs in the same region. We document relationships between coral growth rates and marine productivity, as measured by chlorophyll A concentration, between growth rates and live coral cover, and between coral growth rates and coral species diversity in eutrophic environments.

6.2 Methods.

6.2.1 Study Areas.

A total of 13 reefs were sampled from three regions: the Java Sea, Ambon, and South Sulawesi. These reefs and their physical characteristics are summarised in table 1, and environmental data are summarised in table 2. More complete descriptions of each site are presented in chapter 1 and in various theses (Jompa 1996; Limmon 1996).

Table 6.1. Study Site regions, names, morphologies, and summaries of stresses. Max. depth: maximum depth of coral growth. Water Clarity was measured as average secchi disk extinction depth. Source of stresses summarizes impacts on each reef. More detailed descriptions of each reef can be found in Limmon (1996), Jompa (1996), and Edinger et al. (in review).

Region	Reef Name	reef morphology	max. depth	water clarity	source of stresses
Ambon	Tanjung Setan	fringing reef /wall	40m	>20m	unaffected sites (10m, 3m)
	Hila	fringing reef	20m	20m	bombing, construction, rubble btm.
	Wayame	fringing reef	15m	10m	harbour, sewage, sedimentation
	Wailiha	fringing reef	6m	<5m	sediment, plywood factory
So. Sulawesi	Kapoposan	coral cay/wall	50m	>20m	unaffected (10m), bombed (3m)
	Barang Lompo	coral cay island	25m	17m	bombing, local sewage pollution
	Samalona	coral cay island	25m	18m	anchor damage, pollution from city
	Kayangan	coral cay island	11m	<6m	harbour, industry, sedimentation
Karimunjawa	Pulau Kecil	coral cay island	25m	20m	Java unaffected, overfishing
(Central Java)	Gosong Cemara	coral cay, submerged	25m	20m	Java unaffected, overfishing
	Lagun Marican	mangrove fringe	4m	<3m	carbonate sedimentation
Jepara	Pulau Panjang	coral cay island	8m	<3m	sewage, sediment, aquaculture
(Central Java)	Bondo	fringing reef	5m	<2m	sedimentation, agricultural runoff

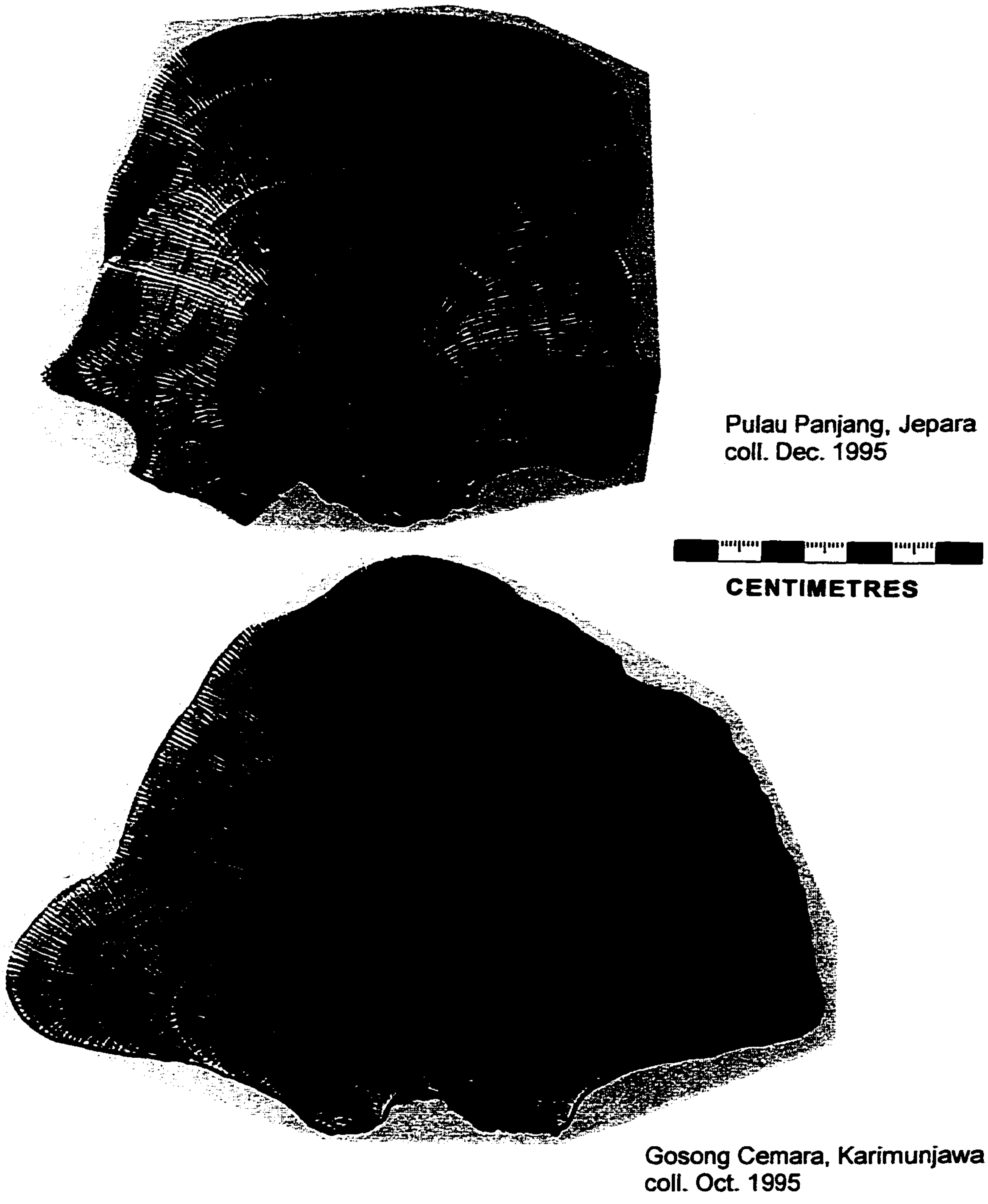


Figure 6.2: X-ray pseudorelief images of rapidly and slowly growing corals. □A: Rapidly growing coral PPS 11, Pulau Panjang, Jepara, average growth rate 16.8m/yr. □B: Slowly growing coral CM5, Gosong Cemara, Karimunjawa, average growth rate 8.5mm/ yr. Annual density bands are clearest in nearshore sites with greater clastic sediment influx during the rainy season.

6.2.2 Coral growth rate measurements.

At least five Porites lobata heads were collected from 1m depth at each reef. All corals were slabbed parallel to the maximum growth axis using a hand-held masonry saw. Axial slabs were cut to approximately 5mm thickness using a diamond-blade rock saw. Annual density bands were marked and measured from X-ray images of the thin slabs, following Buddemeier et al. (1974). A total of 73 corals were measured for this study. Average growth rates for each coral are presented in table 6.3. Raw growth rate data for Java Sea sites are presented in Appendix 3; raw growth rate data for Ambon and Sulawesi are presented in Limmon (1996) and Jompa (1996), respectively.

6.2.3 Line Intercept Transects.

At each reef, we measured 12 replicate 20m line intercept transects, 6 at 3m depth, and 6 at 10m depth for cover of live corals, dead coral, algae, other fauna, and abiotic substrates (e.g. sand and rubble). Other fauna included sessile invertebrates such as sponges, gorgonians, alcyonarian soft corals, zooanthids, and ascidians. On 3 reefs where coral depth did not extend beyond 5m (Wailiha, L. Marican, Bondo; see table 1), we measured transects at 3m only, and at P. Panjang, Jepara, we measured transects at 3m and 6m.

6.2.4 Coral Bioerosion.

Bioerosion of massive Porites lobata heads was measured from X-rays of parallel but non-adjacent slabs through the same coral heads collected for growth rate measurements at the five Java sites (method follows Sammarco and Risk 1990). Cross sectional area of each slab and the borings in it was measured using a hand-held planimeter (method follows Edinger & Risk 1997). Bioerosion intensity is reported as percentage of cross-sectional area removed by boring organisms.

6.2.5 Skeletal Density Measurements and Calcification Rates.

Variations in skeletal density (*sensu* Risk & Sammarco 1991) were measured in corals from three reefs in the Java Sea along an onshore-offshore nutrient and sedimentation gradient: Pulau Panjang South (PPS), Lagun Marican (LM), and Pulau Kecil (PK). In each reef, three corals (4 at PPS) were selected that had at least five years of growth measurements. A total of 74 one year growth increments identified from the X-ray images were cut from ten slabs using a diamond-bladed rock saw. These blocks of skeleton were oven-dried, weighed, and measured with verneir calipers to calculate their volume. Blocks were then embedded in paraffin wax, and their volume was measured as the mass of distilled water displaced from a specially designed pycnometer. Density was calculated as mass per unit volume (g/cm^3). Calcification rates for each coral-year were calculated as density x linear extension rate (g$CaCO_3$/cm^2/yr). The intensity of calicification on individual skeletal elements was estimated as lateral density index, which was calculated as volumetric density/linear extension rate (g/cm^2)

6.2.6 Environmental Data.

A variety of environmental variables were measured at each reef, including chlorophyll A concentration, nitrate and phosphate concentration, suspended particulate matter, concentration, sediment resuspension, water clarity (secchi disk extinction depth), and light intensity (table 2). All variables were measured on at least 3 separate dates; Ambon and Sulawesi data were collected in May - Aug. 1995; Java Sea data were collected in Nov. 1994 - Jan. 1995, July - Dec. 1995, and Aug. - Dec. 1996. Full environmental data for Sulawesi and Ambon sites are reported in Jompa (1996) and Limmon (1996). Chlorophyll sampling and analysis followed Parsons et al. (1984). Suspended particulate matter (SPM) was measured by filtering 1 litre of seawater onto a pre-weighed glass fibre filter, which was subsequently oven-dried and weighed (Cortes and Risk 1985). Sediment resuspension was measured using sediment traps consisting of 30 cm long, 5cm diametre PVC tubes. In Java, traps were deployed on the reef surface at 3m depth and changed monthly or bimonthly in Karimunjawa, and biweekly in Jepara. Sediment traps at the Ambon and Sulawesi sites were deployed 25cm above the reef surface at 3m depth and were changed weekly. Downward irradiance light levels on Java Sea reefs were measured using an Onset HoboJ light logger deployed in a waterproof case. The light logger was placed on the reef for approximately 5 min. each at four depths: 10m, 3m, 1m, and surface, and light extinction coefficients were calculated for each reef. Light intensity at 1m is reported in lumens/sq. ft., and as % of surface light intensity at 1m, and 3m depths, and as light extinction coefficient.

Table 6.2. Environmental parameters measured for each reef in the study. All values are averages of at least 3 measurements, followed by standard deviations (in brackets). Ambon measurements are wet season, while Sulawesi and Java measurements are mostly dry season or transitional. W/W: windward. L/W: leeward. Methods described in text. Light levels reported as light intensity at 1m, % of surface light at 1m and 3m, and as downward light extinction coefficient.

Reef Name	chl. A	NO3	PO4	SPM	resusp	1m light	1m %	3m %	light extinct
(units)	mg/m3	µM	µM	mg/l	mg/cm2/day	lumens/ft2	%	%	K (unitless)
Tanjung Setan	0.39 (0.18)	0.76 (0.40)	0.28 (0.19)	4.49 (1.40)	0.077 (0.018)				
Hila	0.44 (0.21)	0.77 (0.44)	0.38 (0.20)	4.91 (2.66)	0.19 (0.14)				
Wayame	0.38 (0.06)	1.46 (1.01)	0.46 (0.18)	11.15 (3.40)	0.55 (0.23)				
Wailiha	0.46 (0.14)	0.82 (0.32)	0.30 (0.17)	15.30 (10.21)	3.08 (3.13)				
Kapoposan	0.47 (0.05)	0.34 (0.07)	0.18 (0.03)	5.26 (1.24)					
Barang Lompo	0.75 (0.07)	0.63 (0.13)	0.30 (0.11)	8.62 (1.30)	0.70 (0.20)				
Samalona	0.82 (0.05)	0.49 (0.03)	0.31 (0.10)	8.22 (1.30)	0.60 (0.10)				
Kayangan	1.52 (0.53)	0.85 (0.23)	0.41 (0.19)	19.25 (4.61)	2.80 (0.20)				
P. Kecil WW	0.33 (0.08)			9.75 (6.71)	2.03 (0.55)				
P. Kecil L/w	0.29 (0.17)			19.69 (18.27)	1.63 (1.31)	102.69 (45.85)	77	64	- 0.18
G. Cemara W/W	0.40 (0.21)			22.98 (7.56)	4.21 (3.31)				
G. Cemara L/W	0.25 (0.14)			22.26 (7.56)	2.80 (3.62)	146.87 (98.27)	59	35	- 0.22
Lagun Marican	1.24 (0.90)			26.39 (11.58)		71.73 (63.10)	18		- 0.37
P. Panjang W/W	1.23 (0.54)			21.83 (8.40)	26.19 (24.42)	134.27 (37.20)	46	15	- 0.26
P. Panjang L/W	1.09 (0.62)			28.91 (17.86)	31.69 (38.74)	62.22 (14.85)	21	14	- 0.35
Bondo	1.22 (0.52)			21.04 (7.60)	38.5 (25.7)	93.47 (32.20)	23	9.7	- 0.27

6.2.7 Data Analysis.

There were no temporal trends in growth rates of individual corals, or among all corals combined (appendix 3). Therefore we compared coral growth rates among sites using 1-way ANOVA (Logan et al. 1994), treating each annual growth increment as an independent measurement. To standardize among different aged individual corals, we used the 2nd to 6th most recent years of growth in each coral, eliminating measurements from corals less than 5 years in age.

Transect data were summed into cover categories for each transect, which were combined to give average live coral cover values for each reef. Coral mortality index (Gomez 1994) was computed as MI= dead coral cover/(live coral cover + dead coral cover), with values ranging from 0 (all corals live) to 1 (all corals dead). Relationships between coral growth rates, coral cover, percent bioerosion, and environmental variables were assessed using correlation and linear regression analysis. Average growth rates of each coral recorded at each reef (table 6.3) were used for linear regression analyses (multiple Y per X, Sokal and Rohlf, 1973). Linear regression analysis was chosen because it provides a first-order approximation of relationships among environmental variables, bioerosion, and reef health, and because it is possible to calculate significance and estimate the amount of variance attributable to a given environmental variable.

6.3 Results.

6.3.1 Coral growth rates, environmental data, and coral cover , Java.

Porites lobata growth rates were significantly higher on eutrophic nearshore reefs than on offshore reefs with lower nutrient concentrations (fig. 6.3a; 1-way ANOVA, F=7.07, p<0.0001, d.f.=110). Coral growth rates were nearly identical on the two offshore reefs, and had much lower variance than on the nearshore reefs. Highest growth rates were observed at Pulau Panjang, the reef subject to the most sewage pollution, and were slightly lower at Bondo, the site subject to highest sedimentation rates (Tukey Test, table 6.4). Mean coral growth rates on each reef in Java were positively correlated with mean chlorophyll A concentrations (r^2=0.25, p=0.011, n=25), and with suspended particulate matter (r^2=0.21, p=0.021, n=25), and were inversely correlated with light intensity at 1m depth (r^2=0.27, p=0.008, n=25).

Mean total live coral cover was approximately 58% on offshore reefs, and approximately 24% on the nearshore reefs (figure 6.5a,b; 1-way ANOVA, F=10.83, p<0.0001). Coral growth rates on each reef in Java are inversely correlated with total live coral cover (r^2=0.27, p<0.008, n=25), and are positively correlated with mortality index (r^2=0.27, p<0.008, n=25).

Figure 6.3. Average coral growth rates, all sites. A: Java Sea, B: Ambon, C; Sulawesi. Increasing eutrophication and sedimentation to right in all cases.

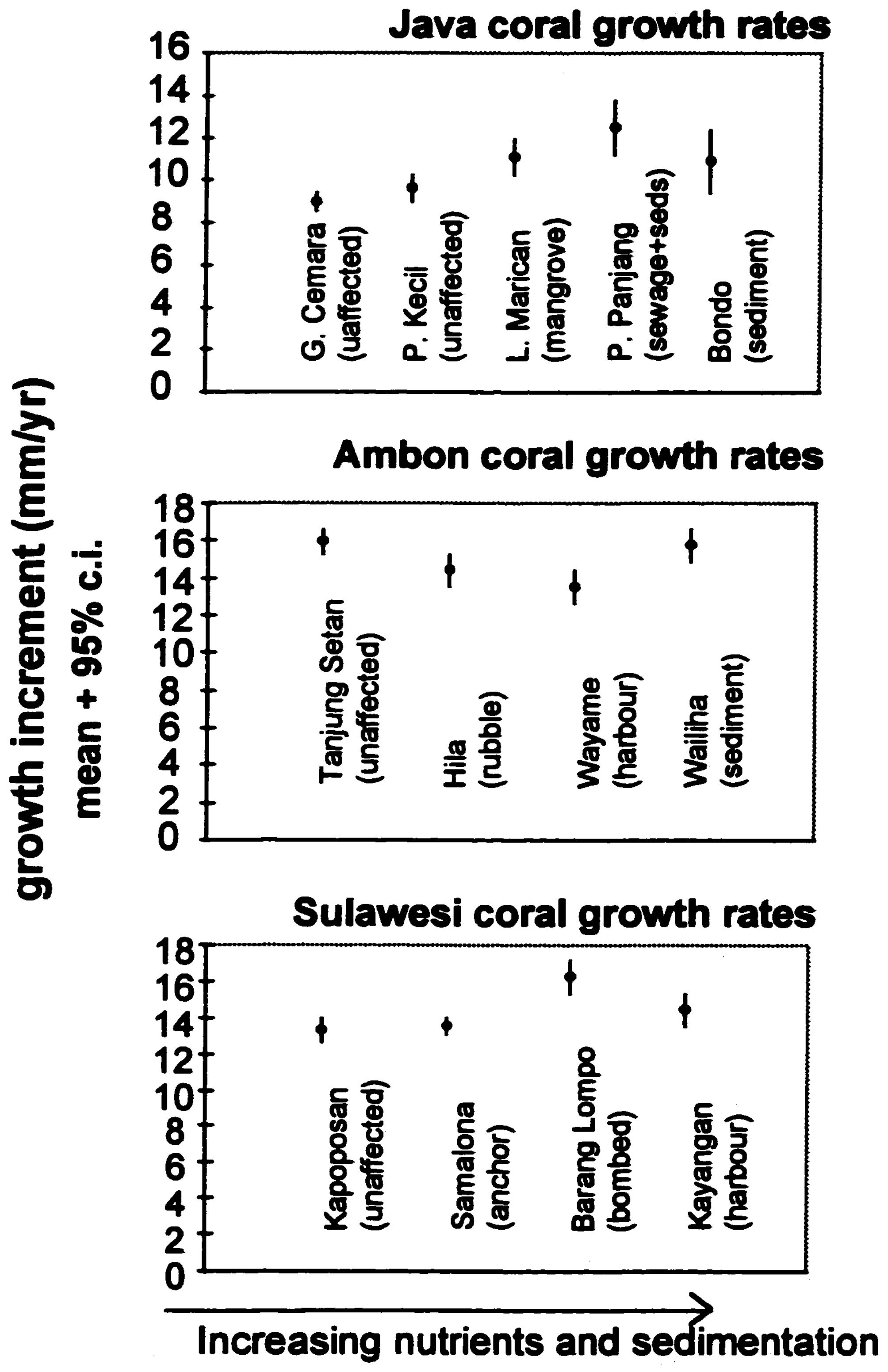
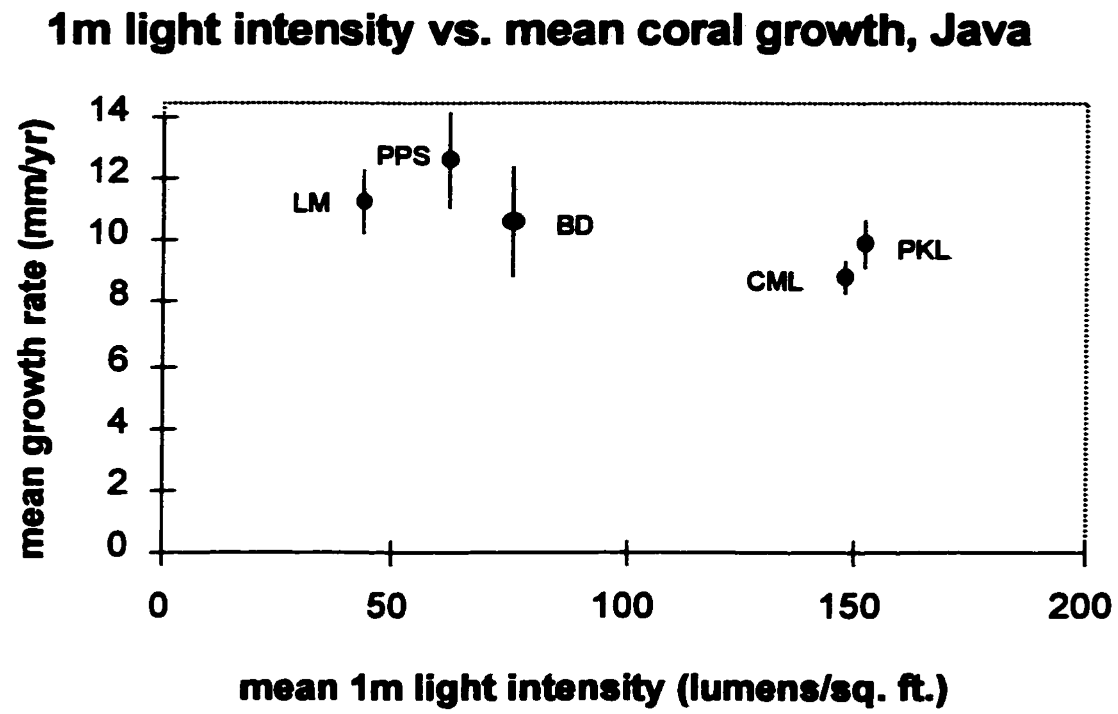


Figure 6.4: 1m light intensity vs. coral growth rates by site, Java. Coral growth rate means ± 95% confidence interval. Light intensity in lumens/sq. ft. (candelas).



6.3.2 Coral growth, environmental data, & coral cover, Ambon.

Coral growth rates at the four reefs sampled in Ambon were highest at Tanjung Setan (cleanest, most oligotrophic site), followed by Wailiha (highest sedimentation site), Hila, and Wayame (highest nutrient concentrations; fig. 6.3b; table 6.3). Growth rates at Wayame were significantly lower than at the other three sites (1-way ANOVA, F=8.14, p<0.0001, d.f.=110). Coral growth rates were negatively correlated with nitrate (r^2=0.37, p<.005, n=21) and phosphate concentrations (r^2=0.50, p<.0005, n=21), but not SPM or sediment resuspension rates.

Total live coral cover on the reefs sampled in Ambon was highest at Tanjung Setan (the cleanest site), intermediate and approximately equivalent at Hila (rubble site) and Wayame (harbour site), and lowest at Wailiha (highest sedimentation site, adjacent to plywood factory; fig. 6.5c,d). Cover at Wailiha is significantly lower than at Tanjung Setan and Wayame (1-way ANOVA, $F=39.27$, $p<0.0001$). Mortality index is lowest at Tanjung Setan, intermediate at Wayame, and highest at Hila and Wailiha, which are statistically indistinguishable (1-way ANOVA, $F=11.0$, $p<0.0001$). Wailiha and Wayame have significantly greater other invertebrate cover than Hila and Tanjung Setan (1-way ANOVA, $F=3.19$, $p<0.05$). Cover of algae and invertebrates combined was positively correlated with SPM ($r^2=0.94$, $p<.001$, $n=7$), but with neither nitrate nor phosphate concentration.

6.3.3 Coral growth, environmental data, and coral cover, Sulawesi.

Coral growth rates were highest at Barang Lompo (intermediate, bombed), followed by Kayangan (most polluted site), Samalona, and Kapoposan (cleanest site; fig.6.3c, table 6.3). Corals at Kayangan grew significantly faster than those at Samalona and Kapoposan (1-way ANOVA, $F=3.03$, $p<0.03$, d.f.=127).

Total live coral cover was highest at Kapoposan (cleanest site), intermediate and approximately equivalent at Barang Lompo and Samalona, and lowest at Kayangan (harbour site, fig. 6.5e.f; 1-way ANOVA, $F=47.27$, $p<0.0001$). Mortality index was lowest at Kapoposan, intermediate at Barang Lompo and Samalona, and highest at Kayangan (1-way ANOVA, F=6.87, $p<0.0001$).

Mortality index was positively correlated with chlorophyll A, nitrate, phosphate, SPM, sediment resuspension, ($r^2>0.75$ in all cases, $p<0.01$, n=7). The average sum of fleshy algae plus other invertebrates cover at 3m was 21.8% at Kayangan, significantly higher than at the other three Sulawesi sites (Samalona: 5.9%; Barang Lompo, 8.4%; Kapoposan, 9.1%;1-way ANOVA, F=11.81, $p<0.0002$). Mean coral growth rates were positively correlated with the sum of fleshy algae plus other invertebrates at 3m ($r^2=0.27$, $p<0.05$, n=4).

6.3.4 All sites combined.

There were no significant correlations between coral growth rates and total live coral cover or mortality index on all 13 sites combined. There was an positive correlation between global mean coral growth rates and cover of other invertebrates ($r^2=0.27$, $p<0.05$, n= 29).

6.3.5 Relationships with coral diversity.

Reefs subject to eutrophication and other land-based pollution are 40-70% less diverse than unaffected reefs in the same region (see chapter 2). In Java, mean growth rates were inversely correlated with diversity ($r^2=0.75$, $p<0.0001$, n=14), using both 3m and 10m transect data. There were no significant linear relationships between growth rates and species diversity in either Ambon or Sulawesi. Diversity data are treated more fully in chapter 2.

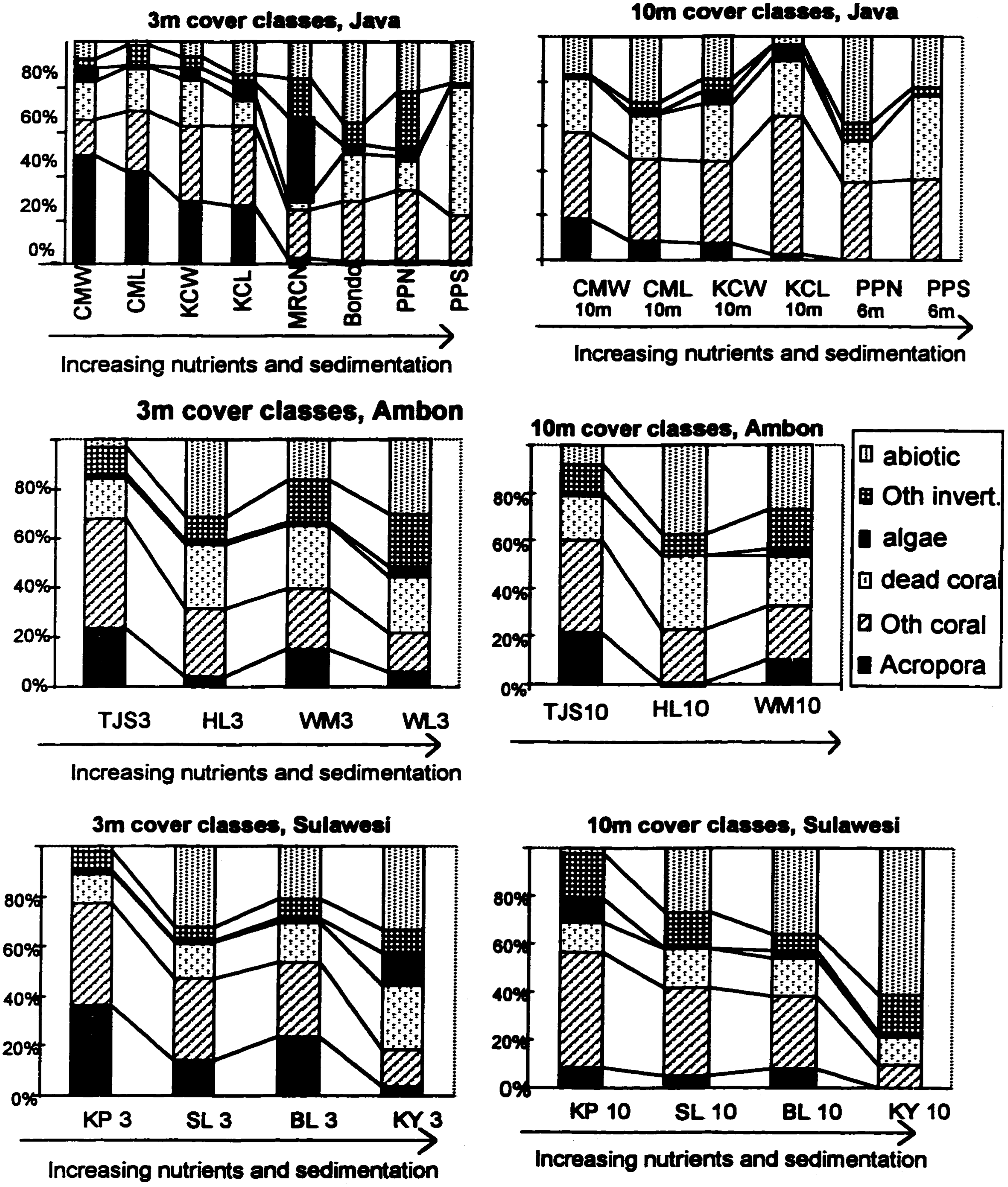
Table 6.3. Average growth rates of individual corals on all reefs sampled. Java Sea data presented as averages of 2nd to 6th latest growth years. Growth chronologies of individual corals presented in Appendix 3. Table arrangement: increasing nutrients and sedimentation to left within each region.

<u>Region</u>	<u>Ambon</u>				<u>*Sulawesi*</u>				<u>Java</u>			<u>Java</u>	
Coral #	WL	WY	HL	TJS	*KY*	*SL*	*BL*	*KP*	Bondo	PPS	LM	CML	PKL
1	16.7	15.0	13.1	15.4	*15.0*	*12.5*	*16.1*	*14.8*	14.3	10.0	10.0	8.6	11.5
2	15.2	12.0	15.9	17.0	*18.7*	*15.0*	*12.9*	*13.4*	17.3	10.4	11.8	10.0	8.9
3	15.4	10.7	12.3	14.8	*11.6*	*14.0*	*19.0*	*10.5*	10.0	14.7	9.9	8.7	10.5
4	15.6	13.7	15.3	15.4	*16.6*	*13.6*	*13.4*	*15.8*	9.4	10.4	13.1		9.1
5	15.7	14.0	15.9	17.0	*12.3*	*13.4*	*15.5*	*12.4*		18.0	13.2		6.8
6				17.0	*12.1*	*13.9*	*16.0*	*15.0*		10.5			
7					*15.3*		*17.4*	*13.5*		15.2			
average	15.7	13.4	14.5	16.1	*14.5*	*13.7*	*16.1*	*13.5*	11.5	12.6	12.0	9.0	9.4
std. Dev.	0.6	1.7	1.7	1.01	*2.6*	*0.5*	*1.8*	*1.4*	3.0	3.1	1.5	1.15	1.4

Table 6.4. Tukey post-hoc test results on Java Sea growth rate data, standardised for coral age using the 2nd to 6th final years in each coral growth chronology. Mean growth rate values for each reef are presented in columns containing statistically homogeneous subsets. Two homogeneous subsets ($p<0.05$) observed: offshore reefs (G. Cemara, P. Kecil), nearshore reefs (L. Marican, P. Panjang). Bondo has extremely high variance in coral growth rates, and overlaps both subsets.

Reef	reef environment	N coral-years	subset 1 (offshore)	subset 2 (nearshore)
Gosong Cemara	offshore	20	9.00	
Pulau Kecil	offshore	25	9.36	
Bondo	high sedimentation	13	11.46	11.46
Lagun Marican	mangroves	20		11.99
Pulau Panjang	sewage + sediment	33		12.62

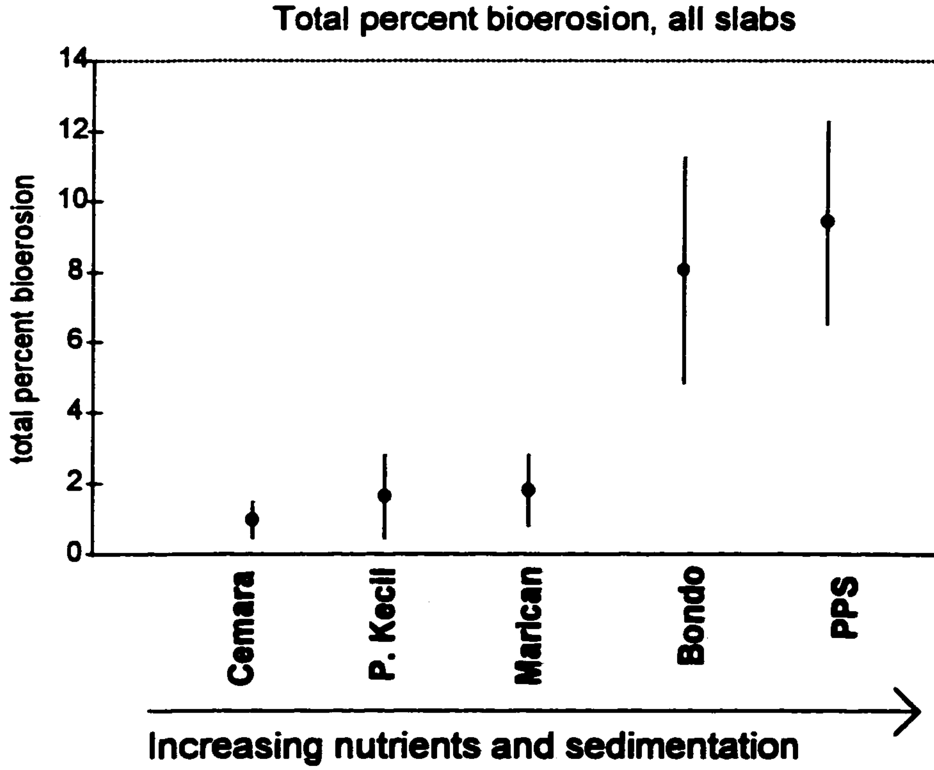
Fig. 6.5. Cover summaries for all reefs. Codes follow table 6.1, table 2.3.



6.3.6 Bioerosion, Java Sea.

Bioerosion of massive corals on the Java Sites was highest at the nearshore reefs (Jepara and Bondo), intermediate at the mangrove site (Lagun Marican), and lowest at the offshore reefs (Pulau Kecil and Gosong Cemara) (fig. 6.6; 1-way ANOVA, F=4.41, $p<0.01$). In Java, bioerosion of massive corals was positively correlated with chlorophyll A concentration ($r^2=0.33$, $p<0.01$, $n=21$). Bioerosion data are treated more fully in chapter 5.

Figure 6.6: Total percent bioerosion, Java Sea. Mean ± 95% confidence interval.

