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**The effects of sedimentation on Indo-Pacific reef corals**

Hodgson, Gregor, Ph.D.

University of Hawaii, 1989

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**THE EFFECTS OF SEDIMENTATION  
ON INDO-PACIFIC REEF CORALS**

**A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE  
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**DOCTOR OF PHILOSOPHY**

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**By**

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"There is something in the psychology of mankind to which coral reefs never fail to appeal."

J. Stanley Gardiner, 1931.

## ABSTRACT

A 12 month study (1986) was made of the effects of coastal logging on terrestrial erosion and sediment discharge from a watershed bordering Bacuit Bay (El Nido), Palawan, Philippines. A complementary study was made of the effects of sedimentation on reef-building corals in Bacuit Bay.

Logging significantly increased soil erosion above natural levels, primarily due to road construction. A large amount of eroded soil entered the main river (Manlag) draining the logging concession. Suspended sediment load was significantly greater there than in a nearby river unaffected by logging. Less than 1% of sediment discharge from the Manlag River in 1986 (39,154 mt) was attributed to natural erosion.

Suspended sediment was transported into Bacuit Bay by low salinity sediment plumes. The effects of Manlag River discharge on Bacuit Bay (low salinity, reduced temperature and high suspended sediment) were not detected beyond a radius of approximately 3 km from the river outlet. Analysis of particle size and calcium carbonate component of sediments deposited in the bay indicated that the deposition rate of sediment of terrestrial origin depended on distance from the Manlag River outlet. The sediment deposition rate at the site closest to the river mouth was significantly greater than the rate at the control site, and high enough to damage corals. Daily Manlag River

discharge records indicated that sedimentation pulses high enough to damage corals could have occurred for 7 days at all study sites except the control. There was little evidence that factors other than increased sedimentation could have damaged Bacuit Bay corals in 1986

Fifty species of corals were used in field and aquarium tests of sedimentation tolerance in Hawaii and the Philippines, and then categorized based on resistance to damage. Tissue necrosis only occurred in areas covered by a sediment layer. Tetracycline in seawater significantly decreased tissue damage and enhanced survival of corals subjected to sedimentation for up to 10 days; it was concluded that tetracycline-sensitive microbes, presumably bacteria, were a causative factor of coral tissue damage and mortality following sediment deposition. One Hawaiian coral species was not damaged by sedimentation. For species that have a high physiological resistance to infection or that can survive partial mortality, sediment clearing ability may be relatively unimportant for survival.

The extent of sedimentation damage to corals appeared to be related to phenotype. Species with large diameter, protrusile polyps were less likely to be damaged by sedimentation than other species. Interactions of growth form with other characters made it difficult to detect a

relationship between susceptibility to sedimentation damage and growth form.

Predictions were made based on a phenotype-sediment tolerance hypothesis. Phenotypes that had been damaged in sedimentation tests were predicted to be less common following 1 year of accelerated sedimentation. Between January and December, 1986, high sedimentation at the site nearest the Manlag River outlet is concluded to have caused a significant reduction in coral cover and number of species and a significant increase in size of dead tissue patches (partial mortality). Pulses of high sediment deposition during peak Manlag River discharge periods are believed to have caused significant overall reduction in coral cover, number of genera and species and increased partial mortality at the 7 treatment sites. Differences in distribution of abundance among phenotypes between January and December 1986 support this idea.

Corals with phenotypes predicted to have a low resistance to sedimentation (low polyp extension ability, small corallite diameter) were significantly more common in January than in December. The statistical linkage of phenotypic characters, especially among the highly abundant acroporids made it difficult to distinguish the effect of growth form on sedimentation damage to corals.

There is little evidence to support the idea that sedimentation resistance has evolved along supra-specific

phylogenetic lineages. Few species appear to be specialized for sediment "refuges", and only one species appears to be restricted to high sedimentation environments. Sedimentation is one of many environmental variables that can affect coral community structure, and at high levels it may limit which species are found at a given site. This limitation will depend on the interaction of physical parameters, especially water motion, with biological parameters including corallite diameter, polyp extensional ability, colony growth form and active resistance mechanisms.

Pocillopora damicornis planulae were unable to settle on glass covered with fine sediment even when only half the available substrate was covered. Planulae may be "discouraged" from settling at sites with fine sediments nearby, even if bare space is available. If the larvae of many species of corals have behavior similar to P. damicornis planulae, then sediment deposition at a much lower rate than required to damage adult corals could significantly reduce planula settlement and perhaps coral recruitment in nature.

## TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS . . . . .	iii
ABSTRACT . . . . .	v
LIST OF TABLES . . . . .	xvii
LIST OF FIGURES . . . . .	xix
CHAPTER I.           GENERAL INTRODUCTION	
Community Structure and the	
Evolution of Phenotypes . . . . .	1
Hard Corals and Coral Reefs . . . . .	3
Sedimentation and Coral Reefs. . . . .	12
Anthropogenic Coral Reef	
Sedimentation . . . . .	13
Project Design . . . . .	16
Study Site . . . . .	19
Palawan Island . . . . .	19
Geological History . . . . .	22
Bacuit Bay . . . . .	23
Bacuit Bay Drainage Basin . . . . .	26



## TABLE OF CONTENTS (continued)

	Page
Logging . . . . .	28
Weather . . . . .	31

## CHAPTER II. TERRESTRIAL PHYSICAL PARAMETERS

Introduction . . . . .	33
Measuring Erosion . . . . .	36
Methods . . . . .	41
Soil . . . . .	41
Rainfall . . . . .	41
Surface Erosion . . . . .	45
Suspended Sediment Discharge . . . . .	49
Results . . . . .	58
Soil . . . . .	58
Rainfall . . . . .	60
Erosion Plot Runoff . . . . .	62
Erosion Plot Erosion . . . . .	64
Suspended Sediment Discharge . . . . .	66
Discussion . . . . .	76
Soil, Rainfall, Runoff and Erosion . . . . .	76
Water and Sediment Discharge . . . . .	82
Conclusions . . . . .	85

## TABLE OF CONTENTS (continued)

	Page
 CHAPTER III. MARINE PHYSICAL PARAMETERS	
Introduction . . . . .	88
Methods . . . . .	93
Temperature and Salinity . . . . .	94
Wind, Waves and Currents . . . . .	94
Turbidity . . . . .	97
Sediment Deposition . . . . .	97
Sediment Characteristics . . . . .	100
Results . . . . .	101
Temperature and Salinity . . . . .	101
Wind . . . . .	103
Waves . . . . .	107
Currents, Turbidity and Sediment Plume Dynamics . . . . .	111
Sediment Deposition . . . . .	121
Trapped Sediments . . . . .	124
Benthic Sediments . . . . .	128
Correlation of Discharge, Wave Height and Deposition . . . . .	131
Discussion . . . . .	132
Bay Temperature and Salinity . . . . .	132
Turbidity . . . . .	133

## TABLE OF CONTENTS (continued)

	Page
Sediment Deposition . . . . .	135
Correlation of Discharge, Wave Height and Deposition . . .	137
Benthic Sediment . . . . .	139
Resuspension Versus Discharge . . . . .	141
Potential Sediment Dilution In The Bay . . . . .	144
Conclusions . . . . .	150

## CHAPTER IV. EFFECTS OF SEDIMENT ON CORALS

Introduction . . . . .	153
Sedimentation and Coral Cleaning Mechanisms . . . . .	154
Sedimentation and Coral Phenotype . . . . .	155
Sedimentation and Coral Damage .	159
Sedimentation and Coral Larvae .	160
Sedimentation and Coral Growth .	161
Complete Burial of Corals . . .	162
Sedimentation and Drilling Mud .	164
Assessing Causality . . . . .	165

## TABLE OF CONTENTS (continued)

	Page
Abrasion . . . . .	166
Light Attenuation . . . . .	166
Microorganisms . . . . .	168
Methods . . . . .	170
Selection of Species and	
Phenotypes . . . . .	170
Growth Form . . . . .	171
Corallite Diameter . . . . .	172
Polyp Extensional Ability . . . . .	174
Sedimentation Resistance	
Hierarchy: Aquaria . . . . .	177
Sedimentation Resistance	
Hierarchy: Field . . . . .	181
Sediment and Planula Settlement	183
Antibiotic Tests: Philippines . . . . .	185
Antibiotic Tests: Hawaii . . . . .	187
Statistics . . . . .	188
Results . . . . .	189
Sedimentation and Tissue Necrosis	189
Sedimentation Resistance	
Hierarchy: Aquaria . . . . .	191
Sedimentation Resistance	
Hierarchy: Field . . . . .	194

## TABLE OF CONTENTS (continued)

	Page
Sediment and Planula Settlement	202
Antibiotic Tests: Philippines .	203
Antibiotic Tests: Hawaii . . . .	205
Discussion . . . . .	207
Sedimentation, Tissue Necrosis And Microorganisms . . . . .	208
Sedimentation Resistance Hierarchy . . . . .	215
Possible Advantages of Certain Phenotypes . . . . .	219
Exceptions to Phenotype- Sedimentation Hypothesis . . .	220
Previous Work . . . . .	223
Partial Mortality . . . . .	225
Sediment Effects on Larvae . . .	226
Conclusions . . . . .	227

## CHAPTER V.

### SEDIMENTATION AND CORAL COMMUNITY

STRUCTURE . . . . .	231
---------------------	-----

Previous Work: Sedimentation and Community Structure . . . . .	234
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## TABLE OF CONTENTS (continued)

	Page
Turbidity and Sediment Deposition	235
What Is a High Sedimentation Rate For Corals? . . . . .	236
Physiological Adaptation . . . . .	237
Potential Damage to Bacuit Bay	
Corals . . . . .	238
Methods . . . . .	240
Statistics . . . . .	246
Results . . . . .	247
Changes in Substrate Composition	248
Changes in Coral Diversity . . .	254
Coral Cover Changes and Phenotype	262
Discussion	
Causal Hypotheses . . . . .	277
Coral Community Changes (January To December, 1986) . . . . .	279
Diversity . . . . .	281
Community Changes and Phenotype	282
Historical Factors . . . . .	283
Unrelated and Linked Characters	284
Physiological Adaptation . . . . .	285
Evolutionary Implications . . .	286
Conclusions . . . . .	291

## TABLE OF CONTENTS (continued)

	Page
APPENDIX A. SOIL ANALYSIS . . . . .	294
Particle Size Distribution . . . . .	294
Calcium Carbonate Determination . . . . .	295
Organic Carbon Determination . . . . .	295
APPENDIX B. TERRESTRIAL DATA . . . . .	296
APPENDIX C. MARINE DATA . . . . .	300
APPENDIX D. CORAL PARAMETERS . . . . .	305
APPENDIX E. COMMUNITY PARAMETERS . . . . .	310
LITERATURE CITED . . . . .	320

## LIST OF TABLES

Table	Page
1.1 Scleractinian Corals (Philippines) . . . . .	5
1.2 Land Use in Bacuit Bay Drainage Basin . . . . .	27
1.3 Details of El Nido Logging Concession . . . . .	28
1.4 Logging Road Area by Type . . . . .	30
2.1 Definitions Concerning Sediment . . . . .	35
2.2 Suspended Sediment: Manlag and Balangoyan Rivers	75
3.1 Settling Velocity of Sediment Particles . . . . .	92
3.2 Tukey Test Matrix: Wave Height . . . . .	111
3.3 Tukey Test Matrix: Secchi Depth . . . . .	116
3.4 Suspended Sediment (Manlag River and Plume) . . .	120
3.5 Tukey Test Matrix: Sediment Trap $\text{CaCO}_3$ . . . . .	128
3.6 Penetration Distance of Sediment Cores . . . . .	131
4.1 Coral Species Used in Sedimentation Experiments .	178
4.2 Planula Experiment Design . . . . .	184
4.3 Contingency Table: CD Versus Damage Group . . . .	199
4.4 Contingency Table: GF Versus Damage Group . . . .	200
4.5 Contingency Table: PEA Versus Damage Group . . .	201
4.6 Planula Settlement and Sediment . . . . .	203
4.7 Number of Species with Each Phenotype Combination Used in Sedimentation Experiments . . . . .	217
4.8 Results of Previous Sedimentation Experiments . .	224
5.1 Definitions of Substrate Categories . . . . .	242



# LIST OF TABLES (continued)

Table	Page
5.2 Two-way Anovas For All Substrate Categories . . .	252
5.3 Two-way Anovas For All Diversity Values . . . . .	258
5.4 Two-way Anova and t-test; Partial Mortality . . .	260
5.5 Number of Species With Each Phenotype . . . . .	263
5.6 Three-way Anovas For Phenotypes X Site X Date . .	264
5.7 Two-way Anovas for Site X Date . . . . .	266
5.8 Distribution of Live Coral Cover: Site 5 . . . . .	275
B.1 Monthly Rainfall and Number of Rainy Days . . .	296
B.2 Weekly Runoff From Erosion Plots . . . . .	297
B.3 Monthly Erosion From Erosion Plots . . . . .	298
B.4 Mean Daily Water and Sediment Discharge . . . .	299
C.1 Mean Monthly Seawater Temperature By Site . . .	300
C.2 Mean Monthly Salinity at Each Site . . . . .	301
C.3 Mean Monthly Wind Speed and Direction . . . . .	302
C.4 Mean Marine Sediment Deposition . . . . .	303
C.5 Mean Non-carbonate Sedimentation . . . . .	304
D.1 Corallite Size and Polyp Extension Ability . . .	305
E.1 S.D. of Percent Substrate (Figure 5.1) . . . . .	310
E.2 Species List For Sites 1-8 . . . . .	312
E.3 Diversity Values and S.D. (Figure 5.3) . . . . .	317
E.4 S.D. of Phenotype Abundance (Figures 5.5-7) . .	318

## LIST OF FIGURES

Figures	Page
1.1 Coral Phenotypic Variation . . . . .	6
1.2 Evolution of the Scleractinian Families . . . . .	8
1.3 Palawan Island and Philippines . . . . .	20
1.4 Inner Bacuit Bay and Drainage Basin . . . . .	24
1.5 Aerial Photograph of Inner Bacuit Bay . . . . .	25
2.1 Manual Raingauge . . . . .	44
2.2 Erosion Plot Design . . . . .	47
2.3 River Gaging Station . . . . .	52
2.4 U-59 Single Stage Suspended Sediment Sampler . . . . .	56
2.5 Manlag and Balangoyan Rivers . . . . .	57
2.6 Particle size of drainage basin soils . . . . .	59
2.7 Mean Rainfall at the 3 Drainage Basin Sites . . . . .	61
2.8 Water Runoff From Erosion Plots . . . . .	63
2.9 Surface Erosion From Erosion Plots . . . . .	65
2.10 Manlag River Hydrograph . . . . .	67
2.11 Manlag River Water Discharge . . . . .	69
2.12 Plot of river height versus water discharge . . . . .	70
2.13 Manlag River Suspended Sediment Discharge . . . . .	72
3.1 Flow Diagram of Sediment Input to Bacuit Bay . . . . .	89
3.2 Design of Water Current Drogue . . . . .	96
3.3 Sediment Trap Design . . . . .	98
3.4 Air and Seawater Temperatures . . . . .	102
3.5 Salinity . . . . .	104
3.6 Wind (Northeast Monsoon) . . . . .	105

## LIST OF FIGURES (continued)

Figures	Page
3.7 Wind (Southwest Monsoon) . . . . .	106
3.8 Diurnal Wind Speed Variation. . . . .	108
3.9 Wave Height . . . . .	109
3.10 Tidal Currents (Incoming and Outgoing) . . . . .	112
3.11 Secchi Depth . . . . .	114
3.12 Sediment Plume (NE Monsoon) . . . . .	117
3.13 Sediment Plume (SW Monsoon) . . . . .	118
3.14 Sediment Deposition . . . . .	122
3.15 Particle Size, Calcium Carbonate, and Organic Matter Components of Trapped Sediment . . . . .	125
3.16 Plot of Silt Content Versus Distance From the Manlag River Outlet . . . . .	126
3.17 Plot of Sediment Particle Size Versus $\text{CaCO}_3$ . . .	127
3.18 Particle Size, $\text{CaCO}_3$ , and Organic Component of Sediments Collected By Hand . . . . .	129
3.19 Plot of Terrestrial Component of Sedimentation Versus Distance From the Manlag River Mouth . . .	140
4.1 Corallite Size Distribution Among Genera . . . . .	175
4.2 Plots of Damage and Mortality to Corals: Aquaria	192
4.3 Plots of Damage and Mortality to Corals: Field	195
4.4 Tissue Necrosis of <u>Oxypora glabra</u> Following Exposure to Sediment and Tetracycline . . . . .	204
4.5 Tissue Necrosis of 3 Hawaiian Corals Following Exposure to Tetracycline and Sediment . . . . .	206

# LIST OF FIGURES (continued)

Figures	Page
5.1 Cover of Each Substrate Category at All Sites . .	249
5.2 Plot of Coral Cover Loss Versus Sediment Deposition . . . . .	255
5.3 Coral Cover and Diversity Values . . . . .	257
5.4 Plot of Partial Mortality Increase Versus Sediment Deposition . . . . .	261
5.5 Number of Colonies With Each PEA (Jan - Dec) . .	268
5.6 Number of Colonies With Each CD (Jan - Dec) . .	270
5.7 Number of Colonies With Each GF (Jan - Dec) . .	272
5.8 Plot of Corallite Diameter Versus Cover Loss . .	276

## I. GENERAL INTRODUCTION

### Community Structure and the Evolution of Phenotypes

According to the organic theory of evolution (Dobzhansky et al. 1977), populations evolve in response to environmental change. Recombination from sexual reproduction, and mutation provide the genotypic and phenotypic variation required for the process of natural selection. For a given environment, natural selection favors some phenotypes leading to a higher fitness as measured by survival and reproduction. Evolution by natural selection leads to adaptation, producing a wide range of genotypes and phenotypes that have allowed adaptive radiation of organisms into almost all environments on earth.

Today many marine organisms may be exposed to a range of environmental conditions that is similar to that experienced over the past few million years (Potts, 1985). If we assume that many existing phenotypic traits are functional and the result of selection, some of these may be more common than others in particular environments (to which they are adapted). This relationship should be most easily discernable in extreme environments where only a few species are able to survive and functional phenotypic characters may be obvious.

A fundamental goal of ecology is to understand the way in which organisms interact with their physical environment

and with other organisms. This goal is achieved by determining how a particular phenotype allows an organism to survive in a given environment. Two approaches to this question are considered here.

One approach is to examine a sample of species from a variety of environments to look for possible correlations between phenotypic characters and environmental characteristics. The limitation of this comparative approach is that of any correlative technique; causality cannot be assessed and there may be more than one causal factor involved. A representative sample is required for both the taxonomic group and the environmental range of the group.

A second approach to this problem is similar to that used in toxicological studies; representative samples of species can be experimentally exposed to different environmental conditions, and injury or mortality can be assessed. The results of this experimental approach can be analyzed with respect to possible correlations between phenotypic characters and degree of injury or percent mortality. The most meaningful test of the effect of different environments on population characteristics would be carried out over several generations.

The results of both the comparative and the experimental approach can be used to formulate predictions regarding the type of environment where species with a

given phenotype may be found. These predictions can then be tested by investigation of additional species at other sites. The comparisons will reveal if the phenotype frequency distributions at some sites are asymmetrical in favor of the phenotype predicted to be adapted to specified environmental conditions. Once correlations between phenotypic characters and specific environmental characteristics are established for a representative sample of organisms, the results can be synthesized with information regarding other factors which may influence abundance and distribution of species, and the importance of the correlations to overall community structure can be assessed.

The objective of the present study was to investigate the relationship between phenotypic characters of reef-forming corals and tolerance of an extreme environment characterized by a high rate of sediment deposition. The results are used to test predictions regarding the role of sedimentation in influencing community structure of corals.

#### Hard Corals and Coral Reefs

Coral reefs are extremely complex ecosystems noted for their high species diversity (Connell, 1978). Scleractinian corals contribute a large proportion of the calcium carbonate necessary for geological coral reef growth (Gladfelter, 1985; Kinsey, 1985), and they form the

framework of the reef (Goreau, 1959; Shinn, 1963). Within the coral reef ecosystem, scleractinian corals are numerically abundant and provide habitat for thousands of species of organisms. Corals also serve as food for many species, both directly and indirectly via such trophic pathways as planktonic feeding on sloughed off coral mucus (Coles and Strathmann, 1973) and coral reproductive products. Although the total primary production of an entire reef system (including for example, a large sandy lagoon) will depend upon the relative areas of algal cover, sand, and mud, some of the highest rates of production have been measured on reef zones with a high percentage of hard coral cover (Smith, 1981; Gladfelter, 1985; Kinsey, 1985). Other types of corals such as alcyonarians (soft corals) or gorgonians (sea fans and whips) may dominate in certain restricted areas, but hard corals form the majority of the living coral cover on most coral reefs. Because of their ecological importance within the coral reef ecosystem, the focus of this work is on hard corals, and from this point onwards, the term "coral" will refer to hard corals of the Order Scleractinia unless otherwise specified.

Although coral taxonomy has been studied for several centuries many genera and species have only been discovered recently (e.g. Hodgson and Ross, 1982; Hodgson, 1985; Veron, 1985). A study of the coral fauna in the Philippines, possibly the region with the highest coral

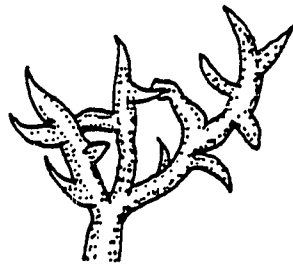


diversity in the world, recorded 478 species, 73 genera and 15 families (Table 1.1; Veron and Hodgson, in press). The total number of Indo-Pacific scleractinian species has not been established but may be between 500 and 550.

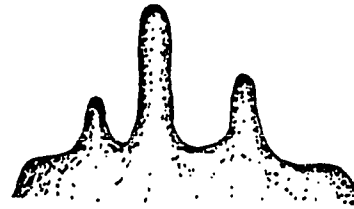
**Table 1.1** Scleractinian coral families, genera and species recorded from the Philippines

No.	Family	Number of genera	Number of species
1	Astrocoeniidae	1	2
2	Pocilloporidae	5	10
3	Acroporidae	4	124
4	Poritidae	3	39
5	Siderastreidae	4	12
6	Agariciidae	5	26
7	Fungiidae	11	36
8	Oculinidae	2	4
9	Pectiniidae	5	13
10	Mussidae	7	19
11	Merulinidae	4	8
12	Faviidae	15	64
13	Trachyphylliidae	1	1
14	Caryophylliidae	4	14
15	Dendrophylliidae	2	8
	Total	73	478

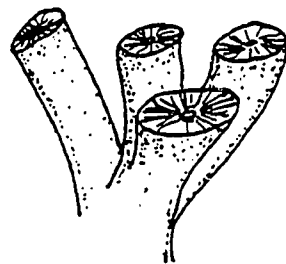
Corals exhibit a wide range of inter- and intra-specific phenotypic variation in both living tissues and skeletal characters (Figure 1.1). This variation may enable corals to inhabit a variety of marine environments. Reef building corals are known to tolerate a wide range in temperature (15-36°C), salinity (20-40 ppt) and other environmental variables such as light (required by



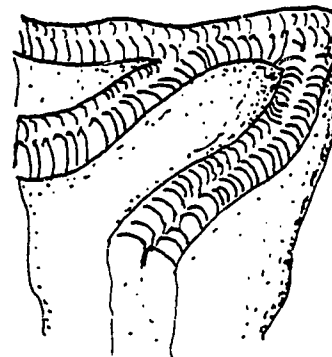
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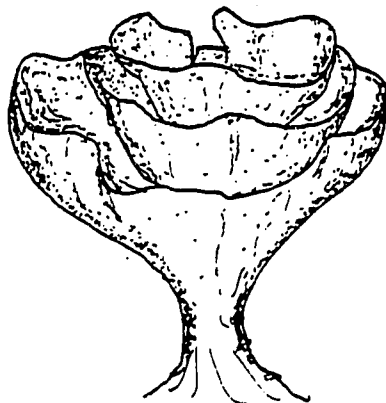
Columnar



Phaceloid



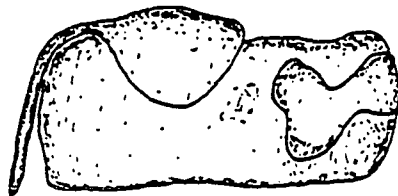
Flabellate



Foliose



Massive



Plate

Encrusting



Solitary

**Figure 1.1** Nine major coral growth form categories. Corals also exhibit wide interspecific phenotypic variation in skeletal characters and polyp shape.

endosymbiotic algae), substrate type and water movement (Wells, 1956). The broad phenotypic diversity of corals and their ability to withstand relatively wide extremes in environmental variation make them versatile research animals for comparative and experimental studies of environmental tolerance.

The earliest fossil Scleractinia are from the Middle Triassic. By the Early Tertiary, 16 of 19 extant Indo-Pacific families had already appeared (Figure 1.2). Comparison of the Indo-Pacific fossil record with extant coral genera and species shows a pattern of slow change since the Pliocene (Stehli and Wells, 1971; Potts, 1984). For example, of 83 fossil scleractinian species recovered from the 2.5 million year old Era Beds in Papua New Guinea, 65 are indistinguishable from extant species, 9 are the apparent ancestors of extant species that have undergone significant evolutionary changes and 9 appear to be extinct (Veron and Kelley, 1988). Assuming complete isolation (no gene flow), a speciation rate of 22.4 species per million years was estimated for all Indo-Pacific species. The range in rate of change in species composition in Hawaii has been estimated to be from 1.6 to 5.3 species per million years (Grigg, 1988). More rapid speciation might be expected in speciose genera such as Acropora (approximately 100 Indo-Pacific species), however, Acropora colonies have delicate branching growth forms and

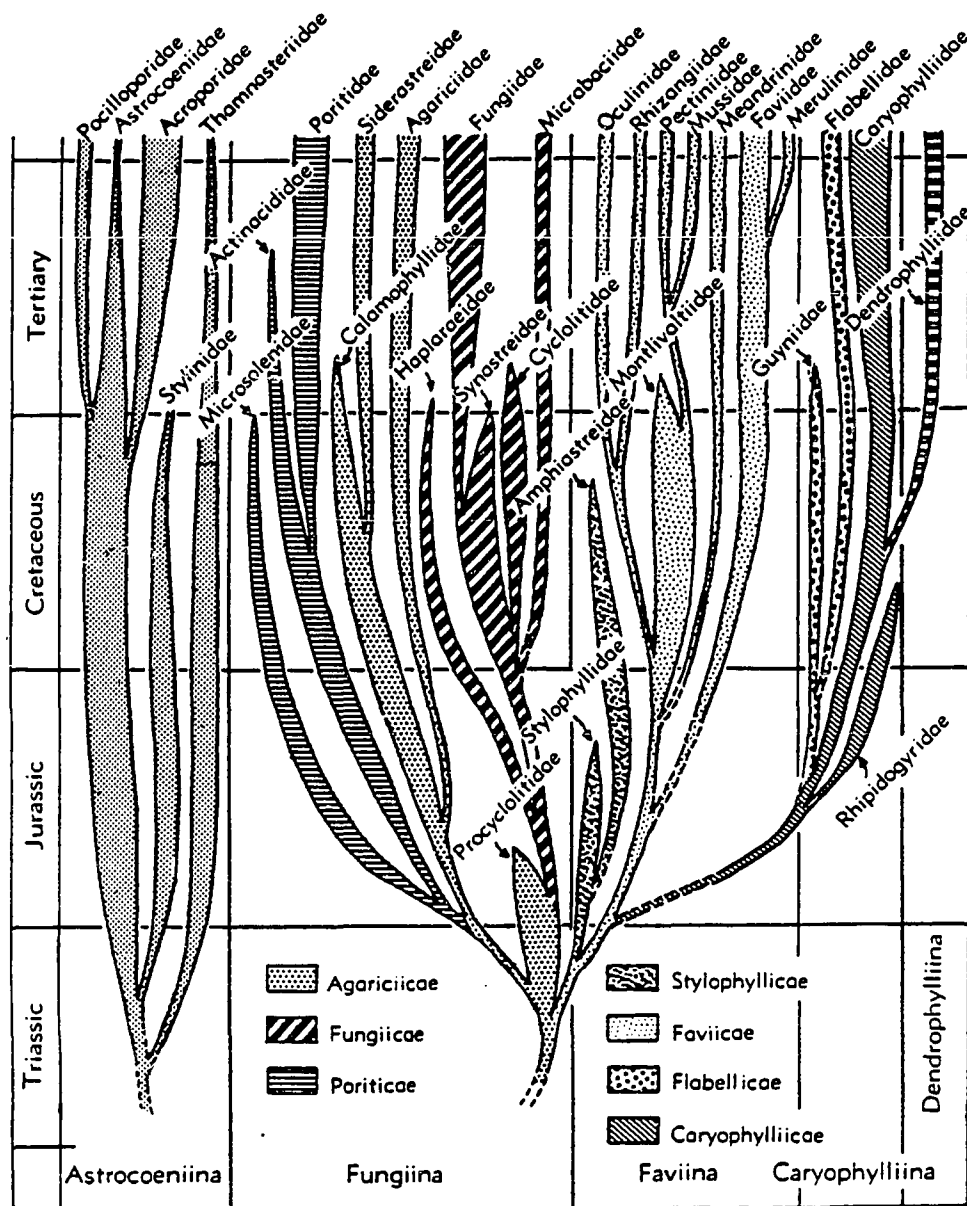


Figure 1.2 Evolution of scleractinian families. Of 19 extant families, only 15 are considered here; 3 (Microbaciidae, Rhizangiidae, and Flabellidae) do not have zooxanthellae and are non-reef building, and 1 (Meandrinidae) is represented by a mono-specific genus Ctenella that has not yet been reported outside of the Indian Ocean. From Wells (1956).

so are poorly represented in fossil beds. In comparison, the approximately 90 scleractinian species endemic to the Caribbean (Wood, 1983) evolved since the closing of the isthmus of Panama 3.5 million years ago (Keigwin, 1978; 1982), a speciation 13% faster than was estimated for the Indo-Pacific (Veron and Kelley, 1988) and several times the Hawaii rate (Grigg, 1988).

Slow evolutionary change within the Indo-Pacific Scleractinia could indicate adaptation to relatively static environmental conditions over several million years as well as a high degree of gene flow among populations. Lack of phenotypic change over this period despite sea level changes and wide geographic and environmental distribution has also been interpreted as a limitation in the underlying genetic variation due to factors such as inbreeding and asexual reproduction (Potts, 1984).

With few exceptions, corals are colonial organisms that reproduce sexually as well as asexually via modes such as colony fragmentation (Highsmith, 1982) and ameiotic larva formation (Stoddart, 1983). These traits and others make corals an especially interesting subject for studies of tolerance to environmental extremes. For example, in contrast to solitary organisms, corals may:

- 1) have different growth forms and physiology at different portions of one colony

- 2) be able to grow and reproduce following death of part of the colony
- 3) have colonies of different sizes that are the same age, or colonies of the same size that are different ages (due to fragmentation and indeterminate growth).

Interpretation of experimental results using corals should take these factors into account. For example, if ability to resist damage due to environmental extremes is related to colony shape, then different portions of one colony may have different levels of resistance. This may lead to certain portions of a colony dying while other portions remain alive. In addition, if environmental tolerance is age related and experimental animals are chosen based on colony size, highly variable results might be expected due to age differences.

The primary objectives of this study could be framed in terms of "sedimentation stress to corals". Unfortunately, the term "stress", although easily understood in everyday usage, has been given many different and often conflicting biological definitions (reviewed by Ulanowicz, 1978 and Lugo, 1978). For example, stress may be viewed as a cause or as an effect. It is also difficult to use the term "stress" meaningfully because it is generally defined with respect to some "normal" condition. For many organisms, and corals in particular, a "normal" condition has rarely been measured and is often unknown

(Brown and Howard, 1985a,b). An attractive alternative to the use of this ambiguous, potentially misleading term, is simply to describe specific changes in the physical or physiological state of individual coral colonies or in the coral community structure as a whole and to assess causality whenever possible. One example is given here to illustrate the reason for not using the term "stress" in subsequent discussion.

If a coral colony is progressively becoming "bleached" due to the loss or expulsion of endosymbiotic zooxanthellae, one major effect is the loss of a metabolic energy source equivalent to the proportion of algal productivity translocated to the coral tissue (Muscatine, 1973). There may be other, unknown effects. The "bleached" condition has frequently been referred to as a stressed condition (Brown, 1987). Eventually, if the coral becomes completely "bleached", it may stop growing, respiration may be reduced, the colony may become diseased and die, or it may regain its normal complement of zooxanthellae. These changes can be measured and described and conclusions reached; e.g., the colony lost 50% of its energy supply due to loss of zooxanthellae or, the colony died after 3 days. To subjectively define a given point in time or an arbitrary magnitude of change of a given parameter as a stressed condition adds no new information or clarification to the description; at best it is

confusing and at worst it may be used in place of real data to support an undocumented conclusion. For this reason, the term "stress" will be avoided in subsequent discussion of the effects of sediment on corals and coral reefs.

### Sedimentation and Coral Reefs

Both Darwin and Dana discussed the effects of sediment discharge from rivers on corals and on coral reef formation. Darwin (1851) wrote, "No doubt brackish water would prevent or retard the growth of coral; but I believe that the mud and sand, which is deposited even by rivulets when flooded, is a much more efficient check" (p. 66). He also wrote, "it appears very probable that the depth at which reef-building polypifers can exist is partly determined by the extent of inclined surface, which the currents of the sea and the recoiling waves have the power to keep free from sediment." Dana (1875) noted the importance of sediments in relation to coral growth. He wrote, "The effects of sediment on growing zoophytes are strongly marked. . . It is natural, therefore, that wherever streams or currents are moving or transporting sediment, there no corals grow; and for the same reason we find few living zoophytes upon sandy or muddy shores." Wood-Jones (1912; p. 242) stated that "sedimentation is the most potent cause of coral death and the most important



influence upon all phases of their existence." The first natural historians believed that sediments control the distribution of corals and that water currents are a primary control of sediment transport.

One of the first experimental investigations of the effects of sedimentation on reef corals was carried out by Marshall and Orr (1931) from December 1928 to June 1929 during the Great Barrier Reef Expedition of the British Museum of Natural History. They concluded that "The movements of sediment play a large part in determining the shape and structure of reefs . . ." (p. 94). More than half of a century later, the effects of sedimentation on corals and the relationship between sedimentation and coral community structure are still poorly understood. Laboratory and field investigations of sedimentation effects on corals will be reviewed in Chapters 4 and 5.

#### Anthropogenic Coral Reef Sedimentation

Increasing attention is being focused on human influence on coastal water turbidity and sediment deposition due to practices such as land clearing, dredging, or sand mining (Maragos et al., 1977; White, 1987). An early account of the possible influence of humans on sedimentation of a coral reef was made by Fairbridge and Teichert (1948). They conducted a geographical survey of Low Isles, where Marshall and Orr had worked previously, and noted the

deleterious effects of terrestrial sediment on the reef. They wrote, "The colossal soil erosion during the last decade or so, engendered by unplanned agriculture in the drier parts of Australia, finds evidence even in the coral seas. . . . We obtained thus an impression, possibly distorted, that continental sedimentation might soon be gaining on coral growth at Low Isles. . . . Much of the coral (of the seaward slopes) was dead and coated in a "fur" of fine brown terrigenous sediment." Goreau (1964) and Banner (1968) suggested that increased runoff and sediment discharge associated with accelerating human land use may produce highly turbid, low salinity waters at the sea surface which may damage corals. The problem with interpreting such accounts is that it is difficult to separate the effects of siltation from those of low salinity.

In addition to poorly planned and managed land use, dredging and construction activity near coral reefs have also been noted to cause increased turbidity and sediment deposition which may reach levels harmful to corals (Brock et al., 1966; Dahl and Lamberts, 1977; Maragos, 1972; Nichols and Towle, 1977; Marszalek, 1982; Hutchings and Wu, 1987). The effects of these human impacts on coral reefs have been reviewed by Salvat (1987) and White (1987). Another cause of sediment discharge in tropical coastal waters is the washing of sugar cane prior to processing.

Grigg (1985) studied the effect of sugar mill discharge on coral reefs in Hawaii and found the extent of measurable impact to be limited to within 2.5 km from the discharge points.

It is logical to expect that increased erosion in coastal regions that include near-shore coral reefs should result in increased sediment deposition on these reefs. However no research to date has specifically documented how a change in land use has resulted in increased erosion, increased sediment discharge from streams or rivers, and increased sedimentation on near-shore coral reefs.

One type of land use that has been shown to consistently increase soil erosion and suspended load of streams is logging, both in temperate and tropical forest areas (BIOTROPE, 1978; Hamilton and King, 1983; Tucker and Richards, 1983). Tree-cutting exposes underlying soil to the direct erosive action of wind and rain by removing layers of leaf canopy (Herwitz, 1987). Dragging of logs by motor driven cables, or by towing is known to increase erosion. But the major cause of erosion due to logging operations has been shown to be road building (O'Loughlin, 1985). A major component of most logging operations is the construction of an extensive road network to allow for log removal. The erosion from logging has been shown to significantly increase the suspended sediment load in streams and rivers, and to significantly reduce fish and

invertebrate biomass and diversity in these freshwater habitats (Cordone, 1956; Graynoth, 1979; Erman and Mahoney, 1983). Although previous studies have inferred a positive relationship between deforestation or land clearing and sedimentation in the marine environment (e.g. Fairbridge, and Teichert, 1948; Smith et al., 1981; Cortes and Risk, 1985; Kuhlman, 1985) this relationship has not been well documented.

### Project Design

The research area addressed in this study is of both theoretical and practical interest. From a theoretical standpoint, an investigation of the effect of sedimentation on coral reefs is one part of the search for environmental factors that may influence coral community structure. From a practical standpoint, anthropogenic sedimentation of coral reefs is one of the general set of pollution problems that may have deleterious effects on coral reef fisheries upon which so many humans depend for protein. Both the theoretical and practical aspects of sedimentation of coral reefs are considered here.

The approach used to study the effects of a high sedimentation environment on reef corals follows the comparative approach outlined above. This requires that a range of environments (biotopes) be located. An ideal study site would include individual coral reefs

historically subjected to a wide range of sedimentation levels and a still-pristine "control" reef area.

In order to control the temporal aspect of the study, a reef area was sought that was subjected to man-made sedimentation beginning at a known date. A site was located in the Philippines where it would be possible to test hypotheses of both theoretical and applied interest by monitoring the effect of coastal logging on coral reefs.

Coastal logging has been implicated as one source of marine sedimentation (Kuhlman, 1985) but this has not been tested. As outlined above, previous work has consistently confirmed that logging operations significantly increase sediment input to streams and rivers in affected drainage areas (Hamilton, 1985). Therefore, for the present study a relative indication was sought of the degree of increased erosion and sediment input to streams given the conditions peculiar to the study site. The applied portion of the study was designed to examine whether a specific human activity, coastal logging, significantly increases erosion and sediment discharge rates from forest lands, and ultimately increases the sediment deposition rate on near-shore coral reefs.

In order to study sedimentation effects on corals, experiments were designed to test tolerance or resistance of corals to different levels of sedimentation. This involves looking for changes in the contribution of a

given phenotype to a sample population in response to sedimentation induced injury and mortality. Several coral species do not begin to reproduce until they reach a size threshold that may take several years of growth (Connell, 1973; Ross, 1984; Szmant-Froelich, 1985; Szmant, 1986) and many coral species are assumed to have indeterminate growth (Szmant, 1986), therefore it would be difficult to measure coral population characteristics over several generations. Rather, an instantaneous effect may be measured which must be assumed to manifest itself in long-term changes in population characteristics.

In order to reach the final goal of the study and relate the results to patterns of coral community structure, it was considered important to use "realistic" experimental exposure to chronic sedimentation rather than exposure to an acute level which may be rare in nature. Therefore, sedimentation rates used in both field and laboratory experiments were based on measurements of local sedimentation rates.

In summary, the design of the present study has two components, terrestrial and marine. The purpose of the terrestrial study was to obtain information on erosion rates under the specific conditions of the study site, and to document changes in sediment load and sediment discharge rate in the main river draining the forest area being logged. Information was also sought which could be used to

compare certain environmental parameters "before" logging and "after" logging, and in primary forest versus logged areas. The marine component of the study was designed to use both comparative and experimental techniques to determine the effect of sediment deposition on individual corals and on coral community structure.

### Study Site

#### Palawan Island

The study site, Bacuit Bay, El Nido, is located near the northern tip of Palawan Island in the southwest Philippines. Palawan's 12,000 km<sup>2</sup> are arranged in a thin, 425 km long strip of land bounded on the East side by the Sulu Sea and on the West by the South China Sea (Figure 1.3). The island is bisected by a central mountain range, leaving only a narrow coastal margin of cultivable land which accounts for about 20% of the total land area (Bureau of Soils, 1980). Ten years ago, Palawan was considered one of the last unspoiled regions in the Philippines, with virgin timber stands and plentiful marine resources, numerous endemic species of plants and animals and a relatively low population density (Pido, 1986). More recently, rapid population growth in combination with industrial expansion in mining and logging has drastically reduced the size of Palawan's remaining wilderness areas.

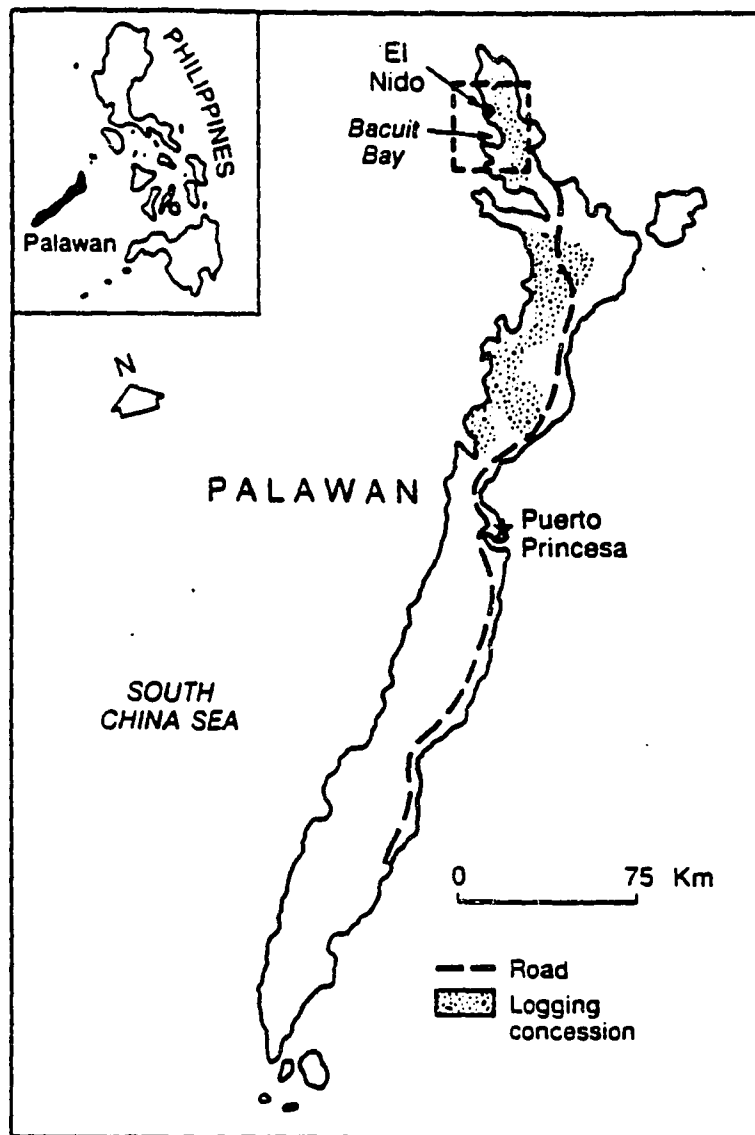


Figure 1.3 Palawan Island and the Philippines (inset).



In 1968, almost 92% of Palawan's land area was forested. Poorly controlled logging, and slash and burn agriculture resulted in a decrease in forest area to 70% by 1980 (Pido, 1986) and perhaps 50% by 1987 (pers. obs.). Present forest consumption is estimated to be 200 km<sup>2</sup> per year, just over 3% of the 1987 forested area.

A high percentage of the total Philippine fish catch is estimated to be taken from the waters surrounding Palawan (Pido, 1986). Previously pristine, the coastal marine environment of southern Palawan has begun to follow the trend seen in most other areas of the Philippines and is now being subjected to increasing fishing pressure, illegal fishing (dynamite, poisons, coral damaging, weighted-scareline or "muro ami" fishing, small mesh nets), siltation and heavy metal pollution from mine tailings. Due to the lack of data, it is not known if these practices have resulted in overfishing of available stocks. Northern Palawan has been the last area affected by increased fishing, partly due to its remote location, the lack of roads and port facilities or other infrastructure. Because of Bacuit Bay's status as a marine tourist reserve, commercial trawling is illegal inside the bay, and this ban is strictly enforced by local and national law enforcement agencies. Artisanal fishing by the local population is allowed.

### Geological History

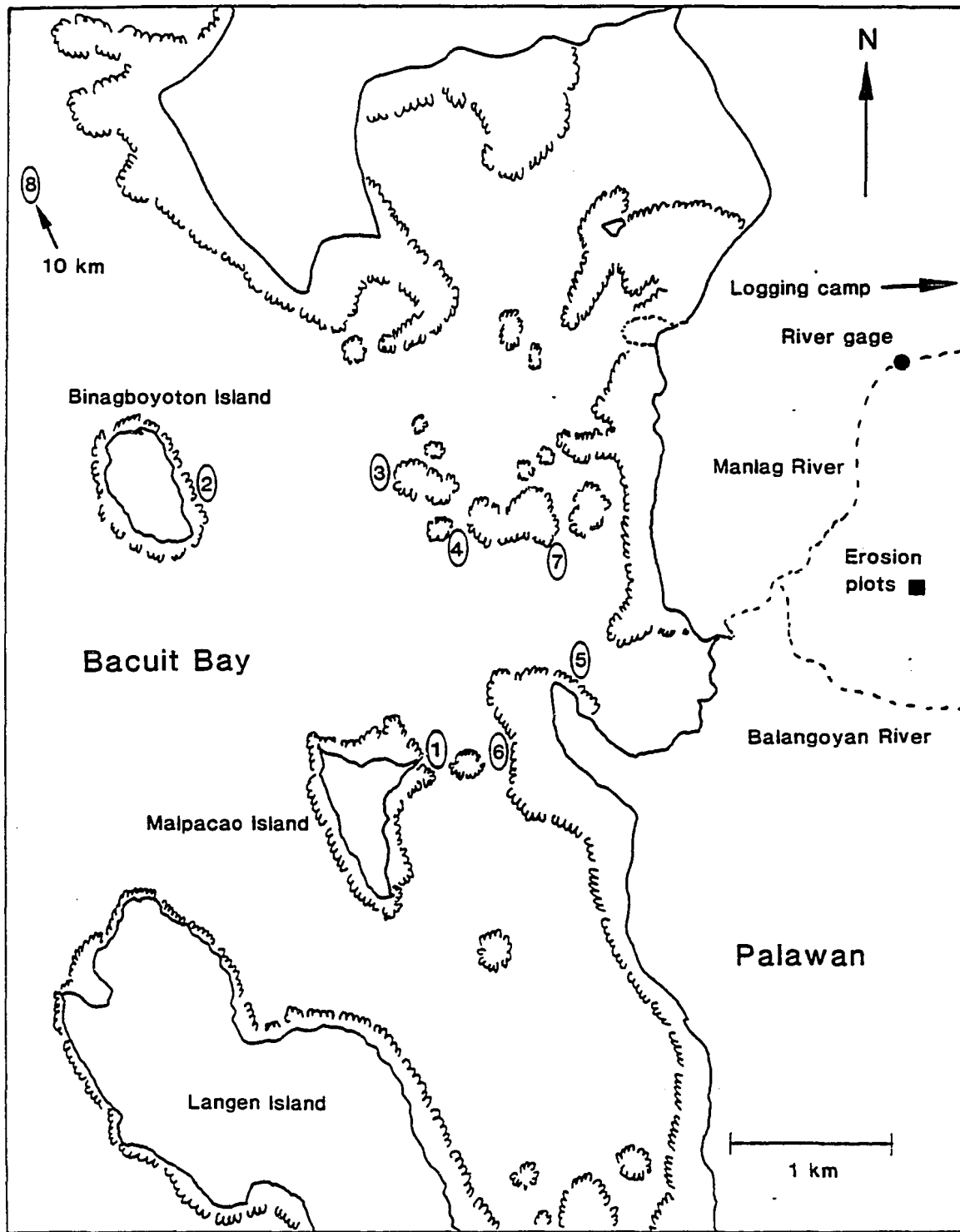
Based on analysis of magnetic anomaly data from the South China Sea, Taylor and Hayes (1983) hypothesize that Northern Palawan originated as a fractional block that broke off from the Asia plate along the proto-China margin due to seafloor spreading in the South China Sea about 100 to 150 million years ago. According to Taylor and Hayes, by the mid-Miocene, about 15 million years ago, the northern Palawan micro-block had moved southward from its original position at about 35° N latitude to its present position at about 10° N. At about that time, the northern and southern halves of Palawan joined together along a NE-SW elongation axis. The origin of the southern half of Palawan is unknown.

The Bacuit Bay region is located in the area bounded by latitude 11°00' to 11°10' N, and longitude 119°15' to 119°30' E. Three geological formations have been described in this region based on fusulinid and conodont fossils: the Liminancong (middle Triassic), Minilog (mid-upper Permian) and Bacuit (middle Permian) Formations (Hashimoto and Sato, 1973). The Liminancong Formation is composed of mostly bedded, frequently hematite-bearing chert, intercalated in some horizons with black slate and reddish tuff layers. This formation is found along the southern bay coastline. The Minilog Formation is composed of black or white, partially recrystallized limestone. This formation is

found throughout the north and east coasts of the bay and on all of the bay islands. The Bacuit Formation underlies the Minilog Formation and is composed of brecciated sandstone, altered tuffs, calcareous sandstone and contorted alternating blocks of sandstone and slate.

### Bacuit Bay

Bacuit Bay (Figures 1.3, 1.4 and 1.5.) encompasses an area of 120 km<sup>2</sup>, contains 5 major islands. There are 9 more islands located on a shelf just outside the bay. The limestone islands of Bacuit Bay have distinct erosion notches at sea level. The bay floor descends seaward in a series of 3 submarine terraces. The near-shore submarine terrace is 0.5 km wide and 8 m below sea level. The second submarine terrace is located at a depth of 18 m and is 2 km wide; the third terrace extends out to the bay entrance at a depth of 40 m. Depths between the outer islands reach 65 m. Flourishing coral reefs surround most islands and form a continuous band along the bay coastline interrupted only by river passes. Due to a eustatic, low sea level stand about 18 thousand years ago (Chappell, 1981), these reefs probably represent a relatively "thin" veneer over the pleistocene limestone.



**Figure 1.4** Inner Bacuit Bay and drainage basin. Site 8 is 10 km past arrow. Note location of Manlag River.

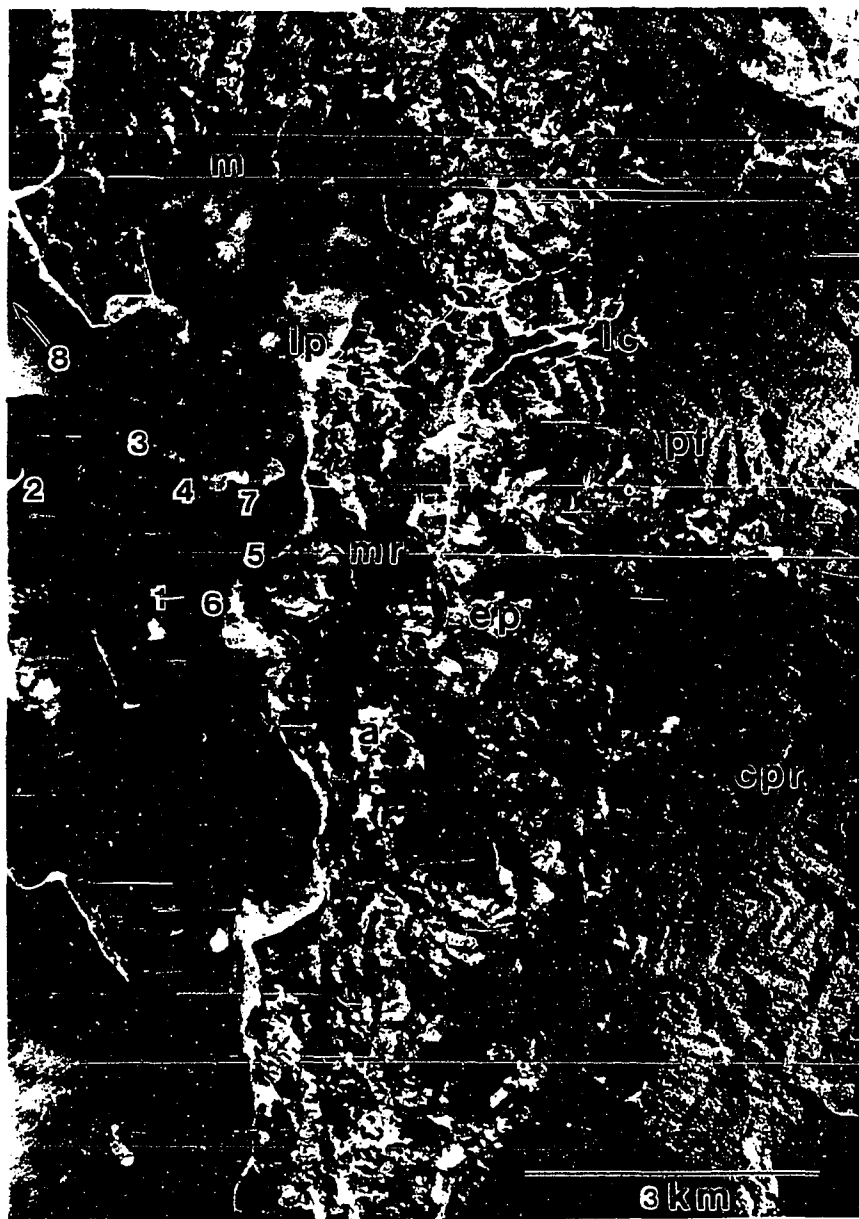


Figure 1.5 Aerial photograph of the inner bay with Study Reefs marked (1-8) and drainage basin. a = agriculture, cpr = Central Palawan Ridge, ep = erosion plots, lp = log pier, lc = logging camp, m = mangrove, mr = Manlag River, pf = primary forest.

### Bacuit Bay Drainage Basin

The terrestrial ecosystem of interest in this study (Figure 1.4 and 1.5) encompasses all land surrounding and draining into Bacuit Bay which will be termed the Bacuit Bay drainage basin (=watershed). The Bacuit Bay drainage basin covers 78.3 km<sup>2</sup> and extends inland to the central Palawan dividing range. It is drained by 4 small rivers and several continuous and seasonal streams that flow into Bacuit Bay. The Bureau of Soils (1980) classified the land system and soil in the upper Bacuit Bay drainage basin as follows. The land consists of steep to very steep (20-50% slope) median, metamorphic hills and ridges with occasional narrow valleys. The soil is moderately deep to deep, clayey, with low to medium fertility. It was formed from basement rocks including chert, schist, slate and quartzite. It has been classified, using the American system, as an Inceptisol (Typic Eutropept) which indicates a young, tropical, brown soil with a cambic horizon but no other diagnostic horizons. A cambic horizon is a non-surface horizon with a high clay content that results from the incomplete weathering of primary minerals (Duchaufour, 1982). The characteristics of the upper drainage basin led the Bureau of Soils to classify the land in the "severe erosion hazard" category.

Prior to the initiation of logging in 1985, 53% of the basin was composed of primary forest. Most of this forest

land is now included within a large logging concession which encompasses most of Northern Palawan. A breakdown of the 1986 land use in the Bacuit Bay drainage area (Table 1.2) shows a low level of agricultural land use. The absence of a high percentage of agricultural land use was one of the desirable characteristics sought during the site selection process for this study.

The town of El Nido is the population center nearest to the bay. It has about 2000 residents and is located on the coast just north of the bay entrance. Three small villages border the bay on the north, east and south coasts. Outside of these villages the population is widely dispersed.

**Table 1.2** Land use in the Bacuit Bay Drainage Basin (1986), measured from aerial photographs

<u>LAND USE</u>	<u>AREA (km<sup>2</sup>)</u>	<u>% OF TOTAL</u>
<b>Forest</b>		
Primary dipterocarp forest	37.0	47.3
Scrub, secondary forest	27.1	34.6
Logged forest	4.8	6.1
Mangrove forest	<u>3.9</u>	<u>5.0</u>
Subtotal	72.8	93.0
<b>Agriculture</b>		
Swidden/cashew	3.6	4.6
Rice paddy	1.1	1.4
Coconut plantation	<u>0.8</u>	<u>1.0</u>
Subtotal	5.5	7.0
<b>Total</b>	<b>78.3</b>	<b>100.0</b>

### Logging

A wide variety of logging techniques is used in the tropics (BIOTROPE, 1978). In order to discuss the effects of logging on erosion and sediment discharge from Bacuit Bay drainage basin, a brief outline of logging methods used in El Nido is presented.

Observations of logging operations were made in August 1985. Logging operations in the area bordering Bacuit Bay commenced in January 1985 and were temporarily suspended by the logging company in January 1986 for one year. By chance, this suspension coincided exactly with the quantitative study period. Details of the concession operations are listed in Table 1.3.

**Table 1.3** Details of logging concession bordering Bacuit Bay, Northern Palawan

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Operator	Pagdanan Timber Products Inc. (PTPI)
Area	969.25 km <sup>2</sup>
Allowable Cut	200,000 m <sup>3</sup> /year
Method	High grade, mechanized
Timber Rotation	85 years
Cutting Cycle	42 years
Harvestable Logs	60 cm Dbh (diameter at breast height) and larger

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Philippine law requires that three trees be planted for each tree harvested (PIADP, 1985a). This level of planting combined with selective logging practices which remove approximately half the number of harvestable classes



of trees will theoretically allow a sustainable yield operation with two harvesting cycles during the 85 year timber rotation (tree growth cycle). Unfortunately, a lack of tree planting, overcutting in low volume timber stands, and excessive felling damage threaten the sustainability of the PTPI concession (PIADP, 1985a).

In order to facilitate logging operations at Bacuit Bay, three construction projects were undertaken. All three might have increased erosion. First, a 100,000 m<sup>3</sup> earthen pier (known as a "logpond" in the industry) was constructed. The pier is used to offload heavy equipment such as trucks and skidders (small tractors used to move logs) shipped in by barge, as a log storage area, and for loading logs onto a barge for transport to the sawmill. Logs of Philippine mahogany (Dipterocarpus spp., locally called "apitong") from this region do not float due to a high resin content and must be transported to sawmill by barge. In order to construct the pier, approximately 100,000 m<sup>3</sup> of soil was pushed down into the bay from an adjacent hillside. With only a bare minimum of protective log pilings, the pier is exposed to the erosive effects of wave action and runoff. The second construction job was to clear a 200 m<sup>2</sup> area for the logging camp, an area used for housing, equipment storage and repair (Figure 1.5). The camp, located about 3 km inland, was cleared almost entirely of vegetation and left bare. The third and

largest construction project was road building (Table 1.4).

Road construction within the hilly drainage basin is generally done by cutting into the hillsides, leaving an exposed vertical face on the uphill side. On the opposite, downslope side the extra soil is pushed over the edge of the road spilling down in a wide swath called a sidecast fill slope. Both the uphill and downhill slopes are thus destabilized by this type of road construction increasing the potential for accelerated erosion.

Three aspects of the design and construction of PTPI concession logging roads which could contribute to increased road failure (small landslides) were cited by PIADP (1985a): lack of drainage canals, and lack of culverts, and excessive road slope angle. During the 1985 rainy season, numerous landslides from cuts above logging roads often halted operations by blocking roads. Such slides were also common during the 1986 rainy season.

**Table 1.4** Logging road area by type (1986), measured from aerial photographs

Type	Width(m)	Length(km)	Area(km <sup>2</sup> )
Primary access (with gravel)	12	16.7	0.20
Secondary	6	20.7	0.12
Tertiary & skid trails	5	18.4	0.09
Total	23	55.8	0.41

Primary access roads are used on a daily basis, e.g. to transport logs to the log pier and usually are partially gravel surfaced. Secondary roads are built to service specific logging zones within the concession and are used only while those areas are productive. Tertiary roads connect secondary roads to the skid trails. Skid trails are the paths cut into hillslopes by bulldozer (caterpillar tractor) to allow skidders access to specific tree stands. Following tree felling by chainsaw, the skidder transports each log to the log truck onto which it is loaded. Skid trails are normally used for only a few days and then abandoned. In this concession they were designed and built perpendicular to the topographical contours thus allowing the greatest possible erosion by maximizing the slope angle for the full length of each skid trail. When fully loaded, log trucks transport logs to the log pier where they are stacked. When a sufficient volume is collected, the logs are loaded onto a barge for transport to the sawmill/veneer plant located 30 km to the south.

### Weather

The results of monitoring of specific weather parameters during 1986 are presented in Chapters 2 and 3. The following section provides an overview of the weather in the El Nido area. The Bacuit Bay weather pattern follows the seasonal Asian monsoon consisting of approximately 6

months of dry season, (November-April), and 6 months of rainy season (May-October). This pattern may shift one or two months in either direction from year to year, and winds are often variable during the transition period. During the dry season northeast winds predominate, therefore this period is called the northeast monsoon. The rainy season occurs during the southwest monsoon (southwest winds predominate). El Nido is not located on a high frequency, tropical typhoon track. A cyclone is defined as a closed atmospheric circulation rotating about an area of low pressure (Joint Typhoon Warning Center, 1982). A typhoon is a cyclone with maximum winds about the center of disturbance greater than (33 m/s, [118 km/h] one minute mean). Over the past 30 years (1957 - 1987) El Nido has not been hit by a major typhoon. The 3 largest storms that passed over El Nido during this period occurred on November 28, 1962 (29 m/s [105 km/h winds]), October 10, 1979 (25 m/s [90 km/h winds]), and October 12, 1981 (21 m/s [75 km/h winds]) (Joint Typhoon Warning Center, 1957-87; PAGASA, 1967-85). Most cyclones pass over the Philippines from East to West. Depending on the precise storm track, all will have to pass over at least one island group of the Visayan Islands before reaching northern Palawan (Figure 1.3). Since cyclones tend to lose strength during passage over land masses, northern Palawan is somewhat protected from cyclones which pass over these islands.

## II. TERRESTRIAL PHYSICAL PARAMETERS

### Introduction

Although the primary emphasis of the El Nido study is on coral-sediment interactions, it is important from both a theoretical and practical standpoint to document the origin and nature of sediment entering Bacuit Bay and potentially affecting corals. In order to do this, a monitoring program was established in the Bacuit Bay drainage basin during 1986. There were 3 objectives of the monitoring program:

- 1) to measure the relative magnitude of increased surface erosion due to logging compared with natural erosion under the specific conditions of the Bacuit Bay drainage basin,
- 2) to measure the effect of logging on suspended sediment load in drainage basin rivers,
- 3) to estimate the rate of sediment discharge from a major river draining the area affected by logging.

Numerous workers have suggested that logging (cutting commercially valuable trees), deforestation (forest removal followed by vegetational change), or land clearing (complete removal of all vegetation) are potential sources of silt pollution in the marine environment (Fairbridge and Teichert, 1948; Brock et al., 1966; Maragos, 1972; Dahl and

Lamberts, 1977; Nichols and Towle, 1977; Marszalek, 1982; Kuhlman, 1985; Hutchings and Wu, 1987; Salvat, 1987 White, 1987) but there is little direct evidence. In order to document the contribution of logging to silt pollution of coral reefs, it is necessary to meet the 3 objectives outlined above. First it must be shown that logging increases erosion and sediment production above natural rates, second that this leads to a high delivery ratio and increased sediment load in water courses flowing out of the logging area, and third that elevated sediment concentration (load) is maintained until the freshwater is discharged into the ocean near coral reefs (Bacuit Bay) (See Table 2.1 for definitions of important terms regarding sediment and erosion). In addition, knowledge of the geographical origin of sediments will help in allowing characterization of their composition. Such knowledge is required for successful prediction of rates of physical processes such as lateral transport of sediment and settling rate in the sea as well as for understanding sediment-coral interactions in nature.

Despite the technical problems encountered when measuring erosion, several studies have successfully demonstrated that logging significantly increases erosion and sediment discharge in temperate and tropical forests (see review by Megahan and King, 1985; Beasley and Granillo, 1988). Since there was no reason to believe the

**Table 2.1** Definitions concerning sediment, erosion and sediment transport.

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Sand	A specific size class of particles (0.0630 to 1.0000 mm).
Silt	A specific size class of particles (0.0629 mm to 0.0040 mm).
Clay	A specific size class of particles (0.0039 mm to 0.0003 mm).
Rainsplash erosion	Detachment and transport of soil particles by rain drops.
Sheet erosion (=surface erosion)	The process of soil particles being sheared from their rest position and transported by overland water flow.
Rill and gully erosion	The process of small channel (rill) formation; continued rill erosion or subsurface tunnel formation and collapse creates gullies.
Mass wasting	The process of large scale slumping or collapsing of earth slopes (=land slides).
Sediment	Soil or other particulate material in suspension, or that settles or has been deposited by a liquid.
Suspended sediment load	Amount (concentration) of sediment (settling and neutrally buoyant) in a defined column of water.
Bed load	Sediment particles on river bottom too heavy to be resuspended.
Sediment	Rate of sediment outflow discharge (=suspended load x river flow; flow of sediment weight/time period).
Sediment delivery ratio	Amount of sediment discharge divided by the amount entering a river.
Sedimentation	The process of sediment settling and deposition.
Siltation	General term; same as sedimentation, but often refers to fine sediments.

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results of logging in El Nido would differ qualitatively from results in other locations, the major terrestrial research effort was focused on accomplishing Objectives 2 and 3, and only limited time and effort were devoted to pursuing Objective 1.

### Measuring Erosion

The effect of rainfall on soil erosion depends on both rainfall and soil characteristics (Wischmeier and Smith, 1978; Duchaufour, 1982; Morgan, 1986). In general, soil erosion is positively correlated with rainfall rate, average raindrop size, and rainfall duration. Before the rain hits the ground, however, it may be intercepted by the forest canopy, various layers of understory, ground cover and plant litter. When rainfall is intercepted by leaves, coalescence of raindrops may result in larger sized water drops hitting the ground. In cases where ground cover has been removed, such as in certain types of agroforestry or where roads have been built, erosion from these larger drops may be greatly increased under high canopy (reviewed by Weirsum, 1984).

A detailed discussion of soil characteristics affecting erodibility is beyond the scope of this work (see Morgan, 1986), however, such factors include soil texture, aggregate stability, shear strength, infiltration capacity and organic and inorganic chemical content. In general,



soils with a high clay to silt ratio are less erodible than soils with a low ratio of these size classes due to the cementing action of clay. In a monsoonal climate with clearly defined dry and wet seasons, soils dry out during the dry months. Dried clay soils become hardened from chemical bonding of clay minerals and act like a solid. Hardened clay has a low infiltration rate (the degree to which water enters a material). During a brief high intensity rainfall, surface clays swell, decreasing pore size between particles, reducing infiltration rate and increasing potential runoff. Runoff volume also varies positively with ground surface slope. A method of determining the characteristic slope of a drainage basin has been proposed by Zecharias and Brutsaert (1985). In general, increased runoff volume will lead to increased erosion due to increased kinetic energy of the water. This process may be counteracted somewhat by soil hardening, since this increases the shear force necessary to dislodge soil particles. Clearly, soil erosion is a complex process that varies greatly with time at a given location.

A wide variety of techniques is available to measure or predict soil loss due to erosion and mass wasting (Morgan, 1986). Soil loss can be measured directly by monitoring soil surface changes, or indirectly using catchment techniques. In order to estimate erosion from areas on the order of several square kilometers, monitoring

is generally needed over a wide area and for a minimum of one year. For this reason, all monitoring techniques tend to be labor intensive. Despite large investments in time and effort, the accuracy of both measurement and prediction of soil loss, particularly from forest land, has proven to be limited. In a review of the status of scientific prediction of erosion from forest lands Dunne (1984) concluded, "The status of techniques and experimental design for erosion measurement in forests is poor. Prediction of erosion and sediment production in forests is qualitative, or at best only roughly qualitative, at present".

A variety of empirical models has been developed to predict erosion from hillslopes and sediment production from watersheds (Morgan, 1986; Hetrick and Travis, 1988). The model most commonly used to predict surface erosion is the universal soil loss equation (USLE; Wischmeier and Smith, 1978). This multivariate equation was derived from results of controlled experiments to estimate surface erosion from gently sloping farmland in the United States. The equation incorporates factors such as soil type, land use, slope angle, slope length and rainfall to estimate surface erosion. Recent work shows that the USLE significantly over-estimates surface erosion under tropical conditions, especially where there are steep slopes (Bureau of Soils, 1986; Liang et al., 1987). Until correction

factors have been field tested, the USLE cannot be used to accurately predict hill slope erosion under tropical conditions. In addition, although often misused, the USLE was designed to predict soil erosion from relatively small, uniform fields, not entire watersheds (Morgan, 1986). For these reasons it was not used in the present study.

Part of the difficulty in measuring sediment production in general may be attributed to problems with definitions of components of the soil loss process: rainsplash erosion, surface erosion, rill and gully erosion, and mass wasting (Table 2.1). Although these terms appear to be clearly defined, they tend to form a continuum. For example, a deep rill may eventually become a gully, but there is no clear division between these terms.

The individual erosion processes are difficult to measure because they often co-occur spatially and temporally and interact synergistically. For example, rainsplash loosens soil particles that are then sheared off and transported by overland flow. But as the runoff layer increases in thickness, rainsplash erosion is diminished. Another problem with measuring soil erosion over large areas is that mass-wasting may be relatively infrequent and difficult to predict, but may contribute a high percentage of total annual erosion (Coats and Collins, 1984).

Few attempts have been made to estimate total soil

loss by measurement of each soil loss component from an entire watershed (Trimble, 1981). This would entail detailed, repeated, surveys and measurements of changes in number and size of rills, gullies, channels and land slumps throughout the watershed. In lieu of this method, a commonly used technique to estimate total erosion relies on a weir system that traps sediment output from a defined catchment area (Kammerer and Batten, 1982; Dunne, 1984). Given the modest financial and man-power resources of the present project, the construction and monitoring of weirs or other large-scale sediment trap networks were not feasible.

In order to demonstrate that coastal logging in Bacuit Bay drainage basin is linked with coral reef sedimentation, it is necessary to show that accelerated soil erosion leads to accelerated transport to Bacuit Bay. Although this seems to be an obvious conclusion, there are alternative hypotheses. For example, despite a high erosion rate due to logging, sediment might be deposited before reaching the Manlag River. Sediment entering the river might be trapped in basins before reaching the bay. Fluvial sediment transport is a complex process. Sediment transport is a function of "stream power"; stream power is a function of water discharge rate times the channel slope ( $Q_w \times S$ ). The lower reaches of the Manlag River have a low slope so theoretically, sediment could be deposited in

storage basins and left undisturbed for many years.

Anderson and Potts (1987) have shown that sediment concentration and turbidity may or may not be correlated with water discharge due to variations in stream power and sediment supply. A model that includes depletion and replenishment functions of discrete sediment compartments has been proposed by VanSickle and Beschta (1983). Simple methods were chosen in order to evaluate the efficiency of sediment transport in the Manlag River.

### Methods

#### Soil

Soils appear uniform throughout the drainage basin and are composed of a reddish-brown clay with a 1 to 2 cm surface layer of dark top-soil. Soil samples for laboratory testing were obtained at 6 sites within the drainage basin and at 3 depths (2 cm, 30 cm, 1 m below the surface) from freshly dug holes. Two of the sites were adjacent to the erosion plots. The samples were analyzed by the Bureau of Soils in Manila for particle size distribution, textural grade, and calcium carbonate content (Appendix A).

#### Rainfall

The nearest Philippine Atmospheric, Geophysical and Astronomical Services Administration (PAGASA) weather stations to El Nido are at Cuyo Island in the Sulu Sea to

the East and at Puerto Princesa, in central Palawan. A network of 34 rain gaging stations was established in central and southern Palawan beginning in 1983 by the Palawan Integrated Area Development Project (PIAPD). Most were not operating in 1986 (PIADP, 1985b) and I was unable to obtain rainfall records for Palawan from PIADP or PAGASA for 1986. The nearest weather station for which there is published data is Clark Airbase, Central Luzon, (elevation 22 m) which is 450 km north of El Nido (National Oceanic and Atmospheric Administration, 1987). In any case, analysis of sporadic pre-1986 rainfall records for south and central Palawan show differences of 2 m or more in annual rainfall over distances of as little as 5 km (PIADP, 1985b). Due to orographic effects of the mountains around El Nido and because of the large distances (>80 km) of PIADP, PAGASA and NOAA stations from El Nido, rainfall data from these stations can not be expected to provide a reliable indication of rainfall in El Nido (PIADP, 1985b). No weather measurements are known to have been recorded at El Nido prior to this study.

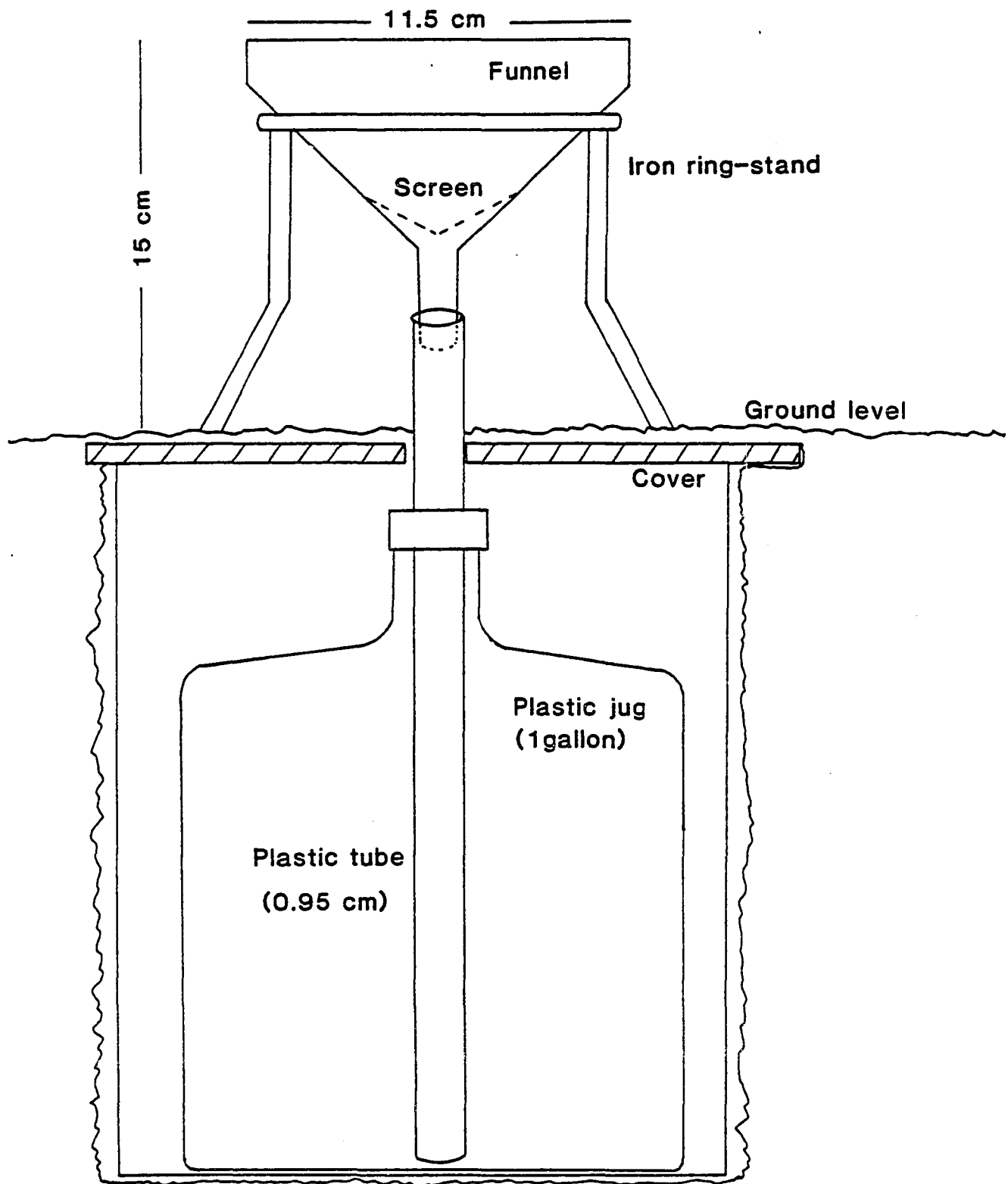
One continuously recording, battery-powered, rain gage (Rainwise Inc., Bar Harbor, ME) was placed in El Nido town. The gage is a "see-saw" or double-tipping-bucket type. It operates by catching rainwater in a funnel and directing it onto one side of a small, double-bucket, balanced in the center. The raised bucket tips and spills when full,

flipping the second bucket into place, and turning a recording dial. The minimum rainfall required to tip the bucket is 2.54 mm. Using this gage, daily rainfall was recorded in the village of El Nido from January 1 to December 31, 1986.

In the U.S., the standard procedure for measuring rainfall is to position a 20 cm diameter rain gage so that its orifice is elevated 3 ft above ground level (Helvey and Patric, 1983). It has been shown, however, that the location of the rain gage orifice near ground level (pit gage) gives more accurate measurements than when the orifice is elevated. This is due to wind effects which cause under-sampling (Helvey and Patric, 1983).

The non-recording gages used in the present study were constructed based on a design for pit gages by Buchanan et al. (1978). Comparative studies have shown that raingages of similar design are at least as accurate as standard gages (Huff, 1955; Kalma et al., 1969). The materials used for each gage were a one-gallon plastic jug, a length of 1 cm diameter, rubber hose, a funnel, a 30 x 30 cm piece of plywood and an iron cooking stand (Figure 2.1). A hole was cut in the top of the plastic jug cap and a section of rubber hose inserted until it reached the bottom. The hose was cut off 3 cm above the cap.

At each gage site, a 25 cm deep hole was dug in the ground and a metal can just larger than the jug was set



**Figure 2.1** Manual raingage.



inside to prevent the earthen walls from collapsing. One jug-hose assembly was placed in each can and a small plywood cover was placed over it and covered with soil. A small hole in the plywood allowed the rubber hose to pass through. An 11.5 cm diameter plastic funnel was tied onto a three-legged, iron, ring-stand and the bottom tip of the plastic funnel was inserted into the rubber hose. The stand supported the funnel on top of the soil-covered plywood. Rainfall on the funnel was trapped in the jug. Three of these pit gages were installed; one in Manlag village (elevation 30 m), one at the cut forest erosion plot and one at the uncut forest erosion plot (both the latter at an elevation of 140 m).

Trials using 2 l of water showed that losses due to evaporation were less than 2 ml over a one week period. Rainfall volume was recorded once per week by emptying the water into a graduated cylinder.

### Surface Erosion

An erosion plot is a patch of inclined ground, cut off from the surrounding area by above- and below-ground walls. This allows water run-off and eroded soil to be collected in a container at the lower end and measured. From these data, an estimate of runoff and soil erosion per unit area can be made.