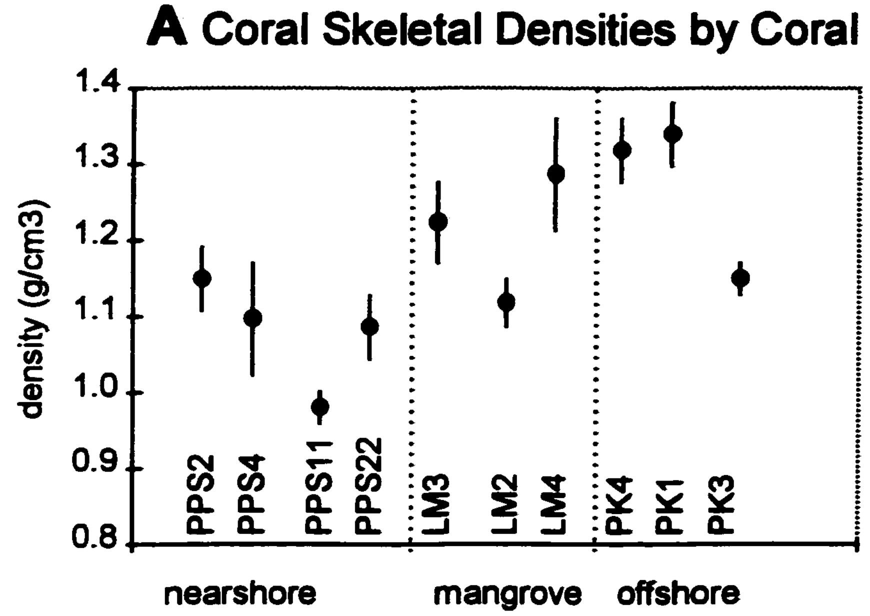


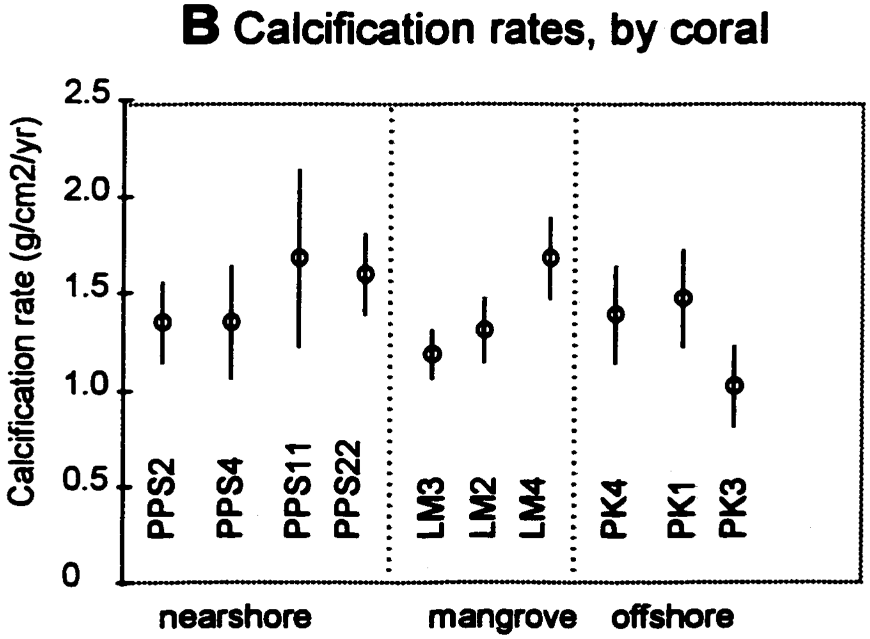
6.3.7 Skeletal Density and Calcification Rates, Java Sea.

Skeletal density of Porites lobata corals was lowest on the nearshore polluted Java Sea reef (PPS), intermediate on the reef adjacent to mangroves (LM), and highest on the clean offshore reef (PK; fig. 6.7a; 1-way ANOVA, $p<0.0001$). Lateral density index, which reflects the intensity of calcification on individual skeletal elements, at PK was more than double that at PPS. These results match previous studies on the Great Barrier Reef, where skeletal density increased offshore (Risk & Sammarco 1991), or decreased through time and with increasing nitrate and phosphate fertiliser runoff (Rasmussen et al. 1992).

Java Sea calcification rates (density x growth rate) were not significantly different among the three sites studied (figure 6.7b, 1-way ANOVA, $F=1.81$, $p>0.15$). There was a weak inverse relationship between density and upward growth when all data points were combined ($r^2=0.07$, $p<0.02$, $n=74$), but not within any one coral or site, except within coral PPS 2, where density was strongly inversely related to growth rate ($r^2=0.83$, $p<0.001$, $n=8$). The slightly higher calcification rates at Pulau Panjang are driven by high linear extension rates, rather than intensity of calcification on individual skeletal elements.

Figure 6.7A: Average coral skeletal density, 3 Java Sea sites, by coral.
Figure 6.7B: Average coral calcification rates, 3 Java Sea sites, by coral.
PPS: Pulau Panjang South; LM: Lagun Marican; PK: Pulau Kecil. Means ± 95% confidence limits.





6.4 Discussion.

Most studies of coral growth rates assume that environmental degradation depresses individual coral growth rates (e.g. Dodge et al. 1974; Highsmith 1979, Tomascik and Sander 1985), and frequently equate rapid coral growth with healthy coral reef growth (e.g. Cortes and Risk 1985; Bosscher 1992; Priess et al. 1995).

Our and other results from eutrophied nearshore reefs partially contradict these studies. Rapid coral growth rates adjacent to sewage outfalls have been observed in several locations (Risk et al. 1993; Dollar 1994). Corals and fringing reefs in Barbados display patterns similar to our results. Juvenile corals were larger on eutrophied reefs, but were less abundant and less diverse than on nearby non-eutrophied reefs; adult coral cover and diversity was lower on eutrophied reefs, and algal cover was higher (Wittenberg and Hunte 1992). Small colonies of Porites porites, (F. Marubini, pers comm. 1997) and adult Montastrea annularis (Tomascik and Sander 1985) growth rates in Barbados increased, then decreased, along a gradient of increasing eutrophication and suspended particulate matter, suggesting that the organic fraction of SPM may be an important food source for corals, and may increase growth rates up to moderate concentrations (Tomascik and Sander 1985). Bioerosion along these same reefs increases with eutrophication and SPM (Holmes 1997).

6.4.1 Factors influencing coral growth rates.

Shallow water corals generally grow autotrophically, using carbon translocated from their zooxanthellae (Muscatine and Porter 1977).

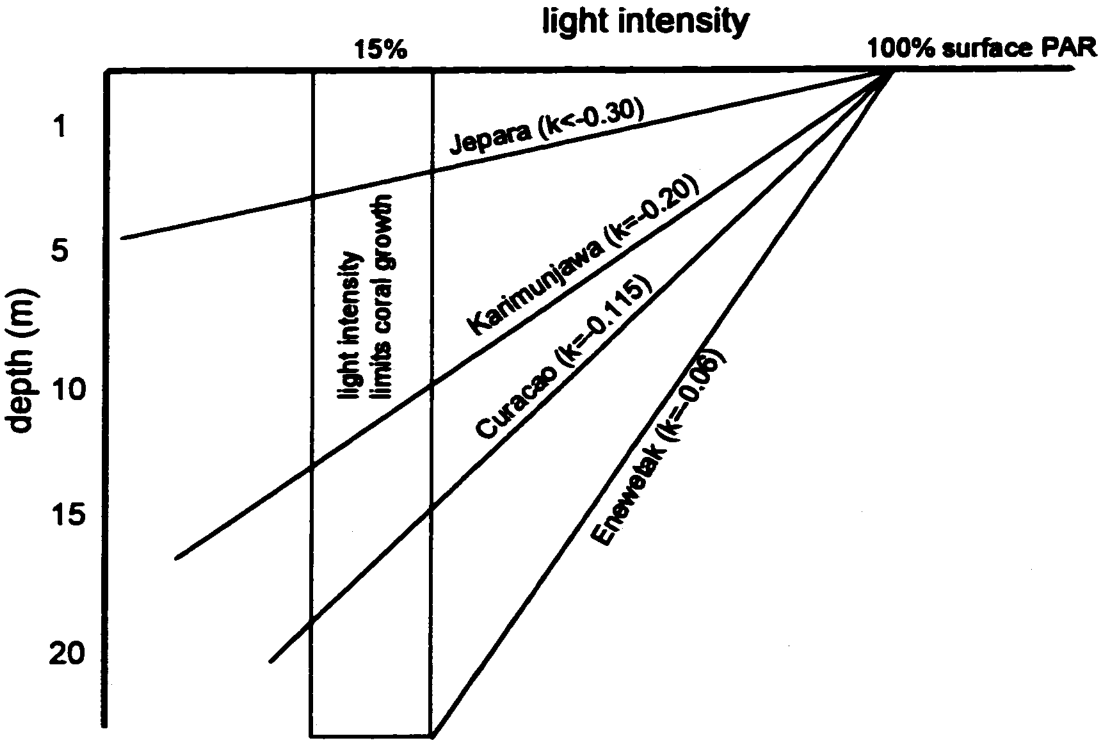
Growth rates are usually positively correlated with light availability up to light saturation (Buddemeier and Kinzie 1976, Highsmith 1979; Bosscher 1992). Reductions in coral growth rates associated with siltation are usually attributed both to reduced light penetration and metabolic stress associated with sediment rejection (Dodge et al. 1974; Dodge and Vaisnys 1977; Rogers 1990).

On the Java Sea sites we studied, coral growth rates are positively correlated with phytoplankton biomass and sedimentation rates, except at the highest sedimentation site (Bondo), where corals showed the growth rate decrease predicted for high sedimentation-high eutrophication conditions (fig 6.1; fig. 6.3a). Dissolved and particulate matter in coastal runoff, including sewage and aquaculture effluent, may contribute to coral metabolism, hence to increased growth rates (Tomascik and Sander 1985; Risk et al. 1994). Moderate sedimentation, through increased turbidity, may indirectly contribute to the observed rapid coral growth rates at some of the nearshore sites. Many of the Porites heads on nearshore reefs have multilobate morphology, which concentrates upward growth within individual lobes, and is generally interpreted as a response to high sedimentation (Goreau 1959).

Java Sea coral growth rates are negatively correlated with light intensity at 1m, the depth at which the corals were collected, but coral growth rates at 1m are probably not limited by light. Montastrea annularis growth rates in Curacao were positively correlated with light up to approximately 15% of surface light intensity, attained at around 15m depth, where the average light extinction coefficient ws -0.115 (Bosscher

1992). The light extinction coefficients of the nearshore reefs (L. Marican, -0.37, PPS, -0.35, Bondo, -0.27) are all well beyond the averages for waters around health reefs (Bosscher 1992; fig. 6.8). On the most heavily polluted nearshore Java Sea reefs, light intensity at 1m depth was already less than 25% of surface light, and was at or below 15% at 3m depth (table 6.2), suggesting that corals growing at depths greater than 1m are critically light limited. For corals on these reefs, rapid upward growth into water with greater light availability would be highly advantageous.

Figure 6.8. Influence of light extinction coefficients on the depths for light saturation with respect to coral growth on various reefs. Data from this study and from Bosscher (1992). Box indicates the range of light intensities at which light limits growth in most species of corals. PAR: photosynthetically active radiation.



6.4.2 Regional variation in growth rates.

Patterns of coral growth rates in relation to nutrient concentrations, sedimentation rates, coral cover, coral mortality, and coral species diversity are different in Ambon than in Sulawesi and Java. On the Sulawesi reefs, coral growth rates were highest on the two reefs with sewage input (Barang Lompo, Kayangan), but were higher on the sewage contaminated reef without high clastic sediment discharges (Barang Lompo) than on the reef in Ujung Pandang harbour (Kayangan). The cleaner water reefs (Kapoposan, Samalona) had significantly lower coral growth rates than did the sewage and sediment contaminated reef (Kayangan). This reef appears to demonstrate the Janus Effect as well, with high coral growth rates, low coral cover, high coral mortality, and high cover of fleshy algae and invertebrates, although we did not measure bioerosion there. The death of the leeward side of Kayangan reef certainly post-dates Dutch accounts from the 1930's (Umbgrove 1947), and probably coincided with the rapid growth of Ujung Pandang as a population and industrial centre in the 1970's and 1980's (Jompa 1996).

In Ambon, coral growth rates were highest at Tanjung Setan, the cleanest site, but were not significantly lower at Wailiha, the high sediment site adjacent to the plywood factory. Corals at Wailiha may be growing fast by ingesting dissolved organic matter from the plywood factory, as suggested by high lignin concentrations in coral skeletons (Limmon 1996). Wailiha had the lowest live coral cover and highest other fauna cover of the Ambon reefs. All the reefs we sampled in Ambon are fringing reefs, and normally receive larger inputs of terrigenous nutrients and sediments than do the offshore reefs in Sulawesi and Java. The increased base level of productivity may account for overall greater growth rates in Ambon, similar to Darwin's island effect (Darwin 1842).

6.4.3 Explanations for rapid coral growth rates under eutrophic conditions.

Three possible explanations can account for the rapid growth of Porites lobata under eutrophic conditions. First, rapid upward coral growth, particularly multilobate morphology, may be a morphological response to high sediment loading and low light penetration, as corals grow into shallower water with greater light availability. Second, they may grow faster by feeding heterotrophically on dissolved and particulate organic matter. Third, rapid calcification may facilitate CO_2 fixation and nutrient uptake under low light conditions (e.g. McConnaughey and Whelan 1997). Some or all of these mechanisms may contribute to the Janus Effect as observed on our sites in Indonesia. The percent cover of submassive corals on a reef, stable isotope data, and skeletal density data may help to elucidate the relative importance of these three processes.

The percent cover of submassive corals is roughly indicative of the frequency of multilobate morphology on the reefs we have sampled, and reflects the degree of morphological change in response to high sedimentation and low light penetration. Submassive corals form a significantly higher proportion of the coral fauna on nearshore polluted reefs in the Java Sea and Sulawesi (24%) than on offshore Java Sea reefs (7.1%) or offshore Sulawesi reefs (10.8%; 1-way ANOVA, F=5.38, $p<0.02$, d.f.=28). On Pulau Panjang, the most polluted reef in our study, submassive corals comprise 27.3% of the corals. The prevalence of submassive corals on nearshore reefs with high growth rates suggests that morphological changes related to low light penetration may contribute to higher coral growth rates.

Within each region, coral tissue $\delta^{\blacksquare}$N values are higher at reefs subject to eutrophication and sedimentation stress than at reefs not under these stresses (Jompa 1996; Limmon 1996; Dunn 1995; Lazier 1997), reflecting the influence of nutrient influx on coral diet and metabolism. Elevated coral $\delta^{\blacksquare}$N values partly reflect a signal of anthropogenic nutrient contamination and, possibly, increased heterotrophy (Dunn 1995, Lazier 1997). Analysis of $\delta^{\blacksquare}$C values in coral tissue can indicate the extent to which corals in eutrophic environments are feeding heterotrophically or autotrophically (Muscatine et al. 1989, Risk et al. 1994, Heikoop 1997). Preliminary $\delta^{\blacksquare}$C results are ambiguous, but indicate that nearshore *Porites lobata* at 1m still exhibit abundant photosynthetic activity (Lazier 1997; Heikoop, pers comm. 1997).

Nitrate and phosphate inputs with sewage contamination may fertilize zooxanthellae, stimulating greater zooxanthellar growth (effect of N), higher within-cell chlorophyll concentrations (effect of P), enabling higher coral growth and calcification rates overall (Steven and Broadbent 1997). Increased availability of dissolved inorganic nitrogen, and phosphorus associated with sewage pollution probably contributes to the rapid coral growth rates on nearshore polluted coral reefs.

Previous studies of environmental variation in skeletal density found that all parts of the skeleton, including septa, dissepiments, and corallite walls, were less heavily calcified on nearshore reefs than offshore reefs (Risk and Sammarco 1991). Other studies attributed increased void space in corals associated with fertiliser runoff to phosphate crystal poisoning (Rasmussen et al. 1992). Our results, likewise, show that skeletal density is lowest on the nearshore reefs, as is the lateral density index (density/growth rate). Calcification rates (density x growth rate) are slightly higher on nearshore polluted reefs than on offshore reefs, but this non-significant trend is driven entirely by rapid upward extension rates on nearshore reefs, overwhelming the differences in density. The density and calcification data suggest that corals on nearshore reefs probably do not calcify more rapidly in order to facilitate photosynthesis under these low-light conditions. In summary, we attribute the rapid coral growth rates observed on heavily polluted nearshore reefs to combined morphological effects and metabolic changes associated with increased organic matter and dissolved inorganic nutrient availability.

6.4.4 Carbonate budgets.

Several researchers have stressed the importance of carbonate budgets to understanding reef health, particularly in the face of land-based pollution and reef degradation (e.g. Birkland 1996; McClanahan 1997). Much previous work has emphasised rapid coral growth rates as an indicator of healthy reef growth (e.g. Cortes and Risk 1985). We have demonstrated rapid individual coral growth rates under eutrophic conditions on three dying Indonesian reefs (Pulau Panjang, Kayangan, Wailiha). We have presented a number of environmental variables and reef health parameters indicating severe degradation on these reefs. Qualitative evidence suggests that each of these reefs growing under severe eutrophication stress also has a negative carbonate budget, i.e. is undergoing net erosion. For example, the reef at Pulau Panjang, Jepara, has the highest average individual coral growth rates we documented in Java, but probably has negative reef accretion rates. Total coral cover is low, cover of non-carbonate producing organisms is high, and bioerosion is high. The Holocene raised reef visible along most of the island's shore is being eroded on all sides, and comparison with 1890's Dutch maps and 1944 US Army maps shows that the size of the island is decreasing (Kamiludin et al. 1991).

Carbonate budgets include carbonate production and carbonate destruction. Generally, carbonate production is estimated as coral calcification plus calcification by calcareous algae, soft corals and other calcareous reef-dwelling organisms, plus inorganic cementation. Carbonate production is usually estimate as carbonate dissolution, sediment export, and bioerosion (Scoffin, et al. 1980). Here, simple carbonate budget calculations are presented for three Java Sea reefs as an example, using our Porites lobata growth rate, density, calcification rate, bioerosion intensity data, and live and dead coral cover data from Pulau Panjang, Lagun Marican, and Pulau Kecil (fig. 6.9, Table 6.5). Carbonate production (kg $CaCO_3/m^2/year$) by corals is estimated as (mean calcification rate x percent live coral cover),

$r_{prod} = (r_{calc} \times \% \text{ cover}_{live})$,

assuming approximately equal calcification rates for all coral species on each reef. Carbonate destruction (kg $CaCO_3/m^2/year$) is estimated as (cross-sectional area bioeroded from 1cm thick *Porites lobata* slabs x skeletal density / average age of corals sampled x the sum (total live coral cover + total standing dead coral cover)) or

$r_{dest} = ((\text{area}_{bioer} \times \text{thick}_{slab} \times \text{density})/\ \text{age}) \times (\text{cover}_{live} + \text{cover}_{dead}))$,

assuming approximately equal internal bioerosion rates for live and standing dead corals of all species. Pulau Panjang has a negative carbonate budget, while Lagun Marican and Pulau Kecil have positive carbonate budgets (table 4), as predicted by qualitative evidence.

These carbonate budgets are very simple, and do not include cementation or calcification by organisms other than corals in carbonate production, nor do they include dissolution and sediment export in carbonate destruction. The simplifying assumptions underestimate carbonate production on the offshore reef, where rapidly calcifying *Acropora* corals are more abundant than at the nearshore reef, and underestimate carbonate destruction on the nearshore reef, where abundant standing dead corals are subject to more intense bioerosion than are live corals (McKenna 1997). Despite these limitations, these calculations provide first order approximations of the carbonate budgets for these three reefs, and the values yielded by these simple calculations are in the same range as more complex models from other regions (Stearn et al. 1977; Scoffin et al. 1980; Hubbard et al. 1990; Guillaume 1990; Conand, et al. 1997).

Figure 6.9: Carbonate budget calculations for 3 Java Sea reefs.

Carbonate Production (kg $CaCO_3/m^2/yr$)

reef	mean calc'n rate	mean % coral cvr	CaCO3 prodn.
PPS	1.49	21.18	3.16
LM	1.43	23.77	3.40
PK	1.29	61.74	7.96

Carbonate Destruction (kg $CaCO_3/m^2/yr$)

reef	mean area bioerosion	mean density	mean age	% live cvr	% dead cvr	CaCO3 destrn
PPS	8.54	1.09	8.00	21.18	58.93	9.32
LM	2.95	1.22	9.00	23.77	5.38	1.17
PK	2.54	1.29	11.60	61.74	13.61	2.13

Total Carbonate Budget (kg $CaCO_3/m^2/yr$)

reef	CaCO3 prodn.	CaCO3 destrn	total budget
PPS	3.16	9.32	-6.17
LM	3.40	1.17	2.23
PK	7.96	2.13	5.84

Table 6.5: Simple Carbonate Budget Calculations for three Java Sea Reefs. All units are in kg $CaCO_3/m^2/year$. Carbonate production by corals is estimated as mean calcification rate x percent live coral cover, assuming approximately equal calcification rates for all coral species on each reef. Carbonate destruction is estimated as cross-sectional area bioeroded from 1cm thick Porites slabs x skeletal density / average age of corals sampled x the sum of (total live coral cover + total standing dead coral cover), assuming approximately equal internal bioerosion rates for live and standing dead corals of all species. All calculations based on leeward reef values.

Reef	reef environment	$CaCO_3$ Production	$CaCO_3$ Destruction	Total $CaCO_3$ Budget
Pulau Panjang	nearshore sewage polluted	3.16	9.32	- 6.17
Lagun Marican	mangrove fringing reef	3.40	1.17	2.23
Pulau Kecil	offshore clean water	7.96	2.13	5.84

6.4.5 Implications for reef management.

The most severely degraded reefs in each region that we studied - Pulau Panjang in Java, Kayangan in Sulawesi, and Wailiha in Ambon - are all probably beyond hope for restoration unless land-based pollution onto them is eliminated. These reefs may soon die completely, as have most of the reef islands in Jakarta Bay (Tomascik et al. 1993), some of which have since subsided below sea level (Brown et al. 1986; Uneputty and Evans 1997). These modern drowned reefs resulting from land-based pollution exemplify the end result of the Janus Effect on modern reefs.

The Janus Effect suggests that coral growth rates can be useful indicators of reef health, but that their interpretation is subject to careful measurement of environmental variables and other parameters of reef health, and that coral growth rates are best considered in the context of carbonate budgets. If we do not see the reef for the corals, we do so at our peril.

6.5 Conclusions.

1. The Janus Effect is the paradoxical combination of rapid individual coral growth rates on dying coral reefs with low or negative reef accretion rates.

2. In all three regions of Indonesia studied, coral growth rates on nearshore polluted reefs are as high or higher than coral growth rates on clear water offshore reefs. Live coral cover on polluted nearshore reefs was lower than offshore.

3. Coral growth rates in the Java Sea are positively correlated with chlorophyll A concentrations and sedimentation rates, and are negatively correlated with light intensity at 1m depth. Coral growth rates were inversely related to live coral cover.

4. In the Java Sea, massive coral bioerosion is higher on nearshore reefs than on offshore reefs.

5. Skeletal density in Java Sea corals is lowest on a nearshore polluted reef, intermediate on a mangrove fringing reef, and highest on an offshore platform reef. Coral calcification rates are not significantly different among these three reefs.

6. The nearshore Java Sea reef has a negative carbonate budget, while the mangrove fringing reef and offshore platform reef both have positive carbonate budgets. Restoration efforts on such heavily polluted reefs will fail unless land-based pollution onto them is eliminated.

7. Eutrophication and other land-based pollution can stimulate individual coral growth rates on nearshore reefs while killing these same reefs.

Chapter 7: Sponge borehole size as a relative measure of bioerosion and paleoproductivity

EVAN N. EDINGER AND MICHAEL J. RISK, 1997. Lethaia 29: 275-286.

7.1 Introduction

Bioerosion is one of several features proposed as measures of paleoproductivity in fossil reefs (e.g. Hallock 1988; Wood 1993). Measuring bioerosion in fossil reefs, however, has been problematic, because many fossil corals are not entire colonies, and because the length of time an individual fossil coral substrate was exposed to bioeroding organisms is difficult to estimate.

In modern corals, which can be collected live, percent area removed from a cross-section of a whole coral head or branch can provide a reasonably accurate measure of bioerosion intensity (Sammarco & Risk 1990). This approach is generally not possible for fossil reefs because highly bioeroded corals break down, and are not available for sampling (Risk *et al.* 1995; Pandolfi & Greenstein 1997). Furthermore, the variability between individual coral heads is often extremely high, necessitating enormous sample sizes (Sammarco & Risk 1990; Risk *et al.* 1995), which are not logistically possible in fossil material.

Separating pre-mortem and post-mortem boring in modern corals is relatively easy: corals are collected live, and there are no post-mortem effects. In fossil material, it can be difficult or impossible to separate pre- and post-mortem boring, except in those borings which were clearly made in growing coral (e.g. Lithophaga palmerae, Krumm & Jones 1993; ichnospecies Gastrochaenolites vivus, Edinger & Risk 1994). Simple counts of boring frequency are likely to combine pre-and post-mortem boring.

Earlier, we proposed the size of individual sponge borings as a relative indicator of bioerosion intensity in fossil corals (Edinger & Risk 1992). We now re-evaluate this idea using both modern and fossil sponge borings. In this paper, we re-analyse data from two previous studies of modern bioerosion across the Great Barrier Reef (Sammarco & Risk 1990; Risk *et al.* 1995). We document the correlation between total bioerosion and Cliothosa hancocki sponge borehole size in modern corals, and we document the limited variation in sponge boring size along a nutrient gradient across the Great Barrier Reef.

We then apply the modern model to a fossil system. We compare the sizes of two boring sponge ichnospecies from Oligocene shelf edge reefs, Oligocene patch reefs, and Miocene patch reefs of Puerto Rico, using corals and boring sponges originally discussed in Edinger & Risk (1994). We found the smallest boreholes in Oligocene shelf edge reefs, intermediate size in Oligocene patch reefs, and greatest size in the Miocene patch reefs. The fossil reefs represent two variables: facies control of bioerosion between shelf edge reefs and patch reefs (e.g.

Keine 1985; Keine & Hutchings 1992) and changes in productivity between the Oligocene and the Miocene (Flower & Kennett 1993).

7.1.1 Nutrient and facies controls of bioerosion

Bioerosion in modern corals varies in relation to many factors, chief among them productivity and nutrient availability (Rose & Risk 1985; Highsmith 1980), fish grazing (Sammarco *et al.* 1986 1987; Keine & Hutchings 1994; Chazottes *et al.* 1995), and length of exposure of dead substrate (Keine &Hutchings 1994; Chazottes *et al.* 1995; Pandolfi & Greenstein 1997).

Numerous workers have documented the correlation between nutrient availability and intensity of bioerosion on modern reefs (e.g. Rose & Risk 1985; Scott *et al.* 1988), and have also implicated eutrophication and consequent increase in bioerosion in the demise of fossil reefs (e.g. Hallock & Schlager 1986; Hallock 1988; Wood 1993; and many others).

Intensity of bioerosion is also facies dependent within the same general nutrient regime, particularly in dead material. Pandolfi & Greenstein (1997) documented greater bioerosion of dead corals at a protected site on Orpheus Island, Great Barrier Reef, than at an exposed site on the same island. Bioerosion of these dead corals was also more intense at deep sites than at shallow sites - in general, inversely correlated with wave energy. They attributed the difference in bioerosion and other skeletal alteration to longer residence time of the dead coral head at the sediment-water interface at the protected site. They predicted that corals at the exposed site would be more rapidly buried or transported away, and therefore unavailable to bioeroding organisms at the sampled sites. Similarly, in Barbados, while boring sponge numbers in branching coral rubble increased along a eutrophication gradient, rubble on exposed reef flats had far fewer sponge borings than rubble in more protected environments (Holmes 1996).

7.1.2 Using sponge borings to measure bioerosion in fossil reefs.

The nutrient control and the facies/taphonomic control follow similar trends, in part because protected sites often have higher nutrient levels than exposed sites (e.g. Wilkinson *et al.* 1984; Furnas *et al.* 1990). Separating nutrient influence and facies/taphonomic influence in the fossil record is especially difficult, because paleoproductivity is difficult to measure directly in reefal carbonates, which generally recrystallise in early diagenesis (James 1983).

Our data on sponge borehole size from Oligocene and Miocene corals of Puerto Rico provide a potential opportunity to test separately the effects of nutrient levels and facies on bioerosion in fossil corals. Most, though not all, boring sponges bore exclusively into dead surfaces of coral, although other parts of the colony may be live (Ruetzler 1975). In addition, the sponge species we consider here, Cliothosa hancocki, Cliona laticavicola, and Siphonodictyon spp., have indeterminate growth, and grow by increasing the size of their chambers, rather than increasing the number of chambers, as in most clionids (Ruetzler 1971 1975; Pang 1973; Bromley & D'Alessandro 1989).

The Oligocene corals come from approximately contemporaneous shelf edge and patch reef facies of the Upper Oligocene Guayanilla and Lares formations in Southwest Puerto Rico. The Miocene corals come from patch reef facies of the Middle Miocene Ponce formation of south-central Puerto Rico. There is ample evidence for increased upwelling and nutrient availability in the Caribbean and elsewhere during the Miocene, including abundant Miocene phosphorite deposits in much of the Caribbean (Riggs 1987; Rodriguez 1989; Cathcart 1989; Ilyin & Ratkinova 1990) and isotopic excursions world-wide (Compton *et al.* 1990 1993; Flower & Kennett 1993, and others).

Oceanic nutrient control alone would predict approximately equal sizes of boreholes in the two Oligocene facies, with much greater borehole size in the Miocene patch reefs. Nutrient levels would be somewhat higher on Oligocene patch reefs than on shelf edge reefs, with some degree of elevated bioerosion as a consequence. Facies control alone would predict equal sizes of boreholes in the Oligocene and Miocene patch reefs, with smaller borehole size in the Oligocene shelf edge reefs. Our results suggest that both nutrient control and facies control are operating, though facies control appears to have been more important.

Our results also illustrate the difficulties in separating the two factors, and suggest that while fossil borehole size may accurately reflect ancient levels of bioerosion, alone it is a poor index of paleoproductivity.

Figure 7.1: Map of central Great Barrier Reef, showing modern sample locations.

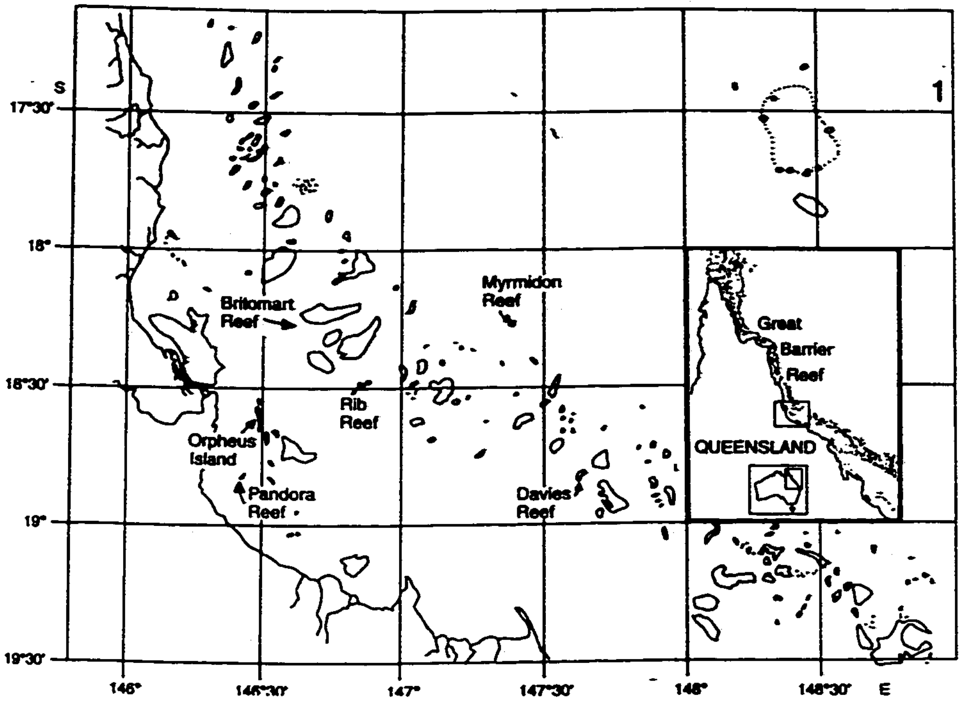
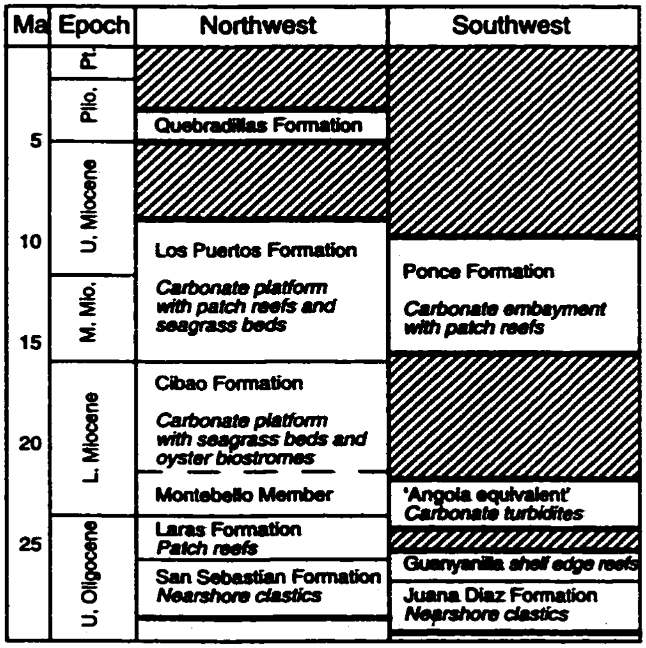


Figure 7.2: Summary of Tertiary Stratigraphy, SW Puerto Rico. Solid horizontal lines indicate conformable contacts; broad grey lines indicate unconformities. Reefs sampled in this study are in the Guayanilla, Lares, and Ponce formations.



7.2 Methods

7.2.1 Modern corals.

One hundred eight massive Porites lobata and 90 branching Acropora formosa were collected from six sites across the Great Barrier Reef (Fig. 7.1) for two studies on cross-shelf trends in bioerosion on the Great Barrier Reef (Porites: Sammarco & Risk 1990; Acropora: Risk *et al.* 1995). Sampling followed a balanced nested ANOVA design, with six massive corals and five branching corals sampled from each of three sites on each of the six reefs. All sites were in the back reef portion of each reef in approximately 10m depth. Three cross-sections were cut from each coral, and bioerosion measured on X-rays of the massive coral cross-sections, or on photographs of one face of each cross-sectional disk of the branching corals. A total of 108 Porites plates and 259 Acropora disks were measured.

Borehole size and total bioerosion in the modern corals were measured using a digitising board interfaced with a personal computer. We separated borers by genus during the original studies, and chose the large unicameral boring sponge Cliothosa hancocki as the best proxy for total bioerosion. Ct. hancocki has indeterminate growth and corresponds to the boring ichnospecies Entobia volzi (Bromley & D'Alessandro 1989) but bears a strong resemblance to Cliona laticavicola borings in the

Caribbean, and to *Entobia convoluta* in fossil material (Edinger 1991; Edinger & Risk 1994).