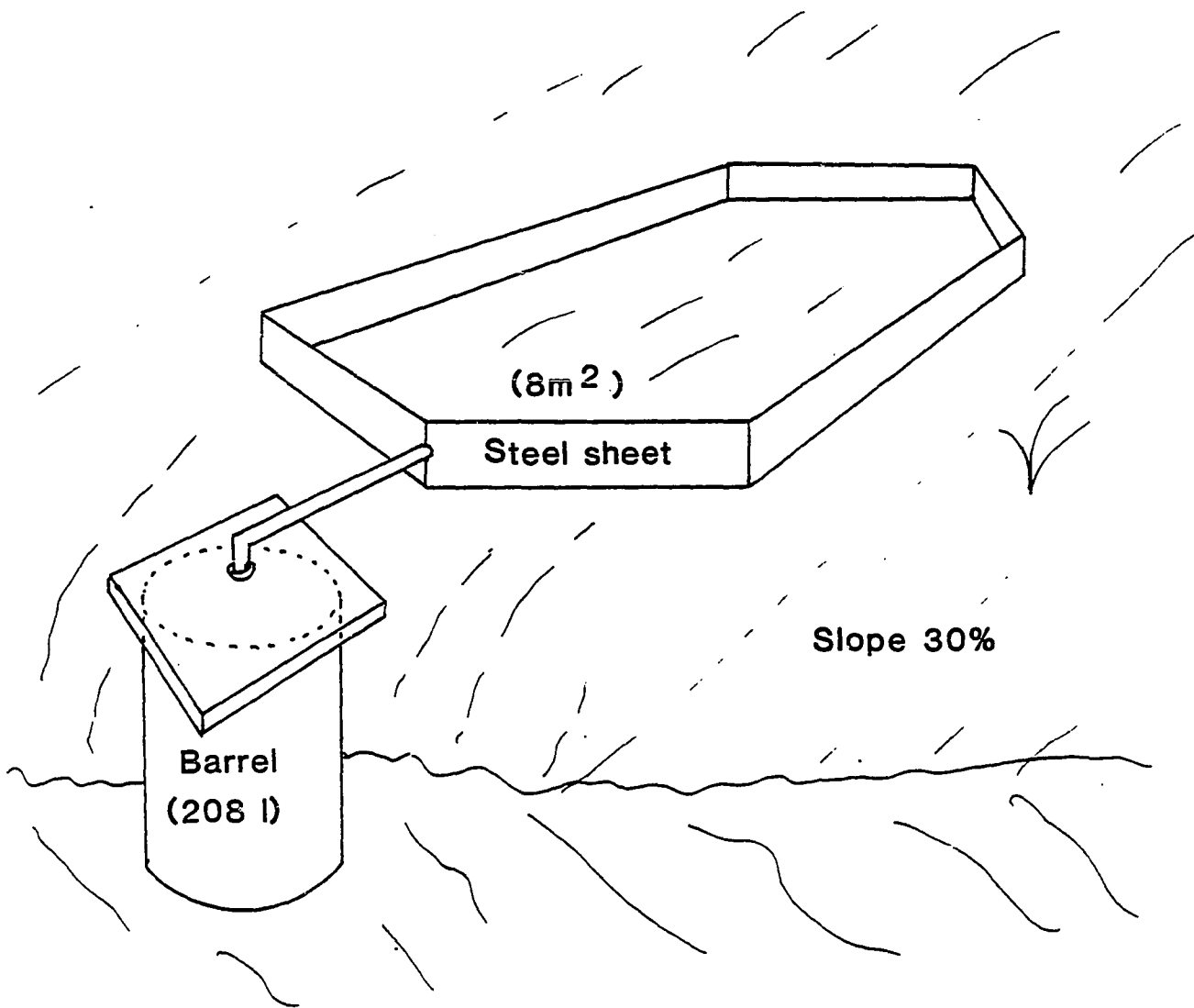
Three erosion plots were situated on a west-facing

hillslope behind Manlag Village where a secondary logging road separated a logged-over patch from a patch of primary forest (Figure 1.5). The advantage of this location was that the 3 plots were situated in different forest conditions but remained close enough to each other (within 20 m), so that differences in rainfall and soil conditions were minimized. The plots were located approximately 3 km from the eastern bay shore and at an elevation of 140 m.

One 8 m<sup>2</sup>, hexagonal, erosion plot was constructed at each of 3 sites: logging road, cut forest (already logged), and undisturbed primary forest, the control for disturbance (Figure 2.2). The slope steepness of all plots was 30% and the slope length was 4.82 m.

Each plot was enclosed by a continuous wall of 33 cm wide, 20 gauge, galvanized iron sheet. The sheet was set vertically in the ground so that half the sheet was above and half below ground. At all times care was taken not to step inside the plots. Only a thin strip of soil was removed to install the walls. At the lower end of the plot, a 20 cm wide plastic sheet was buried 15 cm under the soil to prevent leakage of water built up during torrential rainfall. Runoff water drained from the plot through a hole in the wall at the lower end, and then into a 1.5 m long, 2" diameter, PVC plastic pipe sealed in place with epoxy glue. A 20 X 20 cm square of galvanized 1/2" wire mesh was placed over the hole to prevent clogging by

Figure 2.2 Erosion plot design (not to scale). Barrel is set in ground.



leaves. The lower end of the pipe rested in a notch cut from the lip of a covered 208 l (50 gallon) drum set into a hole in the ground such that the top of the drum was lower than the base of the erosion plot. This allowed gravity flow to drain water from the plot into the drum.

The barrels were examined once per week except during periods of heavy rain when the barrels were monitored as required day and night to prevent over-flow. The wire mesh screens over the plot drain-holes were cleared of debris as necessary. Barrel water volume was measured using a calibrated dip-stick then 2, 1 l water samples were taken by siphon after first stirring vigorously with a plunger using an up-and-down motion. The siphon tube was moved through the entire vertical extent of the water column during collection to insure a representative sample. For each sampling, two, 1 l samples were collected, and the barrels were emptied. The water samples were allowed to stand for 1 week and then the supernatant was decanted and the sediment sun-dried. The sediment was oven dried, weighed and analyzed by the Bureau of Soils in Manila for particle size distribution, organic matter, and calcium carbonate as described in Appendix A.

#### Suspended Sediment Discharge

In order to estimate suspended sediment discharge from the Bacuit Bay drainage basin, a gaging station was established

on the Manlag River. The purpose of the gaging station was to allow measurement of river height (stage), river current velocity and suspended sediment load at one location. Selection of the gaging site was made by a hydrological survey team from the Palawan Integrated Area Development Project (PIADP), Puerto Princesa. Criteria used to select a gaging station site are reviewed by Carter and Davidian (1968). Important features of a gaging site include stable river banks and river bed, and accessibility during storm flow. The site chosen is 1 km upstream from the point where maximum high tide affects stream flow, 10 m downstream of the place where the river passes out of the logging concession and 5 m upstream from a rock riffle associated with a bridge. By locating the station at this site, essentially all suspended sediment could be attributed to natural causes and to logging, as there was no agricultural activity within the drainage basin upstream of this point. Sediment discharge from the Manlag River was used to estimate total erosion from the Manlag River watershed ( $19.6 \text{ km}^2$ ). In order to get a rough estimate of the contribution of natural erosion from undisturbed forest, the rate from the Uncut Forest erosion plot was used.

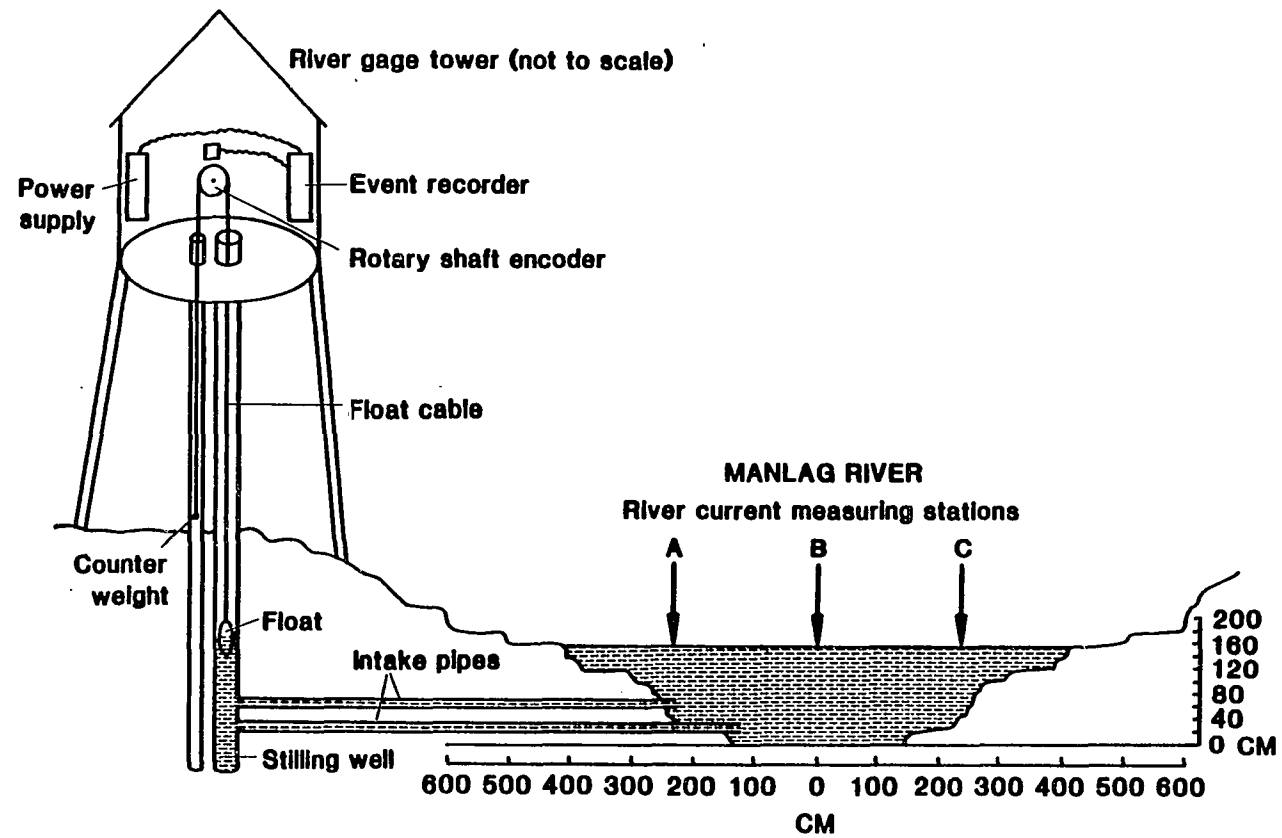
At the gage site, the area of 1 cross-section of the river from the river bed to 2 m elevation was determined by measuring the distance between the opposite river banks at

10 cm vertical intervals. Above this height, distances were measured at 0.5 m vertical intervals. A permanent staff gage was constructed which allowed manual reading of river stage. In addition to the manual gage, a continuous-recording, flood gage was installed on the river bank to automatically record stage height (Figure 2.3). Two horizontal 3" PVC pipes brought water from the river to the gage "stilling well". One of the 2 intake pipes was placed 0.3 m higher than the other to allow adequate flow during high stages. The "stilling well" was the bottom of the 10 cm PVC float pipe. A 6 m high wooden tower was built to hold the recording equipment and to stabilize the upper ends of the float and counterweight pipes. A weighted float was attached to a length of 3 mm flexible steel cable. The cable passed over a rotary recording device and then down a 2.8 cm pipe where it was attached to a counter-weight.

The recording equipment used was a PDL7 microprocessor event recorder, a PSC-2 replaceable-battery power supply converter, and a Ferranti type PYD 241 optical incremental shaft encoder (Data & Research Services Ltd., Milton Keynes, U.K.). In operation, an LCD display of river height on the data logger is initially calibrated to the river height read manually from the staff gage. When the river stage changes, the float moves vertically rotating the shaft encoder. River stage was recorded at 15 minute

**Figure 2.3** River gaging station (not to scale) and river cross-section (to scale).





intervals on modules of solid state, integrated circuit memory called "cachettes". Each cachette holds 42 days of records at this recording frequency. When the memory is full the cachette is replaced. The cachettes were decoded at PIADP facilities in Puerto Princesa.

This automatic data logger functioned until May when battery failure damaged an internal quartz clock. Beginning in May, river height was recorded manually at 07:00 h every day and more frequently during flood periods.

River current velocity (1 minute mean, 3 replicates) was measured by standing in the river daily at 07:00 h with a U.S. Geological Survey (USGS), Price AA rotary current meter following methods given by Guy and Norman (1970). Additional measurements were made during flood periods at which time the bridge just below the gaging station was used as a sampling platform.

Suspended sediment samples were obtained using both a manually operated, USGS DH-48, depth-integrating sampler and a fixed "bank" of 6 USGS U-59 single stage samplers attached in series to a staff gage board (Guy and Norman, 1970). Two 473 ml (1 pint) water samples were collected daily at 07:15 h using the DH-48 sampler following procedures defined by Guy and Norman (1970). The sampler was slowly lowered and raised such that a representative sample of the water column, from the surface to within 9 cm of the bottom, was obtained.

During rising river stage, the bank of U-59 suspended sediment samplers automatically collected one 350 ml sample at up to 6 levels, 0.64, 0.77, 0.96, 1.15, 1.50, and 2.00 m above the river bottom. The samplers are designed so that after the sample bottle is full, an air pocket is trapped in the exhaust tube preventing further water movement in or out of the bottle (Figure 2.4). When used in combination with high flood marks (debris lines) on the staff gage, these samplers were especially valuable to estimate sediment discharge during floods that occurred at night.

River water samples were allowed to settle for one week; the supernatant was poured off and the sediment allowed to sun dry. Sediments were oven dried to constant weight by the Bureau of Soils, Manila.

During 5 one-week periods, suspended sediment samples were collected (DH-48 sampler) from a "control" river (Balangoyan), which drains an area of the concession not yet affected by logging and then joins the Manlag (Figure 2.5). The Balangoyan is similar to the upper Manlag River in width, slope, shape, length and drainage area.

In order to measure sediment delivery in the Manlag River between the flood gage and the river mouth, suspended sediment samples were collected during several levels of discharge over this reach (DH-48 sampler).

No attempt was made to measure bed-load. Bed-load is the portion of sediment that is too heavy to remain

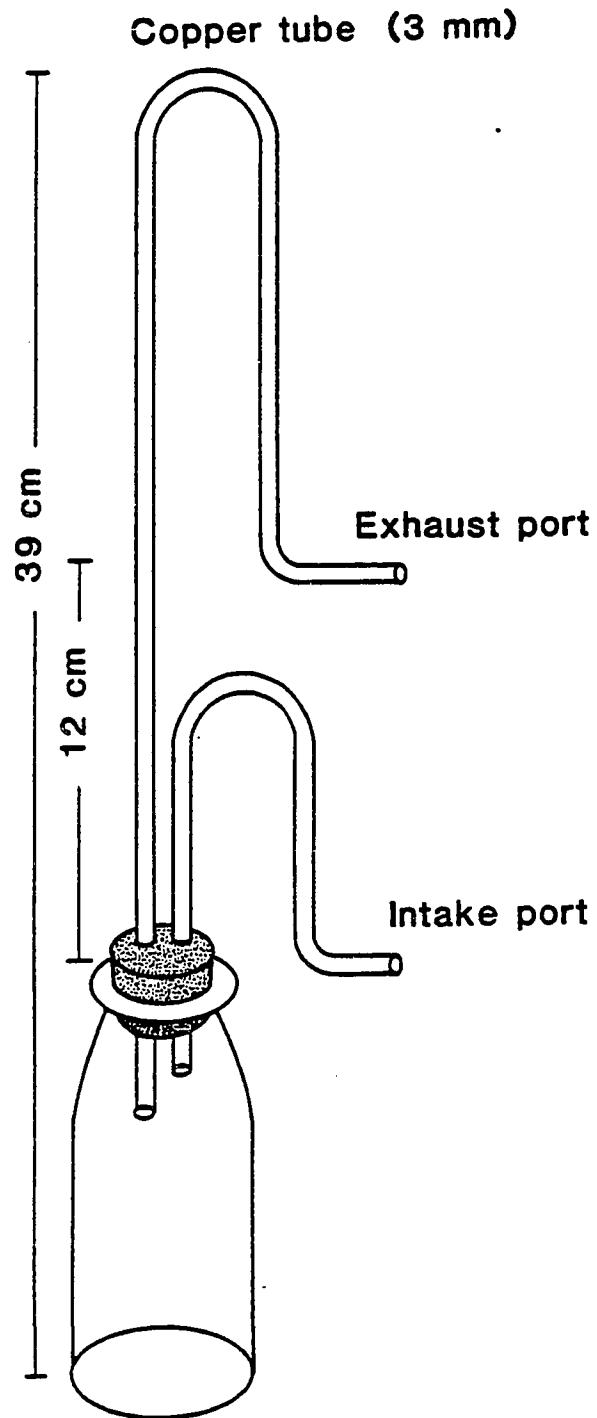
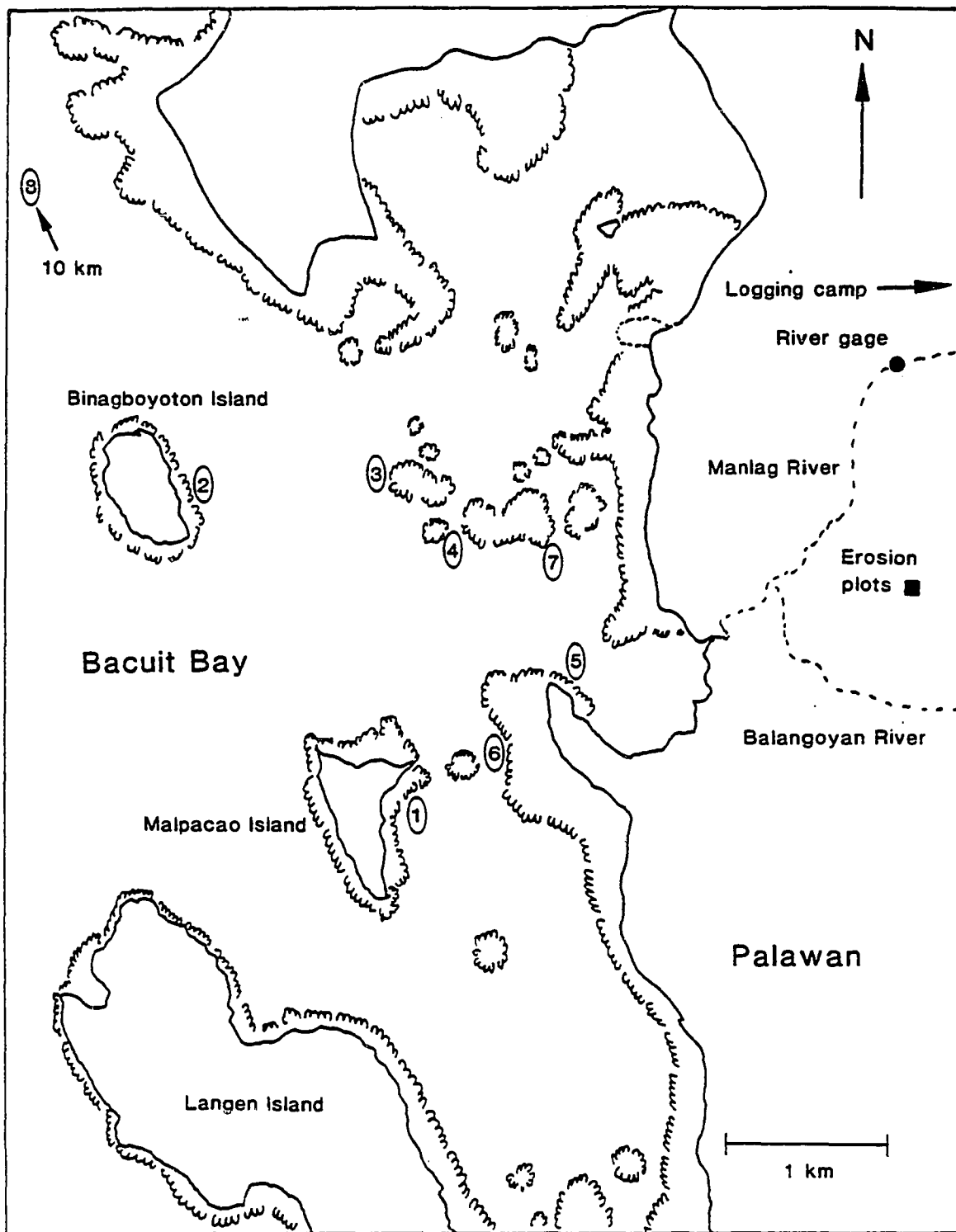


Figure 2.4 U-59 single-stage suspended sediment sampler. Six U-59 units were attached in series to a staff gage to form a "bank" of serial samplers. When the water level reaches the intake port the bottle begins to fill. When the water inside the bottle reaches the lower tip of the exhaust tube, the bottle is effectively sealed.



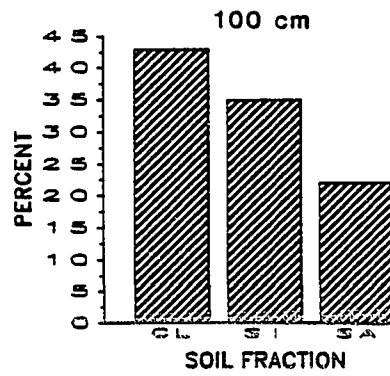
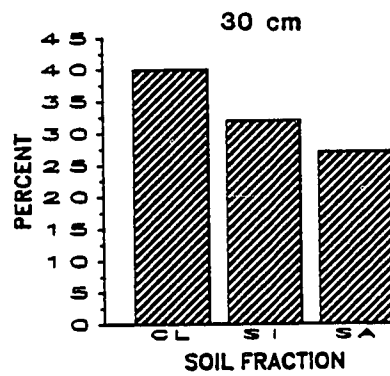
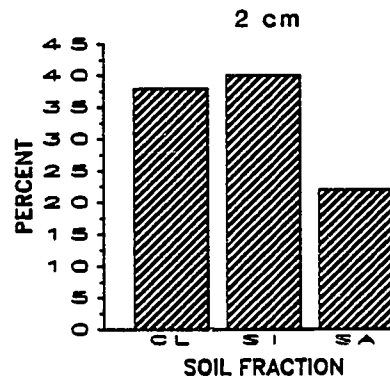
**Figure 2.5** Inner Bacuit Bay and drainage basin. The Manlag River passes through logged forest while the Balangoyan River passes through primary forest. Each number inside an oval marks the location of a coral reef study site (see Chapter 3).

suspended and moves along the river bed by saltation, rolling or sliding (Dyer, 1986). Particles that are not suspended in the relatively rapid river currents would not be expected to be suspended in the bay except during extreme conditions such as might occur during a typhoon. Since El Nido is not commonly affected by typhoons, the effect of river bedload on the bay may be limited to gradual infilling. Since few corals live near the base of the platform and fringing reefs common in Bacuit Bay, it is assumed that Bacuit Bay corals are rarely affected by bedload particles from the rivers, however this was not tested.

## Results

### Soil

Drainage basin soils have a 1-3 cm deep dark layer at the surface with orange, tan or reddish-brown sub-soil. Particle size analysis of soil samples obtained at three depths near the erosion plots (Figure 2.6) show that the 2 cm soil layer had a slightly higher percentage of silt than the deeper layers and less sand and clay. When the results from the 3 depths were averaged, sand formed 23%, clay comprised 36% and silt 41% of the soil. Calcium carbonate was not detected, and the soil pH was acidic (4.5-6).



**Figure 2.6** Particle size of drainage basin soils at 3 depths; 2, 30 and 100 cm below the surface. CL=clay, SI=silt, SA=sand.

### Rainfall

Annual 1986 rainfall measured at Clark Airbase, Central Luzon, (450 km north of El Nido) was 2.32 m, 21% above the 35 year average (National Oceanic and Atmospheric Administration, 1987). Total 1986 rainfall at Bacuit Bay drainage basin sites was 3.4 m (Table B.1, Appendix B). In contrast to the Clark Airbase data, 1986 rainfall was considered average to below average by local farmers. The total 1986 rainfall recorded by the El Nido village gage was 0.5 m less than the lowest rainfall recorded at the 3 other gage sites in the drainage basin. This difference between sites only 15 km apart may be an indication of the difficulty of predicting El Nido rainfall based on rainfall at Clark Airbase.

The rain measurements relevant to the erosion measurements are those from the 3 gages within the drainage basin. Monthly rainfall (Figure 2.7; mean of 3 gages located within the drainage basin) was very light from January through April with peaks in July and August and then again in November. Daily rainfall (Appendix B) was high in November and included the two highest daily totals in El Nido village in 1986, 66 mm and 102 mm.

There was no rain gage at the Road erosion plot site, however, this plot was located between the Cut Forest and Uncut Forest rain gage stations. The mean monthly rainfall at the latter two sites differed by less than 5%. There



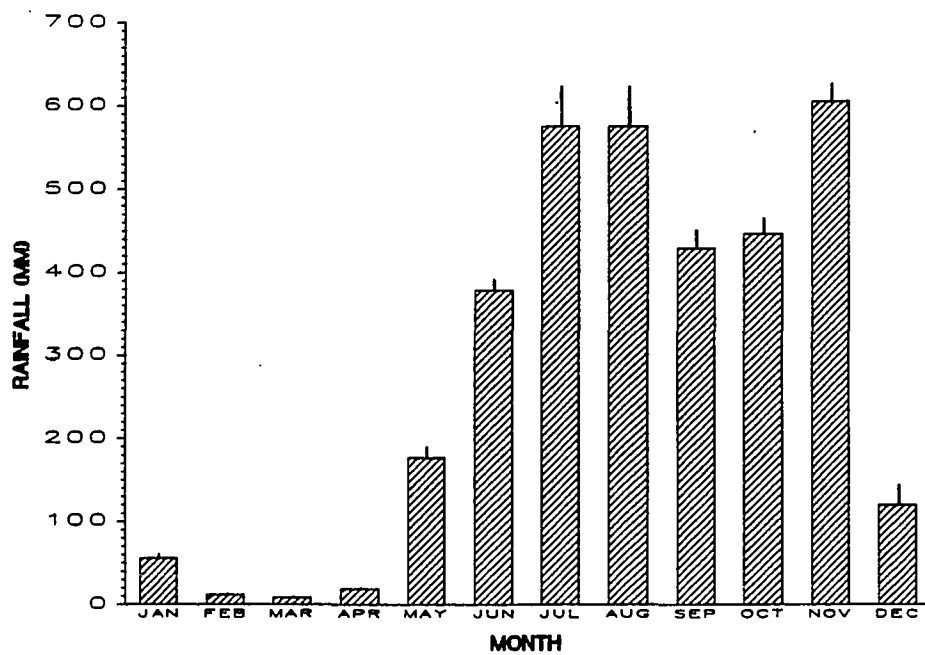


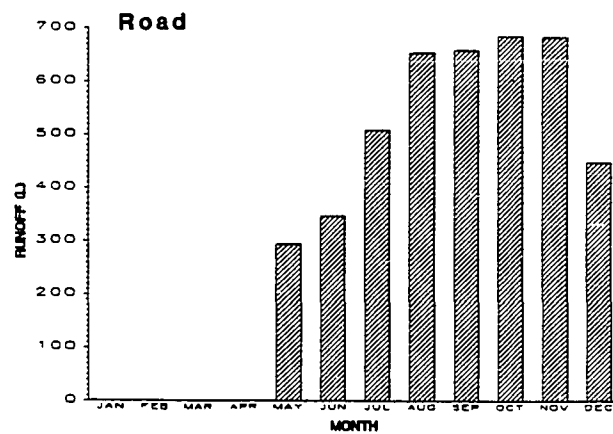
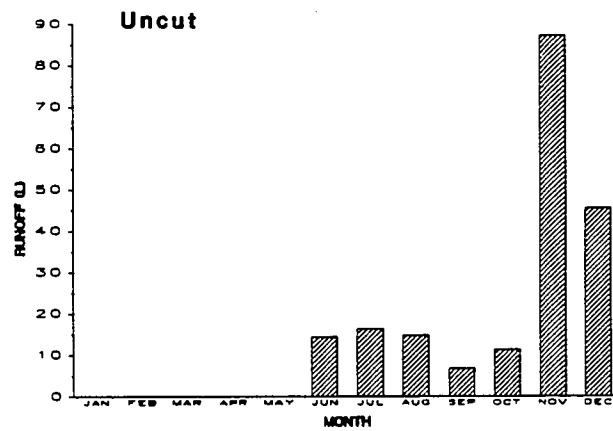
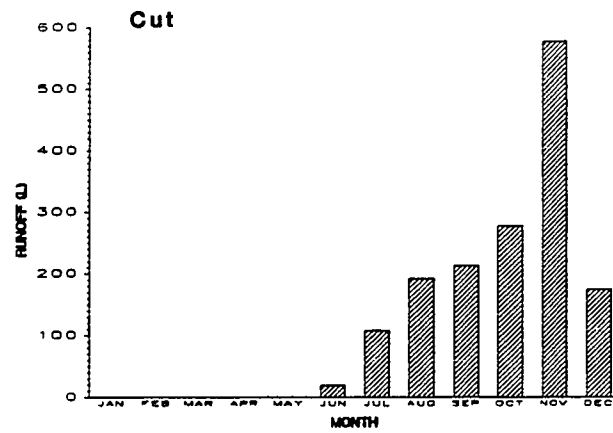
Figure 2.7 Monthly rainfall (mm) 1986; mean of 3 drainage basin sites: Manlag Village near the river gage, Cut Forest and Uncut Forest erosion plots. Error bars = 1 standard deviation.

was no significant difference in mean monthly rainfall among the 4 El Nido sites ( $p>0.05$ ; Tukey test). Therefore it is assumed that there was no significant difference between rainfall (above the vegetational canopy) at the Road site and the other two erosion plot sites.

#### Erosion Plot Runoff

Although above-canopy rainfall volume was assumed to be the same at the 3 erosion plot sites, the quality and quantity of rainfall that reached each plot was probably different. Each plot had a unique weekly, monthly and annual rate of water runoff and erosion. Since each plot was the same size ( $8 \text{ m}^2$ ), data (means and totals) are presented as liters of runoff water per plot. Total monthly runoff volume from the erosion plots is shown in Figure 2.8.

Although mean weekly runoff (Table B.2, Appendix B) from the Cut Forest erosion plot was much greater ( $33.7 \text{ l/week}$ ) than from the Uncut Forest plot ( $4.42 \text{ l/week}$ ) the means are not significantly different (Tukey test;  $p>0.05$ ), but both of these means are significantly less than the mean runoff from the Road erosion plot ( $106.7 \text{ l/week}$ ;  $p<0.05$ ). Since the Cut and Uncut Forest plots had raingages, runoff from these plots can be calculated as a percentage of rainfall volume ( $\text{runoff/rainfall} \times 8 \text{ m}^2 \times 100$ ). Runoff as a percentage of rainfall was 0.7% at the Uncut plot and 5.9% at the Cut plot. Using data from the Manlag raingage

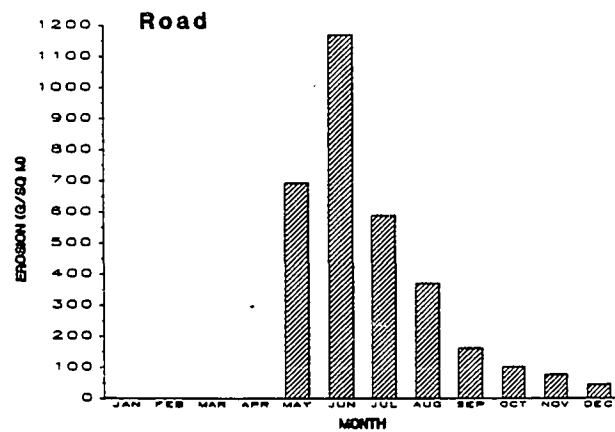
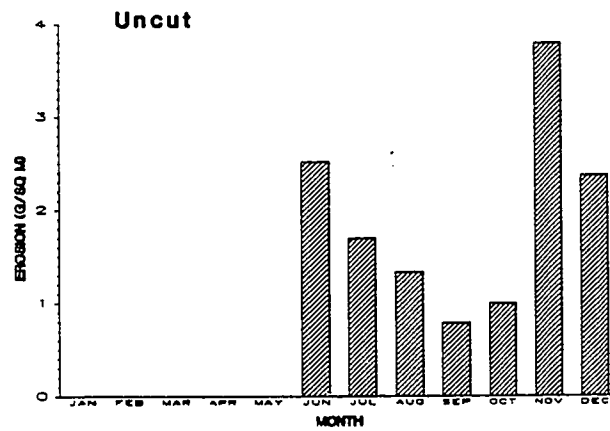
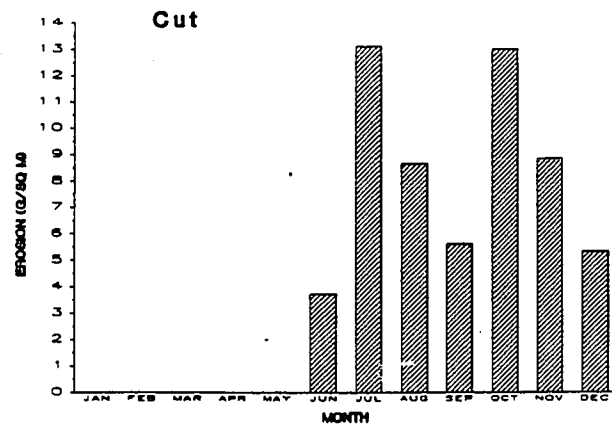


**Figure 2.8** Total monthly water runoff from Cut, Uncut Forest and Road erosion plots.

(which was in an open field) as an estimate of the Road plot rainfall, Road plot runoff was 15.2% of rainfall.

#### Erosion Plot Erosion

The total erosion per month ( $\text{g/m}^2$ ) from each of the 3 erosion plots is shown in Figure 2.9. Although some soil movement may have occurred within the plots during the light dry season rains, rainfall volume was insufficient to cause runoff, therefore no erosion was measured until May or June, when runoff was first collected. Using mean weekly erosion data (Table B.3, Appendix B), there is no significant difference between the Cut Forest ( $2 \text{ g/m}^2/\text{month}$ ) and the Uncut Forest ( $1 \text{ g/m}^2/\text{month}$ ) plots (Tukey test;  $p > 0.05$ ). There is a significant difference between mean weekly erosion from these two plots and that from the Road erosion plot ( $110 \text{ g/m}^2/\text{month}$ ;  $p < 0.05$ ). In addition, the total annual surface erosion from the Road plot ( $3,215 \text{ g/m}^2$ ) is 50 times greater than surface erosion from the Cut Forest plot ( $64 \text{ g/m}^2$ ), and 120 times greater than the rate from the Uncut Forest plot ( $26 \text{ g/m}^2$ ). Bulk density of the soil was not determined. If it is assumed to be  $1 \text{ g/cm}^3$ , then the annual depth of soil loss can be calculated to be: Road plot 3.215 mm, Cut plot 0.064 mm and Uncut plot 0.026 mm. The steady decrease in erosion from the road plot indicates caution should be used when trying to extrapolate these values over longer periods of time.



**Figure 2.9** Total monthly surface erosion from Cut, Uncut Forest and Road erosion plots.

### Suspended Sediment Discharge

At the location where the Manlag River empties into Bacuit Bay, Palawan Island is less than 10 km wide. The straight-line distance from the Central Palawan Ridge crest to the bay shore is about 5 km. The Manlag River shows a 90 m descent from its origin at 100 m elevation within the first 1.5 km, a 7% slope. The remainder of the river has a low slope, however, current velocities recorded at the gaging station during flood stage were occasionally above 1 m/s (4 km/hour). The steepness of the drainage basin slopes combined with the short length of the Manlag River, result in a relatively rapid response (30 min to 1 h rising, and 1 to 2 h falling) of the river to changes in the rate of rainfall as indicated by an example of the Manlag River hydrograph (Figure 2.10). The Manlag River is spring fed and runs all year, however, there are large differences in discharge between the dry and wet seasons. . For example, February discharge in 1986 was less than 4% of June discharge (Table B.4, Appendix B.).

A rough estimate of daily water discharge ( $Q_w$ ) from the Manlag River was obtained by multiplying the "instantaneous" current velocity ( $V_r$ ), by the area of the river cross-section ( $A$ ), corresponding to the river height measured at that time. The equation is:  $Q_w = V_r \times A$

Mean daily Manlag River water discharge in 1986 was 112,402 m<sup>3</sup>/day (1,528,667 ft<sup>3</sup>/day) with a range of 6,154 to

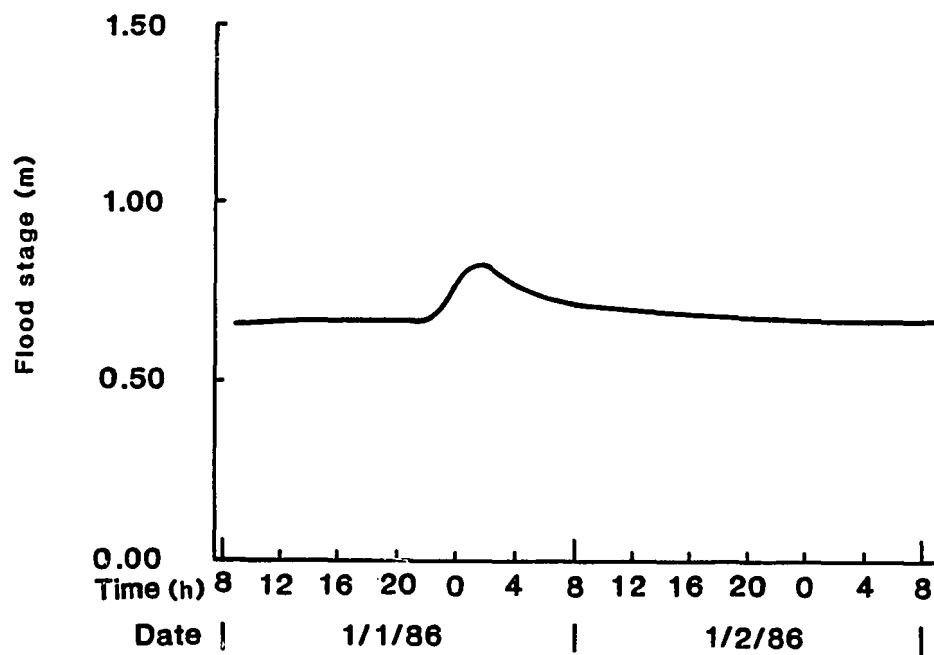


Figure 2.10 Manlag River hydrograph on March 3, 1986. Vertical axis is height above datum in meters. Horizontal axis is time in hours (0 = 24:00 h).

1,877,714 m<sup>3</sup>/day. The mean daily Manlag River water discharge for each month of 1986 is listed in Table B.4, Appendix B. The Manlag River drains approximately 25% (19.6 km<sup>2</sup>) of the 78.3 km<sup>2</sup> drainage basin, therefore mean discharge per unit area was 5,742 m<sup>3</sup>/day/km<sup>2</sup>. During the dry season, monthly water discharge from the Manlag River (Figure 2.11) was closely associated with rainfall, and stayed below 1 million m<sup>3</sup> until May. Monthly water discharge peaked in June, the month with the sixth highest rainfall. From July through the end of the year, rainfall and water discharge were not finely correlated.

A river "discharge rating curve" describes the relationship between water discharge and river flood stage (Carter and Davidian, 1968). The relationship may be linear, or non-linear and complex, depending on the effects of natural structures of the river bed and banks that may control water flow at different flood stages. The relationship may change with time as the features of the river bottom or river bank change. The stage-discharge relationship for the Manlag River in 1986 is shown in Figure 2.12. Linear regression of stage height on discharge was highly significant ( $r^2=0.87$ ;  $p<0.0001$ ). A relatively constant increase in the river cross-section with height to 1.5 m was consistent with the linear relationship (Figure 2.3). Above 1.5 m, the wide shelf would allow increased discharge with a less rapid increase



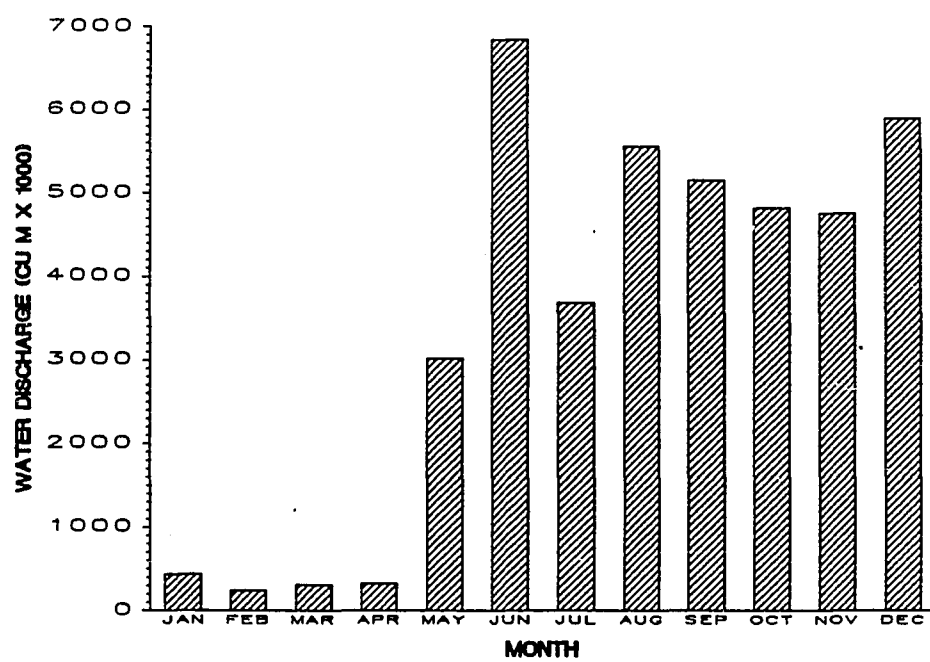


Figure 2.11 Total monthly water discharge from the Manlag River.

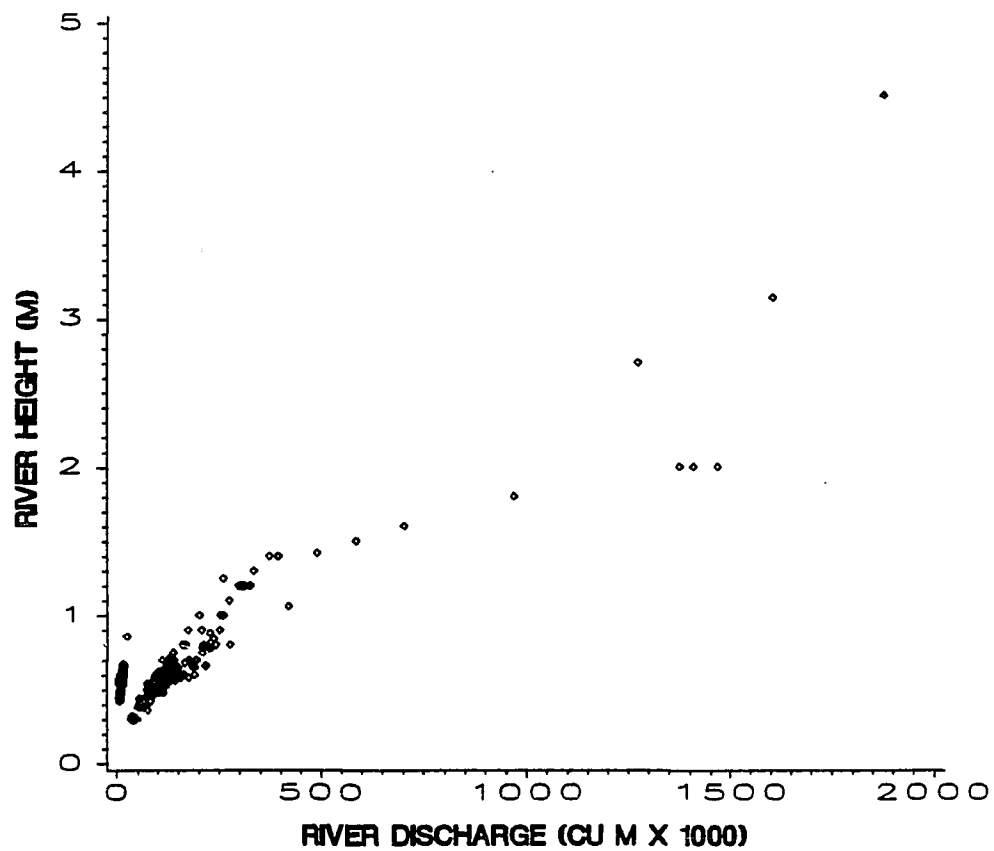


Figure 2.12 Plot of river stage (height) versus water discharge.

in river height. The relationship split into 2 curves above a discharge of 1 million m<sup>3</sup> due to seasonal changes and the location of the bridge span downstream. The lower, asymptotic curve was for unobstructed dry season floods. The exponential increase in river height occurred during December floods when logging debris had accumulated downstream of the gaging station, partially obstructing water flow. In addition, the bridge span obstructed water flow beginning just above 2 m elevation, and acted as a dam as shown by the 3 highest data points.

An estimate of daily suspended sediment discharge ( $Q_S$ ) in metric tons (mt), was obtained by multiplying the suspended sediment load ( $C_S$ ) by the water discharge ( $Q_W$ ) and adjusting for the appropriate units. The equation is:

$$Q_S = C_S \times Q_W$$

Daily suspended sediment load in the Manlag River at the gaging station ranged from 10 to 3200 mg/l (mean  $327 \pm 615$  mg/l). Mean daily sediment discharge per month is listed in Table B.4, Appendix B. Total monthly suspended sediment discharge from the Manlag river (Figure 2.13) ranged from a low of less than 400 mt (metric tons) in February to a high of over 13,000 mt in December. Using natural logarithm transformed values, regression of monthly sediment discharge on the difference between monthly and mean annual rainfall, was significant and produced the following equation where  $x = \ln(\text{monthly-mean rainfall})$  and

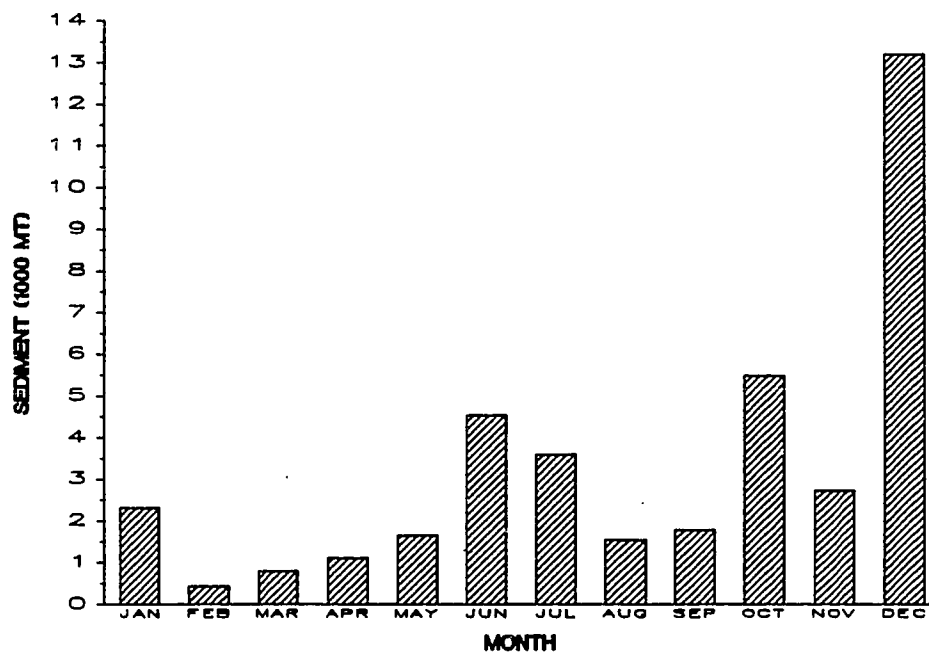


Figure 2.13 Total monthly suspended sediment discharge from the Manlag River.

$y = \ln(\text{sediment discharge})$ : ( $y = 1.33x - 4.95$ ,  $r^2 = 0.33$ ,  $p = 0.05$ ).  
 Using natural log transformed data, regression of monthly sediment discharge on the difference between monthly and mean annual water discharge was also significant ( $r^2 = 0.43$ ;  $p < 0.02$  for the linear equation  $y = 0.49x + 4.49$  where  $y = \ln(\text{sediment discharge})$  and  $x = \ln(\text{monthly-mean water discharge})$ ).

Total estimated suspended sediment output for 1986 was 39,154 mt or 2,000 mt/km<sup>2</sup> (Manlag River and Manlag River watershed (19.6 km<sup>2</sup>) only). Extreme caution should be used in extrapolating soil erosion for an entire watershed based on data from relatively tiny erosion plots due to potential differences in soil conditions, exposure, slope and other factors. For this reason, a sediment budget was not calculated for the Bacuit Bay drainage basin based on erosion plot results and total sediment production was calculated from Manlag River discharge. However, the only data available on erosion from the natural forest is the erosion plot data, and therefore this was used to make an admittedly rough estimate of the percentage of sediment output due to natural erosion. The natural rate measured from the Uncut erosion plot (26 g/m<sup>2</sup>) was multiplied by the area of primary forest remaining in the Manlag River watershed: 19.6 km<sup>2</sup> (Manlag watershed) - 4.8 km<sup>2</sup> (logged forest) = 14.8 km<sup>2</sup> of primary forest. Therefore natural sediment output from undisturbed forest in the Manlag River

watershed was calculated as:  $26 \text{ mt/km}^2$  ( $26 \text{ g/m}^2$ )  $\times 14.8 \text{ km}^2$   
= 385 mt. That is, 75% of the land produced less than 1% of Manlag River sediment discharge in 1986. Even if the erosion plot value underestimates true natural erosion by 100%, it would not alter the conclusion that natural erosion in primary forest land produces a small sediment output when compared with sediment output from accelerated erosion due to logging.

Further support for this conclusion comes from comparison of suspended sediment load between the pristine Balangoyan River and the Manlag River. In 1986, the Balangoyan River drained only uncut primary forest land. The Balangoyan joins the Manlag River about 2 km from the bay, and during 1986 there was always an obvious demarkation between the clear Balangoyan and the muddy, brown Manlag River water. A comparison of mean daily suspended sediment load in the two rivers over a wide range of flood stages during 5 one-week periods shows a significantly greater suspended sediment load in the Manlag River for all periods (t-test; Table 2.2).

Mean daily suspended load in the Manlag River was over 16 times that in the Balangoyan River over these 5 periods. According to interviews with local residents, prior to the onset of logging operations the water quality of the Manlag was similar to that of the Balangoyan River.

Table 2.2 Mean (S.D.) suspended sediment load in the Manlag and Balangoyan Rivers and t-test results. Simultaneous samples obtained during 5 one week periods.

<u>Mean Suspended Sediment (mg/l)</u>					
Period	Balangoyan		Manlag		t-test
Feb 1-7	11	(2)	214	(33)	***
May 1-7	48	(7)	1,157	(172)	***
Jun 15-21	48	(6)	580	(411)	**
Aug 1-7	14	(3)	200	(0)	***
Dec 21-28	103	(7)	1,500	(1,086)	**
Mean	45	(34)	730	(721)	

Significance level in t-test: \*\*  $p < 0.005$ , \*\*\*  $p < 0.0001$ .

During low flow periods ( $< 100 \text{ m}^3/\text{d}$ ), 75% of suspended sediment measured at the gaging station reached Bacuit Bay; the remaining 25% was lost to temporary storage. During moderate flow periods, this delivery ratio increased to 95%. Samples were not obtained during high flood stages. A lack of change in water color and rapid current flow indicate the delivery ratio between the gaging station and the bay may be 100% at high flood stages.

Alternative causes of erosion in the logging area were natural tree-falls due to storms and soil disturbance by animals. Natural tree-falls were uncommon in the logging concession and feral animals such as pigs would be subject to intense human predation. No evidence of either of these factors was seen during 1986.

## Discussion

### Soil, Rainfall, Runoff and Erosion

Soil erosion on ground that is not steeply sloped is often so slow that it is difficult to observe. One way to visually estimate the vertical rate of soil loss was to compare soil protected from rainfall by rocks or other surface litter with surrounding soil. The rapid rate of erosion was especially striking in low-slope sections of the El Nido logging concession previously cleared by bulldozer. As the rainy season progressed, small pieces of hardened soil, pebbles and rocks were left standing on pinnacles at the original soil level while the soil around them was gradually lowered several centimeters.

On the erosion plots, a low level of precipitation, and high evaporation, plant utilization and infiltration apparently precluded runoff or erosion from January through April. Despite nearly 200 mm of rain in May, only the Road plot produced runoff. Factors that may have led to runoff collection from the Road plot one month earlier than from the other 2 plots are soil compaction of the road surface due to previous road use by heavy machinery and the lack of plant cover. Like soil hardening from drying, soil compaction reduces infiltration rate leading to increased runoff. Once clay soil is saturated, the maximum infiltration rate (capacity) may be quite low, allowing substantial runoff. Since rainfall quantity, soil types,



drainage, and slope were similar for the 3 erosion plots, differences in water infiltration capacity among the 3 plots will be affected primarily by soil conditions, rainfall quality and water removal by plants. Plants, especially large trees, remove water from the soil rapidly (Ghosh, et al, 1978). Other factors being equal, soil of plots with fewer plants (and roots) may become saturated with water faster than plots with many plants and root systems.

For the Uncut plot, runoff and erosion did not vary with rainfall, except for a peak in November. Given the very low level of erosion from the Uncut plot compared to the other 2 plots, the steady decline in erosion through September may have been due to stabilization or loss of small amounts of soil next to the wall that may have been disturbed during construction. Following soil stabilization in September, erosion varied in close association with runoff until the end of the year.

With fewer plants on the Cut plot than the Uncut plot less water was probably taken up and more runoff occurred.

For the Cut erosion plot, a steady increase in runoff from June until November could be due to a steady increase in water saturation of the soil. Water saturation increases when the rainfall rate increases faster than evaporation, drainage and plants can remove it. A lack of association between monthly runoff and erosion as occurred at the Cut

plot is not unusual (Wischmeier and Smith, 1978) and may have been caused by cyclical vegetation changes, and soil responses to repeated wetting and drying. Hardening and cracking, could lead to a high runoff period producing little erosion or a low runoff period producing high erosion. With respect to temporary storage, an erosion plot is analogous to a river, complete with micro-basins where detached sediment may be trapped after being transported a very short distance.

The location of the Road plot on a presumably highly compacted surface may explain increased runoff through October, and the erosion peak in June followed by a steady decline. With the exception of September and October, when soil may have been fully saturated with water, Road plot runoff varied closely with changes in rainfall. It appears likely that once an initial surface layer of loose soil was removed, the hard-packed, sun-baked clay surface resisted erosion despite high runoff, even during the high intensity November rains.

A significant percentage of erosion from logging roads is due to losses from cut-and-fill slopes of road shoulders as opposed to from the road surface itself (O'Loughlin, 1985). In contrast to the Road erosion plot, these steeply inclined and non-compacted surfaces are not expected to show such a rapidly declining rate of erosion over time. In fact, the common occurrence of mass wasting (land

slumps) along old roads in the El Nido area indicates that mass wasting will continue for several years after logging road construction, a result documented in other areas (Henderson and Witthawatchutikul, 1984; Schroeder and Brown, 1984).

The location of the Road erosion plot between the Cut and Uncut Forest plots duplicated a common location of logging roads in El Nido. It is likely that this location with respect to Cut and Uncut Forest areas, would expose logging roads to raindrop coalescence and throughfall of large drops from adjacent canopies. At the erosion plot site, the Uncut Forest canopy was completely intact and thick, while the Cut canopy was composed of foliage of widely-spaced, smaller trees that remained following logging. The effects of large-drop throughfall on erosion of the Cut Forest plot were probably minimized by a partial covering of leaf litter, thickly growing grasses, shrubs and a tree sapling. The surface of the Uncut Forest plot was protected by a thick layer of leaf litter, a multi-layered understory and the thick canopy.

Given the large number of site specific variables that affect erosion (Wischmeier and Smith, 1978), the lack of close correlation of runoff, erosion and rainfall among the 3 plots is not surprising. Despite these variables, the annual surface erosion rates measured from the 3 plots in El Nido are comparable to those measured in other

locations. In a review of erosion from undisturbed forest land in the humid tropics, Wiersum (1984) found that annual erosion rates ranged from 3 to 616 g/m<sup>2</sup> (3 to 616 mt/km<sup>2</sup>), median 30 g/m<sup>2</sup>. The median value is similar to the annual Uncut (primary) forest plot erosion rate (26 g/m<sup>2</sup>) in El Nido.

In a study of erosion in a logging concession in Indonesia, the total annual erosion rate from logging roads ranged from 15,480 g/m<sup>2</sup> (newly built road and in use) to 7,380 g/m<sup>2</sup> (2 years after abandonment) (Ruslan and Manan, 1980). If rill and gully erosion provide about 50% of total erosion (O'Loughlin, 1985), then this latter value is in line with the El Nido results for annual surface erosion from the Road plot (about 3,000 g/m<sup>2</sup>). The lack of road use in El Nido may also be an important factor. Reid and Dunne (1984) reported that heavily used logging roads in Washington state produce more than 100 times as much erosion as abandoned roads.

It is instructive to compare an estimate of total erosion expected from the El Nido logging concession with similar estimates for other parts of the world. Rather than estimating total erosion from the entire drainage basin based on data from the 3 small erosion plots, sediment discharge from the Manlag River, should provide a reasonable estimate of erosion.

In order to compare the results from El Nido with

those from other logging areas, a rough estimate of total erosion from the Manlag River drainage area can be made by dividing the total 1986 suspended sediment output from the river (39,154 mt) by the area it drains (19.6 km<sup>2</sup>). This calculation yields an estimate of about 2,000 g/m<sup>2</sup> total annual erosion. In Thailand, which has a monsoonal climate similar to the Philippines, annual surface erosion from a fully operational logging concession was 10,000 g/m<sup>2</sup> based on catchment data (Henderson and Rouysungnern, 1984). Annual sediment yields from a variety of logging operations in the United States are reported to vary widely from about 300 to 200,000 g/m<sup>2</sup> (often expressed as mt/km<sup>2</sup>) (reviewed in Brown and Krygier, 1971). The erosion rate will, of course, depend greatly on the proportion of logging road and cut forest in each location.

Several studies including the present one indicate that erosion from logging roads accounts for most of the erosion due to logging (see also O'Loughlin, 1985; Hodgson and Dixon, 1988). Clearly, the cumulative surface area of all roads within a given concession and their age will be of major importance in determining the rate of erosion and sediment output from that area. In the El Nido case, only 6.1% of the drainage basin was logged during the study. If all remaining primary forest is logged, cut forest (with roads) will amount to 53.4% of the drainage basin. Although some decrease in erosion from old, unused roads is

expected with time (Ruslan and Manan, 1980; Anderson and Potts, 1987; this study), sediment output from the Bacuit Bay drainage basin is expected to increase far above the level measured in 1986 as more of the concession is logged (Hodgson and Dixon, 1988).

#### Water and Sediment Discharge

Annual sediment discharge from the Manlag River (2,000 mt/km<sup>2</sup>) is high when compared with discharge from large river systems around the world e.g. the Amazon (70 mt/km<sup>2</sup>), the Mississippi (110 mt/km<sup>2</sup>), the Ganges (1,500 mt/km<sup>2</sup>) and the Yellow River (2,900 mt/km<sup>2</sup>; Holeman, 1968). Since a sediment budget was not calculated for the drainage basin, it is not possible to determine the ratio of eroded soil entering the Manlag River to suspended load discharged into Bacuit Bay. The most likely location for sediment storage in the Manlag River would be along the lower reach between the gaging station and the bay. This section is characterized by low slope, increased channel width and depth, and tidal influence, all factors favoring low stream power and sediment storage. However, sediment delivery over this section was between 75 and 100%, even during low flow periods. Additional observations indicate that during peak flood stages, temporary sediment deposits would be removed. Although not observed in 1986, during exceptionally dry years, low wet season flow might allow

substantial sediment deposits to build up.

Based on a rainfall of 3.4 m in the 19.6 km<sup>2</sup> Manlag River watershed in 1986 and discharge of 41,026,730 m<sup>3</sup>, 62% of rainfall drained into the Manlag River. Due to the upstream location of the river gage, the discharge value may underestimate discharge at the river outlet, resulting in an underestimate of the percentage of rainfall discharged. The response of Manlag River water discharge to rainfall is attributed to variation in 3 primary factors: the rainfall rate, the water absorbing capacity of the soil, and groundwater flow from the drainage area. No data are available about the latter factor. Exposed limestone cliffs throughout the drainage basin show extensive cave networks and such geological formations are indicative of subterranean drainage outlets that might allow a portion of total rainfall volume to escape from the system. Rainfall rate affects the water discharge rate because a low rate allows more evaporation, and infiltration. Although several light rainstorms can produce the same rainfall volume as one intense rainstorm, all other factors being equal, the intense storm will generate more runoff and water discharge than light storms. As noted previously, the infiltration rate for a given soil changes with time and weather conditions, and this will affect runoff and discharge rates. In addition, statistical correlation between either monthly water or

sediment discharge, and rainfall, may be affected by low frequency monitoring of Manlag River parameters.

A well known problem with measuring sediment discharge is that 90% of annual discharge may occur during a few short, intense storm flows that "clean out" any accumulated deposits from the system (Doty et al., 1981; Ashmore and Day, 1988). The relatively steep hydrograph of the Manlag River indicates that large storm flows can come and go within a few hours. For example, peak sediment discharge from the Manlag River was in December. Ninety-two percent of December sediment discharge occurred during a 4 day period, and 50% during one nighttime flood. Since the bank of U-59 samplers was generally monitored only once per day, multiple storm flows during 24 h could have been missed. Despite this potential sampling error, the linear relationships between log-transformed sediment discharge, rainfall and water discharge were significant.

One potential effect on the relationship between water and sediment discharge is mass wasting. Although the frequency of mass wasting theoretically increases with rainfall (Thomas and Trustrum, 1984), the interaction of other variables makes it difficult to predict the timing of specific land failures. Small land slumps, especially near a river will rapidly increase sediment input and sediment discharge independent of water discharge; a possible explanation of the October Manlag River peak. The standard



deviation of mean daily sediment discharge in October was more than 5 times the mean. In addition, over 30% of October sediment discharge occurred during a single day.

### Conclusions

Samples of El Nido soils are composed of 41% silt, 36% clay and 23% sand;  $\text{CaCO}_3$  was not detectable. A moderately high silt content increases soil erodibility while the clay content decreases water infiltration capacity and increases the potential for runoff.

The dry season in 1986 lasted 4 months (January-April). There was 3.3 m of rain in the Bacuit Bay drainage basin in 1986 with a maximum in November. Although rainfall in Central Luzon (450 km north) was above normal in 1986, El Nido farmers considered 1986 rainfall to be average to below average. There was no significant difference in rainfall among 3 gage sites within the drainage basin and it was assumed that all erosion plots experienced the same above-canopy rainfall.

The lack of runoff from erosion plots until May was attributed to a low level of precipitation, high evaporation, plant utilization of water and infiltration. Despite 200 mm of rain in May, only the Road erosion plot produced runoff, probably because the Road plot was more highly compacted than the other two plots, and lacked plants and a thick leaf litter. Mean weekly runoff and erosion were significantly greater ( $p < 0.05$ ) at the Road

erosion plot than at the other 2 plots.

Total surface erosion from the Road plot in 1986 ( $3,215 \text{ g/m}^2$ ) was 50 times the Cut Forest rate ( $64 \text{ g/m}^2$ ), and 120 times the Uncut Forest rate ( $26 \text{ g/m}^2$ ). Erosion from cut and fill slopes of logging roads was expected to be even higher than the Road plot rate. These erosion rates are similar to rates collected in other tropical logging concessions. The limited data are in agreement with previous studies suggesting that logging operations, particularly logging roads, significantly increase erosion from forest lands. Although some decrease in erosion from old, unused roads may occur over time, annual erosion and sediment output from the Bacuit Bay drainage basin is expected to increase far above the level measured in 1986 as more of the concession is logged.

Due to a short length and steep slope in the upper reaches, the main river (Manlag) draining the El Nido logging concession showed a relatively steep hydrograph. The river stage-discharge relationship was linear up to 1.5 m. Monthly sediment discharge showed a positive linear relationship with both monthly minus mean rainfall and monthly minus mean water discharge after logarithmic transformation of the data. Mean daily suspended sediment load ranged from 10 to 3200 mg/l and was significantly greater (16 times) than suspended load in a nearby "control" river unaffected by logging. Sediment delivery

ratio was high during moderate to high flood stages when the greatest sediment discharge occurred and sediment storage potential was judged to be low. Total sediment discharge from the Manlag River in 1986 was 39,154 mt of which less than 1% was attributed to natural erosion.

In summary, the evidence suggests that logging in the Bacuit Bay drainage basin caused significant increases in: 1) erosion above natural levels, 2) suspended sediment load in the main river draining the basin and 3) sediment discharge to Bacuit Bay.

### III. MARINE PHYSICAL PARAMETERS

#### Introduction

Evidence was presented in the preceding chapter that supports the hypothesis that logging significantly increases erosion and sediment discharge from the Bacuit Bay drainage basin. Suspended sediment discharged from drainage basin rivers into Bacuit Bay is subject to the action of water currents and other physical forces before it settles to the bay floor or is exported to sea. Since physical forces determine where and when a given sediment particle will be deposited, they are important in determining the effects of sedimentation on living organisms, particularly corals. The physical forces that influence sedimentation in Bacuit Bay are the subject of this chapter. Prior to considering methods used in this part of the study, it is useful to briefly review sedimentation theory.

Sediments enter a bay water column through two primary pathways (Figure 3.1). The first major route is sediment delivery from terrestrial sources, especially from rivers and streams. Some terrestrial sediment is derived from shoreline erosion due to wave action, however, in the Bacuit Bay case, little shoreline erosion was evident. The second major avenue of sediment input to the water column is via resuspension of previously deposited sediments from the bay bottom. This second route of sediment input

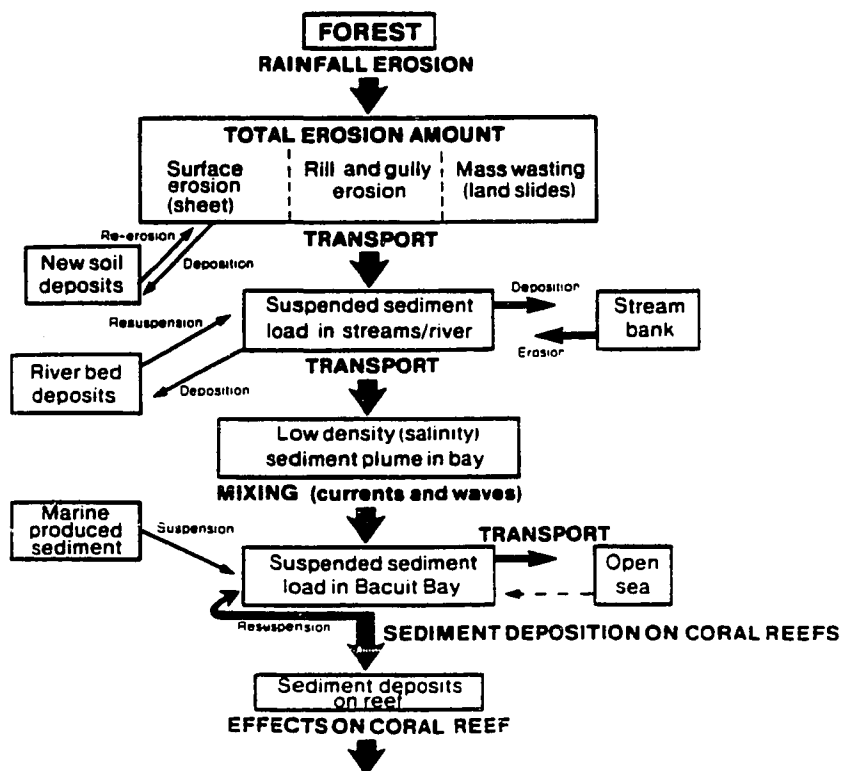


Figure 3.1 Flow diagram of sediment transport from forest to Bacuit Bay. Note the many potential depositional phases that slow sediment transport.

includes resuspension of both terrestrial and marine sediments. The proportion of sediment in the water column that is derived from the first or second major input routes depends primarily on two physical parameters: rainfall rate in the drainage basin and water current velocity (including wave induced currents) and direction in the bay.

As discussed in the preceding chapter, rainfall determines major trends in terrestrial erosion, runoff, suspended load and sediment discharge. Stream power partially determines the distance entrained sediments travel after being discharged into a bay. Following sediment deposition, wind and tidal water currents as well as wave induced bottom currents are the major forces of resuspension. Once resuspended, sediments may be redistributed by water currents.

Advection of entrained sediment in Bacuit Bay is a complex process. Major processes affecting sediment transport in Bacuit Bay are described below. Detailed discussions of bay and estuarine sediment dynamics are given in Dyer (1986) and Mehta (1986).

When sediment-laden freshwater flows into the sea, sediment transport is affected by differences in density between fresh and salt water. Freshwater floats on top of saltwater unless wind or waves induce mixing. During periods of high freshwater discharge and calm weather, low-density freshwater moves rapidly over salt water resulting

in increased horizontal transport prior to mixing. In contrast, during conditions of low freshwater discharge and moderate to high wind and waves, sediment-laden freshwater mixes relatively quickly with salt water. If tidal currents and wind driven currents happen to be in the same direction, lateral sediment transport will be much greater than if these forces are opposed.

In fluids, sediment particles sink at a rate (settling velocity) dependent on particle shape, size and density and fluid density as described by Stokes Law

$$V_s = D^2/18(d_p - d_f/\mu)g$$

where  $V_s$  is the settling velocity,  $D$  is the particle diameter,  $d_p$  and  $d_f$  are the particle and fluid densities,  $\mu$  is the molecular viscosity, and  $g$  is acceleration due to gravity.

In general, large, dense, smooth particles fall more rapidly than small, less dense, flat or rough particles (Table 3.1). For example, if a mixture of different sized sediment particles is transported by horizontal currents in shallow water, the smaller particles will be carried farther than large ones before they settle to the bottom. This maxim of "fining down the transport path" is useful for tracing the origin of sediment deposits. Based on this principle, mean particle size in sediment deposits is expected to decrease with distance from the source. In addition, since less shear force is required to resuspend

small particles than large particles, older sediment deposits tend to have a size distribution skewed towards the larger sized particles (Dyer, 1986).

**Table 3.1** Theoretical settling velocity of spherical quartz particles in seawater<sup>1</sup>.

Sediment Type	Diameter ( $\mu$ )	Settling Velocity (m/day)
Coarse Sand	1,000	14,400
Medium Sand	250-500	3,600
Fine Sand	62-125	300
Silt	30	75
	15	20 <sup>2</sup>
	8	5
	2	0.3
	1	0.07
Clay	0.5 <sup>3</sup>	0.004
	0.25	0.002
	0.12	0.001

<sup>1</sup>Modified from Sverdrup *et al.*, 1940.

<sup>2</sup>Approximate 1 day threshold for settling in water <20 m.

<sup>3</sup>Actual settling velocity of particles <0.5  $\mu$  will be faster due to flocculation.

Another factor affecting sediment transport is flocculation, the binding of sediment particles together to form larger ones. Sediments with a high percentage of clay and organic matter are more likely to flocculate when moving from fresh to salt water. By increasing particle mass, roundness and specific gravity, flocculation



increases sedimentation rates thus decreasing potential horizontal movement (Dyer, 1986). These general principles are the basis for analysis of suspended and deposited sediments. Such analysis reveals details of the history and origin of sediments.

### Methods

Eight monitoring stations were established in Bacuit Bay (Figures 1.4 and 1.5, Chapter 1). Each station was located seaward of a coral reef where permanent transect lines were established for community studies. Site 8 was the fringing reef of Dilumakad Island, near the northern bay entrance. Due to its distance from the Manlag River outlet (16 km), this station was chosen as a control for the effects of logging induced sedimentation.

Since automatic recording instruments were not available, a twice monthly sampling regimen for physical parameters of the bay was carried out in 1986 with the help of several assistants. On the 1st and 14th of each month, temperature, salinity, wind speed and direction, wave height and turbidity were measured using a motorized outrigger boat as a mobile laboratory. Seawater samples were collected during several high river discharge periods. On the first of each month, sediment traps were recovered and samples collected.

### Temperature and Salinity

Water temperature was measured manually with a thermometer held at 10 cm depth (accuracy  $\pm 0.5$  °C). Salinity was measured with a hand-held, temperature adjustable refractometer (accuracy  $\pm 0.5$  ppt; Atago, Inc., Tokyo).

### Wind, Waves and Currents

Wind speed at 2 m elevation over the bay was measured using a hand-held wind speed indicator (Davis Instruments, San Leandro, CA). Measurements were taken at various unobstructed locations throughout the central bay; there was no attempt to sample at a given location and time. The assumption was made that differences over open water would be slight. The instantaneous wind speed was recorded at the end of 5 consecutive one minute periods at 8:00, 10:00, 12:00, 14:00, 16:00, and 18:00 h. Maximum and minimum wind speeds during the 5 minute period were also recorded. Wind direction was measured with a hand-held compass.

Water currents generated by waves, before, during and after breaking are a primary cause of sediment resuspension. As deep water waves move into shallow water, they begin to "set-up", increasing in height. Waves that come into "contact" with the bottom are called breaking waves (Dyer, 1986). The extent of increase in the height of breaking waves depends on several factors, especially the slope of the bottom, water depth, wave

velocity, wave length and amplitude. Total wave energy per unit surface area was calculated from the equation  $E = dg(H^2/8)$  where  $d$ =seawater density,  $g$ =acceleration of gravity, and  $H$ =wave height (Dyer, 1986). From the equation, it can be seen that energy is a function of wave height squared. Thus the potential of waves to resuspend sediment deposits depends on wave height. The height of the highest one-third of all waves was visually estimated at 14 day intervals at each station for a minimum period of 15 minutes.

Current direction and speed were measured from a boat using drogues. The drogue design allowed the submerged portion to be tied off at a variable distance below a float (Figure 3.2). Currents were primarily measured at depths of 0.5 to 1 m; some additional tests were made at 2-3 m. In order to maintain a constant position, bow and stern anchors were deployed to prevent the boat from swinging. A drogue was placed in the water from the boat and a timer was started. Direction of travel was measured using a compass, and distance travelled was measured with an optical range-finder. The range-finder (Model 620, Ranging Inc., E. Rochester, N.Y.) has a range of 15-180 m with an accuracy of  $\pm 0.1$  m at 15 m, and  $\pm 2$  m at 100 m. Depending on current speed, the tests were stopped after the drogue passed beyond 50 m or after 60 minutes had passed, whichever occurred first.

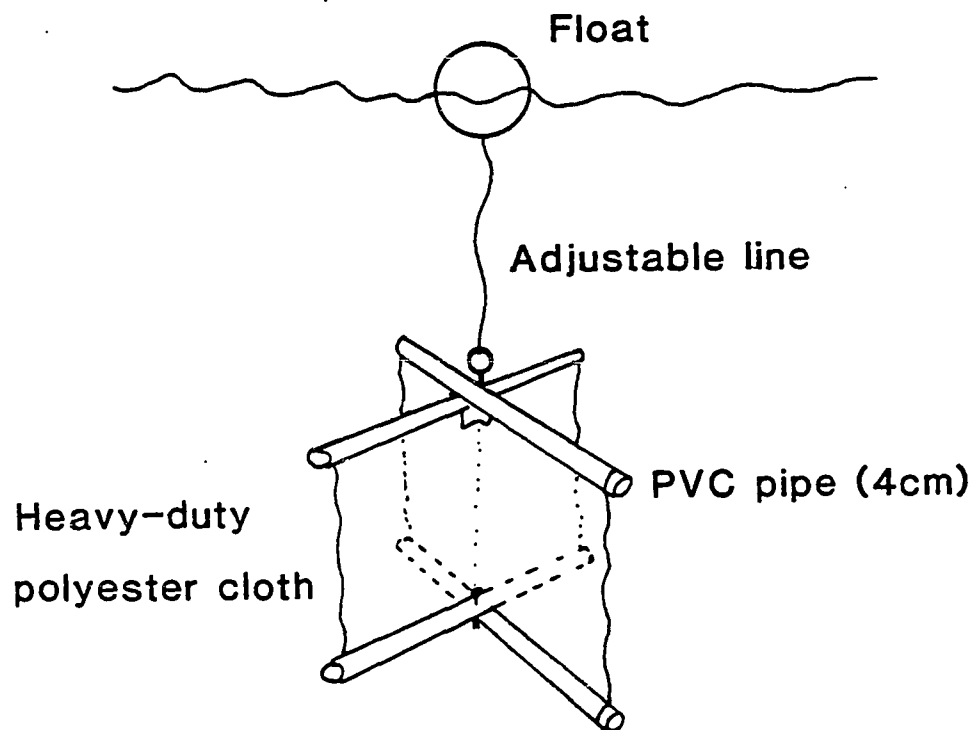


Figure 3.2 Design of water current drogue. Each of the 4 cloth wing-panels is 50 x 50 cm.

### Turbidity

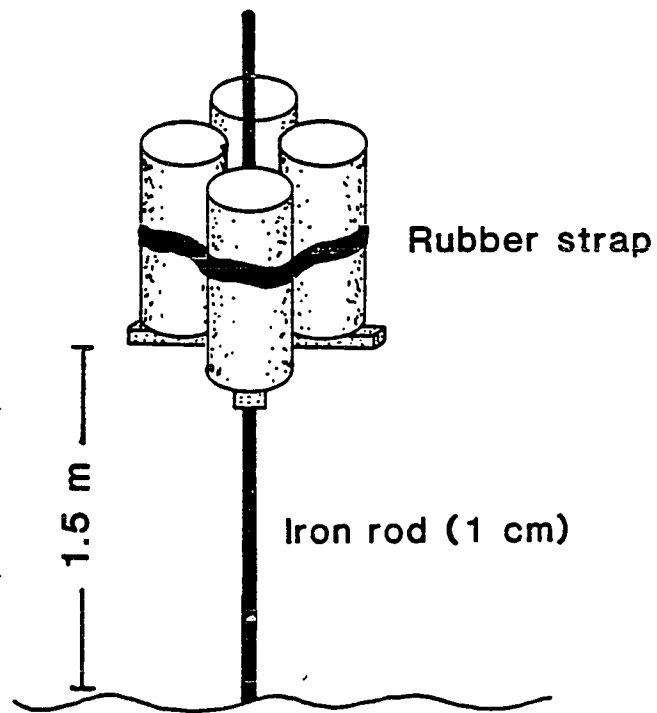
One method of estimating differences in sediment concentration is to measure relative turbidity with a secchi disk. Relative turbidity is an optical property dependent on suspended sediment concentration and characteristics of the sediment such as particle size, shape and composition (Ekern, 1976). Water column turbidity was assessed at 14 day intervals at each station using a 30 cm diameter, white secchi disk. The disk was lowered into the water and depth of disappearance was recorded. A high secchi depth reading indicates clear water and low turbidity. Since the sea surface condition affects the visibility of the disk, the reading was made from the lee side of the boat.

In addition to making secchi depth measurements, a subjective estimate was made of underwater visibility at least bi-weekly throughout the year at each site.

Manlag River plumes were tracked by boat, and velocity was measured by recording the time required for the plume front to travel between reefs. Distances between reefs were obtained from aerial photographs of the bay.

### Sediment Deposition

Sediment deposition was measured with a set of 4 sediment traps at each station (Figure 3.3). Sediment traps were built following design recommendations of Gardner (1980) to



**Figure 3.3** Sediment trap design.

have a diameter to height ratio of between 1:2 and 1:3 to avoid over and under-sampling. A 0.63 cm (1/4") mesh galvanized wire screen was inserted several centimeters inside the top of each trap to exclude fish, crabs and other large organisms. Each set of four traps was attached to a steel bar that had been set into the bottom at 3 m depth. The traps were located 1.5 m above the bottom such that the trap openings were above the level of most corals and at least 1 meter distant from the nearest large colony. This configuration was used to provide a conservative estimate of sedimentation experienced by corals at each site. Additional traps were placed at other depths and locations in the bay used as sites for field experiments.

All traps were recovered on the first of each month. Trapped sediment was poured into bottles and the traps were scrubbed immediately to clean off all fouling organisms and then redeployed. The sediment samples were allowed to stand until settled. Supernatant was decanted, and sediment samples were double-washed with fresh water to remove salts. Samples were sun-dried in plastic containers, then transported to the Bureau of Soils, Manila for analysis (Appendix A).

In order to compare the composition of suspended sediments trapped 1.5 m above the bottom with sediments deposited on the bottom, benthic sediment samples were collected. Five 500 g benthic sediment samples were hand-

collected by pushing plastic containers into the substrate at 10 m intervals along the permanent transect established at each station.

In addition to surface samples of the bay bottom along the transects, the history of sediment deposition at each site was assessed using a 1 m long, 3 cm diameter, clear, flexible, polyethylene plastic pipe (3 mm thick walls) to core the substrate 5 m seaward of the reef-base at each site. Cores were capped and later examined under a dissecting microscope.

Additional information about sediment deposition history was obtained by using the coring tube to test the resistance of the sediment to penetration. The distance the tube could be pushed vertically into the substrate without bending was recorded in five haphazardly chosen locations at the base of each reef, and substrate appearance was recorded.

#### Sediment Characteristics

All sediment samples of 30 g or more were analyzed for percentage particle size, calcium carbonate content, and organic matter content as described in Appendix A. Because of the lack of calcium carbonate in the acidic El Nido soils, calcium carbonate in the sediment trap sediments was assumed to be of marine origin and non-calcium carbonate sediments were assumed to be of terrestrial origin.



Subtraction of the calcium carbonate fraction from total sediment (100%) provided an estimate of terrestrial inputs to sedimentation. The organic component could be of either terrestrial or marine origin.