7.2.2 Fossil corals.

Approximately 20 corals were collected from each of four Oligocene and three Miocene fossil reef localities in Puerto Rico (Fig. 7.2) as part of a study on coral and coral associate evolution and extinction in the Caribbean (Edinger & Risk 1994; Edinger & Risk 1995). We re-examined some of these massive corals from three Oligocene (two shelf edge, one patch reef) and one Miocene patch reef localities, measuring the cross-sectional areas of individual sponge borings of the ichnospecies *Entobia convoluta* (Edinger & Risk 1994; Fig. 7.3A) and *Uniglobites glomerata* (Pleydell & Jones 1988; Fig. 7.3B). Both of these sponge borings are large uni- or bi-cameral borings with indeterminate growth. *Entobia convoluta* and *U. glomerata* are distinguished primarily by shape: *E. convoluta* has a much more convoluted outline than *Uniglobites*. In addition, the apertures in *E. convoluta* are 2-3 times the diametre of those in *U. glomerata* (see sketches and measurements in Edinger & Risk 1994, Fig. 8). *Uniglobites glomerata* (Pleydell & Jones 1988) is probably synonymous with *Entobia glomerata* (Bromley). Modern *E. convoluta* in Caribbean corals are made by *Cliona laticavicola* (Edinger 1991), and modern *U. glomerata* are made by several species of the genus

Siphonodictyon, which occurs in both the Pacific and Atlantic (Ruetzler 1971).

A minimum of five corals from each site were examined, and all borings of each sponge species were clearly marked on the slabs of fossil coral. The slabs of coral were photocopied 1:1, and the area of the marked boreholes were measured using a hand-held planimeter. A total of 141 fossil sponge borings were measured from nine species of fossil corals, with a minimum of 14 and maximum of 33 boreholes per ichnospecies per site. Data were $\log_{10}$ transformed to normalise the distributions, and the two sponge boring ichnospecies were analysed separately using one-way ANOVA.

7.3 Results

7.3.1 Borehole size as a reflector of total bioerosion.

7.3.1a Modern massive corals.

We compared the total size of Cliothosa hancocki borings in each cross-section of Porites lobata with the total % area removed from each cross section (data from Sammarco & Risk 1990). We were unable to compare size of individual boreholes because the data were not tabulated as such. In the vast majority of cross-sections, however, there was not more than one Cliothosa boring, so the total area removed by Cliothosa in most cross-sections is the same as the size of the individual boring.

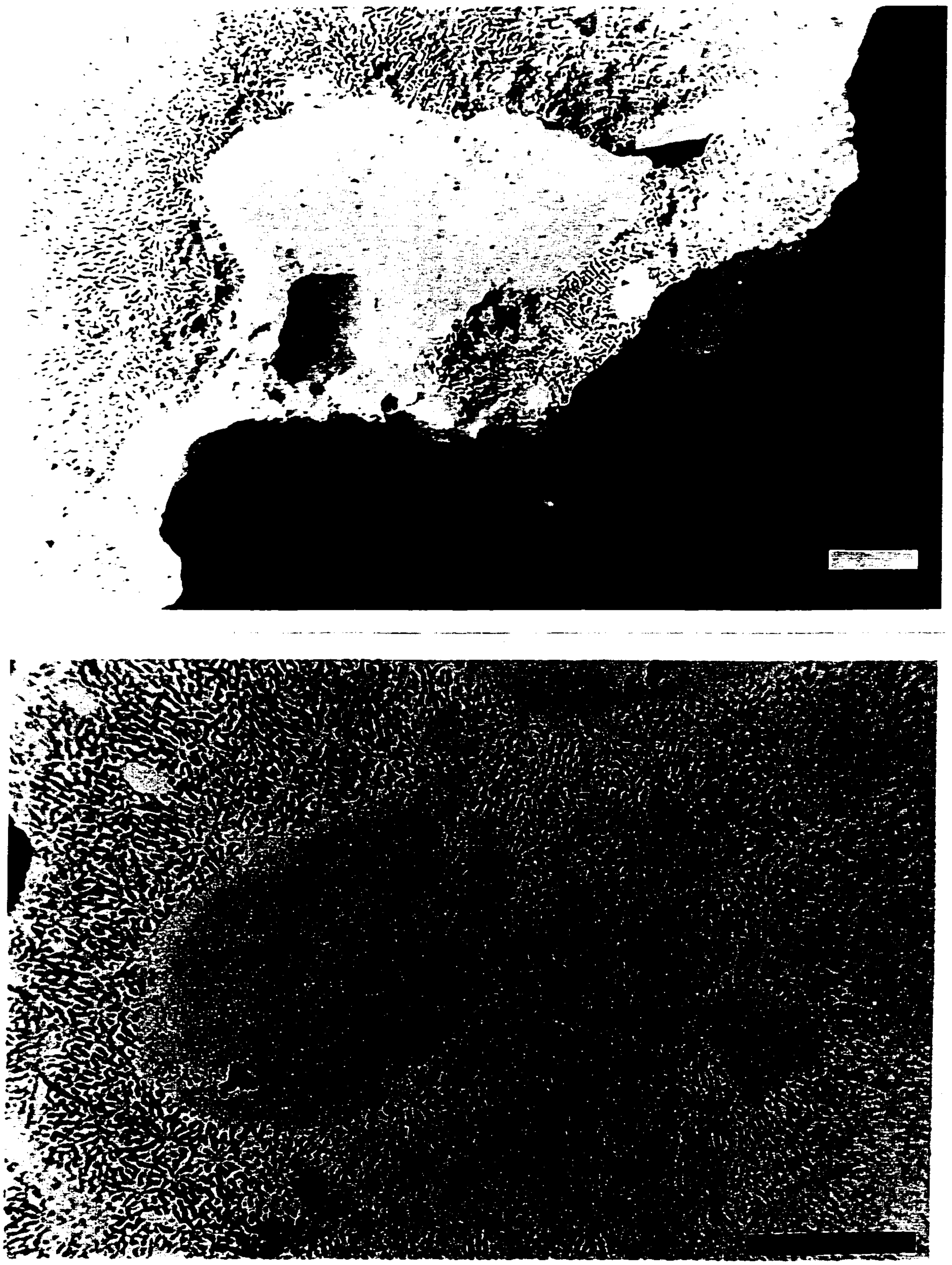


Figure 7.3A - B. Plates of Entobia convoluta, Uniglobites glomerata, Puerto Rico. "□A. Entobia convoluta, in Miocene Psammocora trinitatis.
"□B. Uniglobites glomerata, in Miocene Psammocora trinitatis.

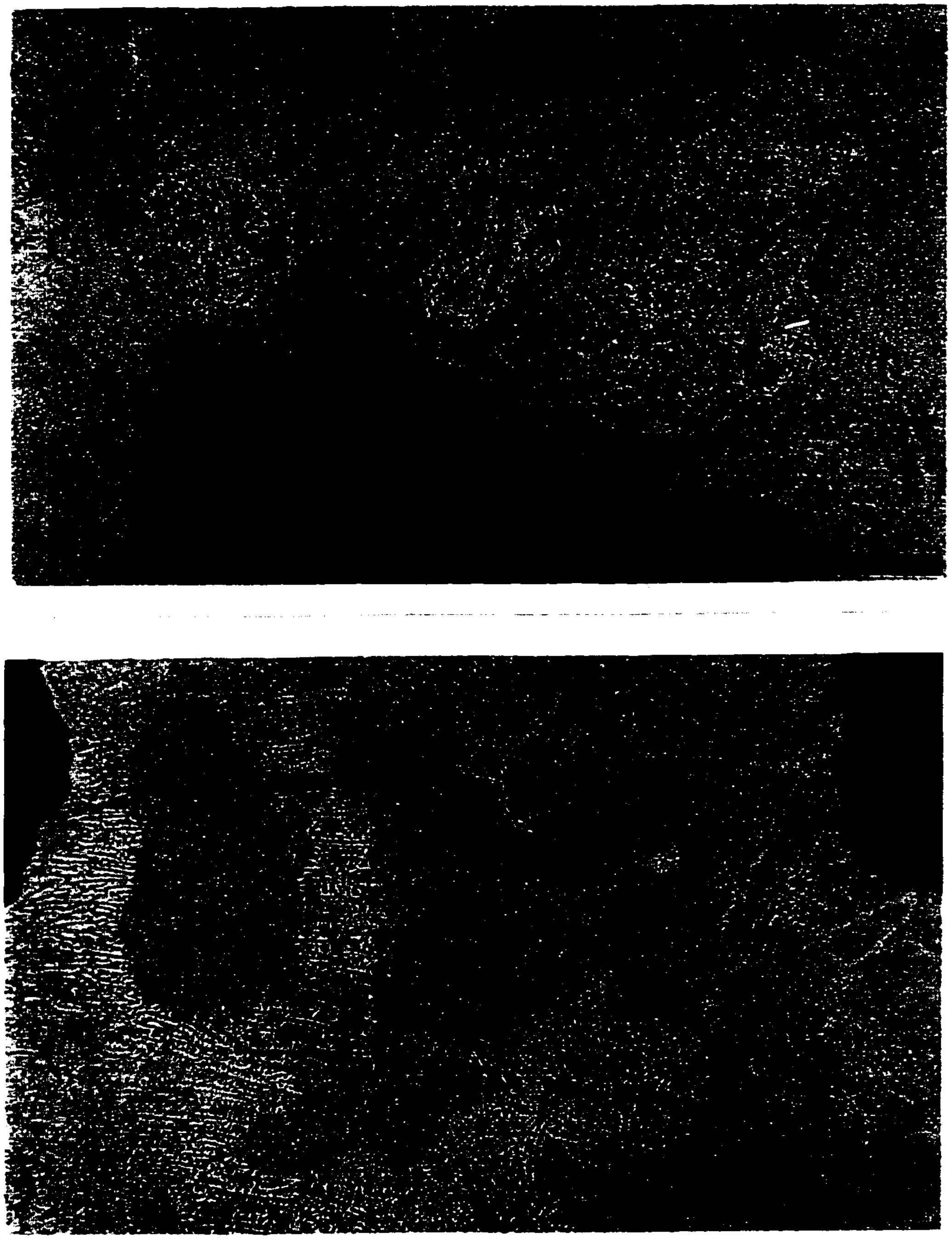


Figure 7.3C - D. Plates of Entobia convoluta, Uniglobites glomerata, Puerto Rico. □C. Both ichnospecies together in Oligocene Porites waylandi. Two-chambered Uniglobites glomerata at left, dumbell shaped, two round chambers joined by connecting filament; single irregular Entobia convoluta chamber at right. □D. Both ichnospecies together in Miocene Psammocora trinitatis. Large irregular Entobia convoluta to right; smaller, rounder Uniglobites glomerata to left appears to have secondarily colonized the E. convoluta borehole. Note small Lithophaga borehole at far right. Original descriptions of both ichnospecies (Edinger & Risk 1994) provide more complete details on shape, on relative proportions of chamber, connecting filaments, and aperture diameters.

Total size of *Ct. hancocki* borings in each cross section is significantly correlated with total bioerosion (r^2=0.142, F=17.53, p<0.0001, n=108). *Cliothosa* borings only rarely accounted for the majority of bioerosion (21 of 108 samples), and on average accounted for 23.3% of total bioerosion (x= 23.3%, s=30.50, n=108). When cross-sections lacking *Cliothosa* borings were excluded, the correlation between *Cliothosa* borehole size and total bioerosion was still evident (Fig. 7.5B), but statistically weaker (r^2=0.058, F=4.35, p<0.05, n=73). In these cases, *Cliothosa* bioerosion on average accounted for 31.4% of the total (x=31.4%, s=31.37, n=73). Total bioerosion decreases significantly across the continental shelf (Table 7.1; Fig. 7.4B; r^2=0.071, F=8.04, p=0.0055, n=108), but cross-sectional area of *Cliothosa* borings does not (Table 1; Fig. 7.4A; square root transformed, r^2=0.0042, F=0.443, p>0.50, n=73).

Figure 7.4 A, B: "A. Cliothosa hancocki borehole size (cm^2) in Porites lobata across the Great Barrier Reef. Site means ± standard error. "B. Total bioerosion in Porites lobata across the Great Barrier Reef. Site means ± standard error. Redrafted from Sammarco & Risk 1990.

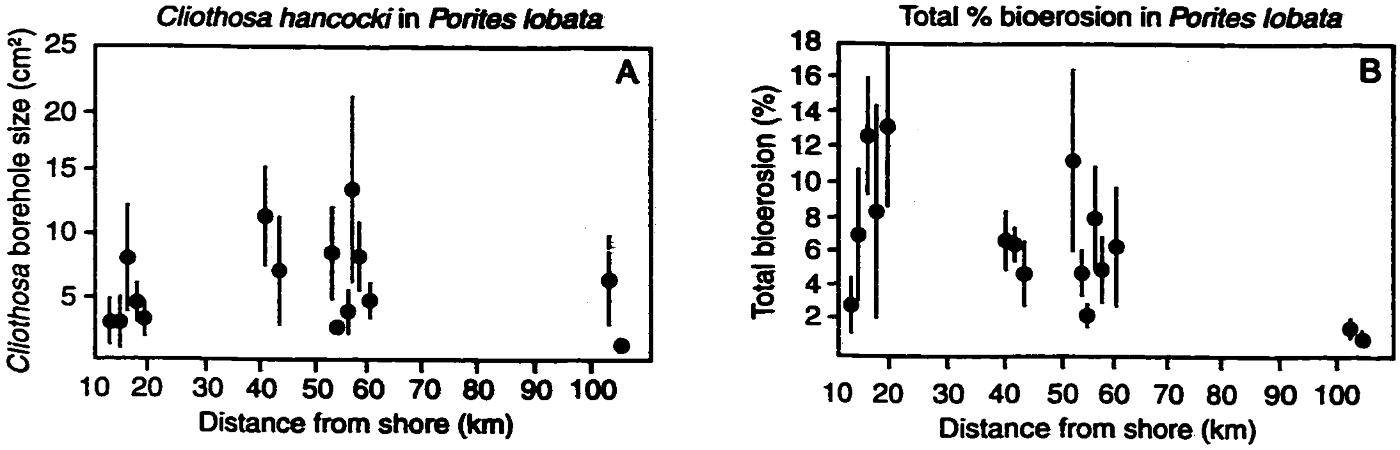


Figure 7.5 "A. Total bioerosion vs. Cliothosa hancocki borehole size, Porites lobata, Site means ± standard error. "B.Total bioerosion vs. Cliothosa hancocki borehole size, Porites lobata, all samples containing Cliothosa boreholes.

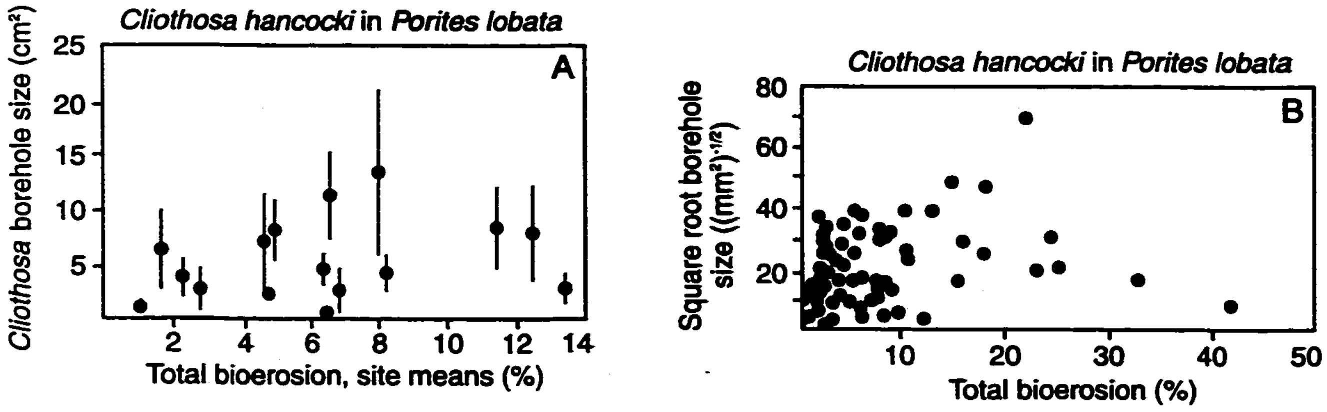


Table 7.1. Area of *Cliothosa* *hancocki* boreholes in modern *Porites* *lobata*, Great Barrier Reef. Total percent bioerosion data from Sammarco & Risk 1990.

reef	distance (km)	statistic	*Cliothosa* size (cm^2)	% bioerosion
Pandora	15	mean	2.544	3.76
		std dev	3.420	6.435
		n	9	18
Orpheus	16	mean	5.067	11.135
		std dev	6.041	11.498
		n	15	18
Britomart	42	mean	6.556	5.877
		std dev	7.776	3.586
		n	12	18
Rib	55	mean	5.116	6.118
		std dev	6.331	8.070
		n	15	18
Davies	58	mean	8.972	6.424
		std dev	11.989	6.485
		n	15	18
Myrmidon	104	mean	4.029	1.233
		std dev	5.627	1.020
		n	7	18

7.3.1b Modern branching corals.

We compared average size of Cliothosa hancocki borings in Acropora formosa with total bioerosion in that species in a transect across the Great Barrier Reef (Risk *et al.* 1995). All of these samples were of dead portions of live colonies, and had been exposed to bioeroding organisms for a similar amount of time, 3-5 years. As with bioerosion of Porites skeletons, the variance in the data is extremely high, and is largely due to within-site variation (Risk *et al.* 1995). Average borehole size is correlated with average percent bioerosion at each site (Fig. 7.7, Table 7.2; 18 sites, 15 samples/site; Spearman rank correlation, $r_s=0.46$, d.f.= 14, $p<.05$). The correlation between borehole size and total percent bioerosion within samples is highly significant ($r=0.204$, d.f.= 736, $p<.001$). Cross-shelf trends in borehole size (Fig. 7.6A) roughly parallel cross-shelf trends in total bioerosion (Fig. 7.6B).

Figure 7.6 "A. Cliothosa hancocki borehole size (mm^2) in Acropora formosa across the Great Barrier Reef. Site means ± standard error. "B. Total bioerosion in Acropora formosa across the Great Barrier Reef. Site means ± 95% confidence limits. Modified from Risk *et al.* 1995.

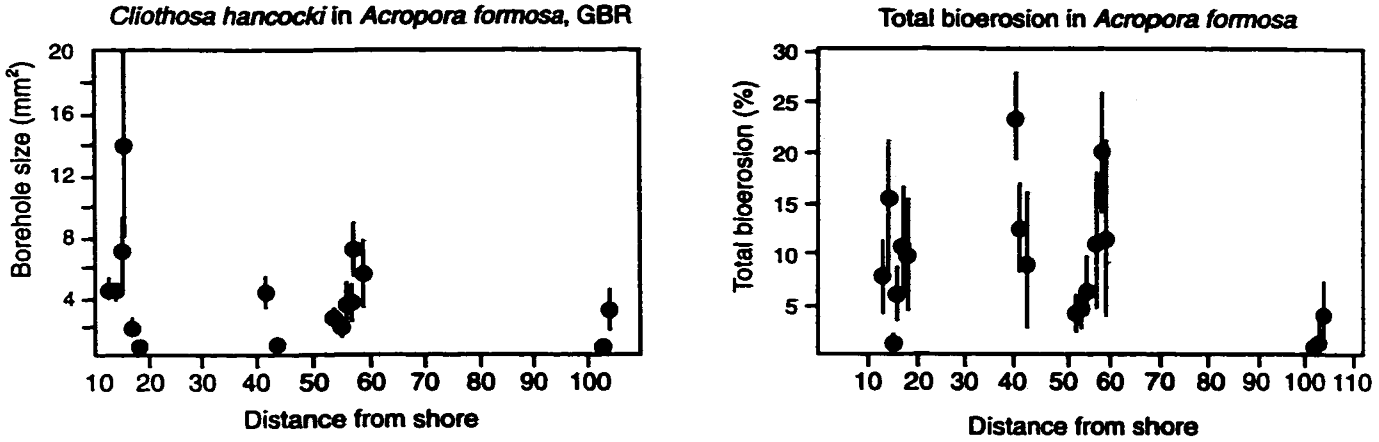


Figure 7.7: Total bioerosion vs. Cliothosa hancocki borehole size (mm^2), Acropora formosa, Site means ± standard error.

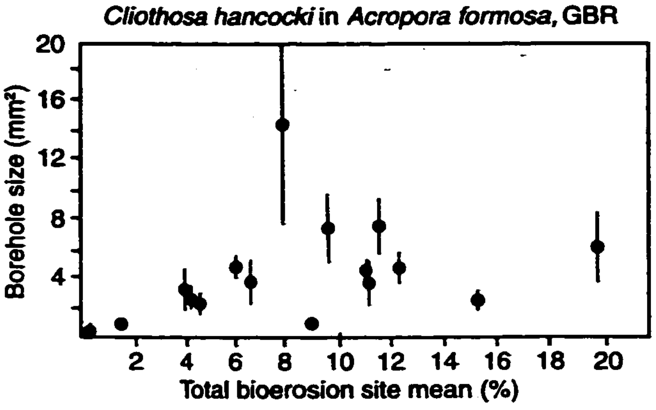


Table 7.2. Modern Cliothosa hancocki boreholes in Acropora formosa, Great Barrier Reef. Total percent bioerosion data from Risk *et al.* 1995.

Reef	distance (km)	statistic	Cliothosa site 1(mm^2)	bioerosion site 1 %	Cliothosa site 2(mm^2)	bioerosion site 2 %	Cliothosa site 3(mm^2)	bioerosion site 3 %
Pandora	15	mean	4.35	6.10	4.15	11.06	6.91	9.64
		stdev	5.07	4.81	7.36	8.61	15.86	10.09
		n	51	15	147	15	47	15
Orpheus	16	mean	13.81	8.03	1.89	15.34	0.72	1.49
		stdev	25.98	6.54	3.01	13.13	0.59	1.88
		n	19	15	26	15	20	15
Britomart	42	mean	3.25	23.6	4.10	12.34	0.56	9.00
		stdev	6.05	7.37	8.42	7.07	0.73	11.12
		n	48	15	69	15	20	13
Rib	55	mean	2.41	4.42	1.95	4.70	3.37	6.58
		stdev	4.07	4.06	6.31	3.90	8.83	5.39
		n	36	15	81	15	39	15
Davies	58	mean	3.21	11.19	6.98	19.97	5.30	11.70
		stdev	6.84	12.26	13.76	11.12	12.00	11.22
		n	22	15	55	15	27	10
Myrmidon	104	mean	0.54	0.33	10.33	1.71	2.97	4.06
		stdev	0.40	0.57	8.72	3.03	6.19	6.59
		n	6	14	5	12	20	15

7.3.1c Fossil Corals.

The borehole size data raw (Fig. 7.8A, 7.9B) and log-10 transformed (Fig. 7.8B, 7.9B) for both sponge boring ichnospecies show a consistent trend: borehole size is smallest in corals from the Oligocene shelf edge reefs, intermediate in corals from the Oligocene patch reef, and largest in corals from the Miocene patch reef. One-way ANOVA found significant trends in both E. convoluta (F=3.223, p=.047, n=61) and U. glomerata (F=3.771, p=.0275, n=79). The median size of each species of boring, however, was almost identical in the Oligocene and Miocene patch reefs (Fig. 8B, 9B). Data summaries are presented in Tables 7.3 and 7.4.

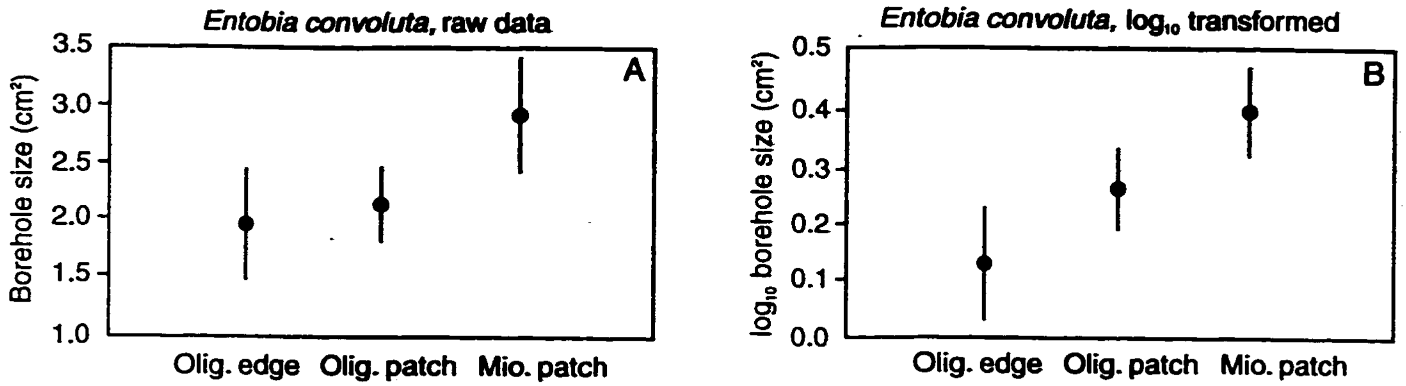
Table 7.3. Borehole size (cm^2) of Entobia convoluta, Oligocene and Miocene, Puerto Rico.

Age and facies	Olig. shelf edge	Olig. patch reef	Mio. patch reef
mean	1.98	2.13	2.91
std dev	2.09	1.46	2.18
median	1.29	1.81	1.84
n	20	21	20

Table 7.4. Borehole size (cm^2) of Uniglobites glomerata, Oligocene and Miocene, Puerto Rico.

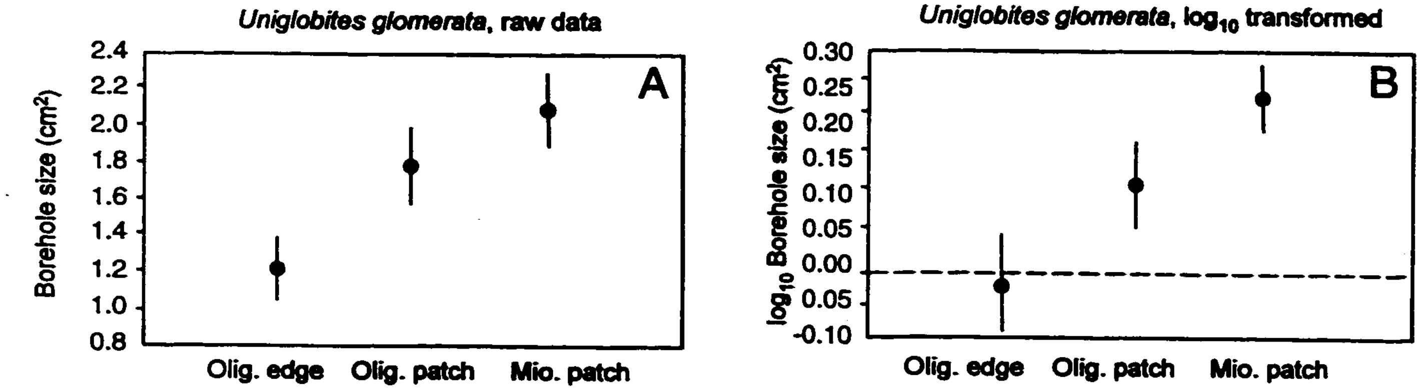
Age and facies	Olig. Shelf edge	Olig. patch reef	Mio. patch reef
mean	1.10	168	2.00
std dev	0.63	1.21	1.15
median	1.00	1.61	1.74
n	14	33	32

Figure 7.8: "A. *Entobia convoluta* borehole size (cm^2) separated by facies, raw data. Mean ± standard error. "B. *Entobia convoluta* borehole size (cm^2) separated by facies, log10 transformed. Mean ± standard error.


Entobia convoluta, raw data

Entobia convoluta, log$_{10}$ transformed

Figure 7.9: "A. *Uniglobites glomerata* borehole size (cm^2) separated by facies, raw data. Mean ± standard error. "B. *Uniglobites glomerata* borehole size (cm^2) separated by facies, log10 transformed. Mean ± standard error.


Uniglobites glomerata, raw data

Uniglobites glomerata, log$_{10}$ transformed

These data, *in toto*, suggest that both facies and inferred productivity differences between the Oligocene and the Miocene contributed to the trends in borehole size, but that the facies difference between the shelf-edge reefs and patch reefs had greater effect than did the inferred oceanic productivity difference between the Oligocene and the Miocene.

7.3.2 Host coral skeletal architecture as a control on borehole size.

7.3.2a Skeletal density.

Skeletal densities of corals vary according to environments (Risk & Sammarco 1991) and species (Highsmith 1981). The rate and pattern of sponge borings in modern corals is partly controlled by the skeletal architecture of the host coral (Risk & MacGeachy 1978). We compared the size of sponge boreholes of the two sponge species combined among the nine species of fossil corals included in our sample (Table 7.5). The differences among species may be partly reflective of facies: among the samples of the seven Oligocene coral species, Hydnophora, Stylocoeniella, Favites, and Siderastrea conferta all occurred only on the shelf-edge reefs, Montastrea and Porites waylandi both occurred only on the patch reefs, and Antiguastrea was represented in the samples from both facies.

Average borehole size in Oligocene samples was greatest in Montastrea and Favites; Miocene Psammocora had the third largest average boring size. Porites in both the Oligocene and Miocene had relatively small average boring size. The smallest average boring size occurred in *Siderastrea conferta*; modern *Siderastrea siderea* has a relatively dense skeleton (Scott 1988). The size differences between borings in different coral species are highly significant (1-way ANOVA, F=6.97, p=.0024, n=141). We did not directly measure density of the fossil coral skeletons, because the density of the fossil material is strongly affected by diagenetic alteration.

We estimated relative skeletal density of the Oligocene corals using two methods. (1) We point counted skeletal material and the amount of infilled pore space (spar and micrite) in transverse thin sections of six Oligocene coral species for which we have good quality thin sections. The ratio of skeletal material to infilled pore space for these corals (Table 7.5) estimates density, and particularly, skeletal resistance to a boring sponge excavating directly down corallites. Mean borehole size in each species is inversely correlated with skeletal density as measured by the ratio of skeletal material to infilled pore space (Fig. 7.10A; r^2=0.73, F=10.82, p<0.03).

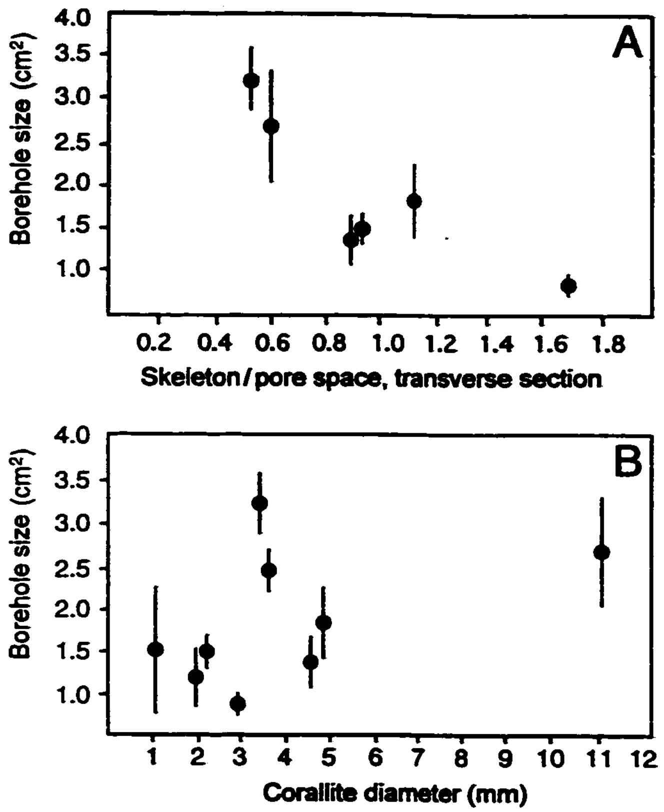
Table 7.5. Size (cm2) of boreholes by fossil coral genus. Entobia convoluta and Uniglobites glomerata combined. Density = ratio of skeletal material to infilled pore space in transverse thin section. diam = corallite diameter, mm., mean of 5 measurements.

coral genus	age	facies	mean	stddev	n	density	diametre
Hydnophora	Oligocene	shelf edge	1.85	1.50	11	1.11	4.8
Stylocoeniella	Oligocene	shelf edge	1.49	2.40	11		1.0
Favites	Oligocene	shelf edge	2.66	1.28	4	0.60	11.0
Antiguastrea	Oligocene	both	1.34	0.73	6	0.89	4.6
Siderastrea	Oligocene	shelf edge	0.85	1.04	7	1.68	3.0
Montastrea	Oligocene	patch reef	3.23	1.23	12	0.51	3.5
Porites waylandi	Oligocene	patch reef	1.48	1.10	37	0.94	2.2
Psammocora	Miocene	patch reef	2.42	1.69	49		3.5
Porites trinitatis	Miocene	patch reef	1.16	0.57	3		2.0

Table 7.6. Bulk density and % pore space of modern relatives of fossil corals. Fossil density = ratio of skeletal material to infilled pore space in transverse thin section, from Table 7.5.

coral genus	bulk density	%pores	fossil density	fossil diameter	mean bore size
Porites	0.98	30.29	0.94	2.2	1.48
Siderastrea	1.44	21.25	1.68	3.0	0.85
Montastrea	1.41	23.71	0.51	3.5	3.23
Favia	1.06	43.46	0.60	11.0	2.66

Figure 7.10"A. Mean borehole size of both ichnospecies combined (cm^2) vs. skeletal density of host coral species, measured as ratio of skeletal material to infilled pore space in transverse thin section. Mean ± standard error. "B. Mean borehole size of both ichnospecies combined (cm^2) vs. mean corallite diameter of host coral species. Mean ± standard error.



7.3.2b Corallite diametre.

Borehole size appears to be somewhat related to corallite diametre (Table 7.5; Fig. 7.10B). Favites polygonalis has the widest corallites of the nine species sampled here (9-11 mm), followed by Antiguastrea (4-5mm), Hydnophora sp. (4 mm), Montastrea costata (3-4 mm), and Psammocora trinitatis (3-4mm). The corals with smallest corallite diametre are Siderastrea conferta (2-3mm) Porites (2 mm) and Stylocoeniella lobatorotundata (1-2 mm, separated by 2-3mm of coenosteum). Mean borehole size is not quite significantly correlated with mean corallite diametre (Fig. 7.10B; r^2=0.253, F=2.38, p=.167; $\log_{10}$ transformed, r^2=0.340, F=3.602, p=0.10).

As a further test, we measured bulk density of four modern corals closely related to corals represented in the Oligocene material: Porites astreoides, Siderastrea siderea, and Montastrea annularis (all from the Caribbean), and Favia matthaii from the Indo-Pacific (Table 7.6), following the method of Risk & Sammarco (1991). We also estimated the percentage pore space in the coral skeleton by measuring the difference in volume displaced by blocks of coral skeleton before and after being impregnated with paraffin. When only these four genera are considered, there was no significant relationship between mean borehole size in fossil corals and bulk density of the modern relatives (r^2=0.0000068, F=0.0000136, p>0.99), nor between borehole size in fossil corals and % skeletal pore space in the modern relatives (r^2=0.118, F=0.269, p>0.65).

7.4 Discussion

7.4.1 Bioerosion intensity.

The size of fossil sponge borings can be used as an indicator of relative levels of bioerosion in fossil corals. Our modern data from both massive and branching corals clearly show that total bioerosion in both massive and branching corals is correlated with size of individual boreholes of Cliothosa hancocki. The patterns in size of fossil sponge borings follow the predictions of facies control on bioerosion and other taphonomic processes (Pandolfi & Greenstein 1997): corals in more protected sites have longer residence times at the sediment-water interface, and are more intensely bored and encrusted than are corals in exposed sites.