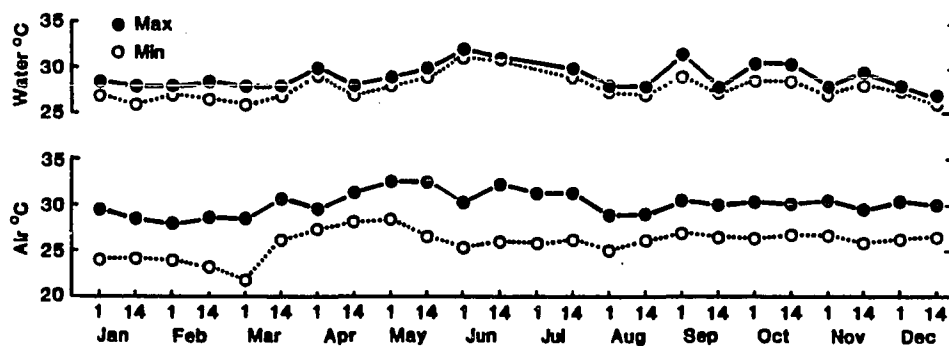
## Results

### Temperature and Salinity

Minimum and maximum daily air temperatures recorded at the river gage station during 14 day periods in 1986 (Figure 3.4) show an annual low of 22 °C in late February and a high of 32 °C in early May.

Maximum and minimum seawater temperatures for the 8 Bacuit Bay sites exhibited a narrow range in 1986 (Figure 3.4). The lowest seawater temperature reading at 10 cm depth was 26 °C at Site 3 in mid-January, and the highest was 32 °C (all sites except 3 and 8) in early June. Mean monthly seawater temperature (n=12 months) ranged from 28 to 29 °C during 1986 (n=24) and there were no significant differences among sites (Table C.1;  $p>0.05$ ; Tukey test). Seawater temperature in the depth range of 3 to 10 m was 1 °C lower than the surface seawater temperature; and in the depth range of 10 to 20 m the temperature was 2 °C below the surface temperature.

Mean monthly salinity was 33 parts per thousand (ppt) at all sites except 1 and 8 where it was 34 ppt



**Figure 3.4** Mean maximum and minimum air temperatures in Manlag Village and mean minimum and maximum seawater temperatures (n=8 sites) in 1986.

(Figure 3.5; and Table C.2, Appendix C). There was no significant difference in mean salinity among the 8 sites ( $p>0.05$ ; Tukey test). The greatest salinity variation occurred at Sites 3, 4 and 7; these were patch reefs in the path of the Manlag River discharge plume. Salinities below 30 ppt were associated with arrival of the Manlag River discharge plume. Underwater observations made at these times revealed that the 1 m layer of sediment-laden freshwater water remained intact for several hours, especially if the wind was light. Details of sediment plume characteristics and behavior are given in the following sections.

### Wind

When the study began in January 1986, the northeast monsoon winds were already in progress and lasted until the end of March (Figure 3.6). The southwest monsoon winds began in April and lasted through September (Figure 3.7). Winds in October and November were variable. The northeast monsoon returned in December, 1986 (Figure 3.6). Mean wind speed and direction for each month are listed in Table C.3. Mean wind speed was high during February, August, September and December with a peak of 4.7 m/s in August. As discussed previously, Bacuit Bay is not on a high frequency typhoon belt. Maximum sustained wind speed (5 minute mean) recorded in 1986 was 10 m/s, gusting to 27 m/s (96 km/h).

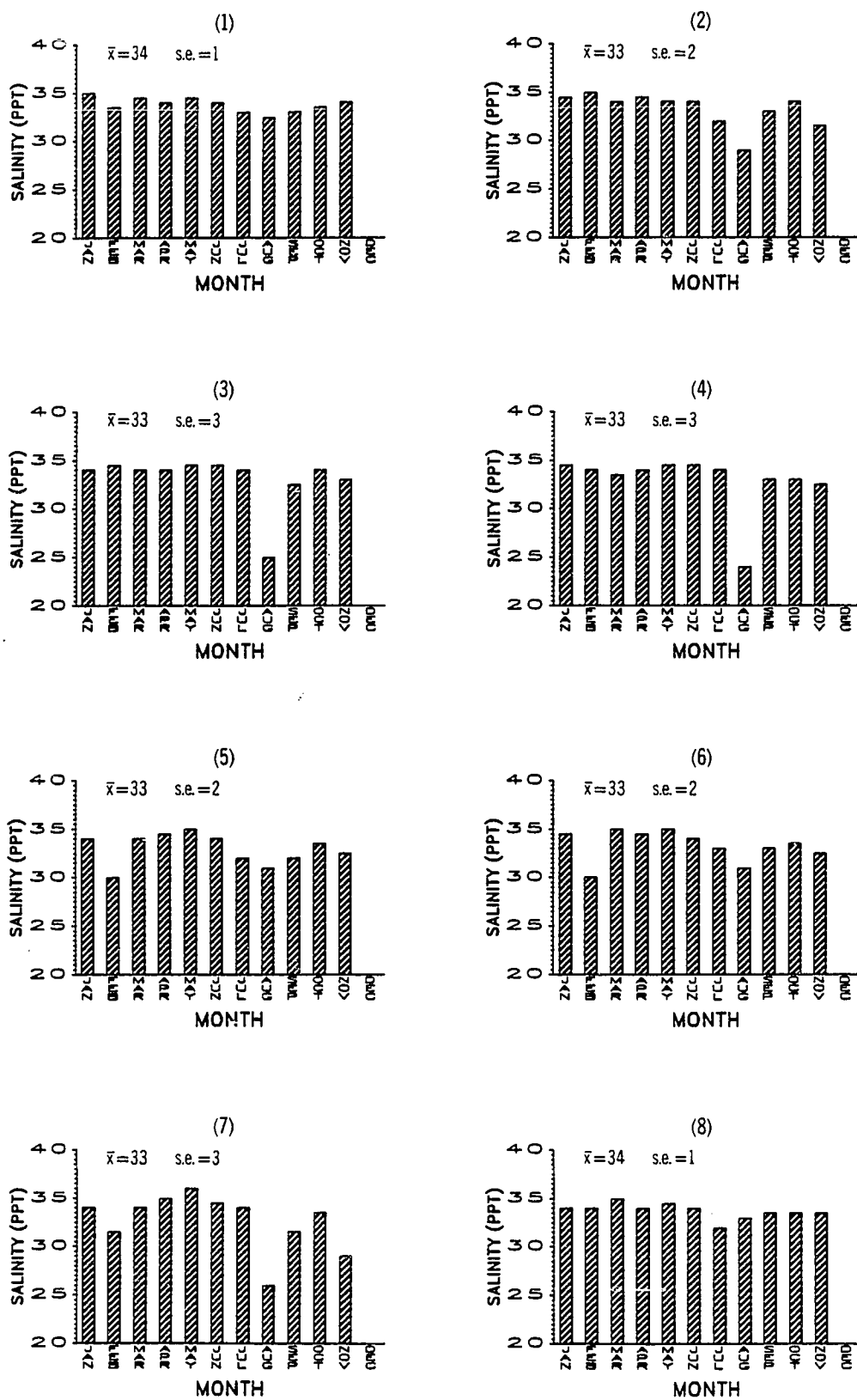
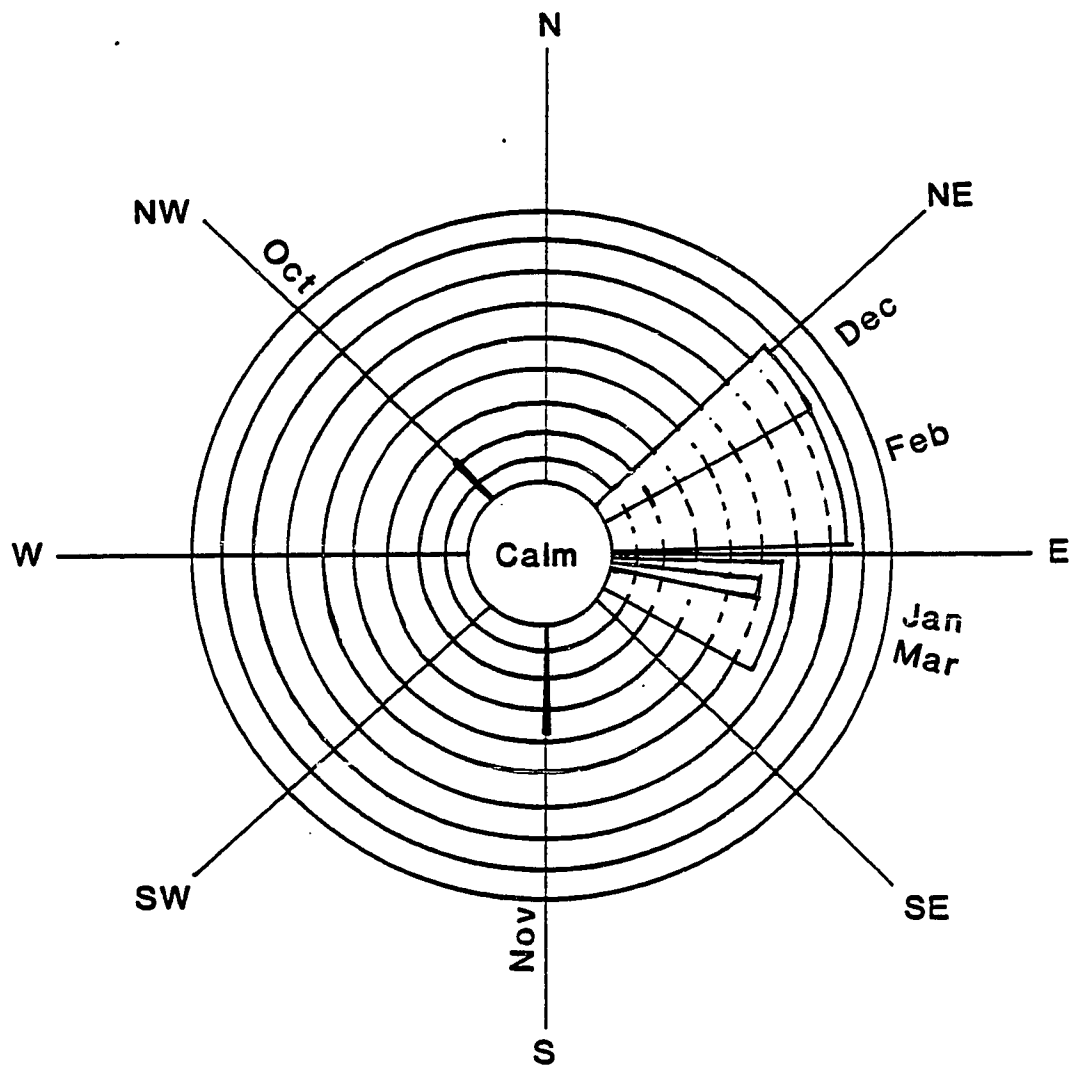
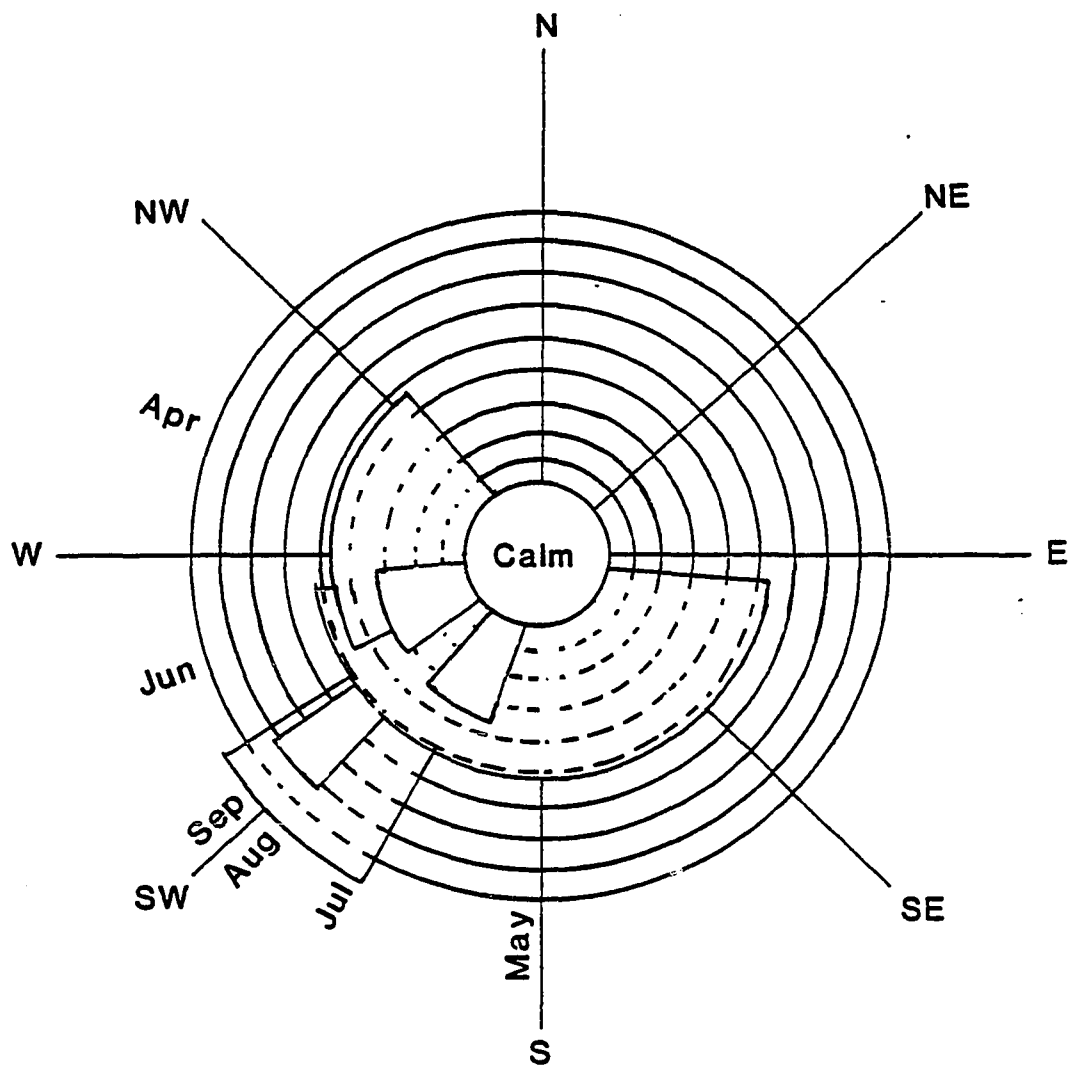


Figure 3.5 Mean monthly salinity (ppt) at Sites 1-8.



**Figure 3.6** Wind speed and direction during Northeast monsoon (October-March) 1986: Calm = 0 m/s and each circular division is 0.5 m/s.



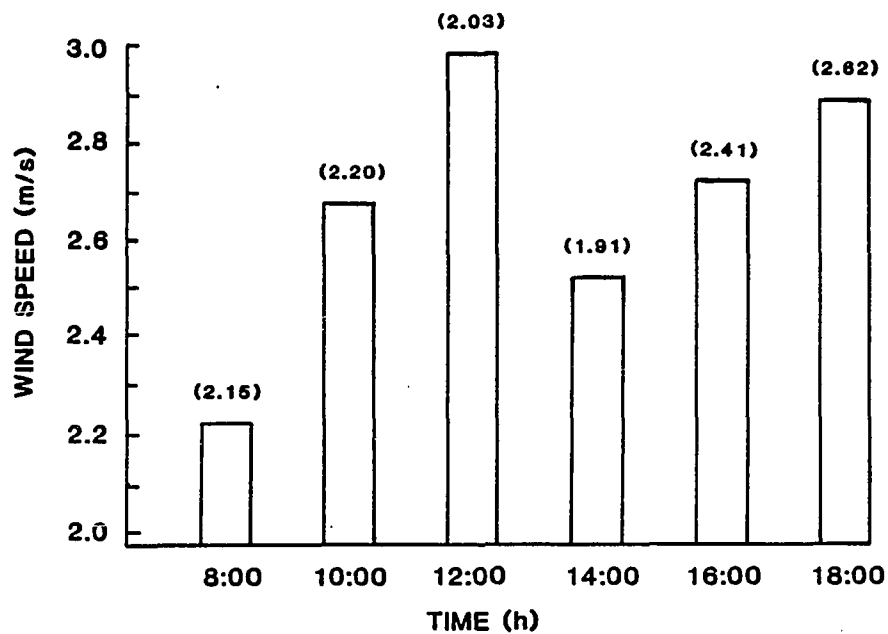
**Figure 3.7** Wind speed and direction during Southwest monsoon (April-September) 1986: Calm = 0 m/s and each circular division is 0.5 m/s.

There was no significant difference in mean wind speed among months, between the two monsoon periods or between morning and afternoon ( $p>0.05$ ; Tukey test) despite an apparent bimodal distribution with peaks at noon and at 18:00 h (Figure 3.8).

### Waves

Two types of waves affected the Bacuit Bay study area: distant storms created long period waves (ocean swell) that entered the bay through channels between the islands at the bay entrance, and short period wind chop was generated by wind blowing inside the bay. The two daily peaks in wind velocity (12:00 and 16:00 h) appeared to cause two matching peaks in sediment resuspension by wind chop, but this was not measured. Due to the orientation of the bay, reefs in the study area were exposed to long period waves only from the north to northwest direction. Maximum fetch for wave generation inside the bay (10 km) was along the northwest-southeast axis. At each study reef the position of the reef front relative to wind and swell direction affected the height of breaking waves.

Mean monthly height of breaking waves at each site is shown in Figure 3.9. The highest mean wave height was recorded at Site 3 in October. Mean wave height at Site 3 was significantly higher than at Sites 1, 2 and 7 ( $p<0.05$ ; Tukey test; Table 3.2). The control reef (Site 8) had the



**Figure 3.8** Diurnal wind speed variation at 2 h intervals between 8:00 and 18:00 h (n=24 days) in 1986. Standard deviations given in parentheses above bars.



**Figure 3.9** Mean monthly height (m) of highest one-third of waves at each station; n=2 estimates per month.

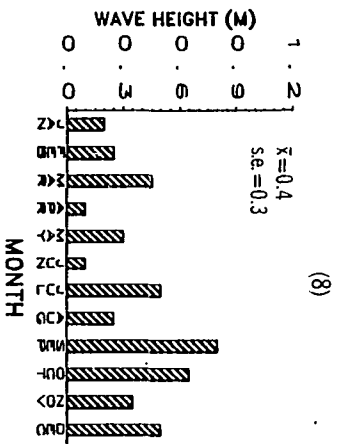
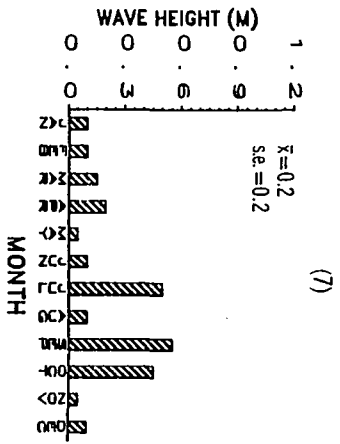
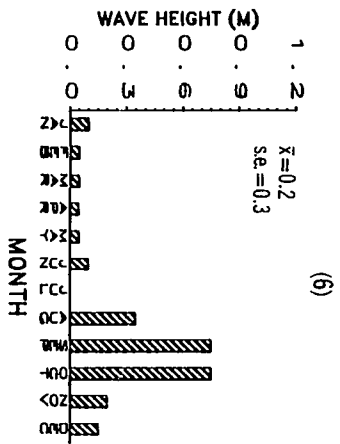
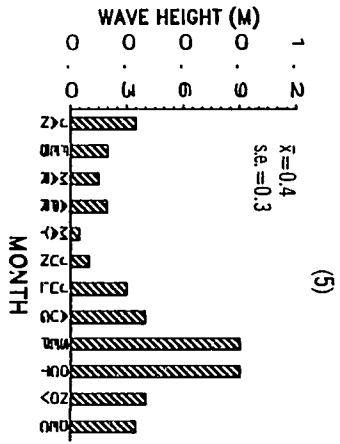
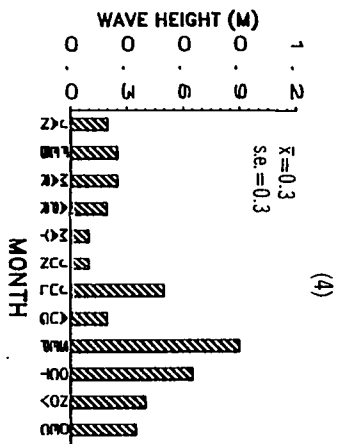
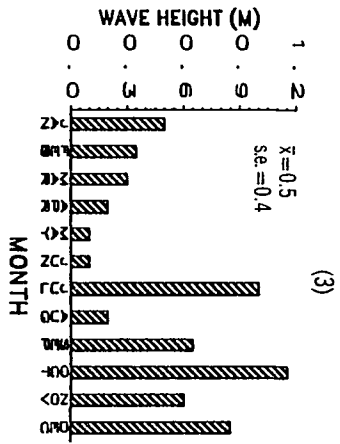
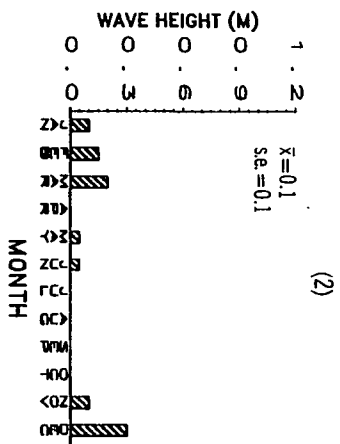
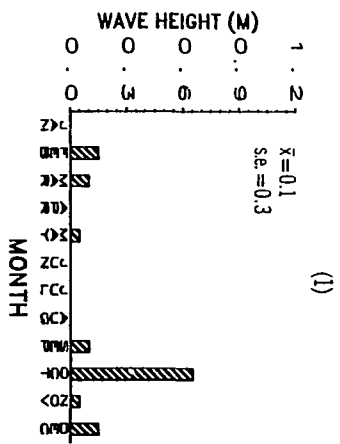


Table 3.2 Matrix of Tukey test results of wave height between all sites in 1986 (n=23 days). Symbols indicate wave height at a site listed on the vertical axis is significantly greater than (+), or less than (-), wave height at the corresponding site on the horizontal axis ( $p < 0.05$ ); ns=not significant.

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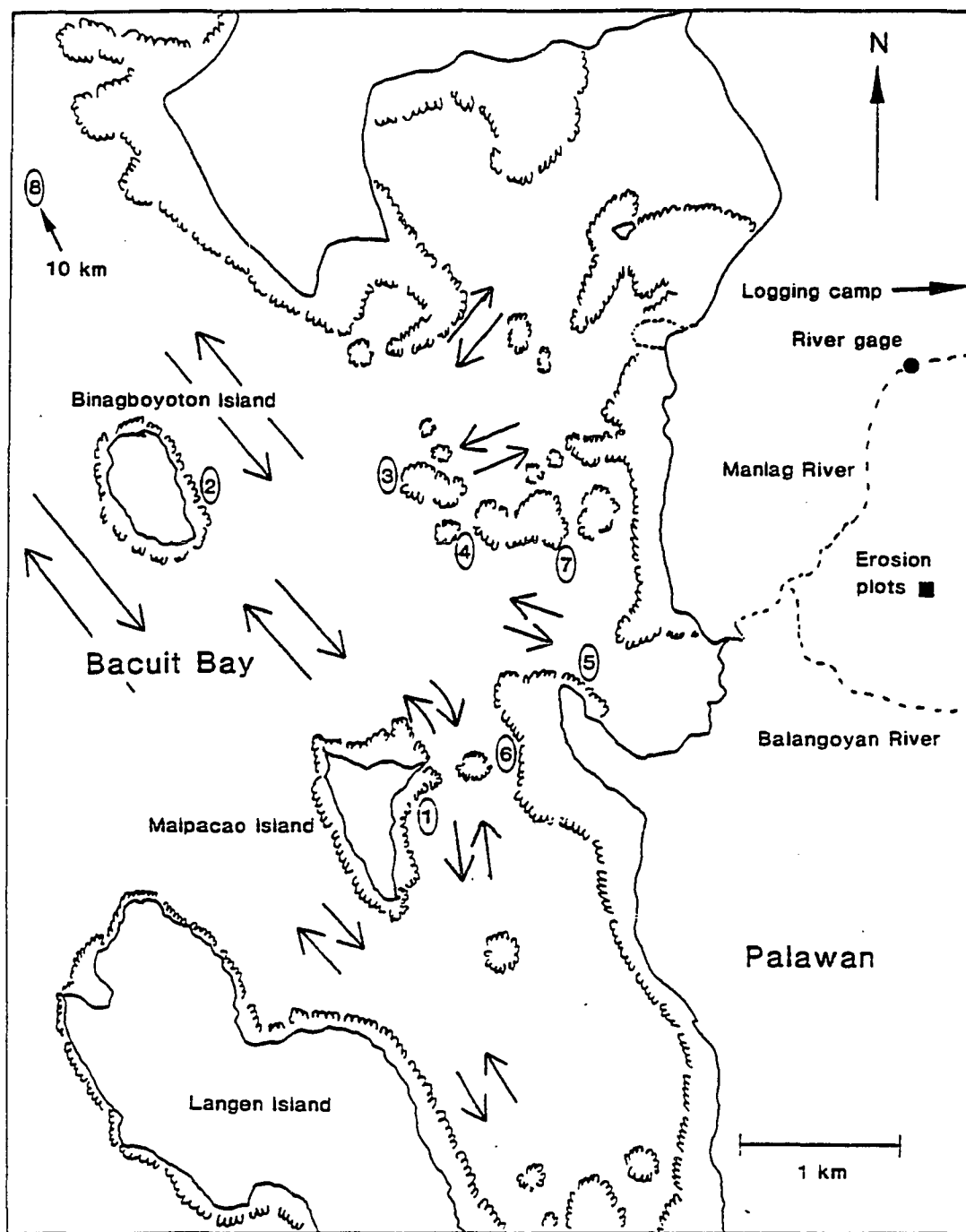
Site										
1										
2	ns									
3	+	+								
4	ns	ns	ns							
5	ns	+	ns	ns						
6	ns	ns	ns	ns	ns					
7	ns	ns	-	ns	ns	ns				
8	+	+	ns	ns	ns	ns	ns			
	1	2	3	4	5	6	7	8	Site	

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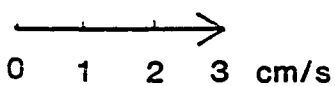
second highest waves. The study reef nearest to the Manlag River discharge point was Site 5. Although Site 5 was far from the bay entrance, it was exposed to waves from the northwest and 1 m breaking waves created by long period oceanic swell were occasionally observed during September and October. The lowest wave heights were recorded at Sites 1 and 2, fringing reefs facing east.

#### Currents, Turbidity, and Sediment Plume Dynamics

Tidal variation in Bacuit Bay was 1.5 m. The lack of narrow channels results in relatively sluggish tidal currents during outgoing tides and calm wind conditions (Figure 3.10). During periods of little or no wind, tidal currents ranged between 0.9 to 3.7 cm/s. Wind driven currents dominated water transport in the bay. Wind



Tidal current velocity



Coral reef

**Figure 3.10** Tidal current speed and direction (incoming and outgoing tides) without wind. Arrow length indicates velocity.

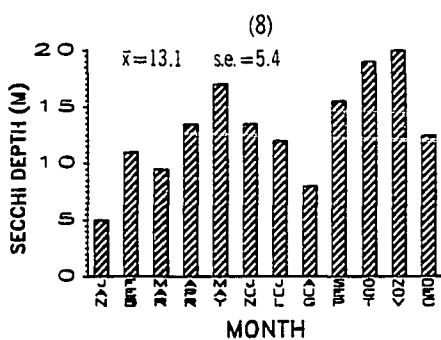
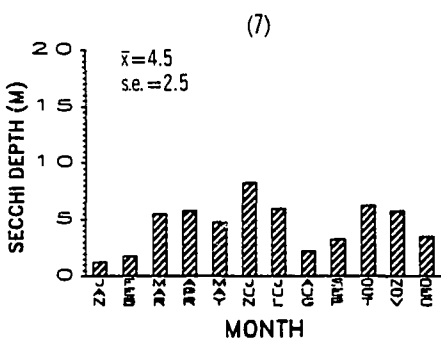
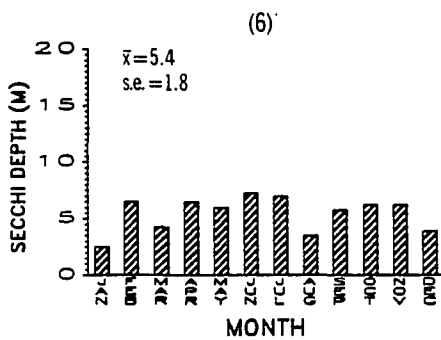
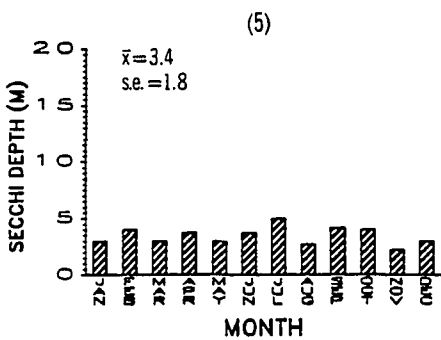
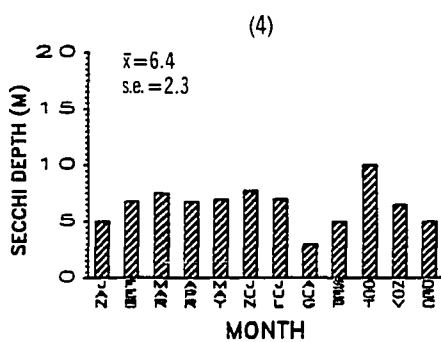
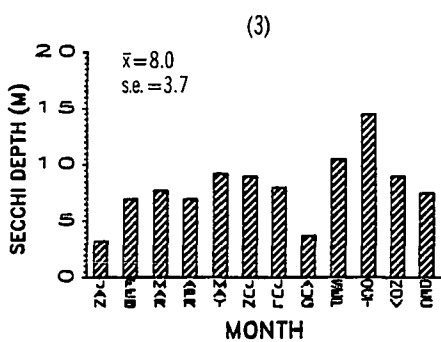
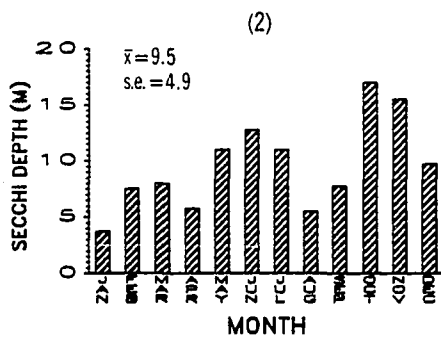
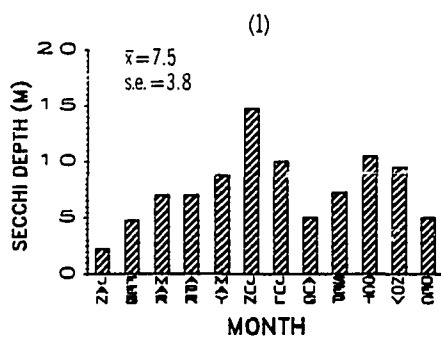
speeds of from 1.7 to 5.8 m/s (170 - 580 cm/s) created surface currents in the same direction ranging between 13.7-33.0 cm/s. Such rapid currents were not recorded below a depth of 1 m. Near the Manlag River outflow point, river discharge and tidal outflow transported entrained sediment up to 30 cm/s.

Secchi depth readings gave an indication of sediment plume dynamics in relation to the study sites. Mean monthly secchi depth at the 8 sites ranged from 1.25 to 20 m (Figure 3.11). Mean secchi depth at the control reef (13.1 m; Site 8) was significantly higher than at all other sites (Table 3.3). The closest site to the river mouth (Site 5), had the lowest mean secchi depth (3.4 m). This was significantly lower than mean secchi depth at the 4 sites farthest from the Manlag River sediment plume.

Underwater observations indicated that the bay was often stratified, with a hazy, low visibility layer beginning near the lower extent of living coral cover at the base of each patch or fringing reef and extending to the bay floor. Stratification disappeared following periods of calm dry weather resulting in relatively high horizontal underwater visibility (up to 15 m) even near the bottom at the two sites nearest the river mouth.

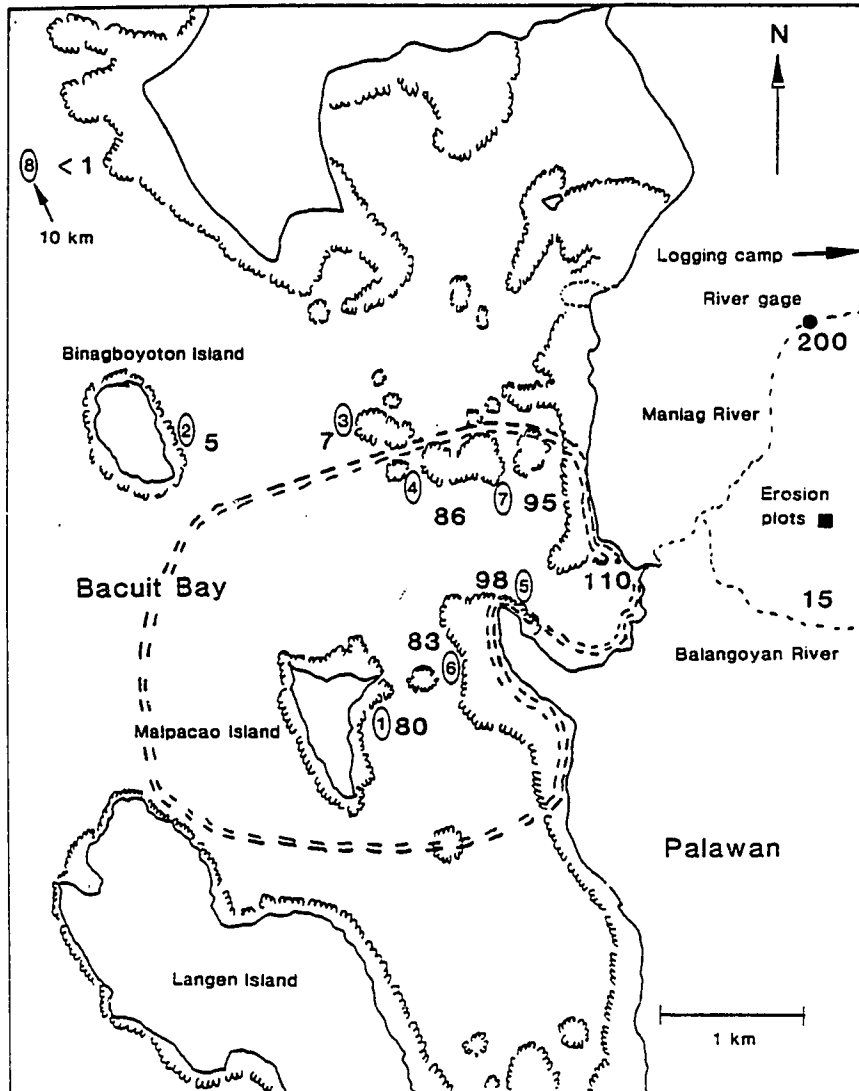
During periods of low rainfall and water discharge, the visible Manlag River plume did not extend beyond Sites 1, 5, 6 and 7. Under these conditions, the lateral

**Figure 3.11 Mean monthly secchi depth at Sites 1-8 in 1986  
(n=2 measurements per month).**









**Figure 3.12** Typical extent of Manlag River sediment plume (double broken line) and suspended sediment concentration (mg/l) in two drainage basin rivers and at Bacuit Bay Sites 1-8 during northeast monsoon (wind 1.7-3.1 m/s; current 25 cm/s) on a falling tide.

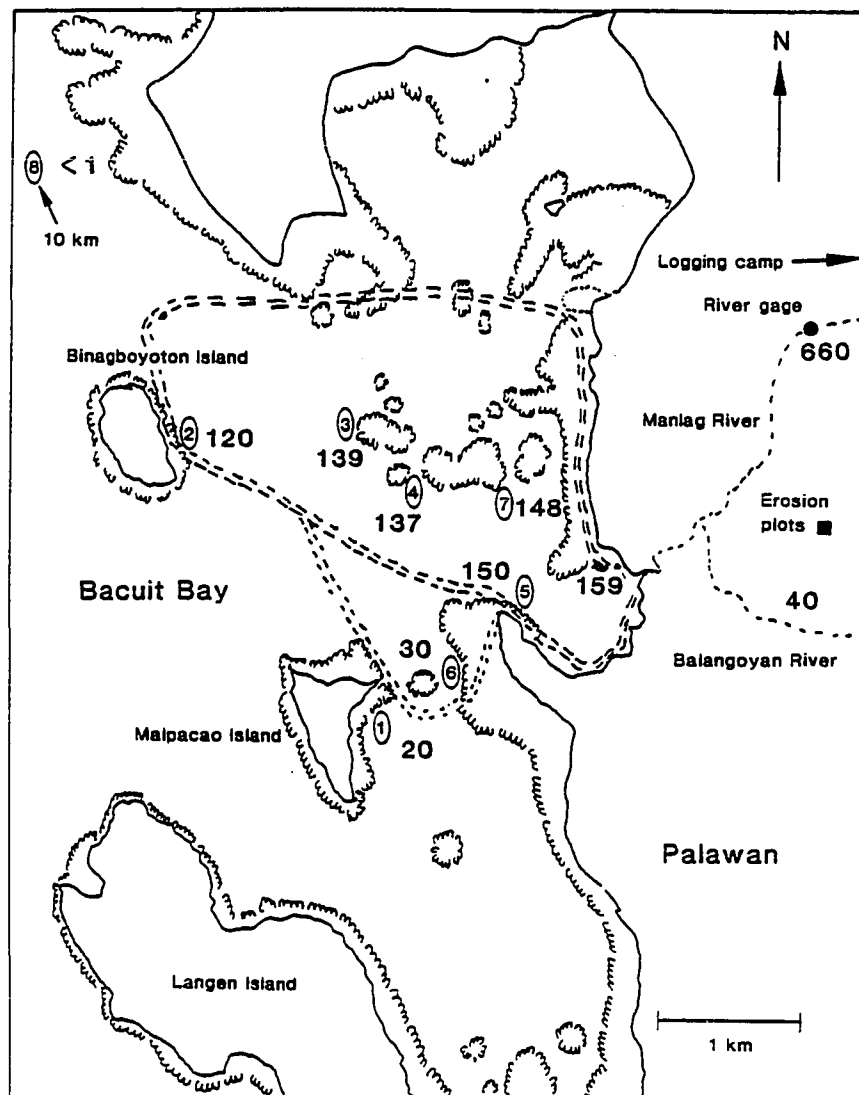


Figure 3.13 Typical extent of Manlag River sediment plume (double broken line) and suspended sediment concentration (mg/l) in two drainage basin rivers and at Bacuit Bay Sites 1-8 during southwest monsoon (wind 2.2-4.4 m/s; current 33 cm/s) on a falling tide. During strong SW winds, the plume may be pushed to the north of Sites 1, 2, and 6. A diluted portion of plume is shown covering Site 6.

turn shoreward. This lateral movement of a diluted portion of the plume is outlined in Figure 3.13 by the dashed line around Site 6. Site 6 was often bypassed by the Manlag River plume especially when southwest winds were strong. Details of two high discharge sediment plumes tracked during the southwest monsoon follow.

During the early morning hours of August 12, 5.6 cm of rain fell and the Manlag River subsequently flooded to a height of 0.9 m. The light-brown sediment plume was first observed flowing out of the river mouth at 9:00 h during an ebb tide of 1.6 m. It moved at an average speed of 30 cm/s until it reached Site 7, 1.55 km away at 10:24 h. There was little wind to cause mixing. Moving beyond Site 7, the plume slowed to 12 cm/s until it reached the outer patch reef (Site 3), 0.7 km beyond Site 7 at 12:00 h. The plume slowed further to about 10 cm/s and reached the area just north of Binagboyoton Island (Site 2), 0.87 km past the outer patch reef at 14:26 h. The wind began to blow from the southwest at 15:00 h, mixing the plume with the surrounding water. At 11:00 h at Site 7, the sediment plume had extended to only 30 cm beneath the surface. Four hours later, just prior to the onset of wind mixing, the turbid layer had descended to a depth of 3 m at Site 7. Changes in the suspended sediment load between the river gage station and Site 3, over 2 km from the river mouth are listed in Table 3.4. Based on river current measurements

and observations of the plume movement in the bay, the suspended load samples are believed to be repeated samples from one water mass as it moved down the river and across the bay.

**Table 3.4** Suspended load of the Manlag River and the sediment plume as the plume moved across Bacuit Bay on August 12, 1986 (4 replicates per site). Control (Site 8) suspended sediment load was <1 mg/l.

Location	Suspended load mg/l (SD)	Time h	Distance from river mouth km
River gage	660 (23)	6:50	2.50
River mouth	159 (14)	9:00	0.00
Site 7	148 (9)	10:24	1.55
Site 4	137 (11)	12:00	1.75
Site 3	139 (8)	14:26	2.25

A second large plume was monitored on August 14 and 15. Heavy rains caused the Manlag River to flood to 2 m height, and estimated water discharge exceeded 1,407,000 m<sup>3</sup>/d, more than 10 times the monthly mean. The Manlag River plume extended beyond Binagboyoton Island and reduced water temperature and salinity at all locations except at Sites 6 and 8 on August 14 and 15. Strong southwest winds prevented the plume from passing over Site 6, and the plume did not reach Site 8. The lowest sea water temperature recorded was 27 °C (Sites 3 and 4) and the lowest salinity recorded was 19 ppt (Site 4; Sites 3 and Site 7 = 22 ppt).

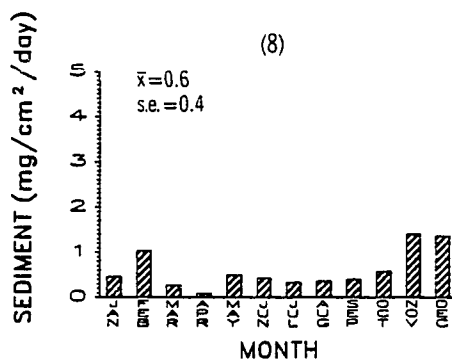
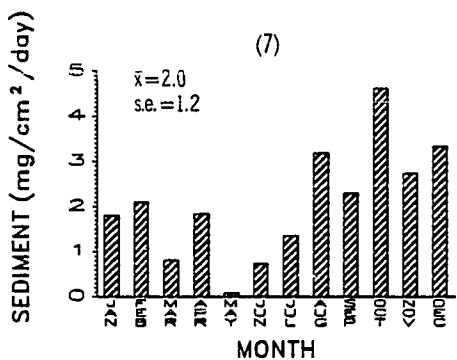
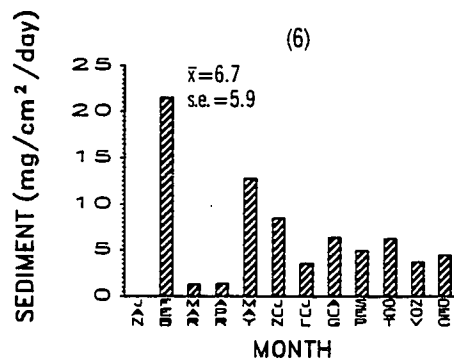
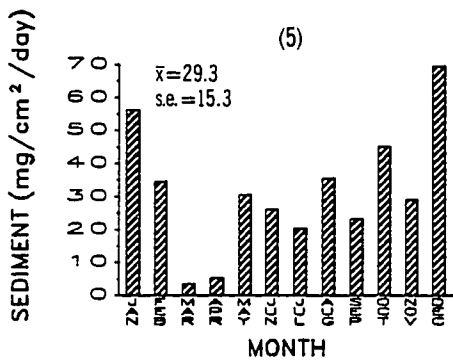
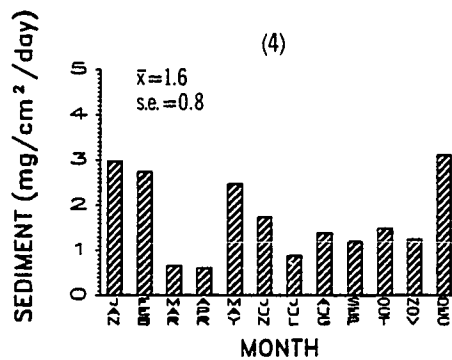
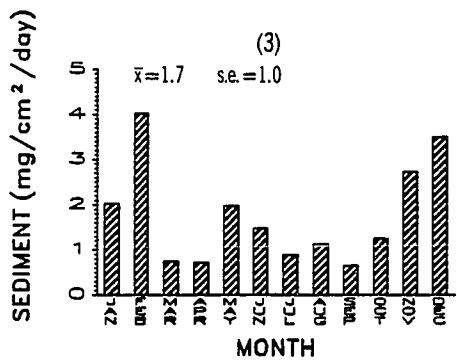
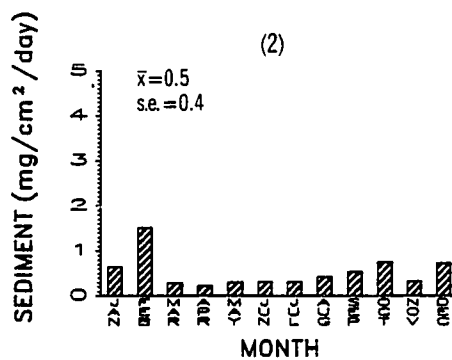
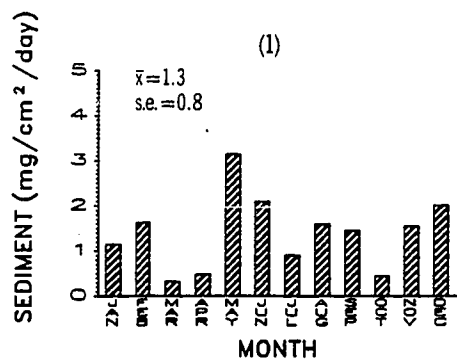
This event is not obvious in Figure 3.4 because air and seawater temperatures had already declined by the previous sampling date (August 1), presumably in a seasonal response to reduced sunlight during the rainy season. It is likely that the effects of several high discharge events on salinity and seawater temperature were not recorded since these parameters were only measured twice monthly.

#### Sediment Deposition

Mean sediment deposition (all sources) in sediment traps ranged from 0.5 mg/cm<sup>2</sup>/d at Site 2 to 31.6 mg/cm<sup>2</sup>/d at Site 5, the site closest to the Manlag River (Figure 3.14 and Table C.4, Appendix C). Sediment deposition at Site 5 was significantly greater than sediment deposition at all other sites ( $p < 0.05$ ; Tukey test). The heaviest sediment deposition occurred at Site 5 during December. Peak sediment deposition did not occur during the same month at all sites. For example at Site 1, peak sediment deposition was in May, at Sites 2, 3 and 6 in February, at Site 4 in December at Site 7 in October and Site 8 in November.

Deposition of terrestrial sediment (total minus the calcium carbonate fraction assumed to be of marine origin) is listed in Table C.5, Appendix C. Monthly variation in deposition of terrestrial sediment followed a similar pattern to that of total deposition.

Figure 3.14 Monthly sediment deposition ( $\text{mg}/\text{cm}^2/\text{day}$ ; mean of 4 traps per site; includes  $\text{CaCO}_3$ ) at Sites 1-8 in 1986. Note the different scales on vertical axes for Sites 5 and 6. Due to rounding, the mean and standard error values differ slightly from those listed in Table C.4, Appendix C.



### Trapped Sediments

Sediments collected by sediment traps ranged from 12 to 41 percent sand, 34 to 67 percent silt, and 12 to 38 percent clay (Figure 3.15). The percentage of silt was negatively correlated with the natural logarithm of distance from the Manlag River mouth ( $p < 0.006$   $r^2 = 0.75$ ; Figure 3.16). Sites 1 and 8 had about double the sand component of the other sites.

In order to obtain a sufficient sample weight for laboratory analysis of particle size, it was necessary to combine consecutive months' samples. This resulted in too few samples for meaningful statistical comparisons of particle size distribution among sites.

Mean percent organic matter of trapped sediment varied little (range 2.1 to 3.6 percent; Figure 3.15)) and was not significantly different among sites ( $p > 0.05$ ; Tukey test).

Mean calcium carbonate content ranged from 17.8% at Site 5 to 48.4% at Site 8 (Figure 3.15). Percentage calcium carbonate was significantly lower at the 3 sites closest to the river mouth (5, 6, and 7) than at Sites 1, 2, 3, and 8 ( $p < 0.05$ ; Tukey test; Table 3.6). In addition, linear regression of percentage calcium carbonate at each site on percentage silt was significant ( $p < 0.002$ ;  $r^2 = 0.82$ ) and showed a negative relationship (Figure 3.17). The highest concentrations of calcium carbonate were associated with a high percentage of sand and low



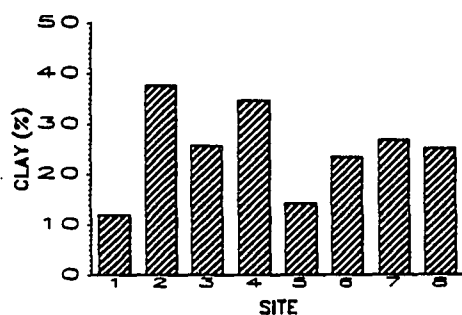
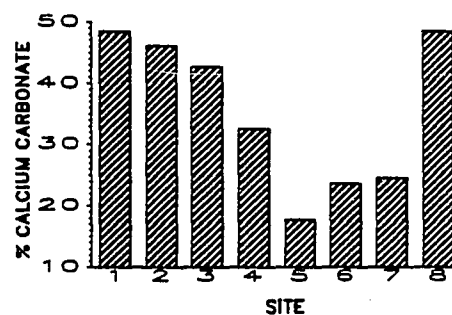
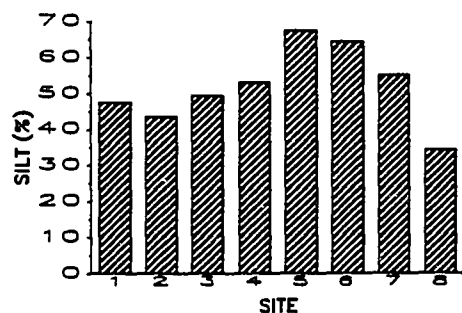
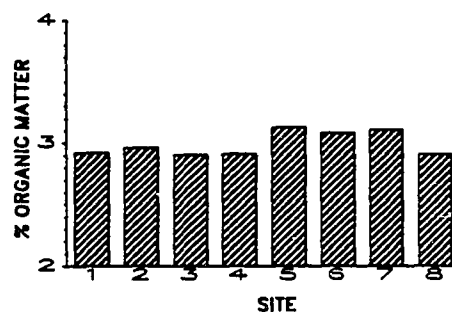
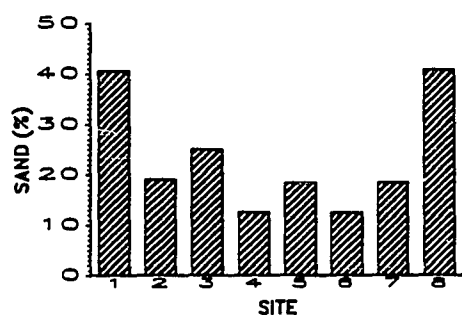


Figure 3.15 Particle size distribution (sand, silt and clay), calcium carbonate, and organic matter components of sediment collected in traps at each site. Sand + silt + clay = 100%;  $100\% - \text{CaCO}_3 = \text{terrestrial component}$ ; organic component may be terrestrial or marine.

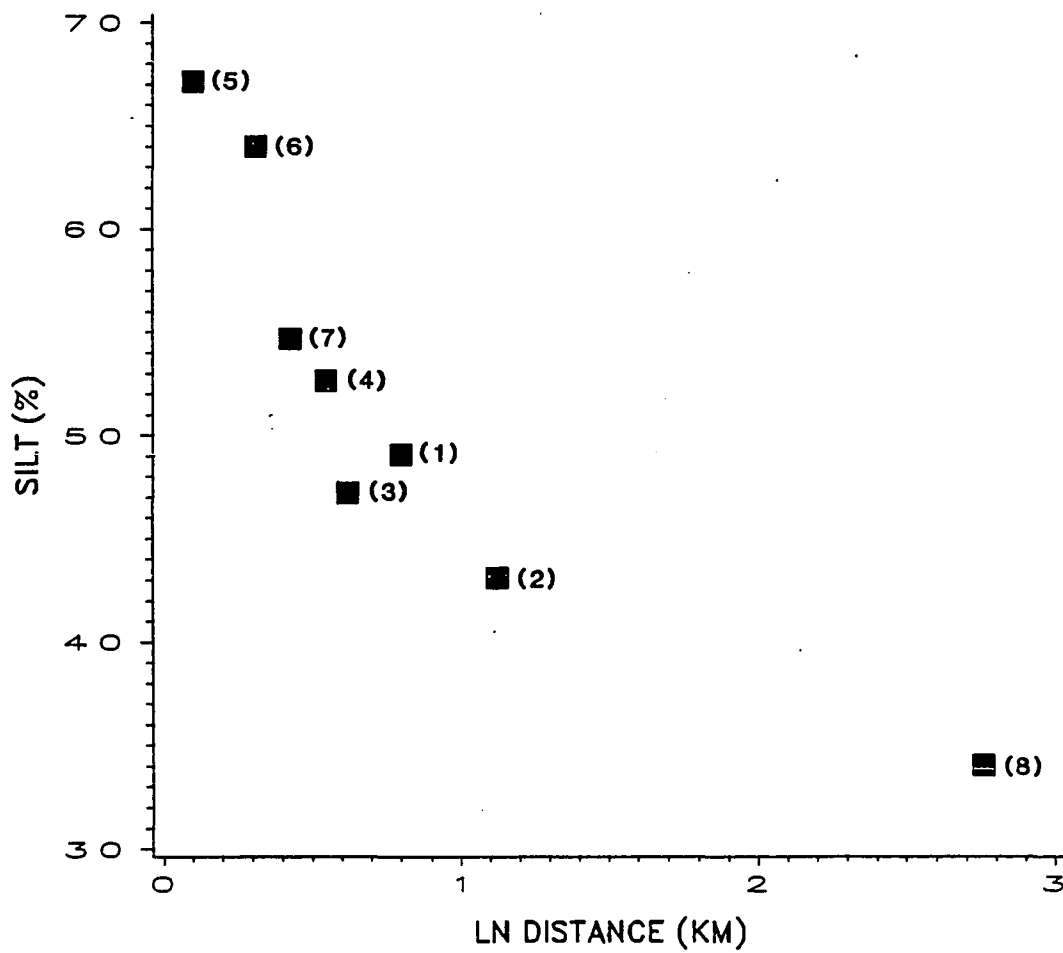


Figure 3.16 Plot of percentage silt content of trapped sediment versus the natural logarithm of distance of each site (1-8) from the Manlag River outlet.

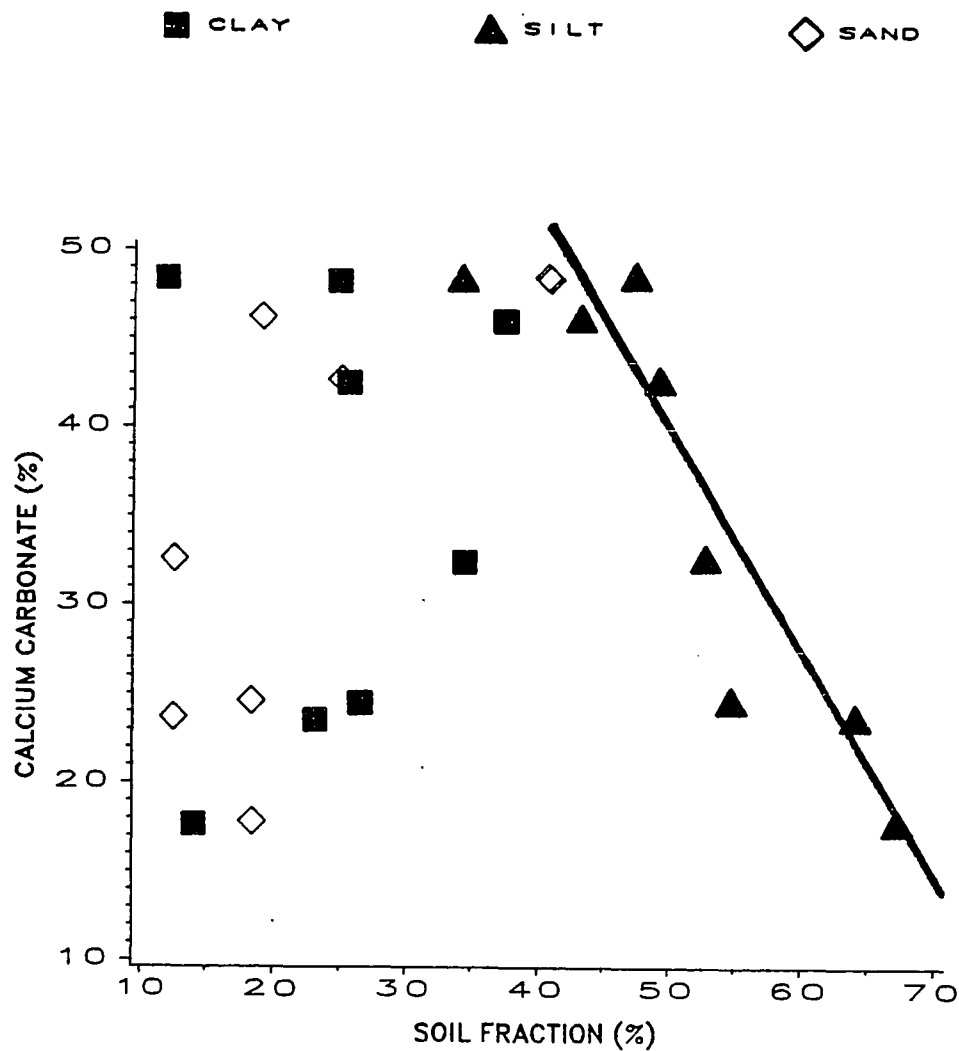
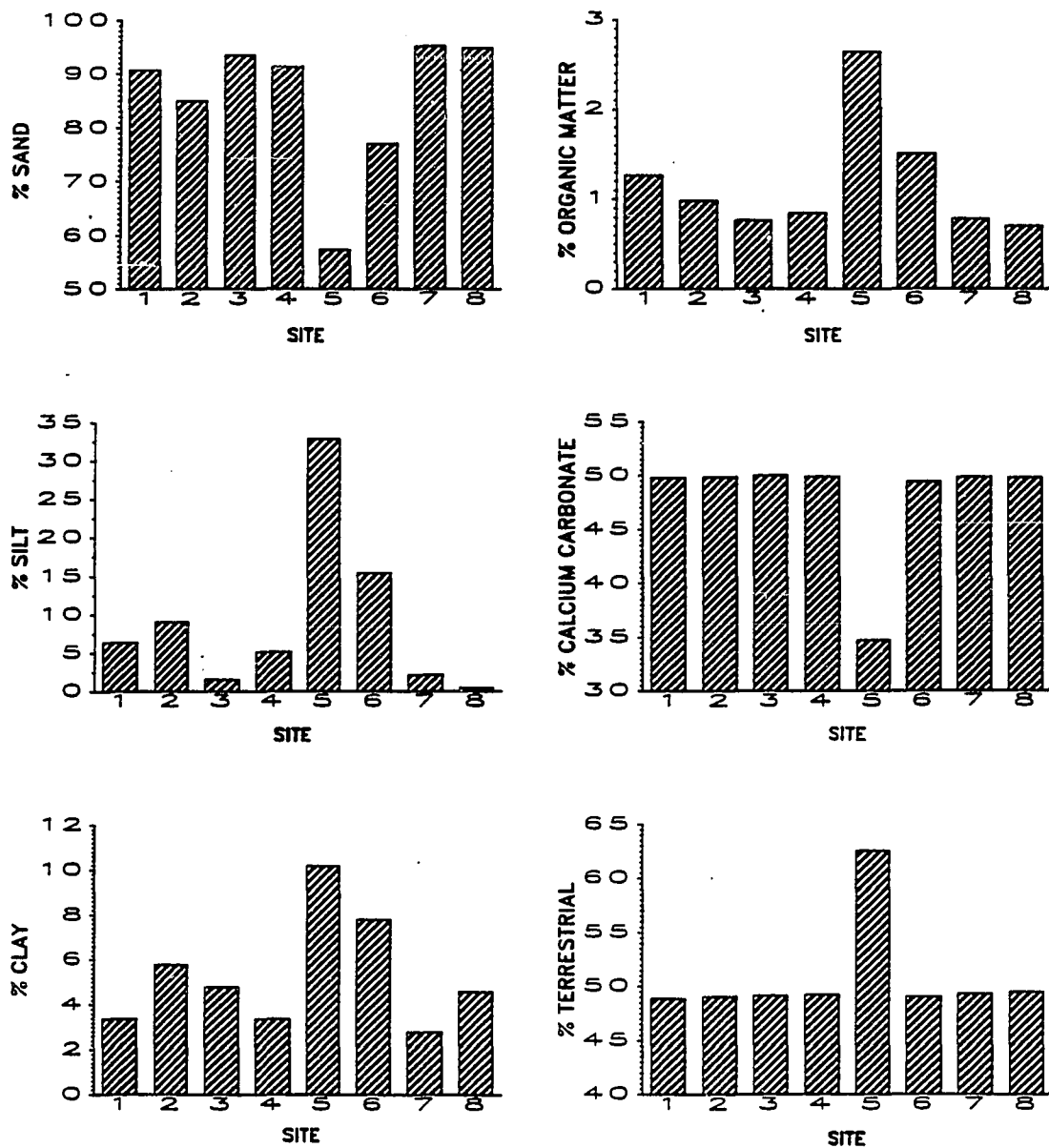


Figure 3.17 Plot of percentage calcium carbonate content (marine sediment) versus percentage of sand, silt and clay in trapped sediment at each site (1-8). Percentage calcium carbonate was linearly related to percentage silt ( $p < 0.002$ ;  $r^2 = 0.82$ ) but not to clay or sand. Note origin of axes is 10%.





**Figure 3.18** Particle size distribution (sand, silt and clay), calcium carbonate, and organic matter components of benthic sediment collected by hand along transects at each site. Sand + silt + clay = 100%.  $100\% - \text{CaCO}_3 \equiv$  terrestrial component; organic component may be terrestrial or marine.

Site 6 ( $p < 0.05$ ; Tukey test). Site 5 also had a significantly higher percentage of clay than all other sites except 2 and 6 ( $p < 0.05$ ; Tukey test). With the exception of Site 5, benthic sediments had a remarkably similar calcium carbonate component of almost 50%. Site 5 had a significantly lower percentage of calcium carbonate and a significantly higher percentage of organic matter than all other sites ( $p < 0.05$ ; Tukey test).

None of the cores taken near the reef-base at each site showed signs of sediment layering. Each core had a uniform appearance with an apparently well-mixed sediment distribution. Core sediments were light-gray in color except at Site 8 where light-brown coral sand predominated. Tube penetration distance at Site 8 was significantly less than at all other sites, and penetration was significantly greater at Site 5 than all other sites ( $p < 0.05$ ; Tukey test; Table 3.6). There were no other significant differences among sites. The fine sediment deposits at Site 5 were probed with a 1 m long wire rod and were found to be deeper than 1 m. In order to get some idea of the time required to form such a thick layer, vertical accumulation of sediment in a set of sediment traps placed directly on the bottom at Site 5 was measured. Deposition ranged between 2 and 10 cm per month.

Table 3.6 Mean penetration distance (cm) of flexible 3 cm diameter plastic tube near the reef base of Sites 1-8. Standard deviations in parentheses (n=5).

Site	Water Depth (m)	Penetration Distance (cm) S.D.	Sediment Grade	Layering
1	15	15.2 (0.8)	silt	none
2	20	8.8 (2.0)	silt	none
3	20	8.0 (1.6)	sand-silt	none
4	10	18.4 (1.1)	sand-silt	none
5	5	53.0 (4.5)	clay	none
6	8	24.8 (6.1)	silt-clay	none
7	8	18.2 (3.3)	sand-silt	none
8	30	4.8 (1.3)	sand	none

#### Correlation of Discharge, Wave Height and Deposition

Local winds, wind direction, long period oceanic waves, and tidal currents all independently affected distribution of terrestrial sediment inputs as well as resuspended sediments in the bay. Relationships between these parameters were investigated with simple and multiple regression using the SAS GLM procedure (SAS, 1985). Neither mean monthly secchi depth nor sediment deposition were correlated with either mean wave height or total sediment discharge for any of the 8 Sites. If wave height is a predictor of sediment resuspension, then it might be expected that mean monthly wave height and sediment discharge would be positively correlated with sediment deposition. Multiple regression using wave height and sediment discharge as co-independent variables was not

significant with either secchi depth or sediment deposition as the single dependent variables (SAS GLM) for each of the 8 Sites.

## Discussion

### Bay Temperature and Salinity

There were 3 physical characteristics of the Manlag River discharge that posed a potential threat to living corals: 1) low temperature water 2) low salinity water 3) a high suspended sediment load. The results indicated that on average days, low temperature and salinity Manlag River water discharge was rapidly mixed with and diluted by seawater soon after entry into the bay. Only during infrequent, high discharge events was bay surface temperature and salinity affected over a large area for longer than one day. Even then, the measurable effects of the freshwater did not extend beyond a 3 km radius from the river mouth.

The lowest Manlag River temperature was 21° C, and the lowest water temperature of the Manlag River sediment plume measured in the bay was 26 °C. This temperature was within the seasonal water temperature range of the control site (Site 8). Water temperatures at near-shore sites were generally higher than at sites further offshore (Table C.1, Appendix C). It appears likely that the relatively low volume of cool river water was rapidly warmed as it passed



over and began to mix with warm, near-shore bay water. The freshwater plume did not need to mix with saltwater for heat transfer to occur.

Sediment plume salinity was an indicator of freshwater-saltwater mixing. Low salinity measured in the bay indicated partial mixing of freshwater discharge with bay saltwater (Table C.2). Although differences in mean monthly salinity among the 8 sites were not significant, a 25% salinity reduction (to 25 ppt) in August at Sites 3 and 4 suggested that biologically important local dilution of bay seawater occasionally occurred. Underwater observations and salinity measurements indicated that low salinity water was limited to the upper 1 m of water. The potential effects of low salinity on corals are discussed in Chapter 5. Since logging has been shown to significantly increase runoff (Hamilton, 1985; this study) and peak stream flow (Hamilton, 1985), the potential for increased freshwater discharge during floods may be increased by future logging of the Bacuit Bay drainage basin.

### Turbidity

Monitoring turbidity is one means of tracking movement of river plumes in near-shore waters. Secchi depth readings were used to interpret: 1) movement of the river plume, and 2) the level of resuspension.

The reduction in suspended sediment load in the Manlag River (Table 3.4) between the gaging station and the river mouth may be partially due to mixing of the muddy Manlag with the clearer Balangoyan River, and later, with bay water. In the bay, both suspended sediment load and location of the plume varied temporally and spatially in response to discharge rate and water currents. During times of calm weather and high discharge, the suspended sediment load of the Manlag River sediment plume remained relatively constant within a radius of 2.25 km beyond the river mouth (Table 3.4). On such occasions, large amounts of sediment were probably transported over 2 km into the bay before deposition.

The combination of weak tidal currents in Bacuit Bay and the location of the sediment plume at the water surface intensified the relative effect of wind on movement and dispersal of sediment discharged from the Manlag River. During strong winds the plume mixed rapidly and was displaced laterally, completely missing reef areas that were within its path during low-wind conditions.

Turbidity was increased both by the arrival of the sediment plume and by wave driven resuspension of bottom sediments. Therefore secchi depth may not be correlated with wind speed and direction at sites directly affected by the sediment plume, especially Sites 1, 2 and 6.

### Sediment Deposition

Sediment deposition measured at the control site (8) in Bacuit Bay ( $0.6 \text{ mg/cm}^2/\text{day}$ ) was similar to "pristine" rates measured at various reefs around the world ( $0.1 - 5 \text{ mg/cm}^2/\text{d}$ ; Randall and Birkeland, 1978; Hubbard, 1987). Only the rate measured at Site 5 ( $31.6 \text{ mg/cm}^2/\text{day}$ ) was similar to rates considered to be damaging at reefs in other regions ( $15 \text{ mg/cm}^2/\text{day}$ , Loya, 1976;  $10-33 \text{ mg/cm}^2/\text{day}$ , Aliño, 1983;  $54.3 \text{ mg/cm}^2/\text{day}$ , Liew and Hoare, 1979;  $160-200 \text{ mg/cm}^2/\text{day}$ , Randall and Birkeland, 1978). In possible contrast to these reports, Hoyal (1986 in Hopely and Woesik, 1988) cite data from northeast Australia indicating that high cover and diversity coral reefs survive chronic sedimentation rates of  $129 \text{ mg/cm}^2/\text{d}$  (7 month mean). Since the sediment trap location (depth and height above the sea floor) are not given it is difficult to evaluate this report.

The location of the sediment trap with respect to both water depth and height above the bottom are known to affect sedimentation. Sedimentation has been shown to increase with depth in a sub-tropical bay environment in Japan (Odhe et al., 1982) and at a tropical reef in the Mallaca Straits (Liew and Hoare, 1979). In Bacuit Bay for example, the study reefs were fringing or patch reefs bordered by large areas of deeper water. Sediment resuspended in shallow water, e.g. from a shallow patch reef, can either settle

again in shallow water or be transported laterally and settle to the bottom in deeper water. In contrast, sediments resuspended in deeper water have a small chance of being carried up and deposited in shallow water due to the small reef flat area and to gravity working against resuspension. In addition, since low to moderate velocity winds are more common than strong winds, shallow sediment deposits are subject to more frequent resuspension than deeper ones.

Due to a significant percentage of calcium carbonate in sediments collected in Bacuit Bay (see below), care must be taken when comparing the particle size distribution of these sediments with those of Bacuit Bay drainage basin soils which contained no detectable calcium carbonate. In comparison to the particle size distribution of forest soil, sediment from sites closest to the river mouth had a higher percentage of silt, and Sites 1 and 8 had higher percentages of sand.

In the absence of currents, turbidity should be correlated with sediment deposition rate. When complex spatially and temporally variable currents affect the water column, turbidity and sediment deposition may not be correlated. In the Bacuit Bay case, mean monthly secchi depth and sediment deposition were not statistically correlated at any site. Mean secchi depth was significantly lower at Site 5 than at the 4 sites farthest

from the river mouth and sediment deposition was significantly greater at Site 5 than at these 4 sites, indicating that sediment deposition and turbidity may be spatially correlated.

Referring back to Figure 3.1 it is evident that turbidity and sediment deposition were dependent upon several processes that transported sediment into the water column. In the Bacuit Bay study area, the primary sediment input routes appeared to be Manlag River discharge and sediment resuspension. When breaking waves were lower than 0.5 m in height, sediment resuspension was minimal due the surface of most reef flats being 0.25 m or deeper at low tide. Sediment resuspension is difficult to measure or model due to the dynamic nature of sediment supply and water currents, so no attempt was made to quantify sediment resuspension in this study. Therefore a detailed sediment budget cannot be modeled for each site.

#### Correlation of Discharge, Wave Height and Deposition

In a study of terrestrial runoff and sewage outflow in Kaneohe Bay, Hawaii (Smith et al., 1981), multiple regression of extinction coefficients against environmental factors including a "short-term" wind factor and runoff also failed to account for a statistically significant part of the variation in water clarity. There are several possible explanations for the lack of

significant statistical association in the El Nido data. Most importantly, the precision of the data was different among the data sets due to differences in sampling schedules. The daily sediment discharge estimate for the river was based on one sample per day. The sediment deposition estimates were cumulative totals based on monthly sampling of traps that collected sediment continuously for the entire year. In contrast, the wave height and secchi depth data were collected on only two days per month. These differences in sampling frequency may be responsible for the lack of clear correlations and suggest that wave height and secchi depth were inadequately sampled. In addition, the amount of sediment lying in shallow benthic deposits that was available for resuspension probably varied temporally and spatially. For example, during a period characterized by low sediment discharge from the river and brisk winds, old shallow sediment deposits might be resuspended and transported away from the reef flat causing low secchi readings. If wave action continued after the benthic sediment supply was exhausted, little additional sediment would be resuspended in that location. Such conditions were observed at the end of the dry season.

It appears that the most important factor affecting the level of terrestrial sediment deposition at sediment trap sites was distance from the mouth of the Manlag River.

When sedimentation rate (terrestrial sediment fraction) was plotted against distance of each of the 8 Sites from the river mouth (Figure 3.19), a clear, steep gradient was evident. The highest sediment deposition was at Site 5, the closest to the river mouth, where there was a large supply of sediment. Site 5 also had a significantly larger terrestrial component than all other Sites (Figure 3.15).

#### Benthic Sediment

Collection and analysis of sediments from deposits along reef transects at each site provided valuable information about sediment movement. As mentioned previously, finer sediments are resuspended more frequently than coarser sediments, and remain suspended in the water column longer. Therefore fines will tend to be transported farther from their point of origin than coarse sediment. For this reason fine sediments tend to settle in the central, deeper portions of a bay or may be transported out. In general, the input of fine sediments must be quite high to allow build-up on a shallow reef area exposed to the scouring effect of waves and lateral currents.

The higher sand fraction found in the Bacuit Bay benthic sediment samples compared with that of sediment trap samples was consistent with the fact that water currents must have a high kinetic energy in order to

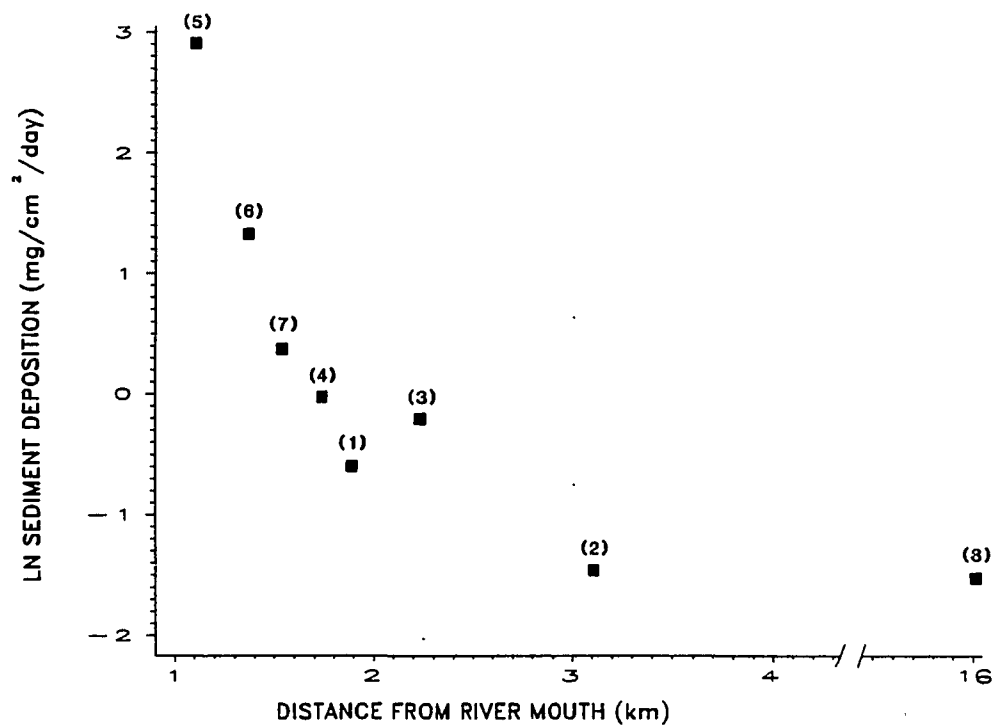


Figure 3.19 Plot of mean monthly deposition of the terrestrial component of total sediment (100% minus percentage calcium carbonate) against distance from the Manlag River mouth for each sediment trap site. Sediment values were natural log transformed.



resuspend large particles. Small particles will tend to be moved higher in the water column more frequently than large particles and so will have a proportionately higher deposition rate in the sediment traps at 1.5 m elevation than on the bottom. The high silt and clay fractions and low calcium carbonate percentage of Site 5 benthic sediments were indicative of high terrestrial sediment input (as opposed to resuspension of marine sediment).

Additional evidence for the high rate of sediment input and deposition at Site 5 was the ease with which the core tube penetrated sediment deposits at the base of the reef (Table 3.7). Local fishermen claimed that prior to the onset of logging, Site 5 had a sand bottom with a large clam population (Hodgson and Dixon, 1988). In comparison to penetration at Site 5, the core tube bent after contacting the sandy bottom at Sites 1, 2 and 7. The sand-silt mixture at Sites 3 and 4 indicated that wave action was mixing finer silt deposits with marine sand. The lack of layering at any site could be due to both disturbance by waves and by marine organisms (see Rhoads and Boyer, 1982 for a review of bioturbation of marine sediments). Bioturbation by a wide variety of benthic invertebrates and fish was commonly observed at all sites.

#### Resuspension Versus Discharge

To fully explain differences in sediment deposition at all

sites it would be necessary to create a separate multivariate model for each site accounting for all the factors so far considered and additional parameters such as detailed reef profiles, surface topography and the location, depth and types of sediment deposits. The data were not sufficient to allow such a detailed analysis, however, some trends can be elucidated regarding the importance of resuspension relative to sediment discharge at each site from a comparison of mean wave height, secchi depth and benthic sediment characteristics. Benthic samples gave an indication of the type of sediments available for resuspension and wave heights indicated the potential kinetic energy available to resuspend sediment deposits. For example, Sites 3 and 5 had the highest mean wave heights of all sites, but sediment deposits "available" for resuspension were quite different.

Site 5 had a significantly greater percentage of fine and easily resuspended silt and clay fractions than Site 3, as well as significantly less sand. In November, mean wave height at Site 3 was 0.6 m while at Site 5 it was 0.4 m (Figure 3.9). Secchi depth was 9 m at Site 3 in November while at Site 5 it was less than 4 m (Figure 3.11). In November, waves were larger at Site 3 than at Site 5 but the water was clearer at Site 3. One explanation of the relatively clear seawater at Site 3 was the lack of fine sediment deposits "available" for resuspension. Referring

back to Figure 2.13 (Chapter 2), sediment discharge in November was only moderate, implicating resuspension at Site 5 as a major source of suspended sediment. These data and observations appear to indicate that there was a greater potential for sediment resuspension at Site 5 than at Site 3 due to a significantly greater quantity of fine sediment deposits available there than at Site 3. In fact Site 3 benthic sediments were composed of over 90% sand. Repeated observations of benthic sediment deposits and turbidity response to wave action at these sites during a variety of weather conditions support this interpretation.

A different situation existed at Site 7. Mean monthly wave height at this protected reef was less than 0.2 m, however, mean secchi depth was the second lowest of all sites (4.4 m) after Site 5. This indicated that sediment input from the Manlag River plume played a relatively larger role in suspended sediment supply at Site 7 than at Site 5 where both resuspension and river discharge appeared to be important.

In contrast, the low sediment deposition rate at Site 6 compared to deposition at nearby Site 5 during the southwest monsoon was consistent with the observation that sediment plumes often bypassed Site 6 during this period.

Sites 1 and 4 had similar clay, silt, and sand fractions in their benthic deposits and they were almost equi-distant from the river mouth. Mean wave height was

slightly higher at Site 4 than at Site 1, and mean secchi depth was slightly higher at Site 4, possibly due to a difference in sand fractions. Sediment deposition was also similar at both sites, with Site 4 slightly higher. These similarities underline the importance of distance from the river mouth in determining the sediment deposition regimen at each site.

Distance from the river mouth and wave exposure may affect sediment composition. Of the 2 sites farthest from the river, Site 2 was located over 3 km from the river mouth and Site 8, the control reef was 16 km away. The sediment plume occasionally reached Site 2 but never reached Site 8. Site 8 was exposed to wave heights of nearly 1 m during the northeast monsoon while Site 2 was almost always calm and had the lowest mean wave height of all the sites. Although sediment deposition at Sites 2 and 8 was equivalent, the sand and calcium carbonate fractions of Site 8 sediments were larger than those at Site 2. It appears that resuspension of marine sand may be a greater contributor to sediment deposition at Site 8 than at Site 2 where there is more influence from suspended sediment derived from terrestrial sources.

#### Potential Sediment Dilution in the Bay

Since the data suggest that sediment output from the drainage basin, and sedimentation in Bacuit Bay were

increased by a logging operation, it is important to consider potential sediment output if the size of the logged area increases in the future. In addition, increased suspended sediment load in Bacuit Bay due to sediment output from logged watershed can be compared with natural and elevated suspended sediment levels documented in other parts of the world that are believed to be damaging corals. Factors which may be important in determining the sediment supply to the bay are: 1) total size of the drainage basin, 2) percentage of the forest area affected by logging and especially road building, 3) soil erodibility and site specific parameters such as those used in the Universal Soil Loss Equation, and 4) sediment delivery ratios of drainage basin rivers.