7.4.2 Alternate measures of paleobioerosion.

Boring lithophagine and gastrochaenid bivalves have also been proposed as indices of relative bioerosion, in relation to productivity gradients (Highsmith 1980), skeletal density (Highsmith 1981), and taphonomic gradients (Pandolfi and Greenstein, submitted). Both groups have been found in corals as old as the Jurassic (Carter 1978; Scott 1988; Oschmann 1989), and putative boring bivalves have even been described from Ordovician rocks (Pojeta & Palmer 1976). Boring bivalves are easily recognised, abundant, and the shells are frequently preserved inside borings, though by no means invariably so.

Unfortunately, simple counts of bivalve apertures (Highsmith 1980 1981) are problematic, because bivalves occur as both nestlers (*sensu*

Kelly & Bromley 1984) and true borers, and this difference in habit can be difficult to distinguish from the aperture alone. In addition, the surface layer of the coral, where the distinctive apertural shape is most readily identified, is often not preserved in fossil material.

Bivalve borings in fossil corals are more difficult to accurately measure in planar cross-section than are sponge borings. Unlike sponge borings, bivalve borings are not randomly oriented, but frequently follow the orientation of corallites. Consequently, as the relative orientation of the bivalve and the plane of section vary in a somewhat unpredictable fashion, measurement error for estimating material removed increases. In many fossil corals, the density contrast between the skeleton and the sediment infill in borings is not sufficient for borings to be quantified in x-radiographs, a technique which is highly effective in modern corals.

Our Oligocene and Miocene fossil corals included both nestling and truly boring Lithophaga and Gastrochaena. Nestlers can be distinguished in those cases where both the shell and the boring are preserved, yet the shape of the boring does not match the shape of the shell. We found examples of boring sponges modifying and expanding bivalve holes, and of Lithophaga colonising vacant sponge borings.

An additional confounding factor may be those lithophagine bivalves that inhibit calcification, rather than actually excavating a borehole (Morton 1983; Morton & Scott 1980). These have been considered a separate subgenus of Lithophaga, Lithophaga (Leiosolenus) (Wilson 1985). Most Lithophaga (Leiosolenus) are host-specific, occurring in one or a few species of coral (Kleemann 1980; Morton &

Scott 1980; Scott 1986). Lithophaga (Leiosolenus) have not been positively identified in fossil material, and are likely to have appeared only in the Pliocene or Pleistocene (Morton 1983).

7.4.3 Paleoproductivity.

The size of sponge borings probably cannot be used alone as an indicator of paleoproductivity. When combined with other types of data, however, borehole size and frequency can help provide rough estimates of past nutrient availability. For example, Holmes (1996) documented an increase in the number of clionid sponge borings in branching coral rubble along a eutrophication gradient in Barbados.

7.4.4 Modern corals.

In the modern corals, sponge borehole size, while significantly correlated with bioerosion intensity, did not significantly decline outward across the continental shelf, in parallel with the known gradient in nutrient availability.

The transect across the Great Barrier Reef represents a gradient in nutrient availability: terrestrially derived nutrient levels, as reflected in chlorophyll A values (Sammarco & Crenshaw 1984; Gagan *et al.* 1987), are high at inner shelf reefs (Pandora, Orpheus), intermediate at mid-shelf reefs (Britomart, Rib, Davies), and low at the shelf edge (Myrmidon). Corals apparently reflect this nutrient gradient in their tissue $\delta^{13}C$ (Risk *et al.* 1994).

Total percent bioerosion clearly decreases across the continental shelf of the Great Barrier Reef in both massive Porites and branching Acropora (Sammarco & Risk 1990; Risk *et al.* 1995), but Cliothosa borehole size does not show a clear statistical trend, although general patterns are similar. Borehole size is correlated with total bioerosion in both corals. The decrease in borehole size across the continental shelf is clearer in Acropora than in Porites, but is still not striking.

Borehole size, like bioerosion in general, reflects several variables, including both nutrient availability (Sammarco & Risk 1990; Risk *et al.* 1995), intensity of fish predation (Risk & Sammarco 1982), and length of exposure of dead surfaces at the sediment-water interface (Boekschoten 1966; Brett & Baird 1986; Pandolfi & Greenstein 1997). The data from our modern corals suggest that other factors, probably chief among them length of exposure to bioeroding organisms, are controlling borehole size to a sufficient extent that borehole size is not an excellent measure of productivity.

7.4.5 Fossil corals.

Mean borehole size for each ichnospecies is smallest in corals from Oligocene shelf edge reefs, intermediate from Oligocene patch reefs, and largest from Miocene patch reefs. The Oligocene sites primarily represent a facies/taphonomic gradient, while the Oligocene-Miocene comparison primarily represents an oceanic productivity gradient, with extensive other documentation of upwelling in the Miocene. Both facies-controlled taphonomic factors and paleoproductivity are apparently reflected in the size of sponge boreholes. Unfortunately, because borehole size may also be influenced by coral skeletal density and corallite diametre, data from multispecies collections of fossil corals must be interpreted with great care.

7.4.6 Skeletal influences on borehole size.

Highsmith (1981) found that total bioerosion was positively correlated with bulk skeletal density in both Caribbean and mid-Pacific corals, and postulated that bioeroding organisms preferentially bore into corals with dense skeletons because denser skeletons provide more effective shelter from predators.

Our results contradict Highsmith's findings, although density was measured in a very different manner. We found borehole size to be significantly inversely correlated with skeletal density as measured by ratio of skeleton to infilled pore space in transverse section. Skeletal density as we measured it is partly determined by the packing of corallites. Sponge boring size and shape are influenced by the mechanical properties of the coral skeleton, so a positive correlation between borehole size and corallite diametre, and a negative correlation between borehole size and skeletal density, are not surprising. Coral species sampled from shelf edge reefs tended to be more dense, but this pattern was not overwhelming (Table 5). Our measurements of bulk density in the modern corals showed no significant relationship with borehole size in the related fossil corals.

Bulk density and corallite diametre appear to influence sponge borehole size, suggesting that differences in coral architecture may confound attempts to measure paleobioerosion and paleoproductivity in multi-species assemblages of fossil corals. Facies-related differences in productivity and residence time of dead corals at the sediment-water interface are probably more important determining factors than are differences in coral architecture, but separating the two may be somewhat difficult.

7.4.7 Limitations of sponge borings as measures of paleoproductivity.

Various studies have documented the enormous variance in rates of bioerosion within facies in the modern. Simply documenting gradients in levels of coral bioerosion along a well-established productivity gradient across the Great Barrier Reef required enormous data sets, particularly for the branching corals (Risk *et al.* 1995). Despite the clearly documented connections between eutrophication and bioerosion on modern reefs, and the correlation between total bioerosion and individual borehole size we document here for modern corals, other controls on bioerosion and borehole size are too important to reliably draw the connections from borehole size to total bioerosion to paleoproductivity. These external factors include residence time at the sediment-water interface, the inability to clearly differentiate pre-mortem from post-mortem boring in fossil corals, and skeletal density and structure of the host coral. Borehole size is a reasonably reliable measure of past bioerosion, and can probably be used as a general indicator of paleoproductivity in conjunction with other kinds of data, but should not be relied upon alone.

7.5 Conclusions

1. Borehole size of Cliothosa hancocki is correlated with total bioerosion in both massive and branching corals across the continental shelf on the Great Barrier Reef.

2. Borehole size of Cliothosa hancocki decreases outward across the shelf in branching Acropora, but does not show a clear trend in massive Porites.

3. Borehole size of Entobia convoluta and Uniglobites glomerata in fossil corals from Puerto Rico is highest in corals from a Miocene patch reef, intermediate in corals from an Oligocene patch reef, and lowest in corals from Oligocene shelf edge reefs. These patterns follow those predicted by both nutrient control and facies/taphonomic control of bioerosional processes.

4. Borehole size in fossil corals can serve as a measure of relative intensity of bioerosion, but is probably a mediocre reflector of paleoproductivity.

5. Borehole size varies significantly among species of fossil corals from Puerto Rico. Original skeletal density and corallite diametre of the host corals may exert partial control on the size of sponge borings.

Chapter 8: Oceanography of modern and ancient epeiric seas.

8.1 Introduction

One of the original aims of this these was to compare coral reefs from a modern epeiric sea, the Java Sea, with fossil reefs in the Middle Devonian Onondaga Formation of Southern Ontario and New York State. This comparison, based on morphological composition data for the modern and fossil reefs, will eventually yield a model for interpreting epeiric reef facies based on the morphology of the reef-building organisms. Some of the modern data is discussed in Chapter 4, but not enough quantitative data from the Onondaga has yet been collected and analysed to do the planned comparisons. Instead, I present here a discussion of paleoceanographic reconstructions of epeiric seas in general and the Onondaga Fmn. in particular, compared with the oceanography and sedimentology of the Java Sea. This chapter forms the prelude to an eventual data-based paper quantitatively comparing the Java Sea and Onondaga Fmn. reefs.

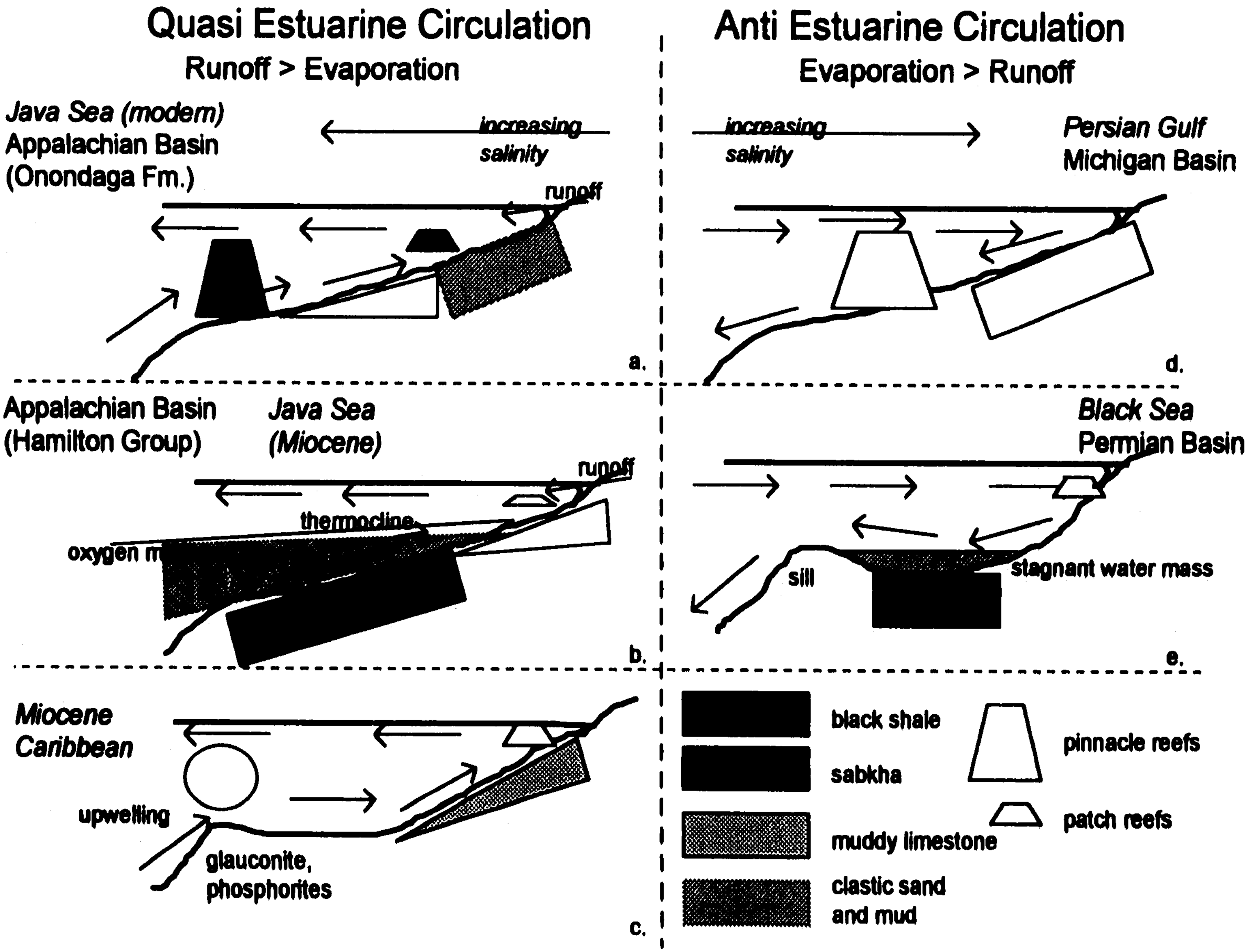
Epeiric seas were common through much of the Phanerozoic, particularly in the Ordovician, Silurian, and Devonian, when many of the best-known reef-bearing carbonate sequences of North America were deposited (Wilson 1975; Copper 1994; many others). Paleozoic epeiric seas were shallow seas, deposited on top of cratonic sequences rather than in ocean basins, and generally inferred to have had somewhat restricted circulation, in part as a result of their shape: wide and shallow (Irwin 1965; Hallam 1981). The centres of many epeiric sea basins are thought to have been sediment starved systems dominated by fine clastic sediments, in some cases, black shales (Sellwood 1986). There are varied interpretations of productivity, and some workers attribute the black shales of some epeiric seas to high productivity (e.g. Pedersen and Calvert 1990), while others invoke restricted vertical circulation and low oxygen conditions in the bottom waters (e.g. Hallam 1981).

8.2 Oceanographic models of epeiric seas.

Paleontologists and sedimentologists quickly recognised that oceanographic patterns of epeiric seas were not identical to those of modern open ocean habitats (e.g. Chamberlin 1882; Schuchert 1910), but specific ideas on how epeiric sea oceanography differed from open ocean environments only crystallised beginning in the 1950's and 1960's (Sloss 1963; Shaw 1964; Irwin 1965). The very low depositional slopes in many epeiric sea basins were thought to have restricted or eliminated tidal circulation in broad nearshore environments of clear-water epeiric seas, resulting in broad facies belts of dolomites and evaporites. Freshwater runoff from the land was not thought to affect this pattern much, except for reducing the amount and extent of evaporite deposition (Irwin 1965), although the model was never meant to apply to clastic sediment dominated basins. Other work examining tidal circulation in modern epeiric seas, however, showed that tidal amplitude is often quite high in broad shallow seas, and increases with greater distance from the shelf edge (Klein & Ryer 1978). Herring-bone ripples, bipolar-bimodal cross-bedding, climbing ripples, tidal scour, and mud cracks, all indicators of tidal paleoenvironments, have all been documented in a variety of Precambrian and Paleozoic epeiric sea environments (Klein & Ryer 1978). Much effort also went into explaining widespread black shale sequences in cratonic interior seaways and elsewhere (e.g. Fisher & Arthur 1977; Hallam 1981; Parrish 1982; Pedersen & Calvert 1990).

More recently, here have been attempts to integrate models for arid environments (e.g. Irwin 1965) with a broader spectrum of climatic, sedimentary, and oceanic environments (e.g. Heckel 1977; Schopf 1980). Circulation systems for epeiric seas have been divided into quasiestuarine (QEC) and anti-estuarine circulation (AEC), applying to regions where freshwater influx exceeds evaporation (QEC; fig 8.1a,b,c) or vice-versa (AEC; fig 8.1d,e). Under QEC conditions, freshwater influx exceeds evaporation, less-dense water flows out of epeiric embayments at the surface, and is replaced by deep, nutrient rich, oxygen depleted water from ocean basins. Anoxic black shale facies can develop with or without a sill separating the embayment from the ocean basin (Witzke 1987). A sharp slope break at the edge of such shelves can lead to upwelling at the shelf edge, promoting zones of high productivity, and possibly of phosphorite deposition (Riggs 1984; Witzke 1987).

Figure 8.1 Epeiric sea circulation models and facies patterns. Modified from Witzke, 1987.



Most modern examples of QEC are in temperate latitudes (e.g. Hudson Bay, Baltic Sea), but the Java Sea also matches a QEC pattern (fig. 8.1,a), including seasonal upwelling at the eastern edge of the Java Sea, adjacent to the deep waters of the Makassar Strait (Roberts et al. 1987 1988; fig. 8.1c). Although there are extensive Tertiary petroleum deposits in the Java Sea - South China Sea system (Nayoan 1975), there is no evidence for Holocene deposition of black shales (Wyrtki 1961; Dewi 1993). During the Miocene sea level and productivity highs (Riggs 1984 1987), the oxygen minimum zone may have extended over much of the Sunda shelf (fig. 8.1b), leading to deposition of source rocks for Java Sea petroleum.Wind-driven upwelling in epeiric seas is thought to have been concentrated in equatorial regions, where equatorial divergence currents caused upwelling, and along the west coasts of land-masses (Parrish 1982). Topographic upwelling (Hallock et al. 1988) around the margins of the Caribbean during the Miocene (fig 8.1c) probably contributed to the lack of Miocene shelf edge reefs in the Caribbean, and may have contributed to the extinction and geographic restriction of Caribbean corals in the early Miocene (Edinger and Risk 1994).

Under anti-estuarine circulation (AEC) conditions, evaporation exceeds freshwater influx, surface waters become hypersaline and dense, and sink, being replenished by nutrient-poor, fully oxygenated surface water from ocean basins (Schopf 1980; Witzke 1987), for example in the modern Persian gulf (fig. 8.1d). Under such conditions, black shale facies will not form, except in the presence of a large sill separating the marginal sea from the ocean basin, for example in the modern Black Sea (fig.

8.1e). Evaporite and mixed carbonate-evaporite facies, however, are common under AEC; AEC conditions most closely approximate the facies described in Irwin's (1965) model, and AEC conditions may have held in many of the low-latitude Paleozoic cratonic seas of North America, such as the Michigan Basin (fig. 8.1d) or the Permian Guadalupe Basin of New Mexico and Texas ((fig 8.1e; Newell 1953; Irwin 1965; Witzke 1987). Various examples of cratonic sequences have been described by QEC or AEC models. Such models have not previously been applied to the Onondaga Formation, or to the Appalachian basin sequence in general.

8.3 Onondaga Formation Paleogeography and Paleoceanography

The Middle Devonian (Eifelian) Onondaga limestone lies at the base of a Middle-Upper Devonian sedimentary sequence in the Appalachian basin, and extends throughout much of the basin in the subsurface, cropping out primarily across New York State, into southern Ontario, and in north-western Pennsylvania (Oliver 1954; Woodrow, et al. 1988). Its lateral equivalents in Ohio and Kentucky are the Columbus Limestone and Detroit River Group. The lower contact is unconformable, resting on the Lower Devonian Bois Blanc Fmn. In western New York and southern Ontario, and on the Lower Devonian Schoharie Fmn. In eastern New York (Oliver 1954; Mesolella & Weaver 1975). The upper contact is gradational into the shales and calcareous mudstones of the Hamilton Group (Oliver 1954; Brett & Baird 1986b). The Onondaga - Hamilton Group portion of the sequence is transgressive (Woodrow, et al. 1988).

The Appalachian basin extended primarily NE-SW, and was bounded on the north and west by the north American cratonic continent, to the east by the Adirondack highlands and the North Atlantic Peninsula of the Old Red Sandstone Continent (Oliver 1977), and to the south opened onto the Iapetus ocean (Woodrow et al. 1988). A structural arch continuous with the Cincinnati Arch separated the Appalachian basin from lateral equivalents in the Michigan basin, such as the Formosa Reef Limestone (Detroit River group; Fagerstrom 1961; Pratt 1988; Woodrow, et al. 1988; see references in Birchard 1990 for more thorough discussion of Middle Devonian paleogeography).

Facies variations within the Onondaga provide much information about regional paleoenvironments. To the south, the Onondaga becomes increasingly silty, then shaley and cherty, toward the basin centre; chert nodules and silicified fossils are common throughout the Onondaga (Oliver 1954), and various authors have proposed an upwelling zone at the southern end of the Appalachian basin (Woodrow et al. 1988), or cool currents from the adjacent open ocean environments (Wolosz & Paquette 1988; Wolosz 1992a). Others have suggested cool water environments in the Onondaga based on the brachiopod fauna (Koch & Boucot 1982).

Patch reefs are exposed in outcrop across southern Ontario and New York state, in the basal Edgecliff Member of the Onondaga (Oliver 1954; Wolosz & Paquette 1988); pinnacle reefs with up to 60m vertical relief are found in the subsurface of south-western New York State and north-central Pennsylvania (Mesolella & Weaver 1975; Mesolella 1978). Paleolatitude at the time of deposition was approximately 10S (Boucot

1988); the climate is thought to have been humid (Woodrow et al. 1988). If a wide belt of carbonates and evaporites existed landward of the patch reef facies currently exposed in outcrop, it has since eroded; there is no evidence of dolomites or evaporites, as would be predicted by Irwin's (1965) model or by anti-estuarine circulation. The abundant black shale in the basal formations of the Hamilton group, the shaley-cherty facies of the subsurface Onondaga, and the proposed upwelling at the SW end of the Appalachian basin all suggest a quasi-estuarine circulation model for the Onondaga formation (fig 8.1a,c).

Following Onondaga time, the Appalachian basin subsided rapidly as a foreland basin and began to receive extensive sediments from the newly rising Acadian orogeny (Woodrow et al. 1988). Extensive carbonate deposition ceased, and there are no reefs known from the remainder of the Middle Devonian of the eastern Appalachian basin (Woodrow et al. 1988), although biostromal corals form a significant portion of the fauna in the Hamilton group and other fossiliferous units in the Middle and Upper Devonian, particularly around the basin margins (Oliver 1954; fig. 8.1b).

The Java Sea and the Onondaga Fmn. have approximately similar paleogeographic, paleoclimatic, and paleoceanographic settings, with the exception of possible upwelling and relatively cool water temperatures in the Onondaga (Koch & Boucot 1982; Wolosz 1992a). Therefore, a comparison of the coral reefs in the two seas seems appropriate. Such a comparison requires a brief review of the context in which Onondaga reefs developed: previous models of epeiric sea coral reefs, and the biogeography of Devonian corals in general.

8.4 Epeiric Sea coral reefs.

Coral reefs of Paleozoic epeiric sea habitats consisted of nearshore fringing and patch reefs in the margins of the seas, as well as pinnacle reefs closer to basin centres (Bourque 1989; Moore 1989). Fringing reefs and shallow water patch reefs in particular grew in mixed carbonate-clastic sedimentary regimes, such as those of the Devonian Onondaga Fm., of southern Ontario (e.g. Wolosz and Paquette 1988), or Silurian patch reefs of Manitoulin Island (Copper and Fay 1989). Niagaran Pinnacle Reefs ringed the Michigan Basin (fig. 8.1d), and are found today along the Bruce Peninsula and the SE shore of Lake Huron (Huh, et al. 1977). Onondagan pinnacle reefs in New York and Pennsylvania may have occupied a similar position within the Appalachian Basin (Mesolella and Weaver 1975).

The morphology and community composition of the reef building organisms (corals, stromatoporoids, bryozoans, sponges) are generally interpreted as dual responses to wave impact and sediment stress (James 1983; Graus and Macintyre 1989; Rosen 1990; many others; but see also Stearn 1982). Among the various Paleozoic framework-building reef organisms, stromatoporoids and tabulate corals are thought to have been photosymbiontic mixotrophs (Wood 1995) similar to modern corals. Reef-dwelling rugosan corals were also probably mixotrophic (Risk et al. 1987; but see also Coates and Jackson 1987).

Patterns of zonation and of ecological succession have been described from some patch reefs and pinnacle reefs of Paleozoic epeiric sea reefs (e.g. Walker and Alberstadt 1975; Huh et al. 1977; Williams 1980; Meyer 1989; Wolosz 1992a; see Gischler 1995 for discussion of a Devonian atoll), and these are viewed in relation to environmental conditions interpreted from the sediments surrounding the reef deposits. Stearn (1982) questioned the viability of any general models of morphological zonation developed for fossil reefs based on modern reef coral zonation, due to unclear and often contradictory patterns of morphological zonation in modern reefs. Rather, reef zonation models based on morphological composition are probably somewhat facies specific; the same probably holds true for the taphonomic processes influencing preservation (Pandolfi and Greenstein,1997; Pandolfi, pers. comm. 1996).

8.5 Devonian Biogeography

Three major biogeographic realms were present during the Early and Middle Devonian. (1) The Malvinokaffrich realm was closest to the Devonian south pole, covering parts of southern South America, southern Africa, and Antarctica, and housed a cold temperate fauna (Boucot 1988; Meyerhoff et al. 1997). (2) The Eastern Americas realm consisted primarily of epeiric and marginal sea environments in eastern and southern North America and northern South America, and is thought to have been tropical to warm temperate in climate (Oliver 1980; Boucot 1988). (3) The third major realm was the Old World realm, found in

Northwest North America, arctic Canada, the Mediterranean region, the Urals, parts of China, and south-eastern Australia (Boucot 1988). The Devonian reefs of the Cordilleran region fringed the western edge of North America, and were the closest to the equator (Moore 1988). A major transcontinental arch separated Old World realm regions of north-west North America from cratonic seas in the Eastern Americas realm (Oliver 1980). With rising sea levels in the Middle Devonian, biogeographic differentiation diminished to a Phanerozoic low during the Famennian (Oliver 1980), although changes in provinciality may not have been caused by transgression (Boucot 1988).

8.5.1 Diversity and Biogeography of Devonian Corals.

Devonian reefs developed in many parts of the world, including the cratonic interior of North America (e.g. Onondaga), shelf-edge reefs of the Canadian Cordillera and Arctic (e.g. Embrie & Klovan 1971; Moore 1988), platform reefs in Brazil (Copper 1977), and the barrier reef of the Canning Basin in Western Australia (Stanley 1986). Of these, the petroleum producing reefs of western Canada have probably received the most study in terms of reef facies (e.g. Embrie & Klovan 1971; many refs. in Moore 1988). More taxonomic and biogeographic work has been done on rugose corals than on tabulates, and much of that has focused on cratonic seas and the Eastern Americas realm (Oliver 1976 1977).

The Eastern Americas realm had a fairly diverse coral fauna, with 28 genera of rugose corals during Onondaga time (Eifelian), of which 18 (64%) were endemic to the Eastern Americas realm (Oliver 1977). By

Givetian time, continued transgression allowed more old world genera to enter the Michigan Basin province of the eastern Americas realm, increasing the total number of genera present to 36, but reducing endemism to 28%. Continued faunal mixing eventually reduced eastern Americas endemism through the Frasnian, culminating in the extinction of most platform-dwelling rugose coral genera at the Frasnian-Famennian (F/F) boundary (Oliver 1977; Sorauf & Pedder 1986). Interestingly, total diversity of corals increased through the Middle Devonian, and through the Frasnian to 47 genera, before collapsing at the F/F boundary; all twelve basin-dwelling (i.e. non-reefal) rugose coral genera survived the F/F extinction (Sorauf & Pedder 1986). These numbers do not include the much less diverse tabulate corals, nor the stromatoporoids. Stromatoporoids were apparently quite rare in Appalachian basin reefs, but more common on reefs of the Michigan Basin (Fagerstrom 1961; Lindemann 1988).

Onondaga reefs, then, grew in the Eastern Americas realm during the height of Middle Devonian coral endemism, and close to the height of Middle Devonian coral diversity. Most of the major reef complexes of the Alberta and Western Canada basins were Frasnian and Famennian in age (Moore 1988), so direct comparisons of faunal lists between these and the Onondaga reefs is not possible. Ideal comparisons would be between onshore patch reefs (in outcrop) , and offshore pinnacle reefs (in core) within the Onondaga, and between offshore pinnacle reefs within the Onondaga and shelf-edge reefs of Alberta, also exposed in core only.

These latter comparisons could be done at the genus level and morphology level only.

8.6 Future Work.

Two specific questions arise for comparing the Onondaga Fmn. reefs and Java Sea reefs: (1) how does the morphological composition of reef-building organisms change between facies within a reef, or between nearshore reefs and offshore pinnacle reefs, and (2) how does the species richness of the fauna vary between facies and between nearshore and offshore reefs. Both these questions will be addressed using the modern reef morphological composition data presented in Chapter 4 and fossil reef coral morphology data still being collected, and will be published separately. A third and related question, how does the species richness of the epeiric sea reefs compare with that of open ocean reefs of the same age, can be addressed using primary taxonomic similarity data from modern reefs from several parts of Indonesia (Chapter 3) and published records of Devonian coral species distributions.

8.7 Conclusions.

1. Paleoceanographic models of epeiric sea circulation derived from Paleozoic examples, applied to the Java Sea, match current systems and surface sediment distributions in the Java Sea.
2. Paleoceanography of the Middle Devonian Onondaga Formation is broadly similar to that of the Java Sea.
3. Both the Java Sea and the Appalachian basin can be characterised as having quasiestuarine circulation, while the Michigan Basin would be better described by antiestuarine circulation, along with the modern Persian Gulf.
4. Patterns of endemicity among Devonian corals were strongly controlled by sea level and degree of interconnection between major paleobiogeographic provinces.

Chapter 9: Conclusions.

The research presented in this thesis has important overall implications for the effects of land-based pollution on modern reefs, nutrient and taphonomic effects on ancient coral reefs, and for facies interpretations of fossil reefs in epeiric seas.

9.1 Modern reef research: pollution and Indonesian coral reefs.

The most important findings of my modern coral reef research in Indonesia are straightforward.

1. There is a dramatic, and statistically significant, decrease in within-site coral species richness, as measured by species-area curves, on reefs subject to land-based pollution, as compared with relatively unaffected reefs in the same regions. Combined sewage pollution and sedimentation have the most severe impact on live coral cover and coral species diversity. Land-based pollution depresses coral species diversity more than mechanical damage does.

2. Total live coral cover is significantly lower on polluted reefs than on their unaffected counterparts. Interestingly, dead coral cover is not significantly higher on nearshore polluted coral reefs than on their unaffected comparators. Mortality index (Gomez 1994), or the portion of all corals along a transect which are standing dead, (MI = dead coral/

(live coral + dead coral)), is highest on nearshore polluted reefs, intermediate on mechanically damaged reefs, and lowest on healthy offshore reefs. Mortality index may be the best overall indicator of reef health derived from transect measurements.

3. Live coral cover and coral species richness are positively correlated at low to medium cover values (<70% live coral cover), but not at high cover values (>70% live coral cover). This pattern fits the intermediate disturbance hypothesis (Connell 1978) of species diversity in relation to disturbance frequency and intensity. Cover and diversity are significantly and positively correlated on reefs along a eutrophication gradient (e.g. Java Sea), but reefs subject to mechanical damage do not show this trend as clearly, suggesting some influence of successional patterns. These patterns indicate limitations to using a linear scale of total live coral cover (Gomez and Yap 1988) as an indicator of reef health.

4. Both species-area curves and similarity analysis based on regional data suggest that Java Sea coral reefs are about 80-85% as diverse as their eastern Indonesian counterparts. The regression line comparing diversity and cover on Java Sea reefs is parallel to a similar line comparing diversity and cover on Eastern Indonesian reefs subject to land-based pollution, but has a lower diversity intercept. These within-habitat diversity differences parallel regional diversity differences between the Java Sea and eastern Indonesia, and may be related to a greater diversity of reef habitats in eastern Indonesia, and/or to a greater intensity of fishing pressure in the Java Sea.

5. Composition of onshore and offshore reefs is different in several crucial ways. Acropora corals typically dominate the shallow (3m) windward and leeward portions of offshore reefs, but drop to near zero abundance on nearshore reefs subject to land-based pollution. The highly significant difference in total live coral cover between all onshore and all offshore reefs is driven almost entirely by Acropora, and only marginally by non-Acropora corals.

The morphological composition of the fauna also changes along onshore-offshore gradients. Submassive corals constitute a much larger portion of the coral fauna on nearshore reefs than on offshore reefs; multilobate (submassive) morphology is a common growth response to sedimentation and reduced light penetration on reefs. Nearshore polluted reefs are dominated almost entirely by massive and submassive corals, with branching and foliose non-Acropora corals, both important constituents on offshore reefs, also dropping to approximately 1% cover. Nearshore polluted reefs clearly separate from all others in r-K-S ternary diagrams based on coral morphology. Ternary morphograms provide a concise method fo classifying reef communities independent of taxonomy, but incorporating successional dynamics, multiple stable states, and morphological complexity.

6. Bioerosion intensity is much higher on nearshore sewage polluted reefs of the Java Sea than on offshore reefs. This pattern is most dramatic for % bioerosion of massive corals, but is also clearly reflected in the bioerosion score of branching coral rubble. Branching coral rubble bioerosion frequency provides an easy, non-destructive

rapid assessment tool for identifying bioerosion, hence excess nutrient loading, on reefs. Both live massive coral and branching coral rubble bioerosion are inversely correlated with transect-based measures of coral reef health. Branching coral rubble bioerosion frequency is more sensitive to gentle eutrophication gradients than is massive coral bioerosion, but is subject to a wider variety of taphonomic factors, and is best used in combination with other indicators of pollution, or of coral reef health.

7. The Janus Effect, the paradoxical combination of rapid individual coral growth rates and slow or negative coral reef accretion rates on eutrophied reefs, is documented on coral reefs in three regions of Indonesia. Rapid coral growth rates do not necessarily indicate healthy coral reefs. In all three areas of Indonesia studied, individual Porites lobata corals on nearshore polluted reefs grew as fast or faster than those on clean offshore reefs. On Java Sea reefs, coral growth rates were inversely correlated with transect-based reef health parameters, such as coral species diversity, total live coral cover, or mortality index. There were no clear linear trends between reef health parameters and coral growth rates on eastern Indonesian reefs.

8. Java Sea coral growth rates, measured by linear skeletal extension, were positively correlated with chlorophyll A concentration in reefal waters; more surprising, coral growth rates were positively correlated with sedimentation rate, and inversely correlated with light intensity at 1m depth. Rapid individual coral growth rates on nearshore reefs can be attributed to combined morphological effects of reduced

light penetration and metabolic changes associated with high organic mattern and nutrient availability. Ongoing tissue and stable isotope analyses (Heikoop et al., in prep.) will help elucidate the metabolic changes associated with rapid skeletal extension in low light high nutrient settings, and determine the extent to which these are driven by autotrophy or heterotrophy.

9. Porites lobata skeletal density is lowest on a nearshore Java Sea reef, intermediate on a fringing reef adjacent to mangroves, and highest on an offsore reef. Skeletal density is inversely related to linear extension rates when all corals are combined, but there are no such trends within individual corals. Individual coral calcification rates are not significantly different between onshore and offshore reefs.

10. Simple carbonate budgets based on coral growth rates, coral bioerosion intensity, skeletal density, and transect measurements, are presented for three Java Sea reefs: Pulau Panjang (nearshore polluted), Lagun Marican (mangrove fringing), and Pulau Kecil (offshore unaffected). Carbonate budgets are negative at the nearshore polluted reef, slightly positive at the fringing reef adjacent to mangroves, and strongly positive at the offshore relatively healthy reef. A positive carbonate budget is necessary for the long term survival of a given reef. Nearshore reefs subject to intense sewage pollution and sedimentation, such as Pulau Panjang, are probably degraded beyond the possibility of restoration, unless land-based sources of pollution impacting these reefs are controlled or eliminated.

11. Carbonate budgets are more strongly dependent on reef scale factors like total live coral cover and bioerosion rates than on individual coral factors like growth and calcification rates. This exemplifies the decoupling of coral growth and reef growth, and suggests that models for fossil reef accretion based primarily on individual coral growth rates need to be re-examined.