The narrow width of Palawan Island, restricts the size of drainage basins. Bacuit Bay drainage basin (78.3 km<sup>2</sup>) is one of the largest in Palawan, but compared to coastal or inland drainage basins in some other locations it is small; e.g., 360 km<sup>2</sup> in Wisconsin (Trimble, 1981), 2,411 km<sup>2</sup> in New Zealand (Graynoth, 1979), 3,339 km<sup>2</sup> in Panama (Larson and Albertin, 1984), and 12,560 km<sup>2</sup> in Thailand (Johnson, 1984). Given similar erosion rates and sediment delivery ratios, the small size of the Bacuit Bay watershed limits the absolute potential for sediment discharge.

At the level measured in 1986 (Chapter 2), soil

erosion due to logging in the Bacuit Bay drainage basin was equivalent to soil erosion measured in other tropical logging areas and sediment discharge per square kilometer of drainage basin was moderate compared to output from logging areas in other tropical and temperate locations.

The area of a watershed affected by logging or other erosion enhancing activities is an important determinant of sediment output. At the end of 1986, 6% of the Bacuit Bay drainage basin had been affected by logging activities. If 100% of the available forest was cut, the logged area would be 37 km<sup>2</sup>, 53% of the drainage basin, almost 9 times the 1986 area. It is logical to assume that sediment output would increase as the area of land affected by logging increases, however, the relationship is probably not linear (Hodgson and Dixon, 1988).

Once sediment enters Bacuit Bay, factors such as sediment characteristics, water currents and potential dilution affect the sedimentation rate at a given location. In still water, the silt and clay particles discharged from the Manlag River would not be expected to sink to a depth of 3 m (the coral transect depth) for between 1 h to several days (Sverdrup et al., 1940), however, the generally sluggish currents measured in the bay would tend to limit lateral transport beyond a 3 km radius as was observed in 1986.

The potential for dilution of Manlag River sediment

discharge ( $Q_S$ ) by mixing in the bay can be calculated by dividing  $Q_S$  by different sized portions of the bay. For example, in the unlikely event that transport and mixing resulted in a rapid, even distribution of suspended sediment throughout the bay, the dilution factor would be quite high. This dilution can be estimated by dividing 1986  $Q_S$  from the Manlag River (39,154 mt) by the entire area of Bacuit Bay (120 km<sup>2</sup>). The resulting sedimentation rate (assuming no export) would be 0.089 mg/cm<sup>2</sup>/day, well below the sedimentation rate measured at the control reef (0.6 mg/cm<sup>2</sup>/day) and in other tropical coastal areas considered to be undisturbed, (1-2 mg/cm<sup>2</sup>/day; Hubbard, 1987). Clearly, 1986 sediment output ( $Q_S$ ) of the relatively small Manlag River would be diluted to a low and probably insignificant level in the unlikely event it were completely and evenly distributed throughout the bay.

Even if distribution of total 1986 Manlag River  $Q_S$  was limited to the area circumscribed by the "treatment" study sites, 1-7 (10 km<sup>2</sup>), the average deposition rate would amount to only 1.0 mg/cm<sup>2</sup>/day, again not very different from "pristine" rates measured at various reefs around the world.

This level of analysis does not preclude the possibility that short term (less than the 1 month sampling period) sedimentation rates may have been significantly higher than the control rate. One way to estimate the

possible occurrence of such short term, high sedimentation pulses at the 7 treatment study sites is to divide the daily suspended sediment output of the Manlag River during peak output periods by the area outlined by the study sites.

The largest sediment plumes observed in Bacuit Bay covered an area of about 6-8 km<sup>2</sup>. Assuming the size of the primary sediment impact area from high discharge plumes was somewhat larger, say 10 km<sup>2</sup> (approximately the area circumscribed by the treatment sites) sediment dilution within this zone can again be calculated. In 1986, the month with the highest sediment discharge was December (412 mt/day). When divided by the 10 km<sup>2</sup> primary impact area, the resulting sediment deposition rate is 4.12 mg/cm<sup>2</sup>/day, lower than the mean deposition rate at Site 6. Recall that the range of mean annual sedimentation at all Sites but 5 ranged from 0.5 to 6.8 mg/cm<sup>2</sup>/day, and only Site 5 was significantly higher (31.6 mg/cm<sup>2</sup>/day) than the others (Appendix C). If only monthly sediment discharge data were available, it might be concluded that insufficient sediment was discharged from the river to significantly increase sediment deposition at any site, even during the month with the highest discharge. But the availability of daily discharge data allows a more detailed analysis of potential sediment deposition rates.

Peak Manlag River sediment discharge occurred on



October 12 (5,144 mt), November 7 (2,569 mt) and December 20 through 23 (5,633, 2859, 2,032, 1,640 mt respectively). Dividing these high daily  $Q_s$  values by the impact area (10 km<sup>2</sup>) gives sediment deposition rates as follows: October 12 (51 mg/cm<sup>2</sup>/day), November 7 (26 mg/cm<sup>2</sup>/day), December 20-23 (56, 21, 28, 20, 16 mg/cm<sup>2</sup>/day respectively). The particle size distribution of trapped sediments is 66 to 94% sand and silt by weight. Based on settling velocity of standard quartz particles (Sverdrup et al., 1940) the sand and silt particles would be expected to settle to 3 m depth within 1 day. Depending on the extent of flocculation, some of the finer, clay particles would remain in suspension for a longer period. These conclusions fit well with observations of clearing time required for turbid water in the bay following high discharge events.

Based on analysis of probable daily sedimentation peaks, it seems likely that significantly increased levels of sediment deposition could have occurred at all treatment sites during these short-term, high discharge periods. However, actual sediment deposition at each site would have been affected by a complex array of factors especially sediment plume dynamics and wind velocity and direction. Suspended load data obtained at various distances from the river mouth (Table 3.4) during high discharge events suggest that at such times the sediment load gradient of the plume was not as steep as the monthly sediment

deposition gradient. During high discharge periods there was only a 15% reduction in suspended load between the river mouth and Site 3, 2.25 km distant. In contrast, monthly sediment deposition data show a 96% decrease over the same distance (Table C.4).

### Conclusions

In 1986, surface circulation patterns in Bacuit Bay were dominated by currents generated by seasonal monsoon winds. Tidal currents were relatively weak. Advection of sediments entrained in the Manlag River sediment plume varied with wind speed and direction. The effects of Manlag River discharge on Bacuit Bay (low salinity, reduced temperature and high suspended sediment) were not detected beyond a radius of approximately 3 km from the river outlet. The potential threat of decreased temperature to living corals does not appear to be important and decreased salinity appears to be important only in the upper 1 m of water. Since logging has been shown to significantly increase runoff (Hamilton, 1985; this study) and peak stream flow (Hamilton, 1985), the potential for greater freshwater discharge was predicted to increase due to planned expansion of logged forest area in the Bacuit Bay drainage basin.

Although concentration of suspended sediment in the river plume decreased little as it moved into the bay,

there was a steep gradient in monthly sediment deposition. Mean secchi depth was significantly lower at Site 5 than at the 4 sites farthest from the river mouth and sediment deposition was significantly greater at Site 5 than at these 4 sites, indicating that sediment deposition and turbidity were spatially correlated.

Monitored on a monthly basis, only sediment deposition at Site 5 ( $31.6 \text{ mg/cm}^2/\text{day}$ ), the study site closest to the river mouth, was significantly greater than the rate at the control site (8), and similar to rates considered to be damaging to corals in other regions. Site 5 also had a significantly larger terrestrial component than all other sites. Sediment deposition measured at the control site (8) in Bacuit Bay ( $0.6 \text{ mg/cm}^2/\text{day}$ ) was similar to "pristine" rates measured at various reefs around the world. In comparison to the particle size distribution of forest soil, sediment from sites closest to the river mouth had a higher percentage of silt, and Sites 1 and 8 had higher percentages of sand.

The most important factor affecting the level of terrestrial sediment deposition at sediment trap sites was distance from the mouth of the Manlag River. Both percent calcium carbonate and distance were negatively correlated with percent silt content of trapped sediments indicating that calcium carbonate was primarily associated with sand and clay fractions, and that silt content was a good

indicator of terrestrial sediment input to Bacuit Bay. The high silt and clay fractions, and low calcium carbonate percentage of trapped sediments and high penetrability of sediment deposits at the base of the reef at Site 5 were indicative of a high terrestrial sediment input (as opposed to resuspension of marine sediment).

Waves appeared to be an important factor influencing sediment resuspension at 3 sites. Turbidity was significantly lower at the control site than at all other sites. Lack of correlation among sediment discharge, wave height and sediment deposition was attributed to inadequate sampling of wave height and different sampling frequencies for different environmental variables.

Total 1986 sediment output ( $Q_s = 39,154$  mt) of the relatively small Manlag River would be diluted to a low and probably insignificant sedimentation level in the unlikely event it were completely and evenly distributed throughout the bay ( $120 \text{ km}^2$ ) or even the area circumscribed by the "treatment" study sites, 1-7 ( $10 \text{ km}^2$ ). Based on analysis of daily discharge records of the Manlag River, sedimentation at all "treatment" study sites (1-7) was estimated to have had a potential range of from 16 to 51  $\text{mg/cm}^2/\text{d}$  for a minimum of 7 days in 1986. It appears likely that sediment deposition at a level considered damaging to corals could have occurred at all treatment sites during short-term, high discharge periods.

#### IV. EFFECTS OF SEDIMENT ON CORALS

##### Introduction

Evidence presented so far supports the hypothesis that logging operations accelerate erosion and sediment discharge from the Bacuit Bay drainage basin resulting in increased sediment deposition on near-shore coral reefs. Previous work has raised three principle questions concerning the effects of sediment on corals. These questions are:

- 1) What is the mechanism by which sediment damages coral tissue and leads to colony death?
- 2) Is there a correlation between sedimentation resistance and phenotype?
- 3) To what extent is coral community structure affected by sedimentation.

Experimental results relating to the first two questions are presented in this chapter, and results relating to the third question are presented in Chapter 5.

Partial reviews of the subject of sediment effects on corals have been made by Levin (1970), Johannes (1975), Rogers (1977), Anderson (1978), Aliño (1983), and Brown and Howard (1985a). In the following paragraphs, important developments in this field will be reviewed.

### Sedimentation and Coral Cleaning Mechanisms

After conducting sediment rejection tests with Caribbean corals, Vaughan (1916) concluded that there are two important mechanisms of sediment removal used by corals exposed to sedimentation. The first is mucus production and the second is ciliary action. Vaughan also noted that these mechanisms may be used in concert to clean the coral surface.

Marshall and Orr (1931) showed the importance of both water motion and biological mechanisms in cleaning corals by placing waxed, fixed coral heads on a shallow reef flat alongside living colonies. Although water currents cleansed some sediments from waxed colonies, living colonies were able to clean themselves much more effectively. These experiments also confirmed Vaughan's ideas that interspecific differences in ciliary action (later studied by Yonge, [1930] and Lewis and Price, [1976]), and mucus production, partially determine the sediment cleaning ability of each species. The results of Marshall and Orr (1931) indicated that coral cleaning efficiency is affected by interactions among sediment particle size, coral growth form and the biological cleaning mechanisms employed.

Yonge (1935) and Abe (1939) described a third mechanism whereby some coral species rid themselves of accumulated sediment. This is accomplished by the coral

taking in water to expand the oral disk so that the sediment slides off. Several species of Fungia, a genus of solitary, free-living coral, are noted for their ability to uncover themselves using this method, even when completely buried under sediment (Wood-Jones, 1912; Marshall and Orr, 1931; Abe, 1939). However, one species, Fungia scutaria, is not able to uncover itself when buried under 1 cm of sand (Jokiel and Cowdin, 1976). Schuhmacher (1977, 1979) determined that the mechanisms used by colonial corals to reject sediment are also used by solitary fungiids.

#### Sedimentation and Coral Phenotype

Vaughan (1916) divided corals into two major groups: strong, firmly attached, massive forms which can withstand rough water and weakly attached, branching forms which can survive only in quiet water. The quiet water group was further subdivided "according to their capacity to resist the deleterious effects of silt". He found that sediment was quickly removed from thin branches by water motion. Marshall and Orr (1931) tested the sediment tolerance of 8 corals (most were identified to the genus level only) at Low Isles (northern Great Barrier Reef). Marshall and Orr noted that corals with large polyps were damaged less than corals with small polyps and concluded that corals can and do live in slightly turbid waters, and for a limited period can tolerate large amounts of sediment falling from above.

Hubbard and Pocock (1972) and Hubbard (1973) studied the sediment rejection capabilities (not susceptibility to damage) of corals in the laboratory. They subjectively assessed the ability of colonies of 26 Caribbean species to remove painted sediment particles of 7 size classes (ranging from 2 mm to less than 62  $\mu$ ) from their surfaces. They did not monitor the effect of sediments on the corals. Hubbard and Pocock (1972) concluded that sediment rejection ability is dependent on sediment particle size and suggested that ability to clean the coral surface of sediments can be predicted from polyp distensional ability and arrangement of corallites (the skeletal cups, including the walls, that hold each polyp), with sediment rejection efficiency increasing in a series from the cerioid arrangement (adjacent corallites share walls), to plocoid (individual walls) and then meandroid (formed in rows). From this work they ranked the 26 species in order of sediment rejection ability and noted reef zones where these corals appeared to be abundant.

The theoretical application of the Hubbard-Pocock model is limited by the fact that the polyp arrangement of many coral species cannot be classified within the cerioid, plocoid and meandroid classifications. For example, about 200 coral species belong to the family Acroporidae. Historically the corallite organization of acroporid species has not been described within this tripartite



classification for the reason that they do not easily fit in such a scheme. Hubbard and Pocock's work could be reevaluated with respect to a more complex classification scheme (Veron and Wallace, 1984) based on corallite shape and coenosteal structure.

The sediment rejection capabilities of 3 of the species tested by Hubbard and Pocock (1972; Siderastrea siderea, Montastrea cavernosa and Diploria strigosa) were also tested in the field at Puerto Rico with similar results (Kolehmainen, 1974). Two of the coral species rated in the Hubbard and Pocock hierarchy as having the ability to reject small particle sizes (Porites astreoides and Acropora cervicornis), were also used in sediment deposition field experiments by Rogers (1977). Rogers used natural sediments collected from the field. In contrast to the results of Hubbard and Pocock (1972), she found the 2 species were unable to clear the colony surface of small particle sized sediments. Rogers suggested that these differences in ability to clear sediment may depend on the mixture of particle size classes used.

Bak and Elgershuizen (1976) exposed 19 Atlantic coral species held in the laboratory to sedimentation using natural sediments and assessed the corals' ability to clean their surfaces. Thirteen of these species had been tested previously by Hubbard and Pocock (1972). The results of Bak and Elgershuizen did not confirm those of Hubbard and

Pocock (1972) and often contradicted them. Bak and Elgershuizen speculated that Hubbard and Pocock may have damaged some corals prior to testing. Bak and Elgershuizen also suggested that the influence of polyp behavior, independent of corallite arrangement, is an important component of the sediment rejection process. Bak and Elgershuizen examined sediment rejection ability in relation to growth form, corallite arrangement, ability to elevate the coenosarc (surface tissue between polyps), polyp extensional ability, tentacle length, polyp diameter, active period, behavioral response to mechanical stimulation, ciliary current strength, and mucus secretion and concluded that there was no correlation between sediment rejection ability and any of these characters. They rejected the notion that there is a general pattern in the efficiency of sediment rejection, and suggested that it is species-specific, and that the large number of independent variables affecting the interaction of sediment with corals makes it impossible to construct a sedimentation rejection hierarchy based on corallite arrangement or other characters.

Lasker (1980) conducted laboratory and field experiments with two morphs of Montastrea cavernosa and determined that colony morphology was important in determining sediment deposition and that coral polyp behavior was important in sediment rejection. Lasker

concluded that a greater area of inclined surface allows biological cleaning mechanisms to work more efficiently.

### Sedimentation and Coral Damage

Beginning with Wood-Jones (1912), sedimentation has often been hypothesized to limit coral growth, but most work has focused on the efficiency of coral cleaning mechanisms and the results of burying corals under a thick layer of mud. Comparatively little experimental work has been done on the effects of sedimentation on corals. Rogers (1983) conducted field sedimentation rejection tests in shallow water using single and multiple applications of coarse calcareous sand on coral colonies of 5 Caribbean species tested in previous studies (Hubbard and Pocock, 1972; Rogers, 1977). She found that large sediment doses (200-400 mg/cm<sup>2</sup>) were required to damage corals, partly due to the rapid cleaning action of waves.

Rice (1985) noted the importance of differentiating between sediment rejection capability and susceptibility to sedimentation damage. For example, Hubbard and Pocock (1972) determined that the coral, Cladocora arbuscula, was poor at rejecting sediments but Rice's results showed that this species is less susceptible to sedimentation damage than Isophyllia sinuosa, a species that Hubbard and Pocock rated as having a high sediment rejection efficiency. These results indicate that sediment rejection efficiency

is only one of many factors that determine the ability of corals to avoid the damaging effects of sediment deposition.

Parnrong and Chansang (1986) tested the sedimentation resistance of 4 Indo-Pacific corals held in aquaria and subjected to sedimentation. At a sedimentation rate of 8 mg/cm<sup>2</sup>/day, time until 50% mortality (2 of 4 colonies) was 4 days for Porites lutea, 7 days for Acropora formosa, 8 days for Pocillopora damicornis, and 21 days for Montipora ramosa. At 33 mg/cm<sup>2</sup>/day, time to 50% mortality was reduced to 2 days for Porites lutea. Interpretation of these results is limited by a lack of controls. In addition, lack of water changes could have caused low oxygen levels.

#### Sedimentation and Coral Larvae

Sediment damage to corals is possible at any stage in their life cycle. Most work on the effects of sedimentation on corals has used adult coral colonies, however, some work has considered the effects of sedimentation on settlement of coral larvae or planulae. Hida (1932) noted that coral planulae do not settle on silt covered surfaces, but generally settle on "clean" surfaces. Lewis (1974) tested the substratum settlement preferences of the planulae of Favia fragum, an Atlantic species. His results showed that "a sprinkling of fine washed sand in

the bottom of test bowls" reduced settlement to less than one-third of the settlement rate on a clean glass surface. A number of other workers have noted the inability of coral planulae to settle on silt covered surfaces (summarized in Maragos, 1972).

#### Sedimentation and Coral Growth

One of the major problems with the use of corals in experiments is that they grow slowly and it is often difficult to measure growth rates (Maragos, 1972). Dodge et al, (1974), Aller and Dodge (1974), and Dodge and Vaisnys (1977) used x-ray photography and autoradiography to estimate growth rates of several massive coral species using yearly banding patterns measured from slices cut from coral skeletons along the axis of growth. Dodge et al., (1974) compared coral growth over several years with sediment deposition in traps located in 3 sedimentation zones. They demonstrated an inverse correlation between sediment deposition and annual coral growth, but their conclusions are weakened by their extrapolation of two weeks of sediment deposition data to annual rates. Dodge and Vaisnys (1977) showed that coral growth bands (rates) were reduced during harbor construction in Bermuda in the 1940's. They inferred a causal relationship between decreased coral growth rates and increased sedimentation which they assumed occurred during harbor construction.

### Complete Burial of Corals

Vaughan (1916) tested the resistance of several Caribbean corals to complete burial under sediment and found that all species were killed after several days under such conditions. Mayer (1918), conducted complete burial experiments at Murray Island, near the northern tip of the Great Barrier Reef. Colonies of 13 coral species were buried under 5 cm of mud. Mayer concluded that near-shore corals are more resistant to sediment burial than corals living near the reef edge. Survival time was 14 hours to 2 days. Edmondson (1928) established a hierarchy of Hawaiian coral species based on survival following complete burial under 10 cm of sand and mud. Survival ability ranged from 12 hours to over 5 days. Marshall and Orr (1931) conducted partial burial experiments and concluded that any portion of a living colony that is buried will die within 1 or 2 days regardless of species. Rice (1985) conducted sediment burial tests with 8 Atlantic coral species and determined that they could survive from 7 to 15 days buried under sediment. A burial depth was not specified but appears to have been several centimeters. The longer period of survival obtained in this experiment compared with previous work may be due to the use of an under-gravel water filter which maintained water and oxygen flow through the sediment layer.

Marshall and Orr (1931) pointed out that complete (bottom-up) burial of corals by sediment is a different process from daily sedimentation (from above), and therefore the experimental results of these two types of sedimentation experiments might differ. They believed that burial would be primarily a test for ability to withstand lack of oxygen, and that sudden burial would be an unlikely event in nature.

Are results of coral burial experiments reliable predictors of resistance of corals to sedimentation? In order to answer this question it should be asked whether corals are commonly exposed to complete burial. Although numerous workers since Darwin have noted the incompatibility of active coral growth with unconsolidated, shifting substrate, e.g. Gardiner (1931), Wells (1957), Goreau and Land (1974) and Johannes (1975), there have been few well documented accounts of recent large-scale coral reef burial under sediments. Maragos (1972) recorded the burial of coral colonies by sediment infilling in Hawaii. Hubbard (1986) reviewed the subject of large-scale, seasonal, current-driven, sediment transport across reefs and concluded that it limits the growth of certain sections of coral reef at St. Croix. But the study did not focus on the mechanism of how sediment limits coral growth, i.e. by abrasion, deposition or other action. R. Schroeder (pers. comm.) has recorded burial of patch reefs several meters in

diameter following storm induced movement of sand banks in Midway Atoll lagoon. The main atoll reef was unaffected.

It may be that as Vaughan (1916) and others have noted, complete burial of coral reefs under sediment is relatively uncommon. More importantly, when it occurs, e.g., during a typhoon, there is little chance that the sediment would be removed soon enough to prevent all corals from dying. Although some species are more resistant than others, all corals tested so far die within a few days after complete burial under a thick layer of mud (Mayer, 1918; Edmondson, 1928; Marshall and Orr, 1931; Rice, 1985). If all buried corals die, there should be little selective advantage in surviving longer. In addition, because the physiological responses may be different in each case, resistance to complete burial may not be correlated with resistance to high sedimentation. Therefore, the results of previous work on survival time of corals following complete burial under several centimeters of mud is not used here as a measure of susceptibility to sedimentation damage.

#### Sedimentation and Drilling Mud

A number of studies have examined the effects of well drilling "mud" on corals (Hudson et al., 1982). Drilling "mud" is an artificial compound that usually contains one or more potentially toxic chemicals, therefore it is



difficult to draw conclusions regarding the effects of natural sediments on corals based on results from drilling mud toxicity experiments. It may be useful to apply the results of this work relating to physical dispersal of mud to analysis of the problem of natural sediment dispersal from a point source (Thompson and Bright, 1980).

### Assessing Causality

So far, experimental tests of the effects of sedimentation on corals have involved only 11 of the approximately 90 Atlantic coral species and 12 of the approximately 500 Indo-Pacific species (Veron and Hodgson, in press).

Despite the lack of thorough experimental tests on the mechanism of coral tissue death due to sedimentation or sediment burial, several workers have speculated that a variety of factors acting alone, or in concert, may be responsible. These factors include abrasion by sediments carried by strong currents, light reduction, smothering by physical blocking of oxygen carrying water currents, microbial action and energy drain due to self-cleaning efforts (Hubbard and Pocock, 1972; Maragos, 1972; Loya, 1976; Rogers, 1977; Lasker, 1980; Aliño, 1983).

Observations and evidence for 3 of these mechanisms, abrasion, light attenuation and microbial action, are considered next.

### Abrasion

Several reports suggest that abrasive scour from sediments may be important in determining where corals can grow (summarized by Levin, 1970). Wave action is one factor which is considered important in determining resuspension of sediment and potential abrasion of living corals (Rogers, 1977; Randall and Birkeland, 1978; Liew and Hoare, 1979). No experiments have tested these ideas.

### Light Attenuation

One possible cause of sedimentation damage to corals is that deposited sediments block out light necessary for photosynthesis by zooxanthellae. Rogers (1977; 1979) used a pair of submerged, 10 m long channels, one covered with clear and the other with black plastic, to monitor the effects of light reduction on coral growth and metabolism. Coral growth and net productivity were reduced to near zero one month after the black plastic was installed, apparently due to shading. Some colonies of the dominant species, Acropora cervicornis, were killed and most corals were bleached. These data were not subjected to statistical analysis. It is questionable whether the low light level achieved beneath the black plastic channel is comparable to the light reduction that occurs during periods of even high turbidity (Loya, 1976; Liew and Hoare, 1979).

Edmondson (1928) conducted burial and light limitation experiments using 15 species of Hawaiian corals. In the latter experiments colonies were kept in complete darkness in screened containers set out on the reef. Some species were more resistant than others and the order of the resistance hierarchy for burial closely matches that of light limitation. The difference in results is that the time until death due to lack of light was much longer than from burial, ranging from 18 to over 45 days. This large difference in the ranges of survival times between the burial and light exclusion experiments has not been noted previously, and is significant to study of the mechanism of coral mortality due to sedimentation. Results of a separate experiment by Yonge et al. (1932) clarify the implications of these results.

Yonge et al. (1932) tested resistance of 4 Indo-Pacific coral species to lack of oxygen and light, by sealing corals in jars filled with deoxygenated water. The survival range of 1 to 6 days is similar to ranges from both sets of sediment burial experiments but much shorter than the range of the light limitation experiments (18-45 days). These results are inconclusive due to a variety of complicating factors such as potential damaging effects of excretory product build-up in the sealed jars. Nevertheless the results seem to indicate that lack of light is not the primary factor responsible for coral

mortality due to sediment burial, and that lack of oxygen or factors acting with similar speed to oxygen deprivation may be more important in this process.

If corals are damaged by light reduction caused by sedimentation, one measurable parameter should be decreased primary production. Using 3 species of Atlantic corals, Rogers (1977), measured the metabolism of colonies subjected to sedimentation and concluded that compared with the results from control colonies, sedimentation reduced net productivity. Parnrong and Chansang (1986) monitored oxygen production and respiration of colonies of the Indo-Pacific coral, Porites lutea, subjected to sedimentation in aquaria. Rapid water currents were used to maintain the desired suspended sediment load. After 3 days of exposure to different sedimentation treatments, oxygen levels in the aquaria decreased at a suspended sediment load of 36 mg/l. Coral respiration decreased at a concentration of 6 mg/l of silt-clay in seawater. Because of a lack of controls, causes other than light limitation could have reduced production. Parnrong and Chansang emphasized the importance of direct effects of sediment on corals rather than indirect effects from light blocking.

#### Microorganisms

Lasker (1980) believes that when sediment deposition on coral surfaces exceeds the removal rate, it may create

anoxic conditions which kill the coral. Other workers have indicated that microorganisms may be involved in the process of sediment damage to corals by creating anoxic conditions. Maragos (1972) noted that sediments provide a surface for bacterial attachment and growth and that bacteria could damage corals. Rogers (1977; 1979), and Parnrong and Chansang (1986) noted a black, sulfide layer located beneath sediment that built up on dying corals. The toxicity of hydrogen sulfide (without sediment) to corals has not been tested.

The following points summarize the state of knowledge concerning sedimentation effects on corals when the present study began:

- 1) A small number of corals had been tested for resistance to damage from sedimentation.
- 2) Corals had been reported to clean their surface of sediment using 4 mechanisms: ciliary movements, mucus net formation, tentacular movements, muscular polyp movements, especially distension aided by water ingestion, and combinations of the above.
- 3) Corals that had been tested showed a wide degree of response ranging from bleaching to death.
- 4) The type of response appeared to depend on a large number of variables, especially sediment type, duration of the sedimentation event, spatial and temporal distribution of sediment deposition, eventual

thickness of sediment deposits and coral morphology and behavior.

Field and laboratory experiments were used to investigate the effects of sediment on corals and to look for correlations between phenotype and degree of effect.

### Methods

#### Selection of Species and Phenotypes

A large number of phenotypic characters are used to differentiate coral species and genera (Wells, 1956). To experimentally determine whether resistance to sedimentation damage is correlated with the presence or absence of certain phenotypic characters, it was important to select species encompassing a wide range of phenotypic variation. Rather than analyze randomly chosen phenotypic characters, 2 characters (coral colony growth form and corallite diameter) were chosen initially that seemed likely to mediate sediment-coral interactions based on personal observations of the process of sedimentation damage, and on previous research. Following completion of field work a third phenotypic character was added to the analysis (polyp extensional ability).

In choosing the characters, two desirable features were sought. First, although intraspecific variability is a well-known feature of corals, it was not the focus of

this study, therefore characters with low intraspecific variability were chosen. Secondly, to facilitate statistical analyses, characters that were easily quantified or categorized were chosen.

### Growth Form

The most obvious taxonomic character of corals (but not necessarily the most conservative) is colony growth form (refer to Figure 1.1). Many workers have noted that the likelihood of sediment particles coming to rest on a coral colony depends on colony growth form (GF) and therefore GF could affect the outcome of a sedimentation event. Colony GF was chosen as the first phenotypic character for analysis with respect to sediment effects. In order to simplify analysis, less common GF variants were grouped into 4 major categories based on similarity. For example, although branching Acropora can be arborescent, bushy or may form flat tables of anastomosing branches, all Acropora GFs were placed in the ramose category for analysis. All GFs (see Figure 1.1) were thus combined into the following 4 categories:

- 1) ramose -- including all branching forms,
- 2) massive -- all solid, hemispherical, encrusting or "head" shaped colonies,
- 3) plate -- all flat, explanate, foliaceous forms,

4) phaceloid -- colonies with nearly parallel branches forming tufts with polyps at the branch tips.

#### Corallite Diameter

Most previous experimental work has focused on the role of phenotypic characters in relation to sediment clearing efficiency as opposed to sedimentation damage resistance; and the conclusions were often contradictory.

Reexamination of Bak and Elgershuizen's (1976) results indicated that the 6 species with the slowest sediment rejection (clearing) times all have small diameter polyps. If it is assumed that a slow rejection time results in a greater chance of coral damage due to sediment build-up, then it follows that polyp diameter might be related to potential sedimentation damage.

Although some data on polyp diameter are available for Indo-Pacific species, a related character, corallite diameter (CD) is considered a primary taxonomic character and is readily available from species descriptions. A corallite is the skeletal cup (including the side walls) that holds each polyp. (Calice [also spelled calyx] diameter [Wells, 1956] is also an important taxonomic character that should not be confused with corallite diameter. Calice diameter is the inner diameter while corallite diameter is the outer diameter of the cup.) When the walls of the cup are thick such as in some Favia spp.,



there may be a large difference between the two measurements.

Mean corallite diameter (CD), the second phenotypic character chosen for analysis, was obtained from a series of 13 publications entitled "Systematic Studies on Philippine Shallow Water Scleractinians" by F. Nemenzo and co-authors Ferraris, Hodgson, and Montecillo and from a second series of 5 publications entitled "Scleractinia of Eastern Australia" by Veron, Pichon, Wallace and Wisjman-Best (see Veron and Hodgson, in press, for these citations and for a complete bibliography of Philippine coral taxonomy). For almost all species, mean CD based on measurements of many specimens were available. In the few cases where published means were not available, they were obtained by measuring 10 corallites shown in photos accompanying species descriptions, and corrected for magnification.

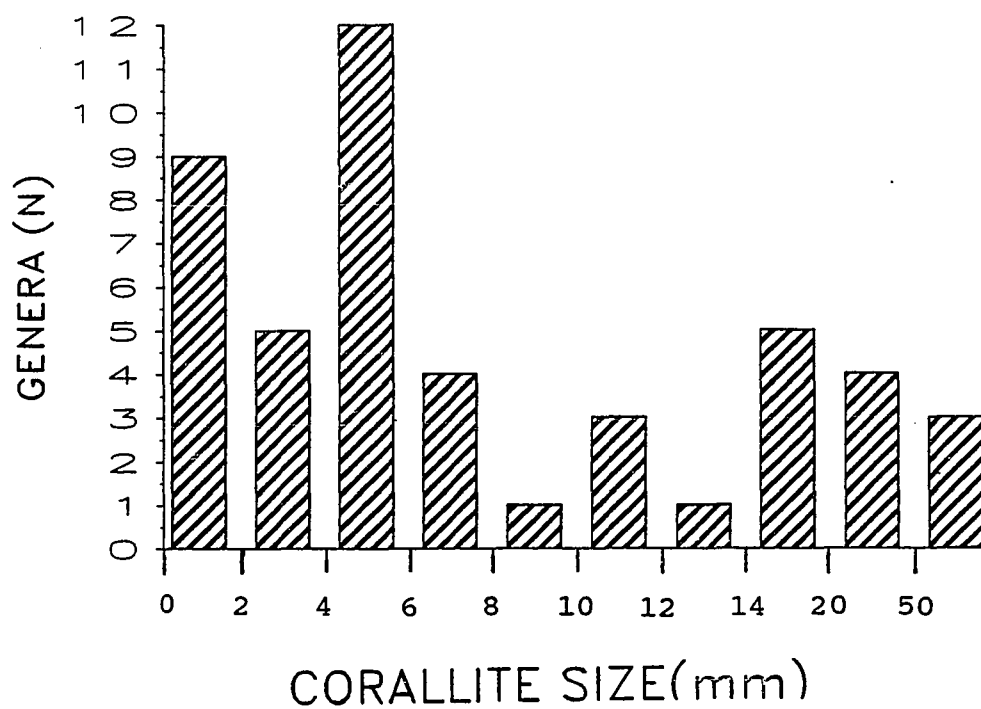
Mean CD of each species is used as both a continuous and categorical variable; in the latter case, species were divided into 3 corallite size classes: small, medium and large CD. Each species was assigned to a CD class using the system of Bak and Engleshuizen (1976) which defines small corallites as those less than 4 mm in diameter, medium corallites as those 4 mm or larger and less than 8 mm, and large corallites as those 8 mm or larger in diameter. Although this system was designed for use with

Caribbean corals, it was found to fit the frequency distribution of the mean CD of Bacuit Bay coral genera (Table D.1, Appendix D), which has peaks at 0-2 mm, 4-6 mm and 14-20 mm (Figure 4.1).

### Polyp Extensional Ability

Previous reports and field observations indicated that active (muscular) and passive (e.g. water current driven) movement of polyps and tentacles sweeps the coral surface, preventing sediment deposition and resuspending sediment, thus allowing sediment to be carried away. A testable hypothesis is that species with long polyps (including tentacles) are less susceptible to sedimentation damage than species with short polyps. Polyp extensional ability (PEA) was chosen to be the third character for analysis with respect to sedimentation damage.

Hubbard and Pocock (1972) used a categorical measure called "polyp distension" in their analysis of sediment rejection efficiency. Although they did not clearly define this term, it implies an increase in both polyp diameter and length. Hubbard and Pocock (1972) concluded that cilia cleared away small sediment particles and polyp distension and tentacle movement were used to clear away large ( $>500\ \mu$ ) particles. To restrict the meaning to polyp length only, I have used the term polyp extension.



**Figure 4.1** The number of genera (n=47) having a mean corallite diameter in the given range (0-2.0, 2.1-4.0, 4.1-6.0, 6.1-8.0, 8.1-10.0, 10.1-12.0, 12.1-14.0, 14.1-20.0, 20.1-50.0, and >50 mm).

Since field work in the Philippines was already completed when this character was added to the analysis, PEA estimates were collected from a variety of sources. In taxonomic descriptions, mean or maximum polyp extension is only included for species with very long tentacles such as species of Euphyllia, Alveopora, and Goniopora. Therefore, polyp extension measurements were obtained from photographs in the taxonomic publications noted above (10 species), and from Faulkner and Chesher (1979; 13 species), Veron (1986; 34 species), Wood (1983; 2 species) and by measuring colonies in the Waikiki Aquarium (6 species). PEA for other species was estimated based on my observations during night dives when most species' polyps are fully expanded (Table D.1, Appendix D).

Since the precision of PEA estimates is limited, this character was treated as a categorical variable with two classes; all species were classified as either high or low PEA. The frequency distribution of PEA among genera has one peak at 1 - 2 mm (13 genera) and another at 8 - 25 mm (13 genera). Taking the midpoint between these peaks, species with polyps and tentacles that can extend more than 5 mm were ranked as having a "high" extensional ability; those with a 5 mm or less maximum extension were placed in the "low" category.

### Sedimentation Resistance Hierarchy: Aquaria

Experiments were conducted in aquaria at El Nido, Palawan to assess the resistance of 22 scleractinian coral species to sedimentation. These 22 species represent 19 genera, and 11 of the 15 families of hermatypic Scleractinia found in the Western Pacific (Table 4.1). In addition, one reef-building hydrozoan (Millepora intricata) was tested.

Five 40 l glass aquaria were set up outdoors as closed systems without circulating seawater or water filtration. The aquaria were continuously aerated with air-stones and were partially shaded under an awning so that water temperature was maintained within 2 °C of ambient water temperature in Bacuit Bay.

Corals were collected from 3-6 m depth at the control station (8) and held in a holding tank until use. Care was taken to disturb the corals as little as possible during collection and transport. For common coral species having abundant small colonies, whole colonies could be used. For large rare species, colonies were broken into several parts with a hammer and chisel, and these fragments (about 15 cm diameter) were allowed to heal for at least two days in the field before collection. There was no difference between the effects of sediment on coral fragments with fresh breaks versus small, whole colonies.

Two aquaria were used to control for aquarium effects and two served as treatment aquaria. For each species

Table 4.1 Coral species used in sedimentation experiments and growth forms (GF): ra=ramose, ma=massive, pl=plate, fo=foliaceous, enc=encrusting, ph=phaceloid, fb=flabellate, fl=free living (GFs combined for analysis; see text). Corallite diameter (CD): S=small, M=medium, L=large. Extensional ability (PEA) is capability of polyp to expand above corallite. In last 2 columns, X indicates use in A=aquarium and F=field experiments.

Family and Species	GF	CD	PEA	A	F
<u>Pocilloporidae</u>					
1 Pocillopora verrucosa	ra	S	Low	X	X
2 Seriatopora hystrix	ra	S	Low	X	
3 Stylophora pistillata	ra	S	Low	X	
<u>Acroporidae</u>					
4 Acropora hyacinthus	ra	S	Low		X
5 Acropora microphthalma	ra	S	Low	X	
6 Acropora palifera	ra	S	Low		X
7 Montipora corbettensis	pl	S	Low		X
8 M. crassituberculata	fo	S	Low		X
9 Montipora florida	fo	S	Low	X	
10 Montipora stellata	ra	S	Low	X	X
11 Montipora turgescens	enc	S	Low	X	
<u>Agariciidae</u>					
12 Pavona cactus	fo	S	Low		X
13 Pavona decussata	fo	S	Low	X	
14 Leptoseris yabei	pl	S	Low		X
15 Pachyseris gemmae	pl	S	Low		X
16 Pachyseris rugosa	pl	S	Low	X	
<u>Fungiidae</u>					
17 Fungia echinata	fl	L	High		X
<u>Poritidae</u>					
18 Goniopora tenuidens	ma	M	High	X	X
19 Porites lutea	ma	S	Low		X
20 Porites sillimaniana	ra	S	Low		X
<u>Faviidae</u>					
21 Barbattoia amicornum	ma	L	High		X
22 Favia stelligera	ma	S	Low		X
23 Favia favius	ma	L	High		X
24 Favia speciosa	ma	L	High	X	
25 Favites abdita	ma	L	Low		X
26 Goniastrea retiformis	ma	M	Low	X	

Table 4.1 (continued) Coral species used in aquarium and field sedimentation experiments and phenotypes. Abbreviations as given above.