9.2 Implications for reef science and management.

The implications of this modern research for reef science and management can be divided into three overall portions: structure and function of nearshore polluted reef coral communities, reef survey and rapid assessment tools, and reef managment policy implications.

9.2.1 Nearshore reef community structure and function.

Ternary diagrams of organismal adaptive strategies (Grimes 1979) provide a useful tool for looking at the overall changes to structure and function of nearshore reefs subject to land-based pollution. The structural fauna (i.e. reef-building corals) is dominated by relatively few species of stress-tolerators (e.g. Porites lobata, various Goniopora and Goniastrea species), which grow quickly but maintain low enough cover values that intraspecific competition between corals cannot account for reduced species diversity. Multilobate morphology of the surviving corals also indicates stress response.

Habitat spatial and topographic complexity is reduced, due to the lack of the competitive dominant canopy species (Acropora's, in particular tabular Acropora), such that the abundance and diversity of accessory organisms is reduced, especially fish. Furthermore, this low diversity low complexity community has a negative carbonate budget, indicating that it is not sustainable. These nearshore reefs, even on slowly subsiding basements, will nonetheless drown due to pollution effects, principally eutrophication and muddy sedimentation. Pollution effects have transformed healthy nearshore reefs into the marine equivalent of dying weedlots.

9.2.2 Reef Survey and Rapid Assessment Techniques.

Coral reef survey techniques for reef management have not changed radically in thirty years, and the range of measurement techniques available all yield data similar enough for managers to use (Risk and Risk 1997). Unfortunately, several of the techniques commonly used for assessing reef health, including coral growth rates and bioersion intensities, are highly destructive, as they require killing entire colonies. Furthermore, the Janus Effect chapter shows the risk of using coral growth rates as indicators of coral reef health. Incidence of bioeroder organisms in live corals or in dead branching coral rubble can be used as a rough indicator of eutrophication stress, or as a rough measure of bioerosion intensity. Likewise, $\delta^{15}N$ and $\delta^{13}C$ stable isotope ratios in coral tissue can elucidate the metabolic status of a given coral, and whether it is shifting from autotrophy to partial heterotrophy in response to high dissolved and/or particulate organic matter content in the water, or large dissolved inorganic nutrient pools.

The following recommendations for reef assessment practices emerge:

1. Coral mortality index is a better overall indicator of reef health status than total live coral cover. The measure of reef health status currently used in Indonesia, based on a linear scale of total live coral cover (Gomez and Yap 1988), should be changed.

2. Recording and presenting data on the morphological composition of coral faunas is important for comparing reef health status of reefs. Morphological composition can be plotted on r-K-S ternary diagrams (Grime 1979) to estimate conservation value. Those reefs plotting in the centre of the diagram have greatest spatial and topographic complexity, and therefore greatest biodiversity potential, fisheries potential, and conservation value.

3. Frequency of bioeroding organism invasions of branching coral rubble reflects overall bioerosion intensity and eutrophication stress to a reef, but cannot be used as a proxy for bioerosion rates in carbonate budgets. The non-destructive nature of the coral rubble technique makes it preferable to massive coral bioersion measures for most reef health purposes.

4. Other associated rapid assessment techniques, such as stomatopod abundance and diversity (Erdmann and Caldwell 1997), carbon and nitrogen stable isotope ratios (e.g. Risk et al. 1993) or butterflyfish abundance and diversity (Reese 1993; but see also Molis 1997) should also be used where possible.

5. Coral growth rates are not reliable indicators of coral reef health, and should not be measured as parts of standard coral reef assessments. Studies on coral growth rates should minimize damage to the reef, particularly on reefs already subject to chronic pollution stress.

9.2.3 Management and Policy Implications

The Indonesian modern reef research in this thesis has several implications for coral reef management policy. First, chronic stresses to coral reefs, such as land-based pollution, are enormously important, and should not be ignored. These stresses pose a greater long-term threat to Indonesian coral reefs than acute stresses causing mechanical damage, such as blast fishing and cyanide fishing, particularly in western Indonesia.

Second, the species and morphological composition of a reef in an important aspect of its health; the loss of nearly all Acropora corals from nearshore polluted reefs accounts for most of the difference in total live coral cover between onshore and offshore reefs. The dominance of nearshore polluted reefs by stress-tolerant massive and submassive corals dramatically reduces the topographic complexity of these reefs, further reducing their habitat potential for fish and other reef associated organisms. Ternary diagrams based on morphology can be used to estimate conservation value from the large volume of life form transect data already collected in Indonesia.

Third, carbonate budgets are largely controlled by coral cover values and bioerosion rates. Carbonate budgets are an important aspect of reef health, and reefs can and do drown on human timescales. The now dead and drowned reefs of Jakarta Bay, combined with the dying and drowning nearshore reefs such as Pulau Panjang in Jepara, or Kayangan reef in Ujung Pandang, illustrate this point most dramatically.

Fourth, reefs such as these nearshore examples are probably degraded beyond the possibility of restoration unless pollution sources are controlled or eliminated. Restoration efforts on such reefs are wasted, except in the context of broader coastal zone management. Folliwing the triage system (Risk 1994), reef restoration efforts should be aimed at reefs that are likely to recover: those affected by acute stresses and mechanical damage, such that the source of coral mortality is no longer acting, and the reef has a real possibility of maintaining a positive carbonate accretion rate.

9.3 Implications for studies of fossil reefs.

Implications of modern reef research in Indonesia for the fossil record are manifold. First, the Janus Effect chapter (chapter 6) confirms and quantifies the hypothesis from the fossil record that excess nutrient availability can cause drowning of reefs and carbonate platforms (Hallock and Schlager 1986). Because live coral cover and bioerosion are the dominant factors in carbonate budget calculations, estimates of growth potential of fossil reefs should include estimates of these variables, and cannot be based upon individual coral growth rates alone. To determine the rate at which a given reef will drown, or its half-life, however, requires both an estimate of its carbonate budget and an estimate of basement subsidence rates.

Second, branching coral bioerosion can be used as an indicator of eutrophication stress on modern reefs, and probably can similarly function as an indicator of paleoproductivity on fossil reefs. For example, the sponge borehole size section (chapter 7) demonstrates the utility of boring sponge borehole size as an indicator of bioerosion intensity and productivity on modern coral reefs, and as a measure of past bioerosion intensity and an auxiliary indicator of paleoproductivity on fossil reefs. Chapter 7 also shows the influence of taphonomic factors on bioerosion intensity in fossil material, as displayed in the facies-related differences in sponge borehole size.

Third, chapter 7 also illustrates the importance of skeletal density on bioerosion (McKenna 1997), and of coral polyp or corallite diametre on sponge borehole size. This chapter illustrates limitations to the simplifying assumptions used in calculating the carbonate budget in chapter 6.

The broader implications for the fossil record of coral reefs in Paleozoic epeiric seas stem from comparisons of species diversity and morphological composition of Java Sea reefs with their eastern Indonesian counterparts. The within-site species diversity of Java Sea coral reefs is about 20% less than that of eastern Indonesian reefs, and is probably attributable to a combination of biogeographic factors and higher fishing intensity in the Java Sea than in eastern Indonesia. The overall similarity of the Java Sea coral fauna to its eastern Indonesian counterparts suggests that epeiric seas are not necessarily much less diverse than their open ocean contemporary faunas. Likewise, at peak Middle Devonian highstand, the rugose coral fauna of the epeiric Eastern Americas realm was 91% as diverse as that of open ocean western and arctic North America (Oliver 1977).

The morphological composition of offshore Java Sea reefs is nearly identical to that of offshore Sulawesi reefs on a broad carbonate shelf open to oceanic circulation. Meanwhile, facies differentiation among the Java Sea reefs is primarily by depth, with very little difference between windward and leeward reef facies. This is largely attributable to the monsoonal circulation and weather pattern prevalent in the Java Sea (Wyrtki 1961). Paleoceanographic models of epeiric seas (reviewed in chapter 8) suggest that monsoonal circulation may have been the dominant pattern in most Paleozoic epeiric seas, implying that little windward-leeward facies differentiation can be expected in Paleozoic epeiric sea reefs, particularly the nearshore reefs typically exposed in outcrop.

By contrast, the considerable variation in morphology between depths is consistent between both windward and leeward sides of Java Sea platform reefs. Depth related facies changes are much more easily identifiable on fossil reefs (Wolosz 1992a). Previous attempts to model facies of fossil reefs based on shapes of modern reef-building organsism were unsatisfactory because there were no consistent morpho-facies patterns among the broad geographic and geomorphological range of modern reefs considered (Stearn 1982).

The greatest difference in morphological composition is related to sedimentary environment, between onshore polluted reefs and offshore relatively unaffected reefs. These broad differences in reef structure have been well recognized in fossil reefs (James 1983; Wolosz 1992b), but attempts at constructing facies models for fossil reefs based on the modern have usually attempted to generalise from a stereotyped view of offshore clearwater oligotrophic reefs (Stearn 1982). Such environments probably do not provide appropriate models for many Paleozoic fossil reefs exposed in outcrop belts of epeiric seas.

Sedimentary facies appears to override the biogeographic differences among reefs in different parts of Indonesia. Future ordination studies will help to clarify whatever differences in species and morphological composition do occur among modern reefs and among fossil reefs in different sedimentary regimes and different depositional basins.

9.4 Summary

Indonesia's coral reefs remain among the world's most diverse and most threatened reefs. This thesis summarizes some of the principal threats to Indonesian coral reefs by quantifying the effects of pollution on within-site coral species diversity, coral bioerosion, coral growth rates, and perhaps most important, coral reef accretion rates. The implications of this research for coral reef management policy and assessment techniques are not radical - the ideas are not fundamentally new, but most of them have not previously been quantified. The applications of this work to coral reef conservation are direct, clear, and common sense: attempts at reef conservation and restoration in western Indonesia that do not address sources of land-based pollution are doomed to mediocrity at best or utter failure at worst. Addressing land-based pollution, however is far easier said than done.

The implications for the study of fossil coral reefs are several. We can infer past levels of bioerosion from sponge borehole size, or from frequency of sponge borings in branching coral rubble. Bearing taphonomic biases in mind, we can interpret patterns of paleoproductivity using patterns of bioerosion. The zonation of fossil reefs in epeiric seas may be outlined more easily by examining the morphological composition of fossil reefs from specific sedimentary facies, and comparing them to modern reefs from the same general depositional environment.

The Janus Effect quantitatively documents in the modern a pattern that has been presumed in fossil reefs: excess nutrient availability can contribute to the demise of reefs and carbonate platforms, even while individual corals on those reefs apparently thrive. The Janus Effect and research presented here can help to explain aspects of reef history, and of reef structure, in epeiric seas, during the Holocene transgression, and in other high nutrient fossil reef settings which have previously remained a mystery.

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Ambon all sites	10m + 3m combined Acroporas corrected	species list				
Genus	species	comment	depthdist	collNo	location	total
Acanthastrea	echinata		3m		HILA	1
Acanthastrea	hilli		3m	SN94	TJS	2
Acrhelia	horrescens		10m		TJS	3
Acrhelia	horrescens		10m		HILA	
Acropora	cerealis		both	SN51	TJS	4
Acropora	cerealis	ACB	3m	SN65A	TJS	
Acropora	cerealis	ACT	3m	SN78	TJS	
Acropora	cerealis	ACT	both	SN9	TJS	
Acropora	cf. divaricata		n/a		WLH	
Acropora	loripes	ACT	3m	SN61A	TJS	5
Acropora	cf. longicyathus	ACB	both	SN30	TJS	6
Acropora	cf. nasuta grp	ACC	10m	SN12	TJS	7
Acropora	cf. pulchra		n/a	TS17	WLH	
Acropora	divaricata	ACT	10m	SN15	TJS	8
Acropora	echinata grp		n/a	TS39	WLH	9
Acropora	florida	ACB	3m	SN65	TJS	10
Acropora	florida		10m		WM	
Acropora	formosa	ACB	both	SN79	TJS	11
Acropora	formosa		3m	WM 48	WM	
Acropora	formosa grp		n/a		WLH	
Acropora	gemmifera		both	SN67	TJS	12
Acropora	horrida grp.		n/a		WLH	13
Acropora	humilis	ACD	both	SN5	TJS	14
Acropora	humilis		3m		HILA	
Acropora	humilis grp.		3m		WM	
Acropora	hyacinthus		3m		WM	13
Acropora	hyacinthus grp	ACT	both		TJS	
Acropora	latistella		10m	WM 30	WM	14
Acropora	loripes	ACT	both	SN10	TJS	
Acropora	loripes grp		both	SN96	TJS	
Acropora	loripes grp	granulosa	n/a		WLH	15
Acropora	loripes grp,	2nd sp.	n/a	TS40	WLH	
Acropora	millepora	ACC	3m	WM59	WM	16
Acropora	nasuta grp		3m		HILA	
Acropora	nasuta grp		10m		WM	
Acropora	palifera		both		HILA	17
Acropora	palifera		both		HILA	
Acropora	pulchra		both	WM29	WM	18
Acropora	pulchra		both	WM29	WM	
Acropora	selago		10m	WM29A	WM	19
Acropora	cerealis	ACT	n/a	TS15	WLH	
Acropora	spicifera	ACB	10m	SN45	TJS	20
Acropora	subulata	ACT	both	SN4	TJS	21
Acropora	valencienesi		10m	SN43	TJS	22
Acropora	valenciennesi	ACT	10m	SN11	TJS	
Alveopora	gigas		10m		WM	23
Alveopora	sp.	juv., no coll.	10m	no coll.	TJS	24
Alveopora	tizardi		n/a		WLH	25
Australogyra	zelli		3m	SN96A	TJS	26
Coeloseris	mayeri		both		HILA	27
Coeloseris	mayeri		both		HILA	
Cyphastrea	japonica		10m		HILA	28
Cyphastrea	microphthalma		both	SN33A	TJS	29
Cyphastrea	microphthalma		both		TJS	
Cyphastrea	microphthalma		3m		HILA	
Cyphastrea	microphthalma		3m		WM	
Cyphastrea	microphthalma		n/a		WLH	
Cyphastrea	serailia	under Acro	10m		TJS	30
Cyphastrea	serailia		3m		HILA	
Cyphastrea	serailia		n/a		WLH	
Diaseris	distorta		10m		HILA	31
Diploastrea	heliopora		10m		TJS	32

Diploastrea	heliopora		10m		HILA	
Diploastrea	heliopora		both		WM	
Diploastrea	heliopora		both		WM	
Echinophyllia	aspera		both	SN17	TJS	33
Echinophyllia	aspera		both		TJS	
Echinophyllia	aspera		3m		HILA	
Echinophyllia	echinoporoides?		10m	WM7	WM	34
Echinopora	gemmacea	big pol, grn	10m		TJS	35
Echinopora	gemmacea		10m		WM	
Echinopora	gemmacea		n/a		WLH	
Echinopora	lamellosa		both		TJS	36
Echinopora	lamellosa		both		TJS	
Echinopora	lamellosa		both		HILA	
Echinopora	lamellosa		both		HILA	
Echinopora	lamellosa		both		WM	
Echinopora	lamellosa		both		WM	
Echinopora	lamellosa	??gemmacea	n/a		WLH	
Euphyllia	ancora		10m	SN27	TJS	37
Euphyllia	ancora		both		WM	
Euphyllia	ancora		both		WM	
Euphyllia	cristata		3m		HILA	38
Euphyllia	glabrescens		both		HILA	39
Euphyllia	glabrescens		10m		WM	
Favia	??laxa	??F.pallida	n/a	no coll.	WLH	40
Favia	*cf.* veroni		10m		HILA	41
Favia	lizardensis		3m		WM	42
Favia	mathaii		10m		TJS	43
Favia	mathaii		n/a		WLH	
Favia	pallida		both		TJS	44
Favia	pallida		both		TJS	
Favia	pallida		10m		HILA	
Favia	pallida		both		WM	
Favia	pallida		both		WM	
Favia	pallida		n/a		WLH	
Favia	speciosa		3m	SN109	TJS	45
Favia	speciosa		both		HILA	
Favia	speciosa		both		HILA	
Favia	stelligera		n/a		WLH	46
Favita	maritima		10m	SN23	TJS	47
Favites	abdita		both		TJS	48
Favites	abdita		both		TJS	
Favites	abdita		3m		WM	
Favites	abdita		n/a		WLH	
Favites	chinensis		3m		TJS	49
Favites	complanata		both	SN5A	TJS	50
Favites	complanata		both	SN90	TJS	
Favites	flexuosa		3m	SN69	TJS	51
Favites	flexuosa		10m		WM	
Favites	halicora		10m		WM	52
Favites	pentagona		n/a		WLH	53
Favites	russeli	under Acro	3m	SN68	TJS	54
Fungia	(*cf.* fungites??)	lost specmn	both	SN17A	TJS	
Fungia	*cf.* coronoa		3m		HILA	55
Fungia	*cf.* fungites		both		WM	56
Fungia	*cf.* granulosa		10m		HILA	57
Fungia	*cf.* repanda		10m		HILA	58
Fungia	*cf.* scruposa	F. Danafungia	3m		HILA	59
Fungia	*cf.* valida		n/a		WLH	60
Fungia	danae		both	SN35	TJS	61
Fungia	danai		both	SN59	TJS	
Fungia	echinata		10m		HILA	62
Fungia	fungites		both		HILA	
Fungia	fungites		both		HILA	
Fungia	fungites		both		WM	
Fungia	moluccensis		3m		WM	63

Fungia	paumotensis		3m	SN99	TJS	64
Fungia	repanda		10m	SN41A	TJS	
Fungia	repanda		10m		WM	
Fungia	scabra		10m	SN41	TJS	65
Fungia	scutaria	juv. Halomitra?	10m		HILA	66
Fungia	simplex		both		HILA	67
Fungia	simplex		both		HILA	
Fungia	sp.	fungites??	both	SN53	TJS	
Galaxea	astreata		3m		TJS	68
Galaxea	astreata		3m		WM	
Galaxea	astreata		n/a		WLH	
Galaxea	fascicularis		both		TJS	69
Galaxea	fascicularis		both		TJS	
Galaxea	fascicularis		both		HILA	
Galaxea	fascicularis		both		HILA	
Galaxea	fascicularis		both		WM	
Galaxea	fascicularis		both		WM	
Galaxea	fascicularis		n/a		WLH	
Gardineroseris	planulata		both		TJS	70
Gardineroseris	planulata		both		TJS	
Gardineroseris	planulata		10m		WM	
Gardineroseris	planulata??	green ctrs, small	10m		HILA	71
Goniastrea	aspera		3m		TJS	72
Goniastrea	aspera		3m		HILA	
Goniastrea	aspera		3m		WM	
Goniastrea	edwardsi		3m		TJS	73
Goniastrea	edwardsi		3m		HILA	
Goniastrea	edwardsi		both		WM	
Goniastrea	edwardsi		both		WM	
Goniastrea	edwardsi		n/a		WLH	
Goniastrea	favulus		10m		TJS	74
Goniastrea	retiformis		3m	SN54	TJS	75
Goniastrea	retiformis		n/a		WLH	
Goniopora	djiboutiensis		3m	SN62	TJS	76
Goniopora	djiboutiensis		both		WM	
Goniopora	djiboutiensis		both		WM	
Heliofungia	actiniformis		10m		TJS	77
Heliofungia	actiniformis		both		WM	
Heliofungia	actiniformis		both		WM	
Hydnophora	excesa		both		TJS	78
Hydnophora	excesa		both		TJS	
Hydnophora	excesa		10m		WM	
Hydnophora	excesa		n/a		WLH	
Hydnophora	microconos		10m	SN28	TJS	79
Hydnophora	pilosa		3m	SN71	TJS	80
Hydnophora	rigida		10m		HILA	81
Leptastrea	transversa		both	SN33	TJS	82
Leptastrea	transversa		both	SN63	TJS	
Leptastrea	transversa		3m		HILA	
Leptoria	phrygia		both	SN49	TJS	83
Leptoria	phrygia		both		TJS	
Leptoseris	explanata		both	SN40	TJS	84
Leptoseris	explanata		both	SN70	TJS	
Lobophyllia	hemprichii		both		TJS	85
Lobophyllia	hemprichii		both		TJS	
Lobophyllia	hemprichii		both		HILA	
Lobophyllia	hemprichii		both		HILA	
Lobophyllia	hemprichii		both		WM	
Lobophyllia	hemprichii		both		WM	
Lobophyllia	hemprichii		n/a		WLH	
Merulina	ampliata		both		TJS	86
Merulina	ampliata		both		TJS	
Merulina	ampliata		3m		HILA	
Merulina	ampliata		10m		WM	
Merulina	ampliata		n/a		WLH	

Merulina	scabricula		10m		HILA	87
Merulina	scabricula		3m		WM	
Montastrea	annuligera		both	SN105	TJS	88
Montastrea	annuligera		both		TJS	
Montastrea	curta		both	SN42	TJS	89
Montastrea	curta		both		TJS	
Montastrea	curta		3m		WM	
Montipora	caliculata	blue encr.	10m	SN32	TJS	90
Montipora	cf millepora		both	WM15	WM	91
Montipora	cf. caliculata		n/a		WLH	
Montipora	cf. hispida	grp 6	10m	SN6	TJS	92
Montipora	cf. millepora		both	WM34	WM	
Montipora	cf. millepora		n/a		WLH	
Montipora	cf. turgescens	grp 14	10m	SN18	TJS	93
Montipora	cf. undata		3m	SN64	TJS	94
Montipora	digitata		3m	SN58	TJS	95
Montipora	digitata		both	WM31	WM	
Montipora	digitata		3m		HILA	
Montipora	foliosa		10m	SN51A	TJS	96
Montipora	foveolata	grp 3	3m	SN98	TJS	97
Montipora	hispida		3m	HL83	HILA	98
Montipora	hispida	(=WM58)	3m	WM39	WM	
Montipora	hispida		n/a		WLH	
Montipora	millepora	grp 2	both	SN3	TJS	
Montipora	millepora		both	SN66	TJS	
Montipora	millepora		both		HILA	
Montipora	millepora		both		HILA	
Montipora	peltiformis		3m	SN76	TJS	99
Montipora	spumosa		3m		HILA	100
Montipora	spumosa		n/a		WLH	
Montipora	verrucosa		10m	SN31	TJS	101
Mycedium	elephantotus		both		TJS	102
Mycedium	elephantotus		bot		TJS	
Mycedium	elephantotus		10m		HILA	
Mycedium	elephantotus		10m		WM	
Oulastrea	crispata		10m		TJS	103
Oulophyllia	bennettae		both	SN39	TJS	104
Oulophyllia	bennettae		both		TJS	
Oulophyllia	bennettae		n/a		WLH	
Oulophyllia	crispa		10m		HILA	105
Oulophyllia	crispa		3m		WM	
Oulophyllia	crispa		n/a		WLH	
Oxypora	glabra		10m	SN7	TJS	106
Oxypora	lacera		10m	SN30A	TJS	107
Oxypora	lacera		both		HILA	
Oxypora	lacera		both		HILA	
Oxypora	lacera		10m		WM	
Pachyseris	rugosa		both		TJS	108
Pachyseris	rugosa		both		TJS	
Pachyseris	rugosa		10m		HILA	
Pachyseris	speciosa		10m		TJS	109
Pachyseris	speciosa		10m		HILA	
Pavona	cactus		10m		HILA	110
Pavona	cactus		10m		WM	
Pavona	clavus		3m	SN112	TJS	111
Pavona	clavus		3m		HILA	
Pavona	decussata		10m		HILA	112
Pavona	explanulata		10m		TJS	113
Pavona	explanulata		10m		WM	
Pavona	minuta		both		HILA	114
Pavona	minuta		both		HILA	
Pavona	minuta		10m		WM	
Pavona	varians		both	SN13	TJS	115
Pavona	varians		both	SN57	TJS	
Pectinia	lactuca		10m	SN29	TJS	116

Pectinia	lectuca		10m		WM	
Pectinia	paeonia		both		TJS	117
Pectinia	paeonia		both		TJS	
Pectinia	paeonia		both		HILA	
Pectinia	paeonia		both		HILA	
Pectinia	paeonia		n/a		WLH	
Physogyra	lichtensteini		both		TJS	118
Physogyra	lichtensteini		both		TJS	
Physogyra	lichtensteini		both		HILA	
Physogyra	lichtensteini		both		HILA	
Physogyra	lichtensteini		3m		WM	
Platygyra	daedalea		both	SN25	TJS	119
Platygyra	daedalea		both		TJS	
Platygyra	daedalea		both		HILA	
Platygyra	daedalea		both		HILA	
Platygyra	daedalea		both		WM	
Platygyra	daedalea		both		WM	
Platygyra	pini		3m	SN54A	TJS	120
Platygyra	pini	near tape	n/a		WLH	
Platygyra	sinensis		both		HILA	121
Platygyra	sinensis		both		HILA	
Platygyra	sinensis		both		WM	
Platygyra	sinensis		both		WM	
Platygyra	sinensis		n/a		WLH	
Platygyra	verweyi		10m	SN45A	TJS	122
Plerogyra	sinuosa		3m		TJS	123
Plerogyra	sinuosa		10m		WM	
Plesiastrea	versipora		10m		HILA	124
Plesiastrea	versipora		n/a		WLH	
Pocillopora	damicornis		both		TJS	125
Pocillopora	damicornis		both		TJS	
Pocillopora	damicornis		both		WM	
Pocillopora	damicornis		both		WM	
Pocillopora	damicornis		n/a		WLH	
Pocillopora	verrucosa		10m		TJS	126
Polyphyllia	talpina		3m		WM	127
Porites	annae		m	SN102	TJS	128
Porites	cf. annae		10m		HILA	129
Porites	cf. nigrescens		3m	SN60	TJS	130
Porites	cylindrica		3m		TJS	131
Porites	cylindrica		both		HILA	
Porites	cylindrica		both		HILA	
Porites	cylindrica		n/a		WLH	
Porites	lichen		10m		HILA	132
Porites	lichen		both		WM	
Porites	lichen		both		WM	
Porites	lobata		both		TJS	133
Porites	lobata		both		TJS	
Porites	lobata		both		HILA	
Porites	lobata		both		HILA	
Porites	lobata		both		WM	
Porites	lobata		both		WM	
Porites	lobata		n/a		WLH	
Porites	c. lutea	msv	3m	SN104	TJS	134
Psammocora	profundicella		10m		WM	135
Psammocora	superficialis		10m		WM	136
Psammocora	superficialis		n/a		WLH	
Sandalolitha	robusta		10m		WM	137
Seriatopora	caliendrum		10m		TJS	138
Seriatopora	caliendrum		10m		WM	
Seriatopora	hystrix		both		TJS	139
Seriatopora	hystrix		both		TJS	
Seriatopora	hystrix		both		HILA	
Seriatopora	hystrix		both		HILA	
Seriatopora	hystrix		both		WM	

Seriatopora	hystrix		both		WM	
Stylophora	pistillata		both	SN16	TJS	140
Stylophora	pistillata		both		TJS	
Stylophora	pistillata		3m		HILA	
Stylophora	pistillata		both		WM	
Stylophora	pistillata		both		WM	
Symphyllia	agaricia		3m		WM	141
Symphyllia	radians		3m		TJS	142
Symphyllia	radians		3m		HILA	
Symphyllia	radians		10m		WM	
Symphyllia	recta	under Acro	both		TJS	143
Symphyllia	recta		both		TJS	
Symphyllia	recta		3m		HILA	
Symphyllia	recta		3m		WM	
Symphyllia	recta		n/a		WLH	
Tubastrea	coccinia	sm. orange	both	SN22	TJS	144
Tubastrea	coccinia		both		TJS	
Tubastrea	coccinia		3m		HILA	
Tubastrea	diaphana		10m		HILA	145
Tubastrea	micrantha		both	SN55	TJS	146
Tubastrea	micrantha	green, azoox	both	SN8	TJS	
Tubastrea	micrantha		10m		HILA	
Turbinaria	frondens		both	SN24	TJS	147
Turbinaria	frondens		both	SN72	TJS	
Turbinaria	frondens		both		HILA	
Turbinaria	frondens		both		HILA	
Turbinaria	mesenterina		10m		TJS	148
Turbinaria	peltata		3m		WM	149
Turbinaria	peltata		n/a		WLH	
Turbinaria	reniformis		both		HILA	150
Turbinaria	reniformis		both		HILA	

<u>Sulawesi all sites</u> 10m + 3m combined species list
Acroporas corrected

Genus	species	comment	depthdist	collNo	site	N spp.
Acanthastrea	echinata		10m		KP	1
Acropora	aculeus		3m	SL27	SL	2
Acropora	bruggemanni	(=kp62,129)	3m	KP113	KP	3
Acropora	cf. formosa grp		both		SL	4
Acropora	cf. selago grp		3m	KP112A	KP	5
Acropora	cf. selago grp		both		SL	
Acropora	cf.formosa		3m		BL	
Acropora	cf.pulchra	bombed	both		BL	
Acropora	clathrata		3m	SL29A	SL	6
Acropora	cuneata		3m		KP	7
Acropora	florida	SL15=SL30	both	SL15	SL	8
Acropora	florida	ACT	3m	SL32	SL	
Acropora	formosa		3m	KP106	KP	9
Acropora	formosa	(=SL24)	both	SL16	SL	
Acropora	formosa		10m	SL24?	SL	
Acropora	horrida	(=kp36)	both	KP110	KP	10
Acropora	horrida	(kp98=kp110)	both	KP36	KP	
Acropora	humilis grp		3m		KP	11
Acropora	humilis grp		10m		SL	
Acropora	hyacinthus		both	SL34	SL	12
Acropora	hyacinthus grp		both		SL	
Acropora	longicyathus		3m	SL14	SL	13
Acropora	loripes		10m	KP31	KP	14
Acropora	microphthalma	KP21=KP52	10m	KP21	KP	15
Acropora	palifera		both		KP	16
Acropora	palifera		both		KP	
Acropora	palifera		both		SL	
Acropora	palifera		both		BL	
Acropora	palifera	bombed	both		BL	

Acropora	pulchra	blue	both	BL2	BL	17
Acropora	pulchra		both		SL	
Acropora	pulchra		3m		KY	
Acropora	selago		3m	KY26	KY	
Acropora	sp.	blue	3m		BL	
Acropora	sp. 2		10m	KP35	KP	
Acropora	sp. 4	no coll	10m		KP	
Acropora	sp. 5		3m		KP	
Acropora	sp. 6	white	3m	KP108	KP	
Acropora	sp. 7		3m	KP112	KP	
Acropora	vaughani		both	BL1	BL	18
Acropora	yongei		10monly	BL9,=KP6	BL	19
Acropora	yongei	blue	3m	SL29	SL	
Alveopora	verrilliana		10m		KP	20
Coeloseris	mayeri		10m		KP	21
Coeloseris	mayeri		3m		BL	
Cyphastrea	japonica		10monly		BL	22
Cyphastrea	microphthalma		10m		KP	23
Cyphastrea	microphthalma		10m		SL	
Cyphastrea	microphthalma		3m		BL	
Cyphastrea	serailia		10m		SL	24
Cyphastrea	serailia		both		BL	
Cyphastrea	serailia		both		BL	
Diploastrea	heliopora		10m		SL	25
Diploastrea	heliopora		3m		BL	
Echinophyllia	aspera		10monly		BL	26
Echinopora	gemmacea		both		KP	27
Echinopora	gemmacea		both		KP	
Echinopora	gemmacea		both		BL	
Echinopora	gemmacea		both		BL	
Echinopora	horrida	near	both		SL	28
Echinopora	horrida		both		SL	
Echinopora	horrida		3m		BL	
Echinopora	lamellosa		10m		KP	29
Echinopora	lamellosa		both		SL	
Echinopora	lamellosa		both		SL	
Echinopora	lamellosa		both		BL	
Echinopora	lamellosa		both		BL	
Echinopora	mammiformis		10monly		BL	30
Euphyllia	ancora		10m		SL	31
Euphyllia	glabrescens		both		SL	32
Euphyllia	glabrescens		both		SL	
Euphyllia	glabrescens		3m		KY	
Favi	speciosa		10m		BL	33
Favia	laxa		3m		BL	34
Favia	lizardensis		10m		SL	35
Favia	lizardensis		10monly		BL	
Favia	mathaii		10m		KP	36
Favia	mathaii		10monly		BL	
Favia	mathaii		3m		KY	
Favia	pallida		10m		KP	37
Favia	pallida		10m		SL	
Favia	pallida		3m		BL	
Favia	pallida		3m		KY	
Favia	speciosa		3m		KY	33
Favia	stelligera		10k		KP	38
Favia	stelligera		both		BL	
Favia	stelligera	columnar	both		BL	
Favites	abdita		both		KP	39
Favites	abdita		both		KP	
Favites	abdita		10m		SL	
Favites	abdita		10monly		BL	
Favites	abdita		3m		KY	
Favites	flexuosa		10m		KP	40
Favites	flexuosa		3m		KY	

Favites	halicora		10monly		BL	41
Favites	halicora		3m		KY	
Favites	pentagona		both		BL	42
Favites	pentagona		both		BL	
Favites	pentagona		3m		KY	
Fungia	cf.fungites		both		BL	43
Fungia	cf.paumotensis		both		KY	44
Fungia	cf.repanda		3m		KY	45
Fungia	concinna		10m		KP	46
Fungia	fungites		both		KP	43
Fungia	fungites		both		KP	
Fungia	fungites		both		SL	
Fungia	fungites		both		SL	
Fungia	fungites		both		BL	
Fungia	horrida		3m		KY	47
Fungia	paumotensis		10m		SL	44
Fungia	repanda		10m		KP	45
Fungia	simplex		10monly		BL	48
Fungia	valida		both		SL	49
Fungia	valida		both		SL	
Galaxea	astreata	columnar	10m		KP	50
Galaxea	astreata	column	10m		SL	
Galaxea	astreata		10monly		BL	
Galaxea	astreata		3m		KY	
Galaxea	fascicularis		both		KP	51
Galaxea	fascicularis		both		KP	
Galaxea	fascicularis		both		SL	
Galaxea	fascicularis		both		SL	
Galaxea	fascicularis		10monly		BL	
Galaxea	fascicularis		both		KY	
Gardineroseris	planulata		10monly		BL	52
Goniastrea	aspera		both		KP	53
Goniastrea	aspera		both		KP	
Goniastrea	aspera		3m		KY	
Goniastrea	edwardsi		10m		KP	54
Goniastrea	edwardsi		10monly		BL	
Goniastrea	edwardsi		3m		KY	
Goniastrea	favulus		10m	KP39	KP	55
Goniastrea	favulus		10m		SL	
Goniastrea	favulus		10monly		BL	
Goniastrea	favulus		3m		KY	
Goniastrea	pectinata		10m		KP	56
Goniastrea	pectinata		10m		SL	
Goniastrea	pectinata		both		BL	
Goniastrea	pectinata		both		BL	
Goniastrea	retiformis		10m		KP	57
Goniastrea	retiformis		3m		SL	
Goniastrea	retiformis		3m		KY	
Goniopora	cf.minor		10monly		BL	58
Goniopora	djiboutiensis		10m		SL	59
Goniopora	djiboutiensis		3m		BL	
Goniopora	somaliensis		10m		KP	60
Goniopora	stutchburyi		10m		KP	61
Goniopora	tenuidens		3m		BL	62
Heliofungia	actiniformis		10m		SL	63
Herpolitha	cf.limax		3m		KY	64
Herpolitha	cf.weberi		3m		KY	65
Herpolitha	limax		3m		KP	
Herpolitha	limax		both		SL	
Herpolitha	limax		both		SL	
Hydnophora	excesa		10monly		BL	66
Hydnophora	excesa		3m		KY	
Hydnophora	microconos		10m		KP	67
Hydnophora	pilosa		10m		KP	68
Hydnophora	pilosa		10m		SL	

Hydnophora	pilosa		10monly		BL	
Hydnophora	pilosa		3m		KY	
Hydnophora	rigida		10m		KP	69
Hydnophora	rigida		10monly		BL	
Leptastrea	purpurea		3m		KP	70
Leptastrea	transversa		10monly		BL	71
Leptastrea	transversa		3m		KY	
Leptastrea	transversa		3m		KY	
Leptoseris	explanata		3m		BL	72
Leptoseris	hawaiiensis		10m		KP	73
Leptoseris	mycetoseroides		10m		KP	74
Lobophyllia	corymbosa		10m		SL	75
Lobophyllia	corymbosa		10monly		BL	
Lobophyllia	hemprichii		10m		SL	76
Lobophyllia	hemprichii		10monly		BL	
Lobophyllia	hemprichii	neartape	3m		KY	
Merulina	ampliata		10m		KP	77
Merulina	ampliata		10m		SL	
Merulina	ampliata		10monly		BL	
Merulina	ampliata		3m		KY	
Merulina	scabricula		3m		KP	78
Montastrea	curta		10m		SL	79
Montastrea	curta		10monly		BL	
Montastrea	curta		3m		KY	
Montastrea	valenciennesi		10m		KP	80
Montipora	aequituberculata		10m		KP	81
Montipora	caliculata	blue encr.	both		KP	82
Montipora	caliculata	blue encr.	both		KP	
Montipora	caliculata	grp 7	both		SL	
Montipora	caliculata	blue.encr	both		BL	
Montipora	cf. caliculata	grp 7	both		SL	
Montipora	cf. foliosa	grp 8	10m		SL	83
Montipora	cf. hispida	grp 4	both		SL	84
Montipora	cf. millepora		10m	KP44A	KP	85
Montipora	cf. millipora	grp2	10m		SL	
Montipora	cf. peltiformis	grp 5	10m		SL	86
Montipora	cf. spumosa	grp6	10m		SL	87
Montipora	cf. turgescens	grp. 14	10m		KP	88
Montipora	cf.caliculata	blue.encr	both		BL	
Montipora	cf.foveolata	grp3	10monly	BL23	BL	89
Montipora	cf.grisea		3m		BL	90
Montipora	cf.mollis	grp11	10monly		BL	91
Montipora	cf.turgescens	grp.14	3m		KY	
Montipora	crassituberculata	grp 12	3m		SL	92
Montipora	danae		10m	KP22	KP	93
Montipora	danae		10monly		BL	
Montipora	digitata		both		SL	94
Montipora	digitata		both		SL	
Montipora	digitata		both		BL	
Montipora	digitata		both		BL	
Montipora	digitata		3m		KY	
Montipora	foliosa		both	KP106	KP	
Montipora	foliosa		both	KP23	KP	
Montipora	foliosa		3m		BL	
Montipora	foveolata	grp 3	10m	KP92	KP	
Montipora	grisea		1m	KP96	KP	
Montipora	hispida		10m		KP	
Montipora	hispida		3m		SL	
Montipora	spumosa	grp6	both	BL26A	BL	
Montipora	spumosa		both	KP101	KP	
Montipora	spumosa		both	KP105	KP	
Montipora	spumosa		both		BL	
Montipora	verrucosa		3m	KP118	KP	95
Mycedium	elephantotus		3m		KP	96
Mycedium	elephantotus		10m		SL	

Mycedium	elephantotus		10monly		BL	
Oxypora	glabra		10m		KP	97
Oxypora	lacera		10monly		BL	98
Pachyseris	rugosa		10m		SL	99
Pachyseris	speciosa		10m		KP	100
Pachyseris	speciosa		10m		SL	
Pachyseris	speciosa		both		BL	
Pachyseris	speciosa		both		BL	
Pavona	cactus		both		SL	101
Pavona	cactus		both		SL	
Pavona	cactus		3m		BL	
Pavona	cactus		3m		KY	
Pavona	cf.varians		10monly		BL	102
Pavona	clavus		10m		KP	103
Pavona	clavus		3m		BL	
Pavona	decussata		10m		SL	104
Pavona	decussata	neartape	3m		KY	
Pavona	explanulata		10m		KP	105
Pavona	explanulata	near	10m		SL	
Pavona	explanulata		10monly		BL	
Pavona	maldivensis		10m		KP	106
Pavona	minuta		10monly		BL	107
Pavona	venosa		10m		KP	108
Pectinia	alcicornis		both		SL	109
Pectinia	alcicornis		10monly		BL	
Pectinia	alcicornis		both		BL	
Pectinia	alcicornis		both		BL	
Pectinia	lactuca		both		SL	110
Pectinia	lactuca		both		SL	
Pectinia	paeonia		both		SL	111
Pectinia	paeonia		both		SL	
Pectinia	paeonia		10monly		BL	
Physogyra	lichtensteini		10m		SL	112
Platygyra	daedalea		10m		KP	113
Platygyra	daedalea		10m		SL	
Platygyra	daedalea		both		BL	
Platygyra	daedalea		both		BL	
Platygyra	daedalea		3m		KY	
Platygyra	pini		10m		KP	114
Platygyra	sinensis		3m		KY	115
Plerogyra	sinuosa		both		SL	116
Plerogyra	sinuosa		both		SL	
Plerogyra	sinuosa		10monly		BL	
Pocillopora	damicornis		10m		KP	117
Pocillopora	damicornis		3m		KY	
Pocillopora	verrucosa		both		KP	118
Pocillopora	verrucosa		both		KP	
Porites	annae		10m		KP	119
Porites	cf. lichen		10m		KP	120
Porites	cylindrica		both		KP	121
Porites	cylindrica		both		KP	
Porites	cylindrica		both		SL	
Porites	cylindrica		both		SL	
Porites	cylindrica		both		BL	
Porites	cylindrica		both		BL	
Porites	lobata		both		KP	122
Porites	lobata		both		KP	
Porites	lobata		both		SL	
Porites	lobata		both		SL	
Porites	lobata		both		BL	
Porites	lobata		both		BL	
Porites	lobata		3m		KY	
Porites	sp. 4		10m	KP45	KP	123
Sandalolitha	robusta		10m		KP	124
Seriatopora	caliendrum		3m		KP	125

Seriatopora	caliendrum		3m		SL	
Seriatopora	hystrix		both		KP	126
Seriatopora	hystrix		both		KP	
Seriatopora	hystrix		both		SL	
Seriatopora	hystrix		both		SL	
Seriatopora	hystrix		both		BL	
Seriatopora	hystrix		both		BL	
Seriatopora	hystrix		3m		KY	
Stylophora	pistillata		10m		KP	127
Stylophora	pistillata		both		SL	
Stylophora	pistillata		both		SL	
Stylophora	pistillata		3m		KY	
Symphyllia	radians		10m		SL	128
Symphyllia	radians		3m		KY	
Symphyllia	recta		10m		KP	129
Symphyllia	recta		both		SL	
Symphyllia	recta		both		SL	
Symphyllia	recta		both		BL	
Symphyllia	recta		both		BL	
Symphyllia	recta	neartape	3m		KY	
Trachyphyllia	???		both	(KY1)	KY	130
Turbinaria	frondens		10monly		BL	131
Turbinaria	peltata		both		KY	132
Turbinaria	reniformis		10monly		BL	133
Turbinaria	reniformis		3m		KY	

Gosong Cemara 10m + 3m combined species list
species list Acroporas corrected

Genus	species	comment	depthdist	collNo	Site	N. spp.
Acrhelia	horrescens		3m		CM3L	1
Acropora	cerealis	ACT	both	CM 7	CM10L	2
Acropora	cerealis		both	CM 7	CM3W	
Acropora	cerealis	ACT n=CM7	10m		CM10L	
Acropora	cerealis		both		CM3L	
Acropora	cf. cerealis		both		CM10W	
Acropora	cf. divaricata grp		both		CM10L	3
Acropora	cf. divaricata grp		both		CM3W	
Acropora	cf. millepora		both		CM3W	4
Acropora	cf. selago grp	ACT	both		CM10L	5
Acropora	cf. selago grp	ACC	3m		CM3W	
Acropora	divaricata		both		CM10W	
Acropora	divaricata grp		both		CM3L	
Acropora	echinata		both		CM10L	6
Acropora	echinata grp		both		CM3L	
Acropora	echinata grp		both		CM10W	
Acropora	echinata grp		both		CM3W	
Acropora	formosa		both		CM10W	7
Acropora	formosa grp		3m		CM3L	
Acropora	formosa grp		both		CM3W	
Acropora	humilis		3m		CM3L	8
Acropora	humilis		both		CM10W	
Acropora	humilis grp		3m		CM3W	
Acropora	hyacinthus		both		CM10W	9
Acropora	hyacinthus grp	ACT	both		CM10L	
Acropora	hyacinthus grp		both		CM3L	
Acropora	hyacinthus grp		both		CM3W	
Acropora	loripes grp		3m		CM3L	10
Acropora	loripes grp		both		CM10W	
Acropora	loripes grp		both		CM3W	
Acropora	nasuta	ss, blue	3m		CM3L	11
Acropora	nasuta grp	ACC	3m		CM3L	
Acropora	nasuta grp	ACT	3m		CM3L	
Acropora	nasuta grp	blue	both		CM10W	
Acropora	palifera		both		CM10L	12

Acropora	palifera		both		CM3L	
Acropora	selago grp	ACT	both		CM3L	13
Acropora	selago grp		both		CM10W	
Acropora	selago grp	ACB	3m		CM3W	
Acropora	selago grp		both		CM3W	
Acropora	sp., ACT, blue	blue	both		CM3W	14
Acropora	tenuis		3m	CM 13	CM3L	15
Acropora	tenuis		both		CM10W	
Acropora	valida		3m	CM 14	CM3L	16
Cyphastrea	microphthalma		10m		CM10L	17
Cyphastrea	microphthalma		both		CM3L	
Cyphastrea	microphthalma		both		CM10W	
Cyphastrea	microphthalma		both		CM3W	
Cyphastrea	serailia		10m		CM10L	18
Diploastrea	heliopora		both		CM10L	19
Diploastrea	heliopora		both		CM3L	
Echinophyllia	aspera		10m		CM10L	20
Echinophyllia	cf. orpheensis		10m	CM 16	CM10W	21
Echinophyllia	orpheensis		10m		CM10L	
Echinopora	gemmacea		3m		CM3L	22
Echinopora	gemmacea		10m		CM10W	
Echinopora	horrida		3m		CM3L	23
Echinopora	lamellosa		both		CM10L	24
Echinopora	lamellosa		both		CM3L	
Echinopora	lamellosa		3m		CM3W	
Euphyllia	ancora		both		CM10L	25
Euphyllia	ancora		both		CM3L	
Euphyllia	ancora		10m		CM10W	
Euphyllia	cristata		10m		CM10W	26
Euphyllia	grabrescens		10m		CM10W	27
Favia	pallida		10m		CM10L	28
Favia	pallida		both		CM3L	
Favia	pallida		10m		CM10W	
Favia	stelligera		3m		CM3L	29
Favites	abdita		10m		CM10L	30
Favites	abdita		3m		CM3W	
Favites	complanata		10m		CM10L	31
Favites	complanata		10m		CM10W	
Favites	halicora		10m		CM10L	32
Fungia	cf. repanda		10m		CM10L	33
Fungia	cf. valida		both		CM3L	34
Fungia	cf. valida		3m		CM3W	
Fungia	fungites		both		CM10L	35
Fungia	fungites		both		CM3L	
Fungia	fungites		both		CM10W	
Fungia	fungites		both		CM3W	
Fungia	repanda		both		CM3L	
Fungia	repanda		10m		CM10W	
Fungia	simplex		10m		CM10L	36
Fungia	simplex		both		CM3L	
Fungia	simplex		10m		CM10W	
Fungia	valida		both		CM10L	
Galaxea	astreata		both		CM10L	37
Galaxea	astreata		both		CM3L	
Galaxea	astreata		both		CM10W	
Galaxea	astreata		both		CM3W	
Galaxea	fascicularis		3m		CM3L	38
Galaxea	fascicularis		both		CM10W	
Galaxea	fascicularis		both		CM3W	
Gardineroseris	planulata		3m		CM3L	39
Gardineroseris	planulata		3m		CM3W	
Goniastrea	aspera		both		CM10L	40
Goniastrea	aspera		10m		CM10W	
Goniastrea	edwardsi		10m		CM10L	41
Goniastrea	pectinata		10m		CM10L	42

Goniastrea	pectinata		3m		CM3L	
Goniastrea	pectinata		both		CM10W	
Goniastrea	pectinata		both		CM3W	
Goniopora	cf. djiboutiensis		10m		CM10L	43
Goniopora	djiboutiensis		both		CM3L	
Goniopora	minor	blue	10m	CM 18	CM10W	44
Goniopora		blue	10m	CM 8	CM10L	
Herpolitha	limax		10m		CM10L	45
Hydnophora	pilosa		3m		CM3W	46
Hydnophora	rigida		3m		CM3L	47
Hydnophora	rigida		3m		CM3W	
Hydnphora	pilosa		10m		CM10L	
Leptastrea	transversa		both		CM10L	48
Leptastrea	transversa		both		CM3L	
Leptastrea	transversa		both		CM10W	
Leptastrea	transversa		both		CM3W	
Leptoseris	explanata		10m		CM10W	49
Leptoseris	hawaiiensis		10m		CM10L	50
Lithophyllon	edwardsi		10m		CM10W	51
Lithphyllon	ewardsi		10m		CM10L	
Lobophyllia	hemprichii		3m		CM3L	52
Lobophyllia	hemprichii		10m		CM10W	
Merulina	ampliata		both		CM10L	53
Merulina	ampliata		both		CM10W	
Merulina	ampliata		both		CM3W	
Merulina	scabricula		3m		CM3L	54
Merulina	scabricula		both		CM10W	
Merulina	scabricula		both		CM3W	
Montastrea	curta		both		CM10L	55
Montastrea	curta		both		CM3L	
Montastrea	curta		3m		CM3W	
Montipora	cf. caliculata		10m		CM10L	56
Montipora	cf. caliculata	blue	both		CM3L	
Montipora	cf. grisea		both		CM10L	57
Montipora	cf. millepora		10m		CM10L	58
Montipora	cf. millepora		both		CM10W	
Montipora	cf. millepora		both		CM3W	
Montipora	danae		3m		CM3L	59
Montipora	danae		10m		CM10W	
Montipora	digitata		3m		CM3L	60
Montipora	foliosa		3m		CM3L	61
Montipora	foliosa		both		CM10W	
Montipora	foliosa		both		CM3W	
Montipora	hispida		3m		CM3L	62
Montipora	hispida		3m		CM3W	
Montipora	peltiformis		both		CM3L	63
Montipora	peltiformis		3m		CM3W	
Montipora	spumosa		10m		CM10L	64
Montipora	spumosa		both		CM3L	
Montipora	spumosa		10m		CM10W	
Montipora	verrucosa		10m		CM10L	65
Montipora	verrucosa		10m		CM10W	
Mycedium	elephantotus		10m		CM10L	66
Mycedium	elephantotus		10m		CM10W	
Oxypora	lacera		3m		CM3L	67
Pachyseris	rugosa		10m		CM10L	68
Pachyseris	speciosa		10m		CM10L	69
Pachyseris	speciosa		both		CM3L	
Pachyseris	speciosa		both		CM10W	
Pachyseris	speciosa		both		CM3W	
Pavona	cactus		10m		CM10L	70
Pavona	explanulata		10m		CM10L	71
Pavona	explanulata		3m		CM3W	
Pavona	varians		10m		CM10L	72
Pavona	varians		10m		CM10W	

Pectinia	alcicornis		10m		CM10L	73
Pectinia	alcicornis		both		CM3L	
Pectinia	alcicornis		10m		CM10W	
Pectinia	lactuca		10m		CM10L	74
Pectinia	paeonia		10m		CM10L	75
Physogyra	lichtensteini		10m		CM10L	76
Physogyra	lichtensteini		10m		CM10W	
Platygyra	sinensis		10m		CM10L	77
Plesiastrea	versipora		10m		CM10L	78
Pocillopora	damicornis		3m		CM3W	79
Pocillopora	verrucosa		3m		CM3L	80
Pocillopora	verrucosa		3m		CM3W	
Porites	cylindrica		both		CM10L	81
Porites	cylindrica		both		CM3L	
Porites	cylindrica		both		CM10W	
Porites	cylindrica		both		CM3W	
Porites	lobata		both		CM10L	82
Porites	lobata		both		CM3L	
Porites	lobata		both		CM10W	
Porites	lobata		both		CM3W	
Porites	nigrescens		3m		CM3W	83
Psammocora	contigua		10m	PK 22	CM10W	84
Sandalolitha	robusta		10m		CM10L	85
Sandalolitha	robusta		10m		CM10W	
Stylophora	pistillata		3m		CM3W	86
Symphyllia	radians		3m		CM3L	87
Symphyllia	radians		10m		CM10W	
Symphyllia	recta		3m		CM3L	88
Symphyllia	recta		both		CM3W	
Syphyllia	recta		both		CM10W	

<u>Pulau Kecil</u> 10m + 3m combined species list
species list Acroporas corrected

<u>Genus</u>	<u>species</u>	<u>comment</u>	<u>depthdist</u>	<u>collNo</u>	<u>site</u>	<u>N spp.</u>
Acanthastrea	echinata		10m		PKW10	1
Acrhelia	horrescens		10m		PKL10	2
Acropora	aspera grp		10m		PKW10	3
Acropora	cerealis		both	(CM7)	PKL10	4
Acropora	cerealis		both	(CM 7)	PKL3	
Acropora	cf. millepora	ACT	3m		PKW3	5
Acropora	cf. pulchra		3m		PKW3	6
Acropora	divaricata		3m		PKL3	7
Acropora	divaricata grp		3m		PKW3	
Acropora	echinata grp	ACBB	3m		PKL3	8
Acropora	echinata grp		both		PKW10	
Acropora	echinata grp		both		PKW3	
Acropora	formosa		both		PKW10	9
Acropora	formosa grp		10m		PKL10	
Acropora	formosa grp		both		PKW3	
Acropora	granulosa	ACT	3m		PKL3	10
Acropora	humilis grp		both		PKL10	11
Acropora	humilis grp		both		PKW10	
Acropora	humilis grp		both		PKW3	
Acropora	humilis grp.		both		PKL3	
Acropora	hyacinthus grp		both		PKL10	12
Acropora	hyacinthus grp		both		PKL3	
Acropora	hyacinthus grp		both		PKW10	
Acropora	hyacinthus grp	ACT	both		PKW3	
Acropora	latistella grp	ACT	3m		PKL3	13
Acropora	loripes grp	ACB	3m		PKL3	14
Acropora	loripes grp		both		PKW10	
Acropora	loripes grp		both		PKW3	
Acropora	nasuta grp	ACT	both		PKL10	15
Acropora	nasuta grp	ACB	3m		PKL3	16

Acropora	nasuta grp	ACT	both		PKL3	
Acropora	nasuta grp		both		PKW10	
Acropora	nasuta grp		both		PKW3	
Acropora	palifera		3m		PKL3	17
Acropora	cerealis		3m		PKW3	
Acropora	selago grp	ACT	3m		PKL3	18
Acropora	selago grp	ACC	3m		PKL3	
Acropora	selago grp		both		PKW10	
Acropora	selago grp		both		PKW3	
Acropora	tenuis	big spoon	3m	(CM 13)	PKL3	19
Acropora	verweyi		3m		PKW3	20
Acropora	valida		3m	(CM 14)	PKL3	21
Alveopora	cf. spongiosa	sp. 1	3m	PK 2 ??	PKW3	22
Alveopora	sp. 1		3m		PKL3	23
Coeloseris	mayeri		3m		PKL3	24
Coeloseris	mayeri		3m		PKW3	
Cyphastrea	chalcidium		10m		PKW10	25
Cyphastrea	microphthalma		both		PKL10	26
Cyphastrea	microphthalma		3m		PKL3	
Cyphastrea	microphthalma		both		PKW10	
Cyphastrea	microphthalma		both		PKW3	
Cyphastrea	serailia		10m		PKL10	27
Cyphastrea	serailia		10m		PKW10	
Diploastrea	heliopora		3m		PKL3	28
Echinophyllia	aspera		10m		PKL10	29
Echinophyllia	aspera		10m		PKW10	
Echinopora	gemmacea		both		PKL10	30
Echinopora	gemmacea		both		PKL3	
Echinopora	gemmacea		3m		PKW3	
Echinopora	horrida		both		PKL10	31
Echinopora	horrida		both		PKL3	
Echinopora	horrida		both		PKW10	
Echinopora	horrida		both		PKW3	
Echinopora	lamellosa		both		PKL10	32
Echinopora	lamellosa		both		PKL3	
Echinopora	lamellosa		3m		PKW3	
Euphyllia	ancora		10m		PKL10	33
Euphyllia	ancora		both		PKW10	
Euphyllia	ancora		both		PKW3	
Euphyllia	cristata		both		PKL10	34
Euphyllia	cristata		both		PKL3	
Euphyllia	cristata		10m		PKW10	
Favia	laxa		3m		PKL3	35
Favia	laxa		10m		PKW10	
Favia	pallida		3m		PKL3	36
Favia	pallida		both		PKW10	
Favia	pallida		both		PKW3	
Favia	stelligera		3m		PKL3	37
Favia	stelligera		3m		PKW3	
Favites	abdita		10m		PKW10	38
Fungia	fungites		both		PKL10	39
Fungia	fungites		both		PKL3	
Fungia	fungites		both		PKW10	
Fungia	fungites		both		PKW3	
Fungia	repanda		both		PKL10	40
Fungia	repanda		both		PKL3	
Fungia	scutaria		10m		PKL10	41
Fungia	scutaria		3m		PKW3	
Fungia	simplex		both		PKL10	42
Fungia	simplex		both		PKL3	
Galaxea	astreata		3m		PKL3	43
Galaxea	astreata		both		PKW10	
Galaxea	astreata		both		PKW3	
Galaxea	fascicularis		both		PKL10	44
Galaxea	fascicularis		both		PKL3	

Galaxea	fascicularis		3m		PKW3	
Gardineroseris	planulata		3m		PKL3	45
Gardineroseris	planulata		3m		PKW3	
Goniastrea	aspera		both		PKL10	46
Goniastrea	aspera		both		PKL3	
Goniastrea	aspera		10m		PKW10	
Goniastrea	edwardsi		both		PKL10	47
Goniastrea	edwardsi		both		PKL3	
Goniastrea	edwardsi		both		PKW10	
Goniastrea	edwardsi		both		PKW3	
Goniastrea	pectinata		3m		PKL3	48
Goniastrea	retiformis		3m		PKW3	49
Goniopora	djiboutiensis	40m	both	PK1	PKL10	50
Goniopora	djiboutiensis		both		PKL3	
Halomitra	pileus		3m		PKW3	51
Heliofungia	actiniformis		10m		PKL10	52
Heliopora	coerulea		3m		PKW3	53
Herpolitha	limax		10m		PKW10	54
Hydnophora	excesa		3m		PKW3	55
Hydnophora	pilosa		3m		PKW3	56
Hydnophora	rigida		3m		PKL3	57
Hydnophora	rigida		both		PKW10	
Hydnophora	rigida		both		PKW3	
Leptastrea	purpurea		10m		PKL10	58
Leptastrea	transversa		10m		PKL10	59
Leptoseris	hawaiiensis		10m		PKL10	60
Leptoseris	mycetoseroides		10m		PKL10	61
Leptoseris	mycetoseroides		10m		PKW10	
Lobophyllia	corymbosa		10m		PKL10	62
Lobophyllia	hemprichii		both		PKL10	63
Lobophyllia	hemprichii		both		PKL3	
Merulina	ampliata		10m		PKL10	64
Merulina	ampliata		both		PKW10	
Merulina	ampliata		both		PKW3	
Merulina	scabricula		both		PKL10	65
Merulina	scabricula		both		PKL3	
Merulina	scabricula		10m		PKW10	
Montastrea	curta		3m		PKL3	66
Montipora	cf. caliculata	blue encr	both		PKL10	67
Montipora	cf. caliculata	blue	both		PKL3	
Montipora	cf. caliculata		both		PKW10	
Montipora	cf. caliculata		both		PKW3	
Montipora	cf. grisea		10m		PKL10	68
Montipora	cf. millepora		10m		PKL10	69
Montipora	cf. millepora		both		PKW10	
Montipora	cf. millepora		both		PKW3	
Montipora	danae		3m		PKL3	70
Montipora	danae		10m		PKW10	
Montipora	digitata		both		PKL10	71
Montipora	digitata		both		PKL3	
Montipora	foliosa		10m		PKL10	72
Montipora	foliosa		both		PKW10	
Montipora	foliosa		both		PKW3	
Montipora	hispida		3m		PKL3	73
Montipora	hispida		both		PKW10	
Montipora	hispida		both		PKW3	
Montipora	peltiformis		3m		PKW3	74
Montipora	spumosa		both		PKL10	
Montipora	spumosa		both		PKL3	
Montipora	verrucosa		10m		PKW10	75
Mycedium	elephantotus		10m		PKL10	76
Mycedium	elephantotus		10m		PKW10	
Oxypora	lacera		both		PKL10	77
Oxypora	lacera		both		PKL3	
Pachyseris	rugosa		10m		PKL10	78

Pachyseris	rugosa	both		PKW10	
Pachyseris	rugosa	both		PKW3	
Pachyseris	speciosa	both		PKL10	79
Pachyseris	speciosa	both		PKL3	
Pachyseris	speciosa	both		PKW10	
Pachyseris	speciosa	both		PKW3	
Pavona	cactus	3m		PKW3	80
Pavona	decussata	both		PKL10	81
Pavona	decussata	both		PKL3	
Pavona	explanulata	3m		PKL3	82
Pavona	varians	10m		PKL10	83
Pavona	varians	10m		PKW10	
Pavona	venosa	3m		PKW3	84
Pectinia	alcicornis	both		PKL10	85
Pectinia	alcicornis	both		PKL3	
Pectinia	alcicornis	10m		PKW10	
Pectinia	paeonia	10m		PKL10	86
Platygyra	daedalea	3m		PKL3	87
Plerogyra	sinuosa	both		PKL10	88
Plerogyra	sinuosa	both		PKL3	
Plesiastrea	versipora	both		PKL10	89
Plesiastrea	versipora	both		PKL3	
Pocillopora	damicornis	3m		PKL3	90
Pocillopora	damicornis	both		PKW10	
Pocillopora	damicornis	both		PKW3	
Pocillopora	verrucosa	both		PKW10	91
Pocillopora	verrucosa	both		PKW3	
Porites	cylindrica	both		PKL10	92
Porites	cylindrica	both		PKL3	
Porites	cylindrica	both		PKW10	
Porites	cylindrica	both		PKW3	
Porites	lobata	both		PKL10	93
Porites	lobata	both		PKL3	
Porites	lobata	both		PKW10	
Porites	lobata	both		PKW3	
Psammocora	contigua	both	PK 9	PKW10	94
Psammocora	contigua	both		PKW3	
Psammocora	digitata	both	PK 10	PKW10	95
Psammocora	digitata	both		PKW3	
Sandalolitha	robusta	3m		PKW3	96
Stylophora	pistillata	10m		PKL10	97
Symphyllia	agaricia	3m		PKL3	98
Symphyllia	recta	10m		PKL10	99
Symphyllia	recta	10m		PKW10	

P. Burung	combined species list			
Genus	species		site	N spp.
Acropora	cerealis	both	BRL10	1
Acropora	cerealis	both	BRL3	
Acropora	cerealis	both	BRW3	
Acropora	divaricata	3m	BRL3	2
Acropora	echinata	both	BRL10	3
Acropora	echinata	both	BRL3	
Acropora	florida	both	BRL10	4
Acropora	florida	both	BRW10	
Acropora	florida	both	BRW3	
Acropora	formosa	both	BRL10	5
Acropora	formosa	both	BRL3	
Acropora	formosa	both	BRW10	
Acropora	formosa	both	BRW3	
Acropora	humilis	both	BRL3	6
Acropora	humilis	both	BRW10	
Acropora	humilis	both	BRW3	
Acropora	hyacinthus	both	BRL10	7
Acropora	hyacinthus	both	BRL3	

Acropora	hyacinthus	both	BRW10	
Acropora	hyacinthus	both	BRW3	
Acropora	loripes	both	BRL10	8
Acropora	loripes	both	BRL3	
Acropora	loripes	both	BRW10	
Acropora	nasuta	both	BRL10	9
Acropora	nasuta	both	BRL3	
Acropora	nasuta	both	BRW10	
Acropora	nasuta	both	BRW3	
Acropora	pulchra	both	BRL10	10
Acropora	pulchra	both	BRL3	
Acropora	sarmentosa	3m	BRL3	11
Acropora	selago	both	BRL10	12
Acropora	selago	both	BRL3	
Acropora	selago	both	BRW3	
Coeloseris	mayeri	3m	BRL3	13
Cyphastrea	microphthalma	both	BRL10	14
Cyphastrea	microphthalma	both	BRL3	
Cyphastrea	serailia	both	BRL10	15
Cyphastrea	serailia	both	BRL3	
Diploastrea	heliopora	both	BRL3	16
Diploastrea	heliopora	both	BRW10	
Echinopora	gemmacea	10m	BRL10	17
Echinopora	horrida	both	BRL10	18
Echinopora	horrida	both	BRL3	
Echinopora	lamellosa	both	BRL10	19
Echinopora	lamellosa	both	BRL3	
Euphyllia	ancora	10m	BRL10	20
Euphyllia	ancora	10m	BRW10	
Euphyllia	crispata	10m	BRW10	21
Euphyllia	cristata	10m	BRL10	
Favia	pallida	both	BRL10	22
Favia	pallida	both	BRL3	
Favia	pallida	both	BRW10	
Favia	pallida	both	BRW3	
Favia	stelligera	3m	BRW3	23
Favia	veroni	both	BRL10	24
Favia	veroni	both	BRL3	
Favia	veroni	both	BRW10	
Favites	abdita	both	BRL10	25
Favites	abdita	both	BRL3	
Favites	abdita	both	BRW3	
Favites	flexuosa	3m	BRL3	26
Fungia	fungites	both	BRL10	27
Fungia	fungites	both	BRW10	
Fungia	fungites	both	BRW3	
Fungia	paumotensis	10m	BRL10	28
Fungia	scutaria	both	BRL10	29
Fungia	scutaria	both	BRW3	
Fungia	simplex	both	BRW10	30
Fungia	simplex	both	BRW3	
Galaxea	astreata	10m	BRL10	31
Galaxea	astreata	10m	BRW10	
Galaxea	fascicularis	both	BRL10	32
Galaxea	fascicularis	both	BRL3	
Galaxea	fascicularis	both	BRW10	
Galaxea	fascicularis	both	BRW3	
Gardineroseris	planulata	3m	BRW3	33
Goniastrea	edwardsi	10m	BRL10	34
Goniastrea	edwardsi	10m	BRL3	
Goniastrea	edwardsi	10m	BRW10	
Goniastrea	favulus	both	BRL10	35
Goniastrea	favulus	both	BRL3	
Goniastrea	retiformis	3m	BRL3	36
Goniopora	djiboutiensis	3m	BRW3	37

Goniopora	minor	both	BRL10	38
Goniopora	minor	both	BRW10	
Goniopora	minor	both	BRW3	
Halomitra	pileus	10m	BRL10	39
Hydnophora	exesa	10m	BRL10	40
Hydnophora	microconos	3m	BRL3	41
Hydnophora	pilosa	both	BRL10	42
Hydnophora	pilosa	both	BRL3	
Hydnophora	rigida	both	BRL10	43
Hydnophora	rigida	both	BRL3	
Hydnophora	rigida	both	BRW10	
Hydnophora	rigida	both	BRW3	
Leptastrea	purpurea	10m	BRW10	44
Leptoseris	explanata	10m	BRW10	45
Leptoseris	papyracea	10m	BRW10	46
Lobophyllia	hemprichii	both	BRW10	47
Lobophyllia	hemprichii	both	BRW3	
Merulina	ampliata	both	BRL10	48
Merulina	ampliata	both	BRW3	
Merulina	scabricula	both	BRL10	49
Millepora	sp.	both	BRL10	
Millepora	sp.	both	BRL3	
Millepora	tenella	both	BRW10	
Montipora	caliculata	10m	BRL10	50
Montipora	foliosa	both	BRL10	51
Montipora	foliosa	both	BRL3	
Montipora	hispida	3m	BRW3	52
Montipora	millepora	both	BRL10	53
Montipora	millepora	both	BRL3	
Montipora	spumosa	3m	BRL3	54
Montipora	tuberculosa	3m	BRL3	55
Montipora	verrucosa	10m	BRW10	56
Mycedium	elephantotus	10m	BRW10	57
Oxypora	glabra	10m	BRW10	58
Pachyseris	rugosa	10m	BRL10	59
Pachyseris	rugosa	10m	BRW10	
Pachyseris	speciosa	both	BRL10	60
Pachyseris	speciosa	both	BRL3	
Pachyseris	speciosa	both	BRW10	
Pachyseris	speciosa	both	BRW3	
Pavona	cactus	10m	BRL10	61
Pavona	cactus	10m	BRW10	
Pavona	venosa	3m	BRW3	62
Pectinia	alcicornis	10m	BRL10	63
Pectinia	lactuca	10m	BRL10	64
Physogyra	lichtensteini	10m	BRW10	65
Pocillopora	damicornis	both	BRL10	66
Pocillopora	damicornis	both	BRL3	
Pocillopora	damicornis	both	BRW10	
Pocillopora	damicornis	both	BRW3	
Pocillopora	edouxi	both	BRL10	67
Pocillopora	edouxi	both	BRL3	
Pocillopora	edouxi	both	BRW10	
Porites	annae	10m	BRW10	68
Porites	cylindrica	both	BRL10	69
Porites	cylindrica	both	BRL3	
Porites	cylindrica	both	BRW10	
Porites	lobata	both	BRL10	70
Porites	lobata	both	BRL3	
Porites	lobata	both	BRW10	
Porites	lobata	both	BRW3	
Porites	lutea	both	BRL10	71
Porites	lutea	both	BRL3	
Porites	nigrescens	10m	BRL10	72
Psammocora	digitata	10m	BRW10	73

Sandalolitha	robusta		both		BRL10	74
Sandalolitha	robusta		both		BRW3	
Seriatopora	hystrix		10m		BRL10	75
Stylophora	pistillata		3m		BRW3	76
Symphyllia	agaricia		10m		BRW10	77
Symphyllia	radians		3m		BRL3	78
Symphyllia	recta		both		BRL10	79
Symphyllia	recta		both		BRL3	
Symphyllia	recta		both		BRW3	

Pulau Panjang 6m + 3m combined species list
species list Acroporas corrected

Genus	species	comment	depthdist	coll No.	site	sp. no.
Acropora	humilis grp		3m		PPS3	1
Acropora	loripes grp		3m		PPN3	2
Acropora	nasuta		3m		PPS3	3
Alveopora	sp. 1		both		PPN3	4
Alveopora	sp. 1		both		PPN6	
Alveopora	sp. 1		6m		PPS6	
Alveopora	sp. 2		both		PPN3	5
Alveopora	sp. 2		both		PPN6	
Australogyra	zelli		6m		PPS6	6
Coeloseris	mayeri		3m		PPS3	7
Cyphastrea	microphthalma		3m		PPS3	8
Cyphastrea	serailia		6m		PPS6	9
Diploastrea	heliopora		3m		PPN3	10
Echinophyllia	aspera		6m		PPN6	11
Echinophyllia	aspera		3m		PPS3	
Echinophyllia	orpheensis		6m		PPS6	12
Echinopora	gemmacea		3m		PPN3	13
Euphyllia	ancora		6m		PPN6	14
Euphyllia	ancora		both		PPS3	
Euphyllia	ancora		both		PPS6	
Favia	cf. veroni		both		PPN6	15
Favia	cf. veroni		both		PPS3	
Favia	cf. veroni		both		PPS6	
Favia	laxa		both		PPN3	16
Favia	laxa		both		PPN6	
Favia	matthaii		3m		PPN3	17
Favia	pallida		both		PPN3	18
Favia	pallida		both		PPN6	
Favia	pallida		both		PPS3	
Favia	pallida		both		PPS6	
Favia	stelligera		6m		PPN6	19
Favia	stelligera		3m		PPS3	
Favites	abdita		both		PPN3	20
Favites	abdita		both		PPN6	
Favites	abdita		3m		PPS3	
Favites	halicora		both		PPN3	21
Favites	halicora		both		PPN6	
Galaxea	fascicularis		both		PPN3	22
Galaxea	fascicularis		both		PPS3	
Galaxea	fascicularis		both		PPS6	
Galaxea	fasciculata		both		PPN6	
Gardineroseris	planulata		6m		PPN6	23
Goniastrea	edwardsi		6m		PPN6	24
Goniastrea	favulus		3m		PPN3	25
Goniastrea	favulus		both		PPS3	
Goniastrea	favulus		both		PPS6	
Goniastrea	pectinata		both		PPS3	26
Goniastrea	pectinata		both		PPS6	
Goniopora	djiboutiensis		both		PPN3	27
Goniopora	djiboutiensis		both		PPN6	
Goniopora	djiboutiensis		both		PPS3	

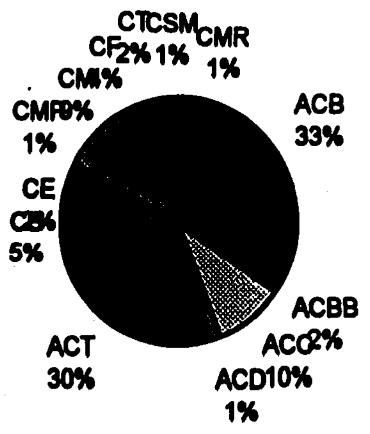
Goniopora	djiboutiensis	both	PPS6	
Goniopora	sp. 2	6m	PPN6	28
Heliofungia	actiniformis	6m	PPS6	29
Hydnophora	excesa	3m	PPN3	30
Hydnophora	excesa	3m	PPS3	
Hydnophora	pilosa	both	PPN3	31
Hydnophora	pilosa	6m	PPN6	
Lithophyllon	edwardsi	6m	PPN6	32
Lithophyllon	edwardsi	both	PPS3	
Lithophyllon	edwardsi	both	PPS6	
Lobophyllia	corymbosa	6m	PPS6	33
Lobophyllia	hemprichii	3m	PPN3	34
Lobophyllia	hemprichii	both	PPS3	
Lobophyllia	hemprichii	both	PPS6	
Merulina	ampliata	3m	PPN3	35
Merulina	ampliata	both	PPS3	
Merulina	ampliata	both	PPS6	
Montastrea	curta	6m	PPN6	36
Montipora	cf. grisea	3m	PPS3	37
Montipora	cf. millepora	both	PPN3	38
Montipora	cf. millepora	both	PPN6	
Montipora	cf. millepora	6m	PPS6	
Oxypora	lacera	6m	PPS6	39
Pavona	decussata	3m	PPS3	40
Pectinia	alcicornis	both	PPS3	41
Pectinia	alcicornis	both	PPS6	
Pectinia	paeonia	both	PPN3	42
Pectinia	paeonia	both	PPN6	
Pectinia	paeonia	both	PPS3	
Pectinia	paeonia	both	PPS6	
Platygyra	daedalea	3m	PPN3	43
Platygyra	sinensis	both	PPN3	
Platygyra	sinensis	both	PPN6	44
Platygyra	sinensis	both	PPS3	
Platygyra	sinensis	both	PPS6	
Plesiastrea	versipora	3m	PPS3	45
Pocillopora	damicornis	3m	PPS3	46
Porites	cylindrica	3m	PPS3	47
Porites	lobata	6m	PPN6	48
Porites	lobata	both	PPS3	
Porites	lobata	both	PPS6	
Symphyllia	radians	3m	PPS3	49
Symphyllia	recta	3m	PPN3	50
Symphyllia	recta	both	PPN6	
Turbinaria	peltata	6m	PPN6	51

Lagun Marican	combined			
Genus	species	depthdist	site	N spp.
Acropora	palifera	3m	LM3	1
Acropora	pulchra	3m	LM3	2
Cyphastrea	microphthalma	3m	LM3	3
Echinopora	gemmacea	3m	LM3	4
Euphyllia	ancora	3m	LM3	5
Favia	laxa	3m	LM3	6
Favia	lizardensis	3m	LM3	7
Favia	matthaii	3m	LM3	8
Favia	pallida	3m	LM3	9
Favia	speciosa	3m	LM3	10
Favites	abdita	3m	LM3	11
Favites	chinensis	3m	LM3	12
Galaxea	fascicularis	3m	LM3	13
Goniastrea	edwardsi	3m	LM3	14
Goniopora	minor	3m	LM3	15
Heliofungia	actiniformis	3m	LM3	16
Hydnophora	rigida	3m	LM3	17

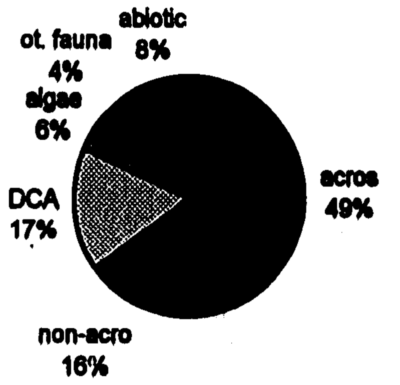
Montastrea	curta	3m	LM3	18
Montipora	millepora	3m	LM3	19
Oxypora	glabra	3m	LM3	20
Porites	lichen	3m	LM3	21
Porites	lobata	3m	LM3	22
Porites	lutea	3m	LM3	23
Stylophora	pistillata	3m	LM3	24

Bondo	combined species list			
Genus	species	depthdist	site	N spp.
Acropora	divaricata grp	3m	BND3	1
Acropora	nasuta	3m	BND3	2
Alveopora	sp. 1	3m	BND3	3
Coeloseris	mayeri	3m	BND3	4
Cyphastrea	microphthalma	3m	BND3	5
Diploastrea	heliopora	3m	BND3	6
Echinophyllia	orpheensis	3m	BND3	7
Euphyllia	glabrescens	3m	BND3	8
Favia	lizardensis	3m	BND3	9
Favia	lizardensis	3m	BND3	10
Favia	matthaii	3m	BND3	11
Favia	pallida	3m	BND3	12
Favia	speciosa	3m	BND3	13
Favites	abdita	3m	BND3	14
Favites	c. chinensis	3m	BND3	15
Favites	pentagona	3m	BND3	16
Galaxea	astreata	3m	BND3	17
Galaxea	fascicularis	3m	BND3	18
Goniastrea	aspera	3m	BND3	19
Goniastrea	edwardsi	3m	BND3	20
Goniastrea	favulus	3m	BND3	21
Goniastrea	retiformis	3m	BND3	22
Goniopora	djiboutiensis	3m	BND3	23
Goniopora	minor	3m	BND3	24
Heliofungia	actiniformis	3m	BND3	25
Leptastrea	transversa	3m	BND3	26
Lithophyllon	edwardsi	3m	BND3	27
Montipora	millepora	3m	BND3	28
Pectinia	paeonia	3m	BND3	29
Platygyra	daedalea	3m	BND3	30
Platygyra	sinensis	3m	BND3	31
Porites	annae	3m	BND3	32
Porites	lobata	3m	BND3	33
Symphyllia	radians	3m	BND3	34
Symphyllia	recta	3m	BND3	35
Turbinaria	peltata	3m	BND3	36

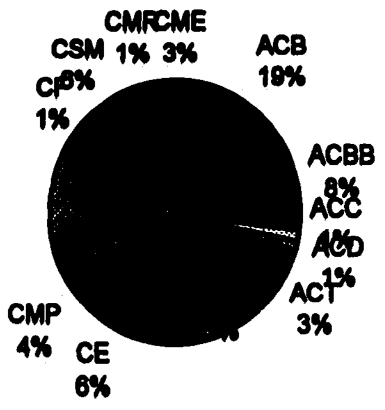
Appendix 2: cover and morphologies of Java Sea reefs by reef, exposure, and depth: Gosong Cemara windward.



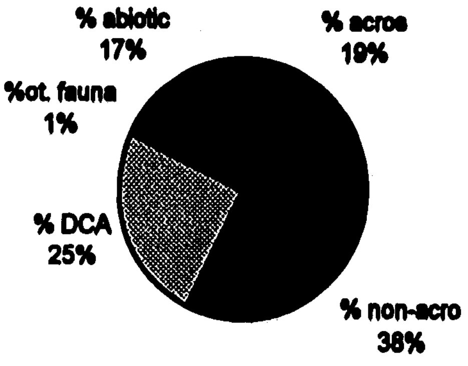
G. Cemara W/W 3m



G. Cemara w/w 3m cover classes



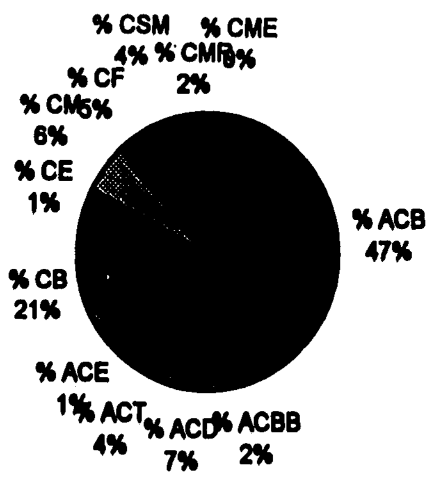
G. Cemara w/w 10m cover classes



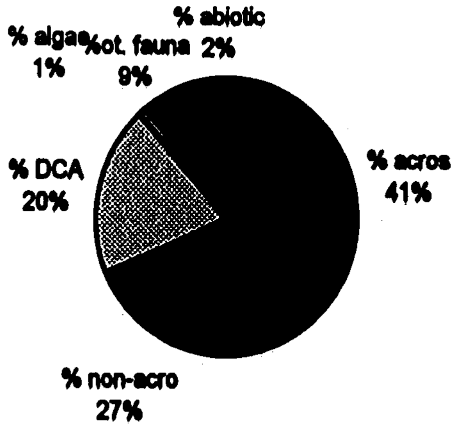
G. Cemara w/w 10m cover classes

Appendix 2: coral cover and morphology by reef, depth, and exposure: Gosong Cemara leeward.

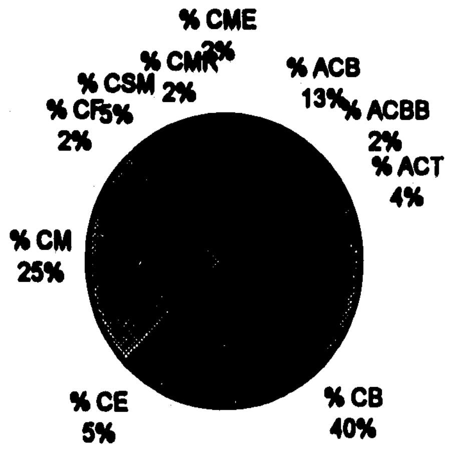
G. Cemara l/w 3m coral morphs



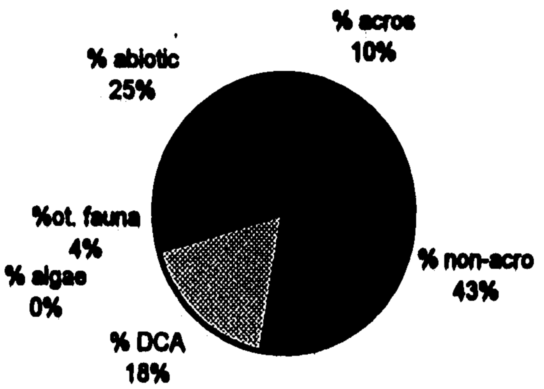
G. Cemara l/w 3m cover classes



G. Cemara l/w 10m coral morphs

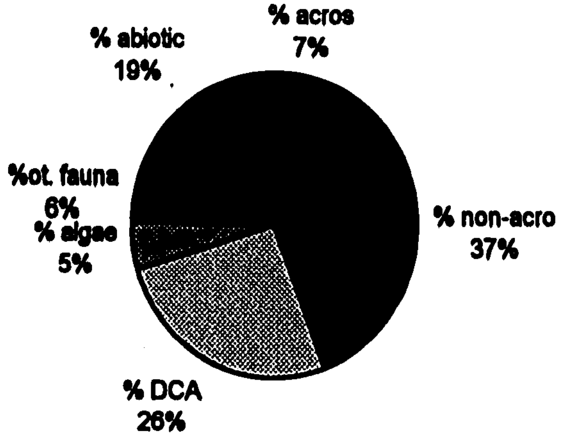


G. Cemara l/w 10m

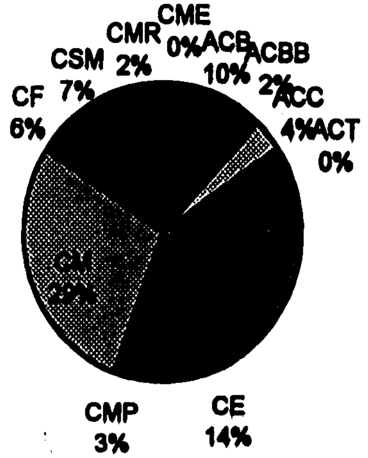


Appendix 2: coral cover and morphology data by reef, exposure, and depth: Pulau Kecil leeward.

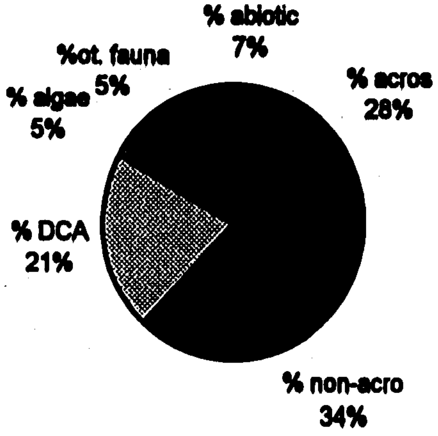
P. Kecil w/w 10m



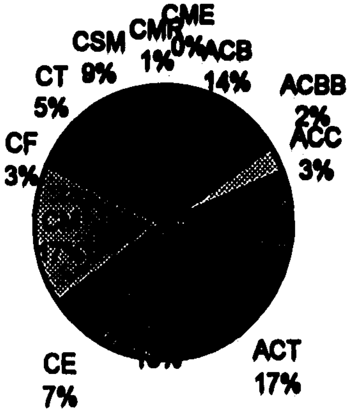
P. Kecil w/w 10m coral morphs



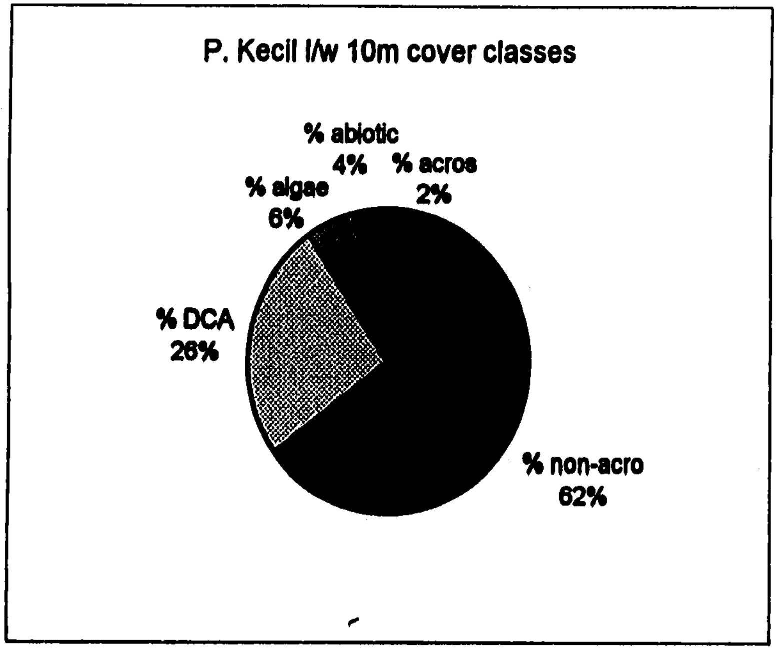
P. Kecil w/w 3m cover classes

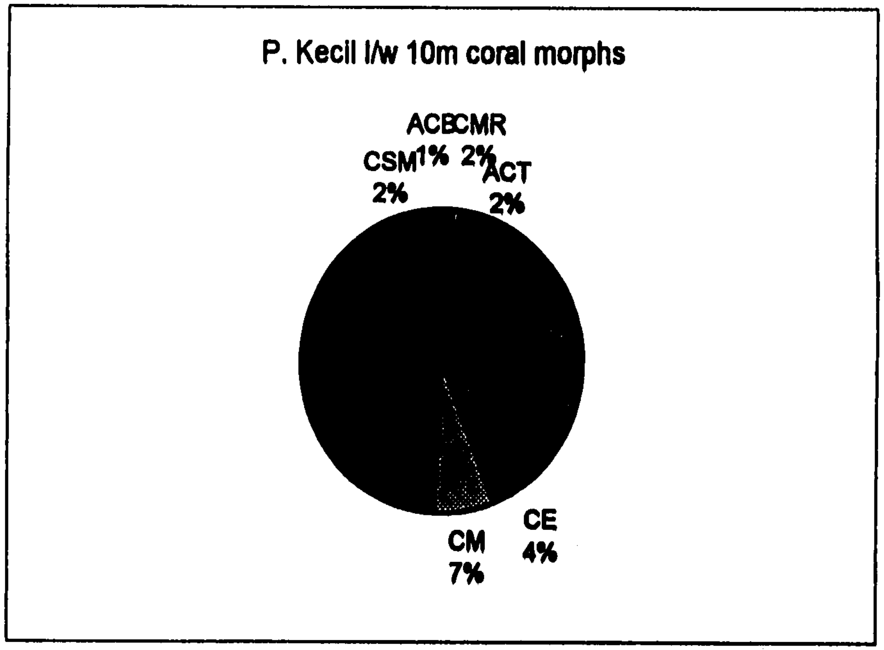


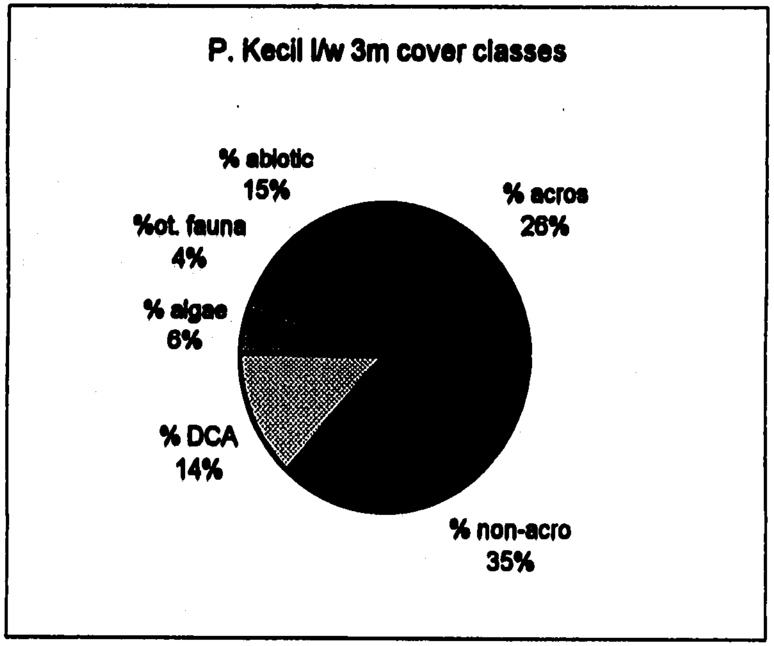
P. Kecil w/w 3m coral morphs

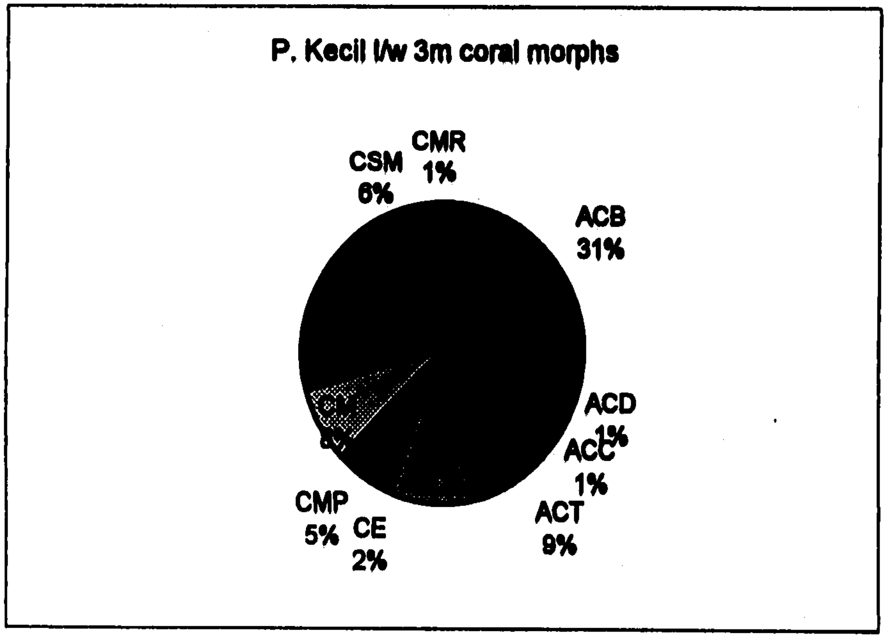


Appendix2: coral cover and morphology by reef, exposure, and depth: Pulau Kecil leeward


P. Kecil l/w 10m cover classes

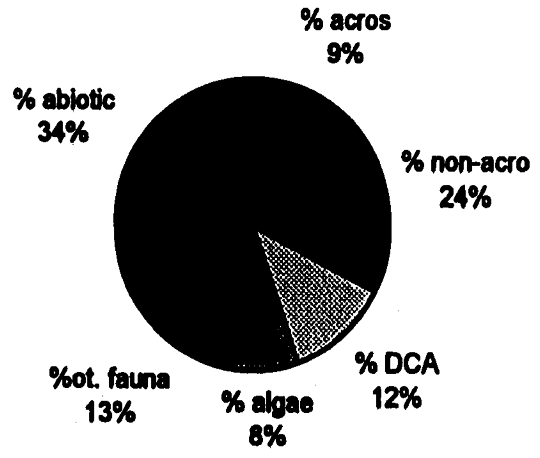

P. Kecil l/w 10m coral morphs


P. Kecil l/w 3m cover classes

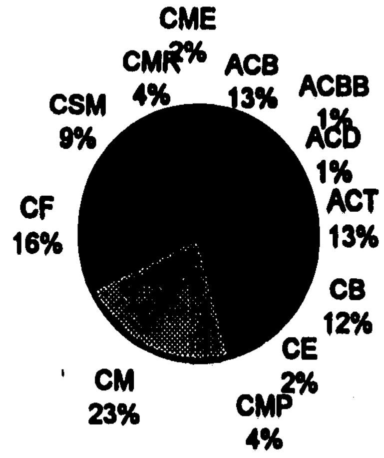

P. Kecil l/w 3m coral morphs

Appendix 2: coral cover and morphology by reef, exposure, and depth: Pulau Burung windward

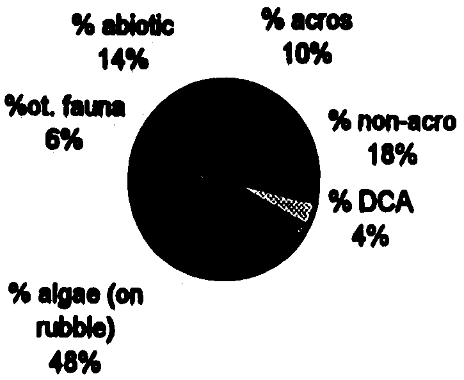
P. Burung w/w 10m cover classes



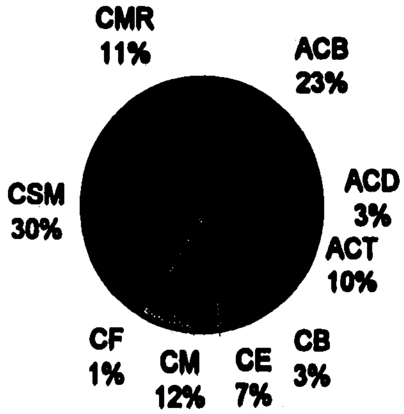
P. Burung w/w 10m coral morphs



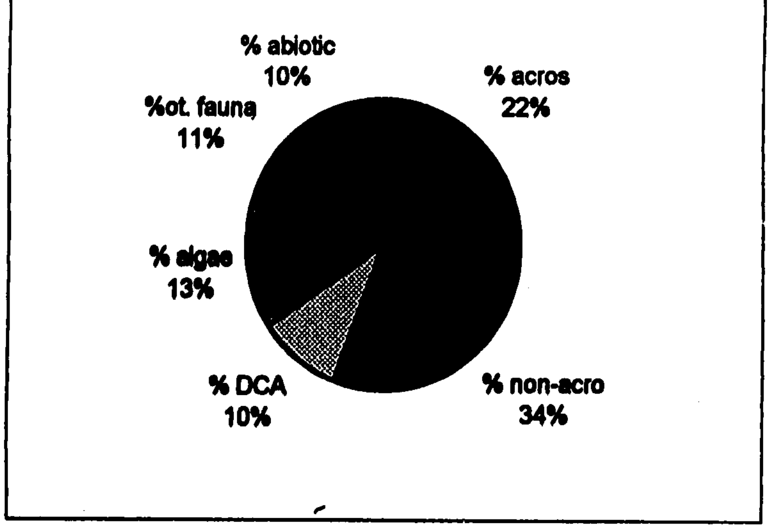
P. Burung w/w 3m cover classes



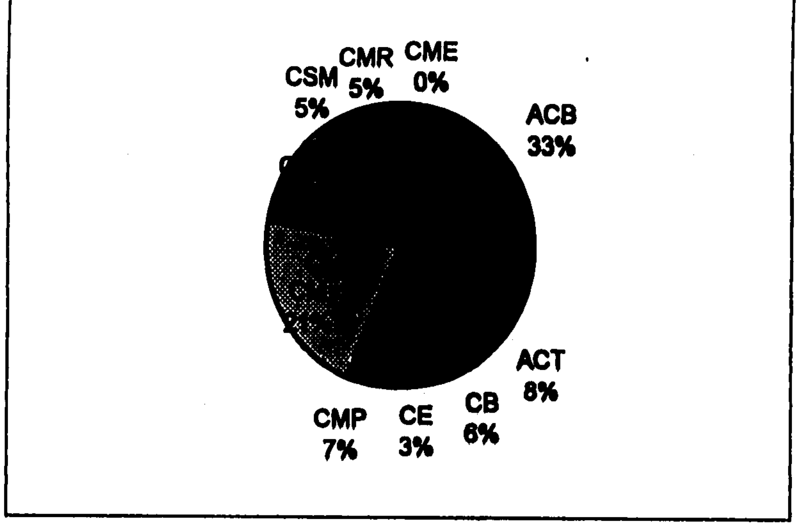
P. Burung w/w 3m coral morphs



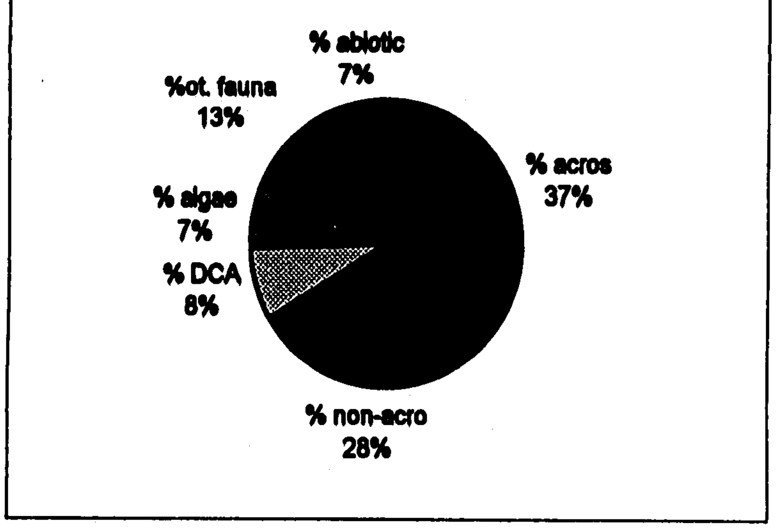
Appendix 2: coral cover and morphology by reef, exposure, and depth: Pulau Burung leeward



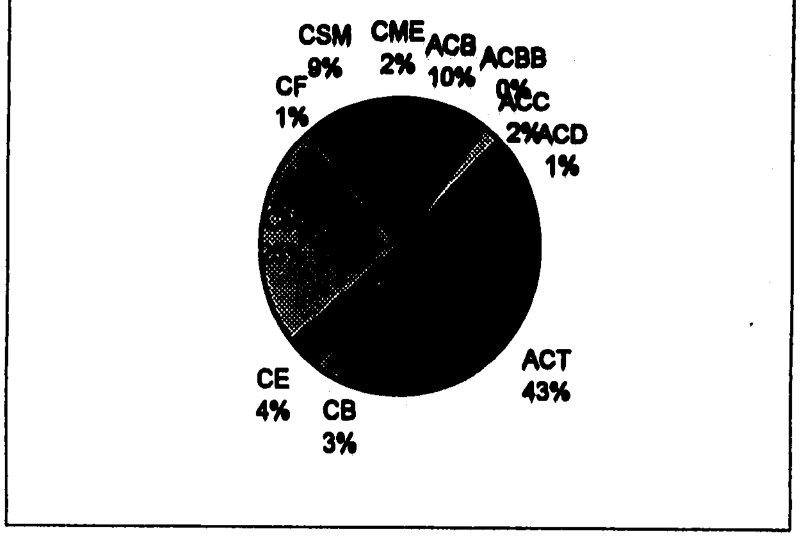
P. Burung l/w 10m cover classes



P. Burung l/w 10m coral morphs

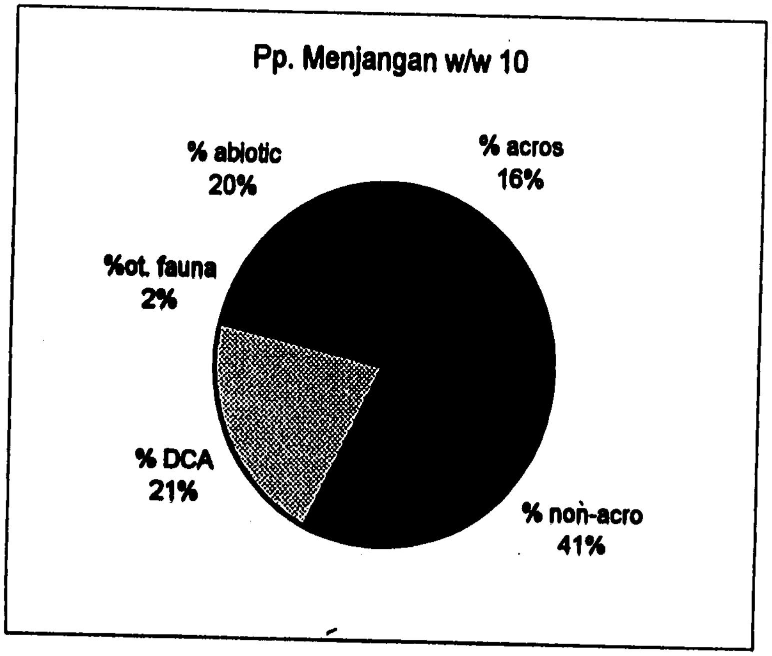


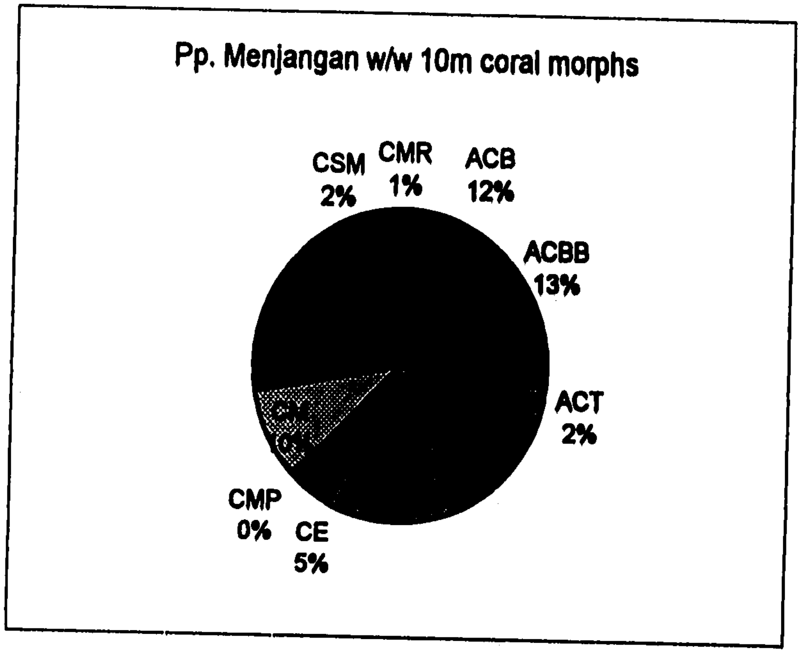
P. Burung l/w 3m cover classes

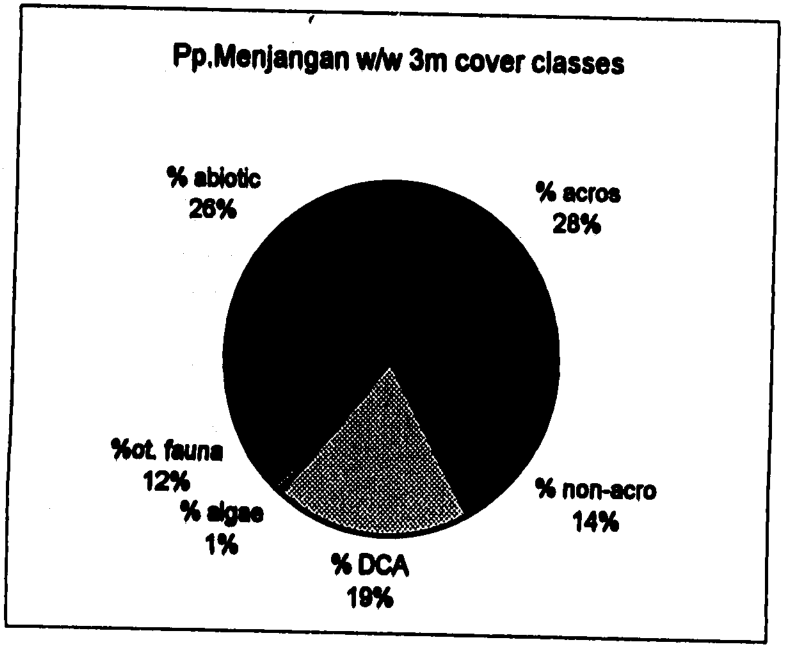


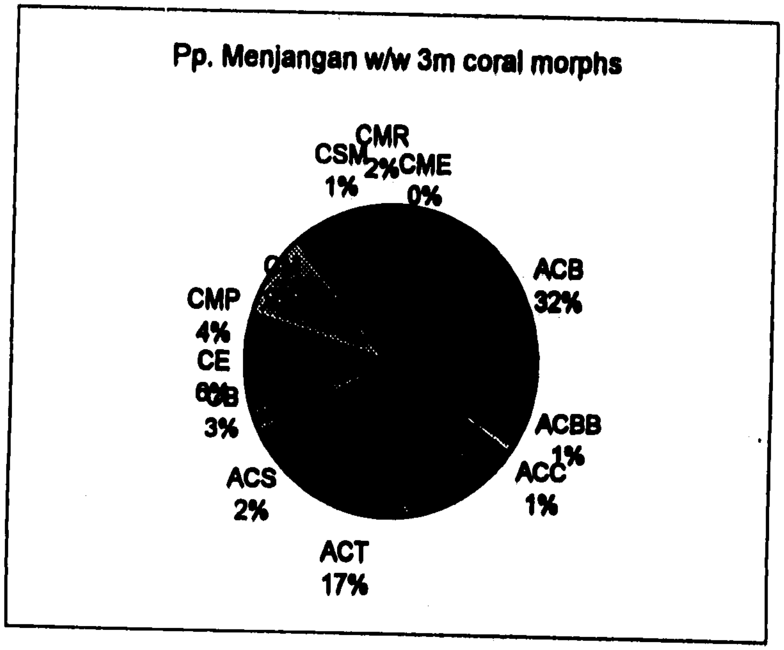
P. Burung l/w 3m coral morphs

Appendix 2: coral cover and morphology by reef, exposure, and depth: Pp. Menjangan windward.


Pp. Menjangan w/w 10

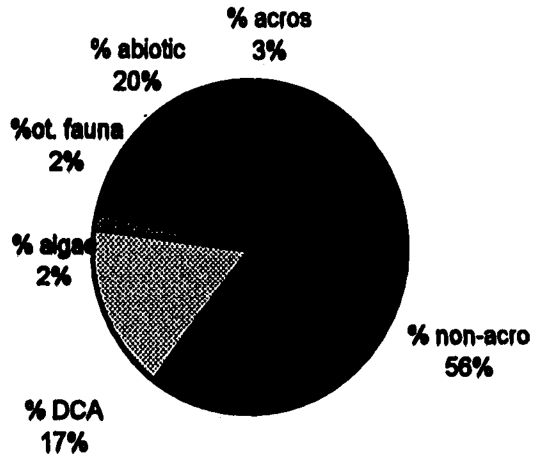

Pp. Menjangan w/w 10m coral morphs


Pp.Menjangan w/w 3m cover classes

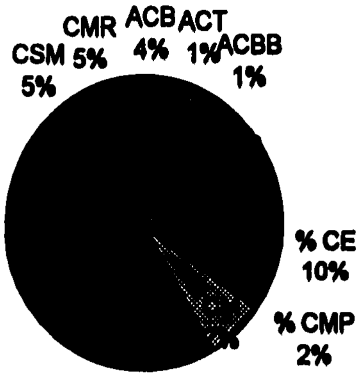

Pp. Menjangan w/w 3m coral morphs

Appendix 2: coral cover and morphology by reef, exposure, and depth: Pp. Menjangan leeward

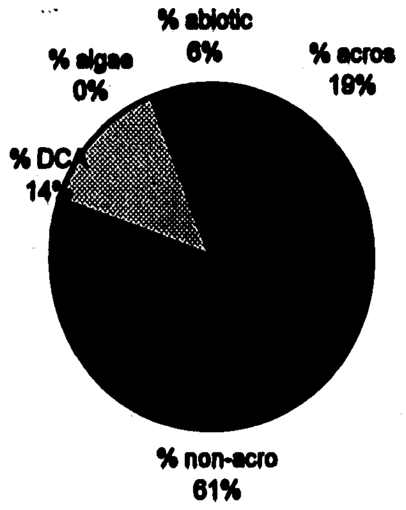
Pp. Menjangan l/w 10m cover classes



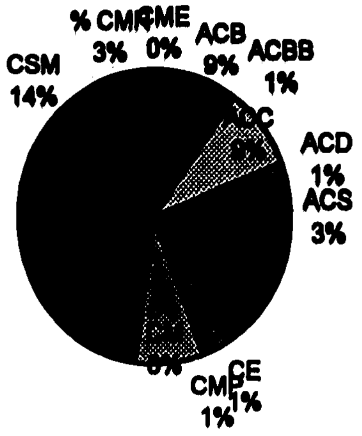
Pp.Menjangan l/w 10m coral morphs



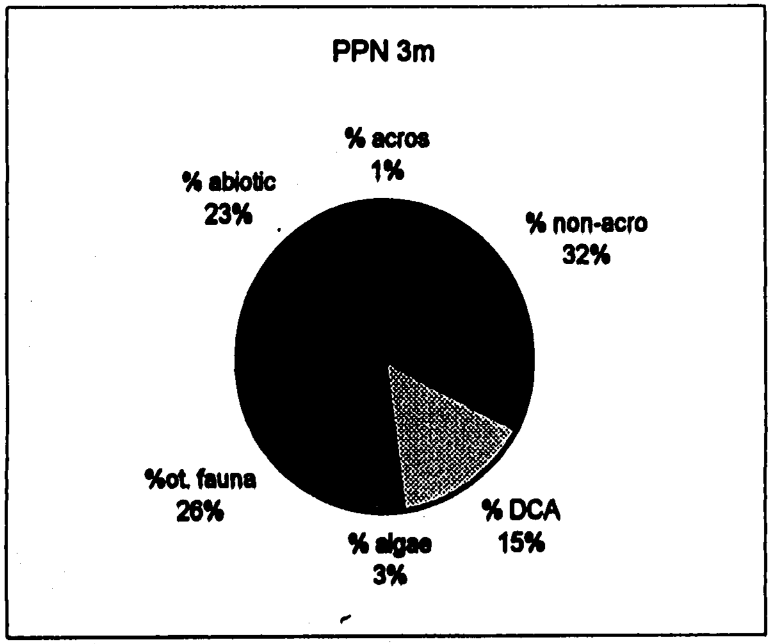
Pp. Menjangan l/w 3m cover classes

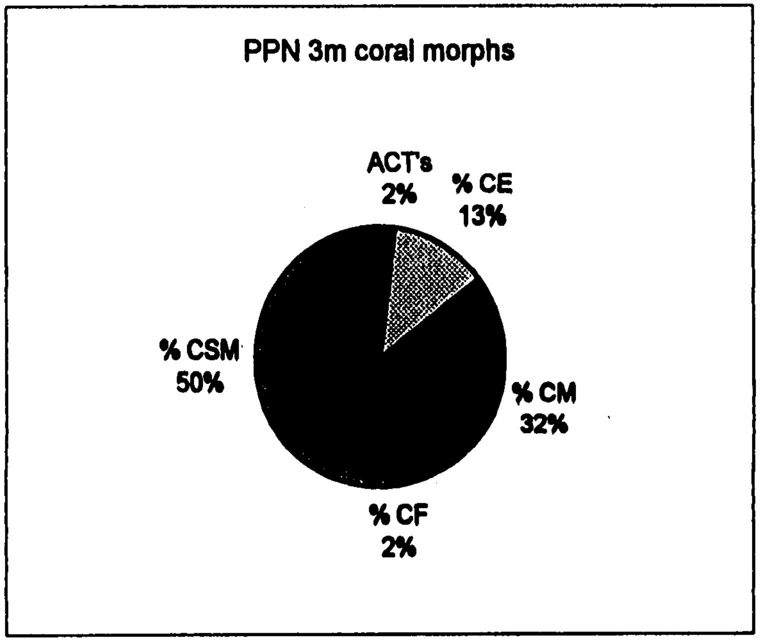


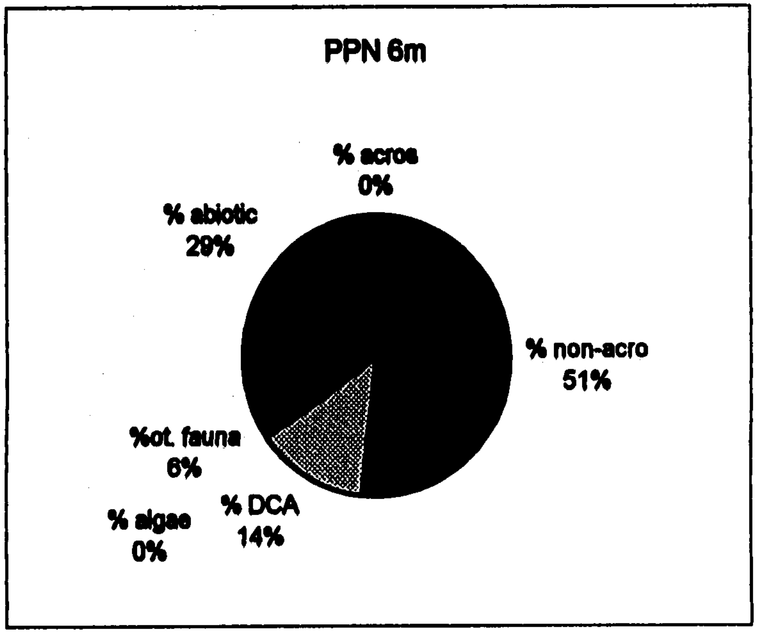
Pp. Menjangan l/w 3m coral morphs

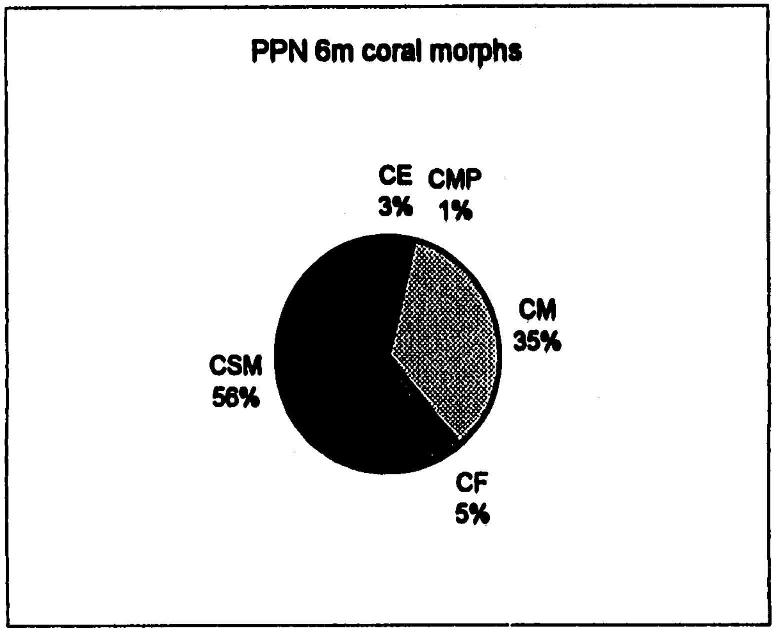


Appendix 2: Morphological Composition by Reef, Depth, and Exposure, Java Sea sites: Pulau Panjang North, 3m, 6m.

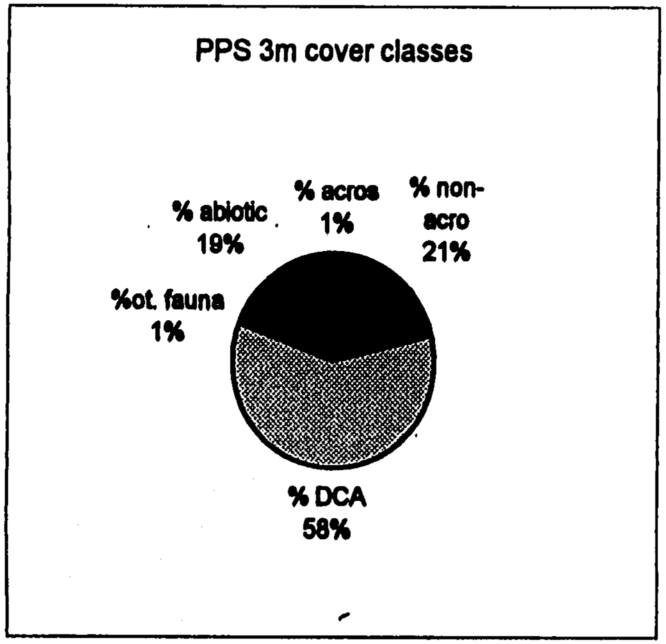

PPN 3m

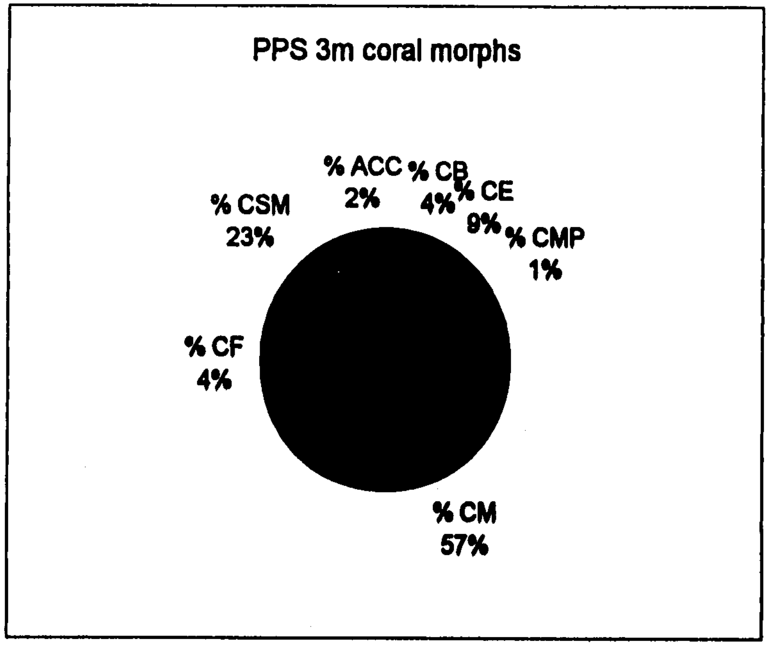

PPN 3m coral morphs

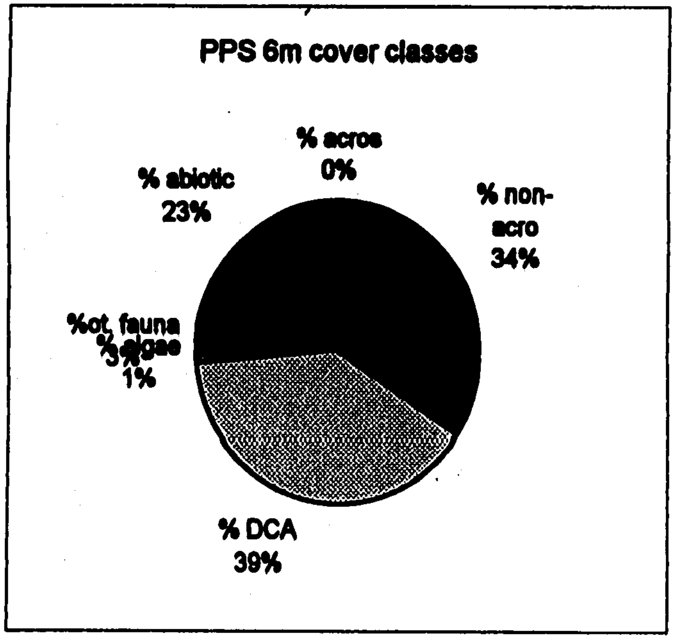

PPN 6m

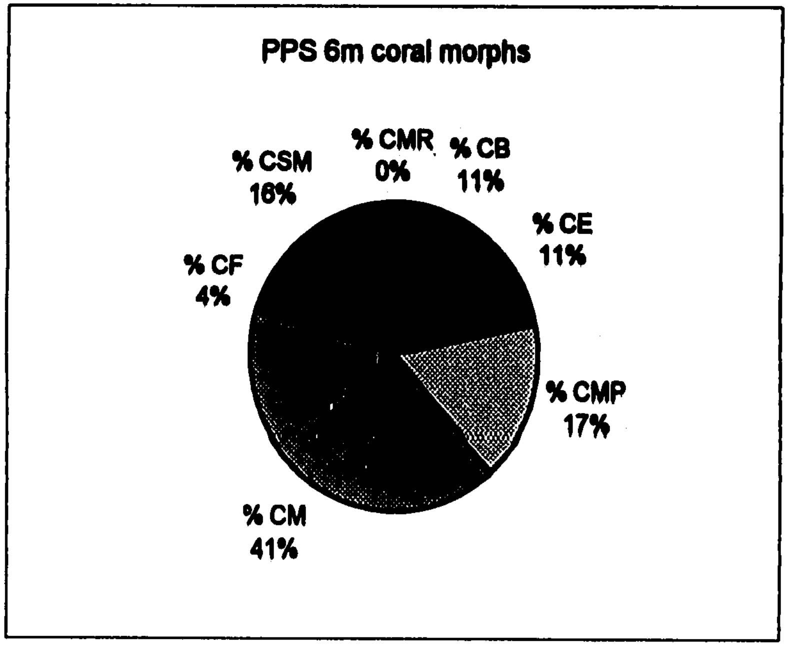

PPN 6m coral morphs

Appendix 2: coral cover and morphology data by reef, depth, and exposure: Pulau Panjang South, 3m, 6m.

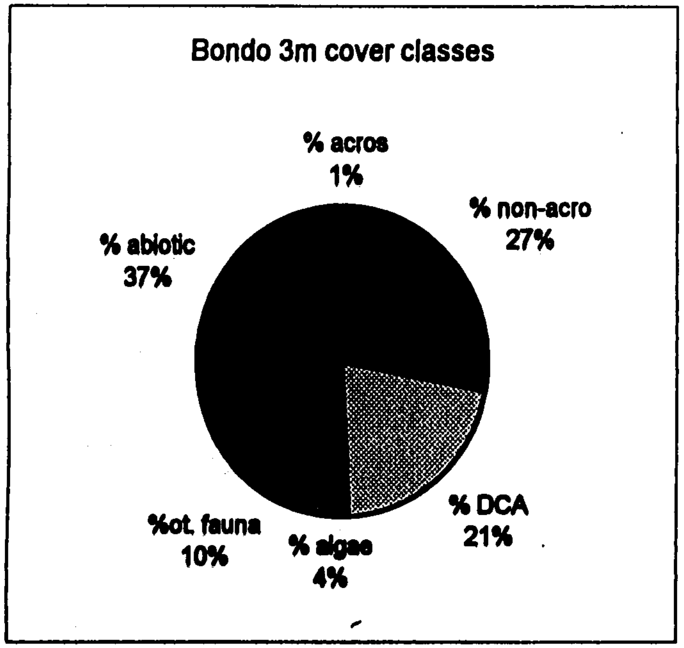


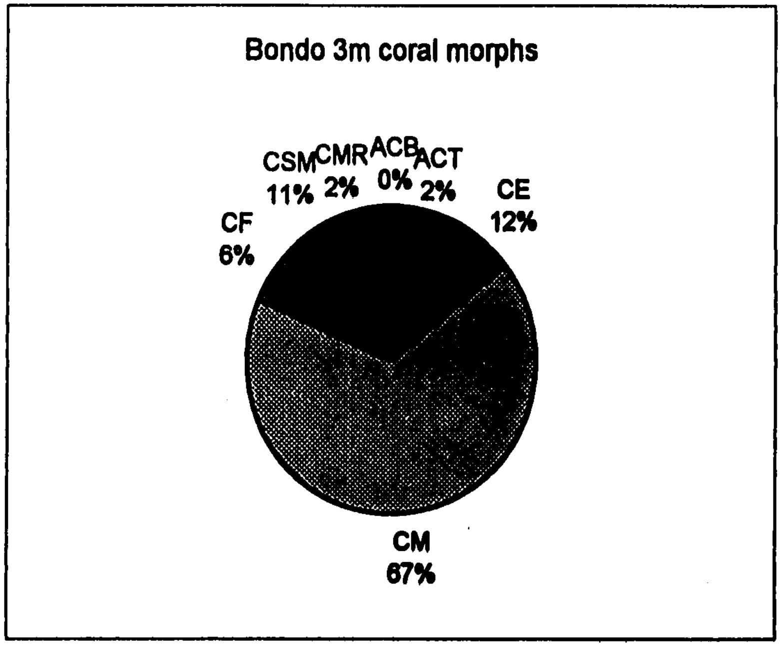


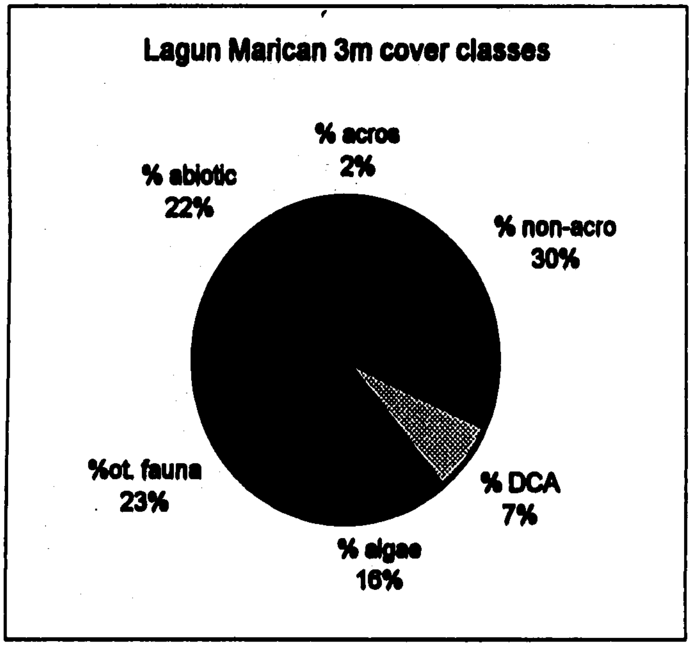


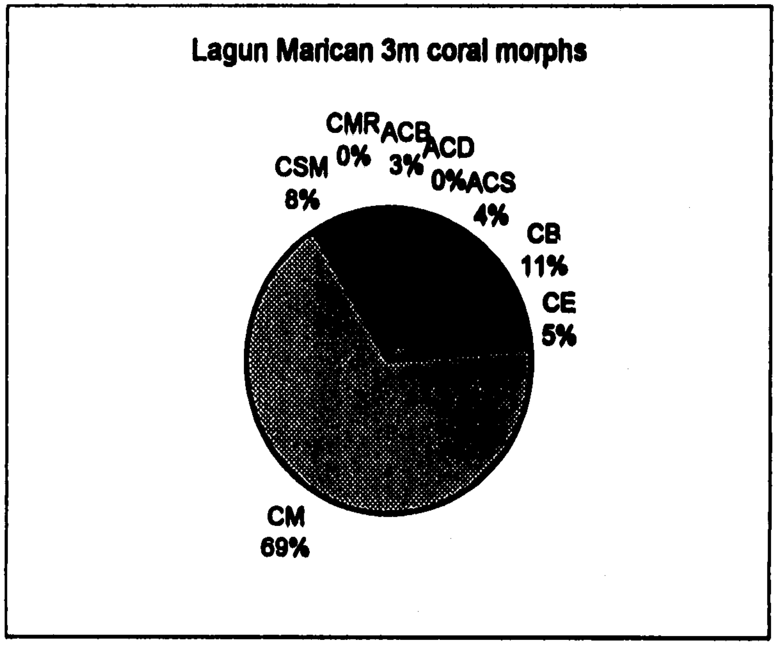


Appendix 2: coral cover and morphology data by reef, depth, and exposure:
Bondo, Lagun Marican.


Bondo 3m cover classes


Bondo 3m coral morphs


Lagun Marican 3m cover classes


Lagun Marican 3m coral morphs

Appendix 3: Individual coral growth rate measurements by site, coral and year. All values in mm/yr.

site	Cemara			P. Kecil					L. Marican				
year	KJ 1.2	KJ 4.4	KJ 5.1	PK1.5	PK 2.2	PK 3.3	PK 4.4	PK 5.4	LM 1.3	LM 2.5.2	LM 3.5	LM 4.6	LM 5.
1996				13	14	6	12	9	8	6.5	7	10	10
1995	6	10	8	13	12	11	15	8.5	11	12.8	11	9	10
1994	10	8	9	9	6.5	10	11	8	10	12	9	13	16
1993	7	9.5	9	11.5	11.5	7	11	6	11	14	8.5	12	13
1992	9.5	10.5	8	11	6.5	11.5	9	6		9	11.5	17.5	10
1991	9	9	8.5	13	8	13	8.5	5.5		11	9.5	14	17
1990	7.5	13	9	16	7	10	6	6.5		10	10.5	11	10
1989	7	15	9	11	9.5	12	8.5	8		10.5	10.5	13	11
1988	9	10	7.5	6	7	10	10	7		10	10	17	10
1987	8.5	10		12	7.5	11.5		7			8	15	
1986	12	11.5		8	7	9		12			7	13	
1985	8	9				13.5		9				12	
1984	7	9				11.5		8					
1983	8					11.5							
1982	9												
1981	9												
1980	10												
1979	7												

Appendix 3: Individual coral growth rate measurements by site, coral and year. All values in mm/yr.

Jepara								Bondo				site
PPS 1	PPS 2	PPS 4	PPS 5	PPS 11	PPS 12	PPS 21	PPS 22	B 2.1	B 4.1	B 9.6	B 15.3	year
						4	5	5	11	7	9	1996
7.5	6	7	8	12	18	5	15	15	14	12	12	1995
13	14	14	10	23	20	13	16	18	20	10	7.5	1994
12	8	14	9	19	14	13	18	19		10.5	5.5	1993
8	12	14	10	18		11	14			8.5	11.5	1992
7	9.5	14	10	12			12			9	10.5	1991
10	8.5	17.5	13							11.5	8	1990
	12	13								8.5	9	1989
	18	17.5									10	1988
	14	14									13	1987
	17										6	1986
	12											1985
												1984
												1983
												1982
												1981
												1980
												1979

Appendix 4: Environmental Data: chlorophyll concentrations averaged among seasons.

		Cemara l/w			Lgn Marican			P. Kecil l/w			PPN			PPS					
		date	conc.	average	date	conc.	average	date	conc.	average	date	conc.	average	date	conc.	average			
"Wet Season" 94	Nov and Dec 94	22-Nov-94	0.06133					19-Nov-94	0.06948		10-Nov-94	0.29584		10-Nov-94	0.58094		season avg		
		17-Dec-94	0.3598					17-Dec-94	0.36548		21-Dec-94	1.03086		21-Dec-94	0.65064		Cem l/w		
				0.220465						0.21748			0.66336			0.61579	dry	wet	all
"Dry Season" 95	July to Oct 95	5-Oct-95	0.08419		5-Oct-95	0.15583		10-Oct-95	0.08618		13-Oct-95	0.28084		30-Sep-95	0.39988		0.19783	0.362012	0.279921
					5-Oct-95	0.14118					29-Oct-95	1.51836		13-Oct-95	0.57954		Mron		
					12-Oct-95	2.5834					6-Aug-95	0.3008		29-Oct-95	1.27722		dry	wet	
					29-Jul-95	0.33828								6-Aug-95	0.40786		0.718456	1.50333	1.109893
					30-Jul-95	0.36359											P. Kecil l/w		
				0.08419			0.718456			0.08616			0.699287			0.66607	dry	wet	
"Wet Season" 95	Nov and Dec 95 .	8-Nov-95	0.2862		12-Nov-95	2.28086		9-Nov-95	0.52859		4-Dec-95	1.74186		4-Dec-95	1.69194		0.173707	0.343328	0.258517
				0.2862			2.28086			0.52859			1.74186			1.69194	PPN		
"Dry Season" 96	Sept and Oct 96	24-Sep-96	0.33914					28-Sep-96	0.2953		13-Sep-96	1.5491		13-Sep-96	0.60016		dry	wet	
		24-Sep-96	0.79742					28-Sep-96	0.1855		20-Sep-96	1.21108		20-Sep-96	0.60356		0.740417	1.639087	1.189757
		29-Sep-96	0.24284								29-Oct-96	1.018		29-Oct-96	0.69512		PPS		
				0.459733						0.2404			1.259367			0.632947	dry	wet	
"Wet Season" 96	Nov and Dec 96	24-Nov-96	0.22712		23-Nov-96	0.72568		25-Nov-96	0.36592		15-Nov-96	3.28032		15-Nov-96	3.34284		0.798257	1.145128	0.971691
		24-Nov-96	0.20374								29-Nov-96	1.48168		29-Nov-96	1.4165				
											6-Dec-96	0.59044		6-Dec-96	0.73184				
				0.21543			0.72568			0.36592			1.77748			1.830327			
Average			avg	0.249204		avg	1.241039		avg	0.28731		avg	1.228293		avg	1.087415			
stdev			stdev	0.14306		stdev	0.900627		stdev	0.166563		stdev	0.539786		stdev	0.617228			
Average wet season data and dry season			wet/dry	0.279921		wet/dry	1.109893		wet/dry	0.258517		wet/dry	1.189757		wet/dry	0.971691			
Not Used		Cemara w/w						P. Kecil w/w											
		22-Nov-94	0.12039					17-Dec-94	0.32203										
		17-Dec-94	0.31058					20-Dec-94	0.40759										
		8-Nov-95	0.57586					25-Nov-96	0.25086										
		24-Sep-96	0.44632																
		24-Sep-96	0.7328																
		8-Oct-96	0.12861																
		24-Nov-96	0.44086																
		24-Nov-96	0.4476																

Appendix 4. Environmental data: suspended particulate matter measurements, Java Sea sites, by date, location, and depth.

date	Location	side	mg/l =	avgs	
30-Jul-95	B.Lawang	L/W	28.8		
22-Sep-96	Bondo		23.29	Bondo	
16-Nov-96	Bondo		20.43	21.03714	BND
30-Nov-96	Bondo		10.96		
21-Sep-96	Bondo 1		23.06		
30-Oct-96	Bondo 1		24.33		
21-Sep-96	Bondo 2		22.57		
21-Sep-96	Bondo 2		22.61		
27-Sep-96	Burung	L/W	19.69	19.69	BRL
25-Sep-96	Burung	W/W	4.45	4.45	BRW
28-Jul-95	Cemara	L/W	33.6	Cem L/W	
5-Oct-95	Cemara	L/W	10	20.26	CML
6-Oct-95	Cemara	L/W	15		
8-Oct-95	Cemara	L/W	25		
8-Nov-95	Cemara	L/W	20		
24-Sep-96	Cemara	L/W	17.3		
29-Sep-96	Cemara	L/W	20.92	Ceml/w10	
28-Jul-95	Cemara	L/W 10m	30.7	30.7	CML10
6-Oct-95	Cemara	W/W	25	Cem w/w	
8-Oct-95	Cemara	W/W	25	22.9775	CMW
8-Nov-95	Cemara	W/W	20		
24-Sep-96	Cemara	W/W	21.91		
12-Nov-95	L Marican	sfc	30	L Marican	
30-Jul-95	L Marican		24.8	26.386	Lmarican
5-Oct-95	L Marican		35		
23-Nov-96	L Marican		10.53		
30-Jul-95	L. Pinggir		21.6		
12-Nov-95	L. Pinggir		40		
27-Nov-96	P. CemBer	L/W	6.11	6.11	PCemBer
12-Nov-95	P. CemKcl	L/W	30	30	Pcem Kcl
10-Oct-95	P. Kecil	L/W	45	PKL	
9-Nov-95	P. Kecil	L/W	20		
28-Sep-96	P. Kecil	L/W	2.14		
25-Nov-96	P. Kecil	L/W	12.35	19.8725	PKL
10-Oct-95	P. Kecil	W/W	5	PKW	
25-Nov-96	P. Kecil	W/W	14.49	9.745	PKW
4-Oct-95	P. Kumbang		15		
30-Sep-95	PPN	sfc	24.1	PPN	
13-Oct-95	PPN	sfc	20	21.33	PPN
4-Dec-95	PPN	sfc	40		
13-Sep-96	PPN		19.59		
20-Sep-96	PPN		20.54		
29-Oct-96	PPN		20.33		
29-Oct-96	PPN		21.43		
15-Nov-96	PPN		18.56		
6-Dec-96	PPN		7.42		
16-Oct-95	PPS	5m	25	PPS 5m	
16-Oct-95	PPS	5m	15	20	PPS 5m
16-Sep-95	PPS	sfc	25	PPS sfc	
30-Sep-95	PPS	sfc	35	28.91333	PPS sfc
13-Oct-95	PPS	sfc	20.9		
16-Oct-95	PPS	sfc	5		
29-Oct-95	PPS	sfc	25		
4-Dec-95	PPS	sfc	80		
13-Sep-96	PPS		22.26		
20-Sep-96	PPS		25.65		
29-Oct-96	PPS		22.02		
15-Nov-96	PPS		20.86		
29-Nov-96	PPS		31.83		
6-Dec-96	PPS		33.44		
27-Nov-96	T. Gelam		15.27	15.27	T. Gelam

Appendix 4: Sediment resuspension rates, individual values and averages by site, Java Sea.

Averages	rates	sediment	resusp.	in traps						
site	CMW3	CML3	CMW10	CML10	CMW20	CML20	PKW3	PKL3	PKW10	PKL10
rate	2.292994	2.672307	8.0350318	10.33083	5.866242	2.740755	2.394904	1.324841	1.15499	1.749469
(mg/cm2/d)	51.32537	1.150136	2.3293904	1.6305732	1.728844	1.091902	2.547771	0.509554	1.93631	1.732484
		1.121019	24.106688	1.1767516	11.13004	2.853503	1.808316	3.070594	3.12183	5.703291
		9.066348		3.0640127		7.945329	1.355397		4.35372	8.269958
		0								
average	26.80918	2.801962	11.49037	4.0505419	6.24171	3.657872	2.026597	1.634996	2.64171	4.3638
stdev	34.67113	3.628513	11.292351	4.2634171	4.711832	2.969546	0.549372	1.308388	1.39874	3.204728
n	2	5	3	4	3	4	4	3	4	4

Appendix 4: Sediment resuspension rates, individual values and averages by site, Java Sea.

Averages	rates	sediment	resusp.	in traps		
PPN1	PPN3	PPS1	PPS3	PPS6	Bondo1	site
15.91029724	16.34156	23.872081	9.210014154	20.79352	74.47689	rate
43.88989991	62.7434	54.954504	7.881104034	8.176752	1542.588	(mg/cm2/d)
123.0989711	12.40813	284.61253	16.56050955	15.15074	110.8621	
737.9458599	273.6288	35.666515	41.56050955	33.9172		
52.55459509	13.28253	5.5711253	106.3535032	51.25199		
		43.651805	8.587352138	9.194023		
				51.03857		
				9.970428		
194.6799246	75.68089	80.93535	31.69216544	27.07469	575.9758	average
306.2505224	112.6598	115.26561	38.74767799	18.54775	837.3088	stdev
5	5	5	6	7	3	n