Family and Species	GF	CD	PEA	A	F
<u>Faviidae cont.</u>					
27 Goniastrea edwardsi	ma	M	High		X
28 Platygyra lamellina	ma	L	High		X
29 Hydnoophora microconus	ma	S	Low		X
30 Hydnoophora ridgida	ra	S	Low		X
31 Cyphastrea microphthalma	ma	S	Low	X	X
32 Echinopora horrida	ra	M	Low		X
33 Echinopora mammiformis	pl	M	Low		X
<u>Oculinidae</u>					
34 Galaxea fascicularis	ph	L	High	X	X
35 Achrelia horrescens	ra	S	Low		X
<u>Merulinidae</u>					
36 Merulina scabricula	pl	S	Low		X
<u>Mussidae</u>					
37 Acanthastrea echinata	ma	L	High		X
38 Lobophyllia corymbosa	ph	L	High		X
39 Lobophyllia hemprichii	ph	L	High	X	
40 Symphyllia radians	ma	L	High		X
<u>Pectiniidae</u>					
41 Oxyphora glabra	pl	M	Low	X	X
42 Oxyphora lacera	pl	M	Low	X	
43 Mycedium elephantotus	fo	L	Low	X	X
44 Pectina alcicornis	fo	L	High	X	
45 Pectinia lactuca	fo	L	High		X
<u>Caryophylliidae</u>					
46 Euphyllia ancora	fb	L	High	X	X
47 Euphyllia glabrescens	ph	L	High		X
<u>Dendrophylliidae</u>					
48 Turbinaria peltata	pl	M	High	X	X
<u>Trachyphylliidae</u>					
49 Trachyphyllia geoffryi	fl	L	High	X	X
<u>Milleporidae (Hydrozoa)</u>					
50 Millepora intricata	ra	S	Low	X	

tested, 8 colonies were used per run; 4 colonies were placed in control aquaria (2 in each) and 4 colonies in treatment aquaria (2 in each). Since water filter systems were not used during experiments, all aquaria were given a 50% seawater change every other day. Half the water was siphoned from the top of each aquarium and replaced with fresh bay seawater.

Sediment was collected from Site 5, washed in freshwater and dried. After placing coral colonies in aquaria, 50 g dry weight of sediment was sprinkled evenly over the water surface of treatment aquaria and then the water was stirred to mix the sediment evenly resulting in a 1.25 g/l concentration. The sediment was allowed to settle resulting in a deposition rate of 40 mg/cm<sup>2</sup>. Hand-stirring with a spatula was done at 8:00 h and 18:00 h daily until most sediment was resuspended. This procedure was chosen because it mimics the sediment resuspension/deposition/resuspension process observed in the field (resuspension during windy periods; see Chapter 3) and allows examination of the entire coral surface following stirring. The current produced by bubbles from the air-stone was not powerful enough to keep sediment in suspension. Tests showed that without stirring, the water became clear after 24 h.

It was not necessary to add additional sediment following water changes because almost all sediment had



fallen below the halfway point within a few hours of stirring, therefore only clear water was siphoned from the aquarium. Coral colonies were examined daily at 18:00 h following water stirring and changes in their appearance were noted. The size of patches affected by bleaching, or tissue necrosis was estimated by measuring 2 perpendicular axes of each colony with a ruler (to the nearest millimeter) and then measuring the size of the patches. For ramose colonies, only upward facing surface areas were measured. Onset of tissue necrosis was defined as tissue breakdown with holes in the coenosarc visible. Each experiment ran for 7 days. Aquaria were carefully washed and dried between experiments to avoid buildup of microorganisms.

#### Sedimentation Resistance Hierarchy: Field

To monitor sedimentation effects on corals in the field, corals from the control reef (Site 8) were transplanted to an area with a known high sedimentation rate; the bay floor (7.5 m depth) at Site 7. Water depth and the location were chosen to avoid wave action and low salinity which potentially affected Sites 5 and 6. An underwater platform standing 50 cm above the bottom was anchored 10 m south of the Site 7 reef face. The horizontal platform consisted of a 2 m x 1 m wood frame covered with 5 cm mesh galvanized fencing.

Corals were collected from the control reef (Site 8) at 6-8 m depth and transported by boat in 700 l live wells to Site 7. As with the aquarium experiments, species were chosen to represent a wide taxonomic range and all major growth forms. Thirty-six species representing 27 genera and 12 families were tested (Table 4.1). Four colonies of each species were placed on the platform and adjusted so that they rested in their natural growth position. Four additional colonies of each species were transported back to the control reef (Site 8) and placed on a large rock at 7.5 m depth to control for effects of collection and transportation.

The colonies were monitored underwater at least once per week for the first 4 weeks, and then biweekly for 120 days. Sediment deposition at the platform (7.5 m depth) was measured with a sediment trap unit. Mean deposition was  $20.8 \text{ mg/cm}^2/\text{day}$  (S.E. = 7.6), more than 10 times the rate measured at 3 m depth at this site. Changes in the appearance of the colonies were recorded as discussed for the aquarium experiments.

Several unsuccessful attempts were made to experimentally separate effects of sedimentation from effects of light reduction on corals. Sedimentation "tents" were designed that would act as umbrellas when placed over coral colonies and block sediment deposition from above. Tents were built using metal or wooden frames

covered with clear plastic sheet. Both pyramid and A-frame tent designs of several sizes were tested by placing them over coral colonies. In each test, vertical sediment deposition was blocked, but a 1 cm opening at the base of the tent skirt allowed horizontal currents to carry sediment into the space beneath the umbrella. After entering the tent, water currents apparently slowed allowing sediment deposits to build up. If the plastic sides of the tents were extended to reach the bottom, all sedimentation was blocked but the colonies were rapidly killed, perhaps due to lack of oxygen and buildup of wastes. Since these experiments were unsuccessful despite very slow horizontal currents, it seems that it will be difficult to use umbrella designs to separate light from sedimentation effects on corals.

#### Sediment and Planula Settlement

This experiment was designed to test the ability of coral planulae to settle on sediment covered surfaces. Thirty 250 ml glass jars covered with plastic lids were used as experimental containers. Air was supplied to an airstone in each jar from a tube passing through a small hole in the lids. Prior to each experiment, the jars were filled with seawater and allowed to sit for 2 days so that a biological film could form on the glass surfaces.

Pocillopora damicornis planulae were collected by

allowing colonies to planulate naturally in aquaria (i.e. planulation was not artificially induced by heating seawater or other treatment). Twenty planulae were placed in each of 30 jars. There were 5 different treatments and 1 control with five replicate jars for each. Treatments consisted of adding different amounts of dried sediment. The control jar was used to approximate a "natural" settlement rate on a glass jar bottom without sediment. In preliminary trials planulae settled primarily on the jar bottom. The critical factors affecting planula settlement appeared to be depth of the sediment layer on jar bottoms and percentage of jar bottom covered with sediment. Treatments were designed to encompass a range of these factors (Table 4.2).

**Table 4.2** Treatments for planula settlement experiments. Control (not shown) used no sediment. "Cover (%)" indicates the percentage of the jar bottom covered with sediment. "Thickness" is the depth of the sediment layer.

	<u>Treatment</u>				
	A	B	C	D	E
Sediment (g)	40	30	20	15	10
Cover (%)	100	100	95	90	50
Thickness (mm)	2	1	<1	<1	<1

It was not possible to measure sediment layers less than 1 mm thick. Jar bottoms were inspected under the dissecting microscope to determine the extent of sediment particles.

When sediment cover was less than 100%, patches without sediment were defined as "bare" surface to contrast them with sediment covered surfaces. Of course, these bare patches were actually covered with a biological film.

The planula settlement experiments were run for 10 days. The number of settled coral planulae was counted every day. Coral planulae can temporarily attach to hard surfaces using strands of mucus. This type of attachment is easily distinguished, and was not counted as settlement. Successful settlement was judged based on a flattening of larvae on the glass and initiation of primary corallite deposition. The experiment was repeated 3 times.

#### Antibiotic Tests: Philippines

Sedimentation experiments using adult coral colonies in aquaria were first carried out in Palawan without antibiotics. Oxypora glabra, a plate forming coral was found to be susceptible to sediment damage within 2 days, therefore it was chosen as a test species for the antibiotic experiments in Palawan. Antibiotic experiments were conducted later in Hawaii using other species.

Tetracycline, a broad-spectrum, water soluble antibiotic active against gram-negative and gram-positive bacteria, was chosen for these experiments. Tetracycline was tested by Barnes (1971, in Buddemeier and Kinzie, 1976) as a potential skeletal stain for coral growth studies and

found to be unsuitable. An initial test was made to determine if tetracycline alone has a deleterious effect on corals in aquaria. Coral colonies were collected from 3 m at the control reef (Site 8) and 4 colonies were placed in each aquarium. Aquaria were filled with seawater and a different amount of medical grade tetracycline powder was added to each to attain the concentrations 0, 1, 5, 10, and 100 mg/l. The corals were monitored for 7 days and changes in appearance noted. There was no visible effect on the corals except in the 100 mg/l treatment which produced a mean of  $30\% \pm 10\%$  tissue breakdown after 5 days. Based on results of this trial run, the concentrations 0, 1, 10, and 100 mg/l tetracycline were used in the sedimentation experiment with Oxypora glabra. Although 100 mg/l tetracycline in seawater damaged O. glabra, this concentration was included in case lower concentrations showed no effect on rate and extent of tissue necrosis. As in previous experiments, marine sediment collected from Site 5 was washed in freshwater and then dried. Fifty grams dried fine sediment were added to aquaria and vigorously stirred twice per day at 8:00 h and 18:00 h. Changes in color and integrity of the coral surface were recorded, and size of affected patches was measured. Colonies were photographed at the end of the experiment. The experiment was run twice.

### Antibiotic Tests: Hawaii

A second series of antibiotic tests was carried out in Hawaii using common Hawaiian coral species (Porites lobata, Pocillopora meandrina, Montipora verrucosa) collected from Kaneohe Bay, Oahu. The experiments were performed in 665 l black plastic tanks with concrete bottoms (area 9,500 cm<sup>2</sup>) at the Hawaii Institute of Marine Biology. Both M. verrucosa and P. lobata have a wide range of growth forms. For this experiment, plate-like forms were collected and broken into several pieces of about 100 to 200 cm<sup>2</sup>. Branch clusters of P. meandrina were broken from large colonies. Forty colonies of each species were required for each run; 10 colonies of each species were placed in each of 4 tanks. Tank 1 held untreated seawater, Tank 2 held tetracycline treated seawater, Tank 3 held tetracycline treated seawater with sediment and Tank 4 held seawater with sediment. Colonies were allowed to heal and adjust to tank conditions with flow-through seawater for 5 days, then the water was turned off, leaving an air stone to supply oxygen.

Medical grade tetracycline was added to treatment tanks achieving a concentration of 10 mg/l. Fine sediment was collected from a reef flat near Coconut Island and washed in freshwater. Three hundred grams (dry-weight) of sediment was added to each tank and stirred producing a concentration of 0.5 g/l and a deposition rate of 30 mg/cm<sup>2</sup>/day. The water was stirred to resuspend the

sediments once per day at 09:00 h. Every second day, one-half the water was siphoned from the top of each tank and replaced with fresh seawater. Additional tetracycline was added to maintain a constant concentration in treatment tanks. It is not known if tetracycline activity changes with time under the experimental conditions. Changes in the color and integrity of the coral surface were measured and recorded and colonies were photographed after 10 days. The experiment was run twice.

### Statistics

To determine if the results of sedimentation experiments were dependent on phenotype, tests of independence (also called tests of association; Sokal and Rohlf, 1981) were performed using Model II, 2 x 2 contingency tables. In these tests, the observed number of species with each phenotype that was damaged was compared with the expected number, and the observed number that was not damaged was likewise compared with the expected number. The null hypothesis was that the number of coral species that was damaged or undamaged was independent of phenotype. The expected number for each cell was calculated by multiplying observed row by column totals and dividing by the total number of species used in the experiment. The test statistic was calculated using Proc Fncat (SAS, 1985) and is approximately distributed as chi-square. The test



statistic was compared with the appropriate chi-square value with one degree of freedom.

## Results

### Sedimentation and Tissue Necrosis

Qualitative observations of sediment-coral interactions are important to an understanding of quantitative results. In the experiments, the shape and slope of the coral surface affected sediment deposition. When sediment fell on a coral colony, it tended to lodge on relatively flat or concave areas. Areas which were markedly convex such as pinnacles or thin branches did not generally accumulate sediment, even in calm water. In the absence of water currents, a sedimentation rate greater than the biological cleaning rate resulted in sediment buildup. Despite high suspended sediment loads, water currents in the field were able to prevent sediment build-up even on concave surfaces.

Following sediment deposition, the entire surface of a plate-like coral was normally covered with a thin layer of gray-brown sediment. Corals repeatedly cleared off sediment between stirring periods. If there was a thick layer of sediment, sediment was lodged in depressions, or the tissue was damaged, the colony was often not able to clear off the sediment. Each time sediment was resuspended by stirring, the coral surface was checked for tissue damage.

Inspection of 2:1 macrophotographs of damaged areas showed that the first sign of tissue damage was "bleaching" (loss of zooxanthellae) followed by extrusion of white mesenterial filaments. Coral tissue changed from firm and even in color to slimy and mottled, often with 1 mm diameter holes in the tissue. As necrosis progressed, tissue broke up into strands leaving bare white skeleton exposed. Sediment overlying damaged coral tissue changed color, becoming dark, grayish-black and gave off an odor of hydrogen sulfide. Inspection of borders of damaged patches under the dissecting microscope revealed a network of filaments had formed over damaged areas. When sediment was washed away from these patches the tissue necrosis was clearly visible. Patches of tissue necrosis slowly grew in size under the sediment layer. It is important to note that once started, patches of tissue necrosis were not contagious and did not spread to areas that, due to morphology were not covered by sediment, e.g. small convex knobs, unless the entire colony was near death. Not a single case was recorded of tissue necrosis originating from an edge of a broken coral fragment. Necrosis always began on a flat or concave sediment covered surface.

No experiments were conducted to test recovery of corals placed in clean water following sediment damage nor to determine when the colonies died. It is difficult to determine when a coral colony has completely died. Few

colonies survived after a large portion of their surface area (>80%) was damaged even if sedimentation was stopped and clean water was added.

#### Sedimentation Resistance Hierarchy: Aquaria

For each species that was damaged percent dead tissue (necrosis) and number of live colonies (of 4) were plotted against time in days (Figure 4.2). The plots were arranged in a sedimentation resistance hierarchy with the least resistant species (most quickly damaged) placed first. No control colonies showed any sign of damage.

The coral species were assigned to 3 categories based on degree of damage due to sedimentation. The "Mortality" category consists of species in which one or more of the four colonies tested died during the experiment. In Figure 4.2, the first 6 coral species beginning with Oxypora lacera belong to this category. The "Damage" category consists of the next 7 species beginning with Pavona decussata. These species suffered some tissue necrosis but no mortality. The last category consists of 10 species that showed no deleterious effects. Species in this "No Detectable Damage" category are listed in alphabetical order below: Euphyllia ancora, Favia speciosa, Galaxea fascicularis, Goniopora tenuidens, Millepora intricata, Pachyseris rugosa, Pectinia alvicornis, Pocillopora verrucosa, Trachyphyllia geoffryi, Turbinaria peltata.

### Mortality Category

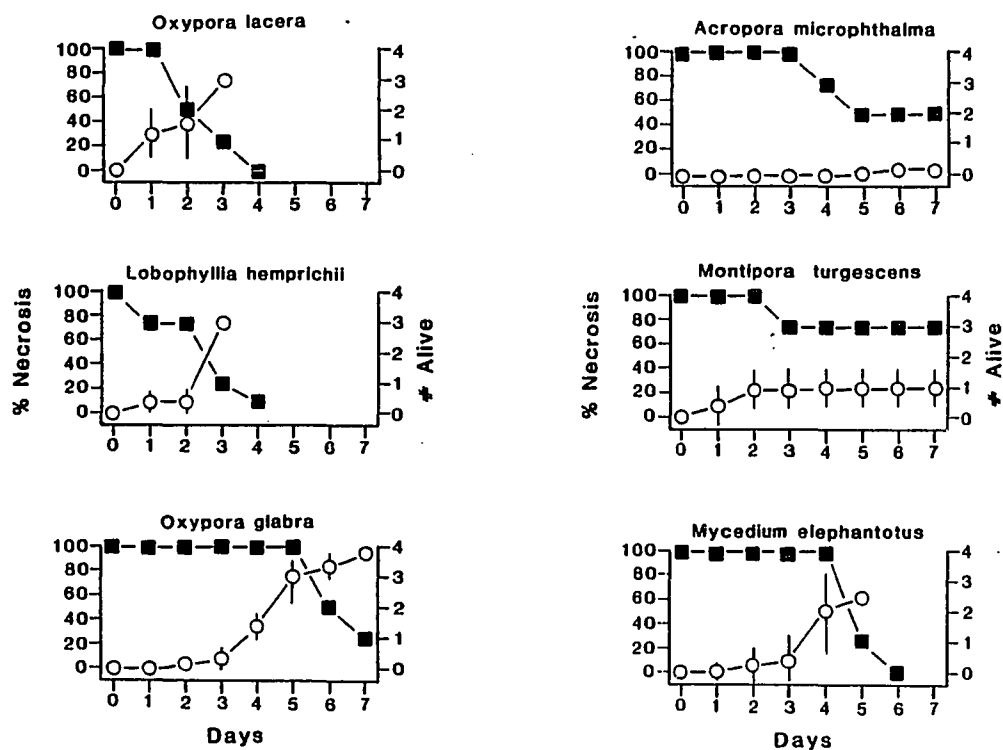


Figure 4.2 Plots of damage and mortality to colonies (n=4) of 13 coral species subjected to sedimentation in aquaria for 7 days. Necrosis = circles. Mortality = squares.

# Damage Category

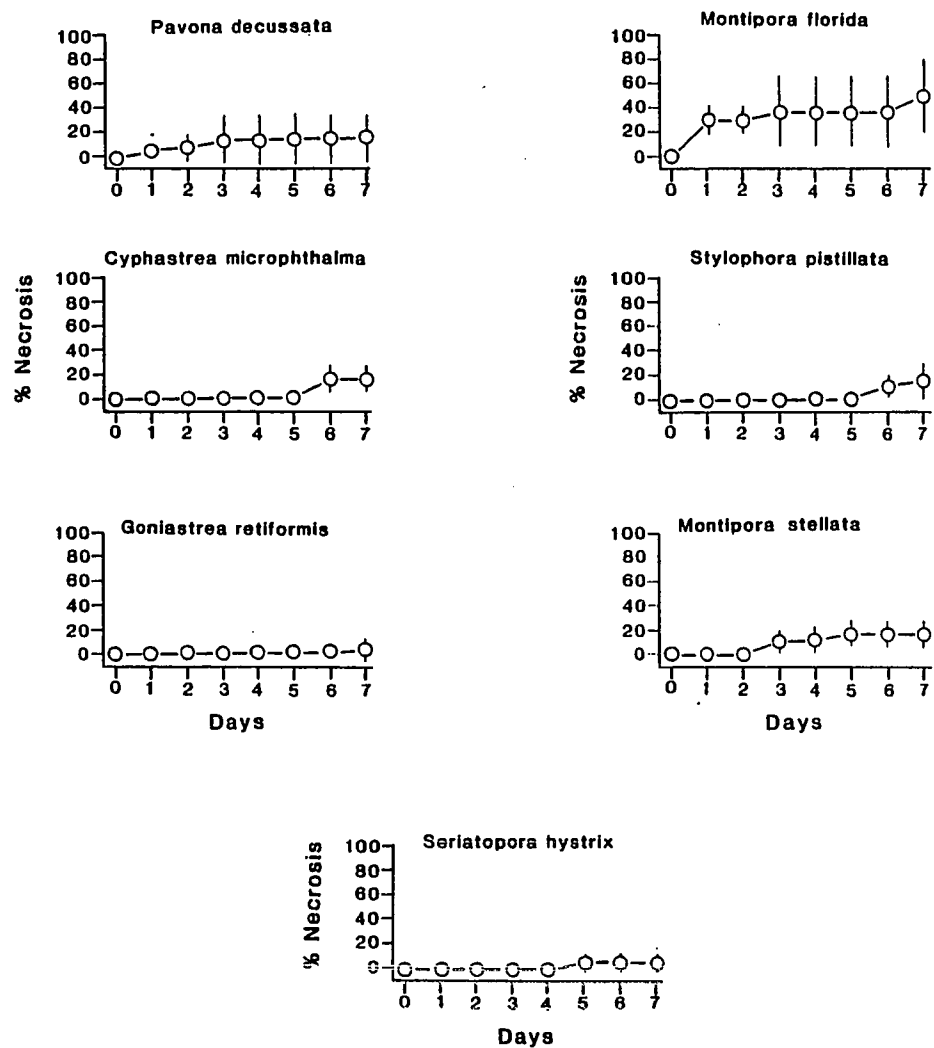


Figure 4.2 continued. Plots of damage to corals (n=4) subjected to sedimentation in aquaria. Necrosis = circles.

### Sedimentation Resistance Hierarchy: Field

For each species damaged in the field experiment, percent dead tissue and number of live colonies were plotted against time in weeks (Figure 4.3). The plots were arranged in a hierarchy with the least resistant species (most quickly damaged) placed first. No control colonies that were returned to the reef showed any sign of damage.

The species were divided into the same 3 categories as were used in the aquarium experiments except that the time scale was based on 17 weeks (120 days) instead of 7 days. The "Mortality" category consists of 7 species, all of which suffered some mortality during the 120 day experiment. The "Damage" category consists of 13 species all of which were damaged but did not suffer mortality during the 120 day experiment. Seventeen species showed no deleterious effects during the 120 day experiment and so belong to the "No Detectable Damage" category. These species are listed in alphabetical order below:

Acanthastrea echinata, Euphyllia ancora, Favia amicorum,  
Favia fava, Fungia echinata, Galaxea fascicularis,  
Goniastrea edwardsi, Goniopora tenuidens, Leptoseris yabei,  
Lobophyllia corymbosa, Pachyseris gemmae, Pavona cactus,  
Pectinia lactuca, Platygyra lamellina, Pocillopora verrucosa,  
Trachyphyllia geoffryi, Turbinaria peltata.

Eight species were used in both the aquarium and field experiments and so are found in both Figures 4.1 and 4.2

### Mortality Category

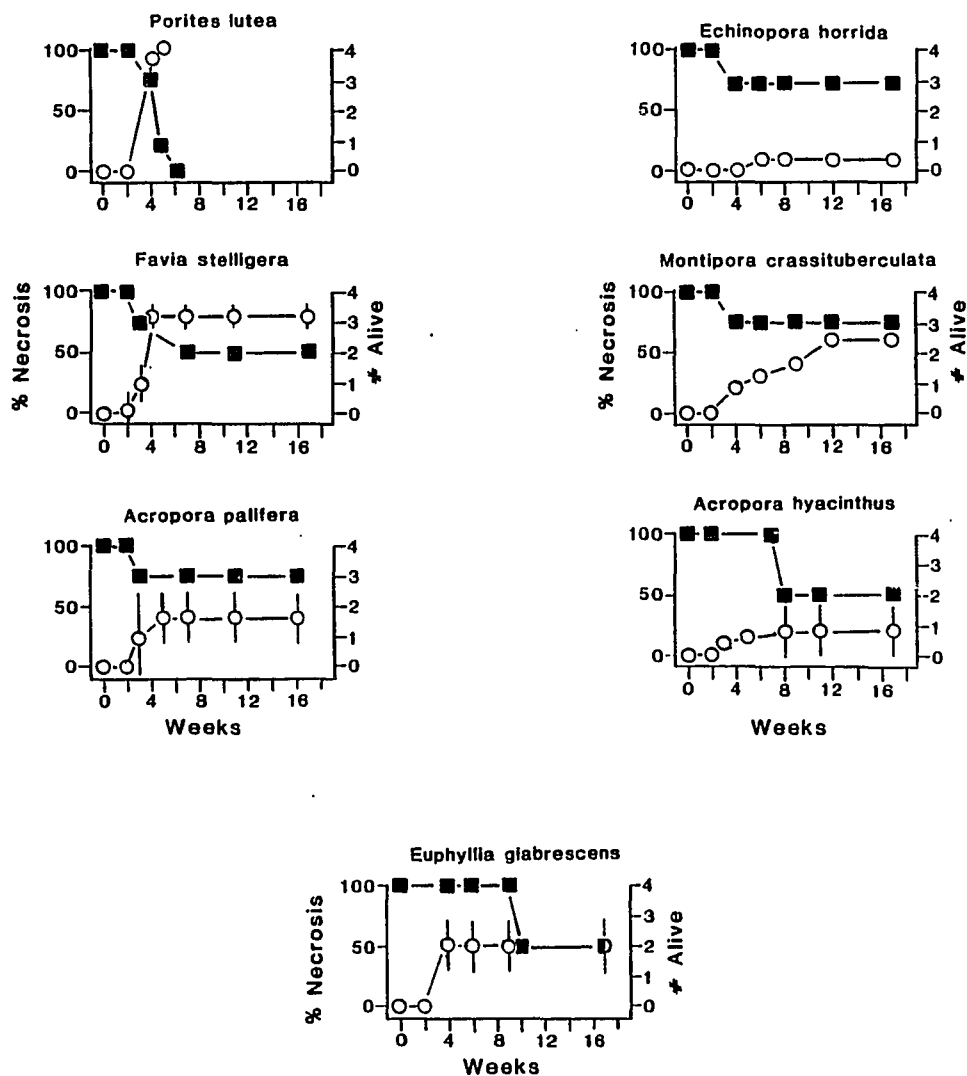


Figure 4.3 Plots of damage and mortality to colonies (n=4) of 20 coral species subjected to sedimentation in the field for 17 weeks. Necrosis = circles. Mortality = squares.

### Damage Category

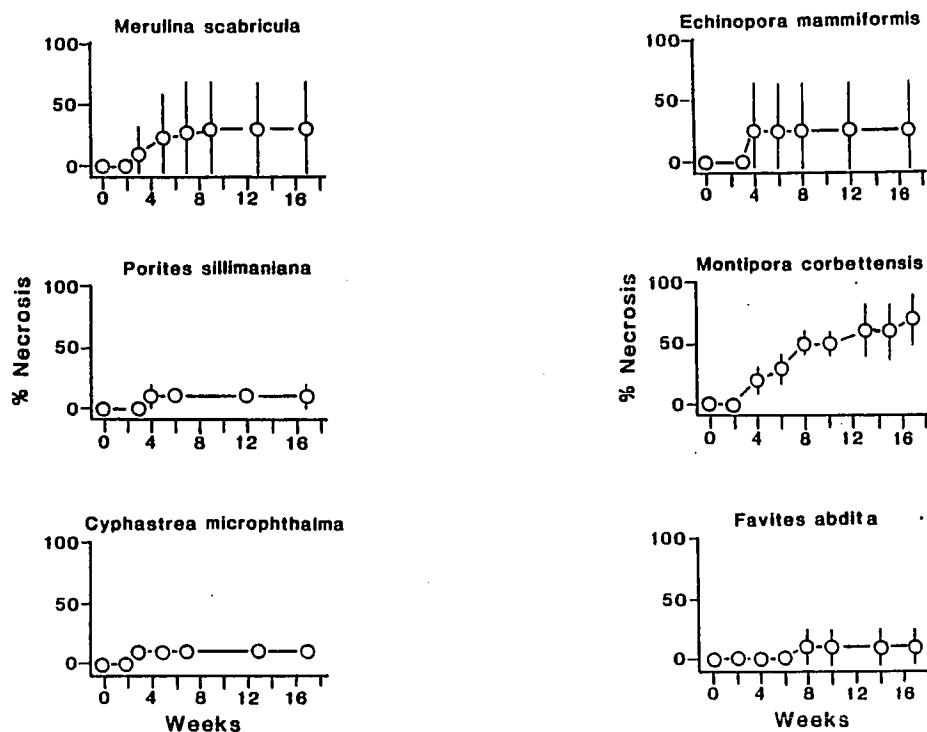


Figure 4.3 continued. Plots of damage and mortality to colonies (n=4) of 20 coral species subjected to sedimentation in the field for 17 weeks. Necrosis = circles.



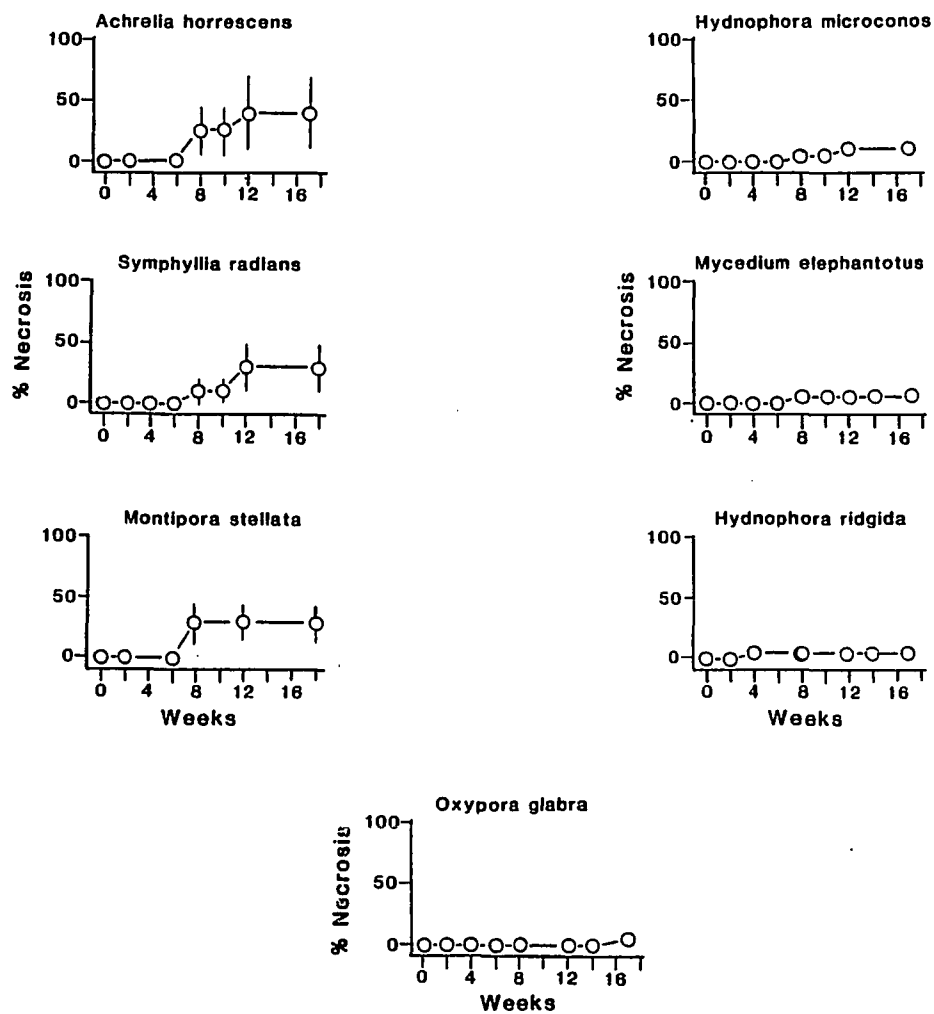


Figure 4.3 continued. Plots of damage and mortality to colonies (n=4) of 20 coral species subjected to sedimentation in the field for 17 weeks. Necrosis = circles.

and the above lists. The purpose of conducting both aquarium and field experiments was to determine if the sequence of events following sedimentation and ending in coral tissue necrosis was similar regardless of coral phenotype and under both field and aquarium conditions; i.e., that damage was not an aquarium effect. Since the primary purpose was not to investigate potential differences between field and aquarium results, it was not necessary to use all the same species in both experiments.

The sediment deposition rate used for the aquarium experiment (40 mg/cm/day) was about double that measured during the field experiment (20.8 mg/cm/day), however, the aquarium sediment was resuspended twice daily by stirring. This stirring may have given temporary relief to cleaning mechanisms but also may have distributed bacteria throughout the aquarium. Due to the protected location of the field experiment (Site 7) there was probably little current action to clean the colonies.

Damage to corals in aquaria occurred much faster than in the field. Two of the 8 coral species used in both experiments (Mycedium elephantotus and Oxypora glabra) had colonies that died at the higher rate of deposition used in the aquarium experiments, but not at the lower, field rate. Therefore these species were placed in the "Mortality" category in the aquarium hierarchy but the "Damage" category in the field hierarchy. There were no category

differences among the remaining 6 species used in both experiments i.e. each of the 6 species was placed in the same category, therefore the results of field and aquarium experiments were pooled for analysis.

The pooled data were arranged in contingency tables; 1 table for each of the 3 phenotypic characters (Table 4.1): corallite size-class (CD), growth form (GF) and polyp extensional ability (PEA).

In each contingency table, the columns were made up of observed and expected number of species with the specified character state, that were either damaged (or killed) or undamaged by sedimentation.

The results were analyzed first with respect to CD (small, medium and large; Table 4.3).

**Table 4.3** Contingency table of corallite size class versus resistance group with observed and expected cell values for N species with the specified characteristics. Test of independence of damage from corallite size ( $p < 0.02$ ).

Corallite Diameter	N	Damage Group			
		<u>Damage</u>		<u>No Damage</u>	
		Obs.	Exp.	Obs.	Exp.
Small	25	19	15	6	10
Medium	8	5	5	3	3
Large	17	5	10	12	7
Total	50	29	30	21	20

The test indicates a significant departure from expected cell values, therefore the null hypothesis that damage was independent of corallite diameter was rejected. Of 19 species that were damaged, fewer species with large CDs and more species with small CDs were damaged than expected. It appears that species having large CDs were the most resistant to sedimentation. Out of 17 species in the large CD class, 70% were not damaged. Species with a small CD were least resistant to sedimentation with 76% being damaged.

Next, results of the 2 sedimentation experiments were analyzed with respect to GF (plate, phaceloid [bushy, often composed of wide, trumpet-shaped branches of even height], ramose or massive; Table 4.4). Since GFs may vary intraspecifically, only GFs used in the experiments were considered here.

**Table 4.4** Contingency table of growth form versus resistance group. Cell numbers are observed and expected number of N species with the specified growth form. Test of independence of damage from growth form ( $p < 0.17$ ).

Growth Form	N	Damage Group			
		<u>Damage</u>		<u>No Damage</u>	
		Obs.	Exp.	Obs.	Exp.
Plate	16	9	9	7	7
Phaceloid	6	2	4	4	2
Ramose	12	10	7	2	5
Massive	16	8	9	8	7
Total	50	29	29	21	21

The test of independence was not significant, therefore the null hypothesis that damage was independent of growth form was not rejected. Although not statistically significant, the results for ramose GF may indicate a trend; 83% of ramose species were damaged compared with 56% of plate, 50% of massive and 33% of phaceloid species.

Patterns in susceptibility of corals to sedimentation damage were next analyzed with respect to PEA (high or low; Table 4.5). The test of independence indicates there were significant differences between observed and expected results. The null hypothesis that damage was independent of polyp extensional ability was rejected. Far fewer species with a high PEA were damaged (16%) than species with a low PEA (81%).

**Table 4.5** Contingency table of polyp extensional ability versus resistance group. Cell numbers are observed and expected number of N species with the specified extensional ability. Chi-square test using N ( $p < 0.0001$ ).

Polyp Extensional Ability	N	Damage Group			
		<u>Damage</u>		<u>No Damage</u>	
		Obs.	Exp.	Obs.	Exp.
High	18	3	10	15	8
Low	32	26	19	6	13
Total	50	29	29	21	21

Possible interaction among phenotypic characters and degree of damage can be assessed qualitatively, however,

statistical techniques such as categorical modelling (SAS, 1985) require a larger sample size per cell than was available and therefore were not used in this analysis. Statistical interaction between phenotypic characters is evident. For example, 9 of 11 small CD, low PEA, ramose species were damaged, but only 3 of 13 massive or phaceloid, large CD, high PEA species were damaged. The unequal sample for each phenotype combination, although reflecting nature, makes it difficult to separate possible influences of individual phenotypes on sedimentation resistance. Thus it is not possible to conclude from the tests of independence for CD, GF and PEA that, for example, small CD alone causes increased susceptibility to sedimentation damage. The phenotype combination for each species must be considered.

#### Sediment and Planula Settlement

Mean planula settlement was significantly higher in controls (no sediment) than in all treatments (Table 4.6;  $p < 0.05$ ). Over the 10 day period no planulae were able to settle when 95% or more of the jar-bottom was covered with fine sediment. Low settlement occurred in jars with 50 and 90% of the bottom covered. Although there was 40% less sediment cover in Treatment E than in Treatment D there was no significant increase in settlement.

Table 4.6 Results of planula settlement and sedimentation experiment. For Tukey test groups, means with different letters are significantly different ( $p < 0.05$ ) (3 runs with  $n=5$  jars per treatment and 20 planulae per jar).

Treatment	Sediment		Settled Planulae		Tukey Test Groups
	Thickness mm	Cover %	mean	s.d.	
A	2	100	0	0	A
B	1	100	0	0	A
C	<1	95	0	0	A
D	<1	90	0.9	0.7	AB
E	<1	50	1.1	0.7	B
Control	0	0	5.9	2.6	C

#### Antibiotic Tests: Philippines

The results of sediment trials with Oxypora glabra using tetracycline are presented in Figure 4.4. Colony mortality is indicated by 100% necrosis. Tetracycline alone showed no effect on Oxypora glabra coral tissue between 1 and 10 mg/l (final percent necrosis = 0%) at the 3 concentrations and so these data were not plotted. At a concentration of 100 mg/l tetracycline alone, 2% of the coral surface was damaged on day 5 and by day 7 tissue breakdown had reached 30%. The plot of tissue necrosis when sediment and 100 mg/l tetracycline were used together is similar to the results of 100 mg/l tetracycline without sediment. After 7 days, the two final percentages for the latter tests were not significantly different (t-test;

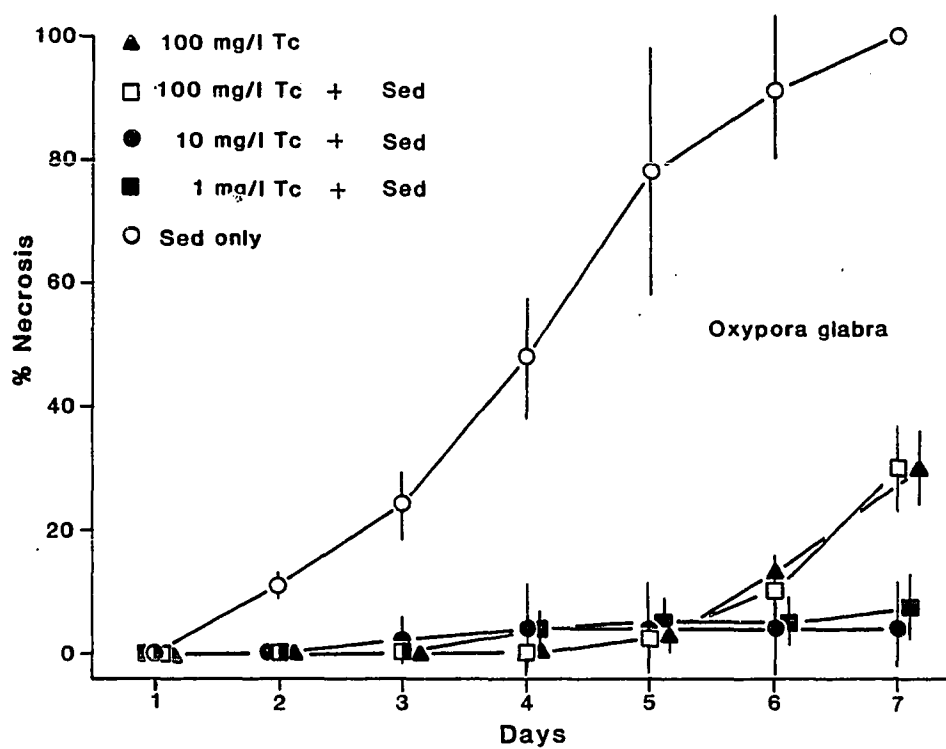


Figure 4.4 Mean percent tissue necrosis (n=8) on Oxypora glabra following exposure to the specified concentrations of sediment (sed) and tetracycline (Tc) for 7 days. Error bars are  $\pm 1$  standard deviation.



$p > 0.05$ ), but showed significantly greater damage than all other treatments except sediment without tetracycline (Tukey test of means;  $p < 0.05$ ). When sediment was added without tetracycline, all coral colonies developed patches of tissue necrosis by day 2, and all died within 7 days. After 7 days, tissue necrosis was significantly greater (100%) in the no tetracycline treatment than for all others ( $p < 0.05$ ; Tukey test). Mean percent damage in 1 and 10 mg/l tetracycline with sediment were not significantly different from 0% damage. The tetracycline clearly prevented colony death for 7 days at all 3 concentrations.

#### Antibiotic Tests: Hawaii

No corals exhibited tissue damage or partial mortality following exposure to 10 mg/l tetracycline treatment for 10 days (Figure 4.5). Porites lobata colonies appeared to have slightly more mucus on their surface in the tetracycline treatment than in plain seawater. Montipora verrucosa was not damaged by either sedimentation alone or sedimentation with tetracycline. For both Porites lobata and Pocillopora meandrina, mean percentage damaged area with the sediment only treatment was significantly greater than percent damaged area for both the sediment with tetracycline treatment and controls (plain seawater and tetracycline treated seawater; t-test;  $p < 0.05$ ). For P. lobata and P. meandrina, the results of the tetracycline plus sediment

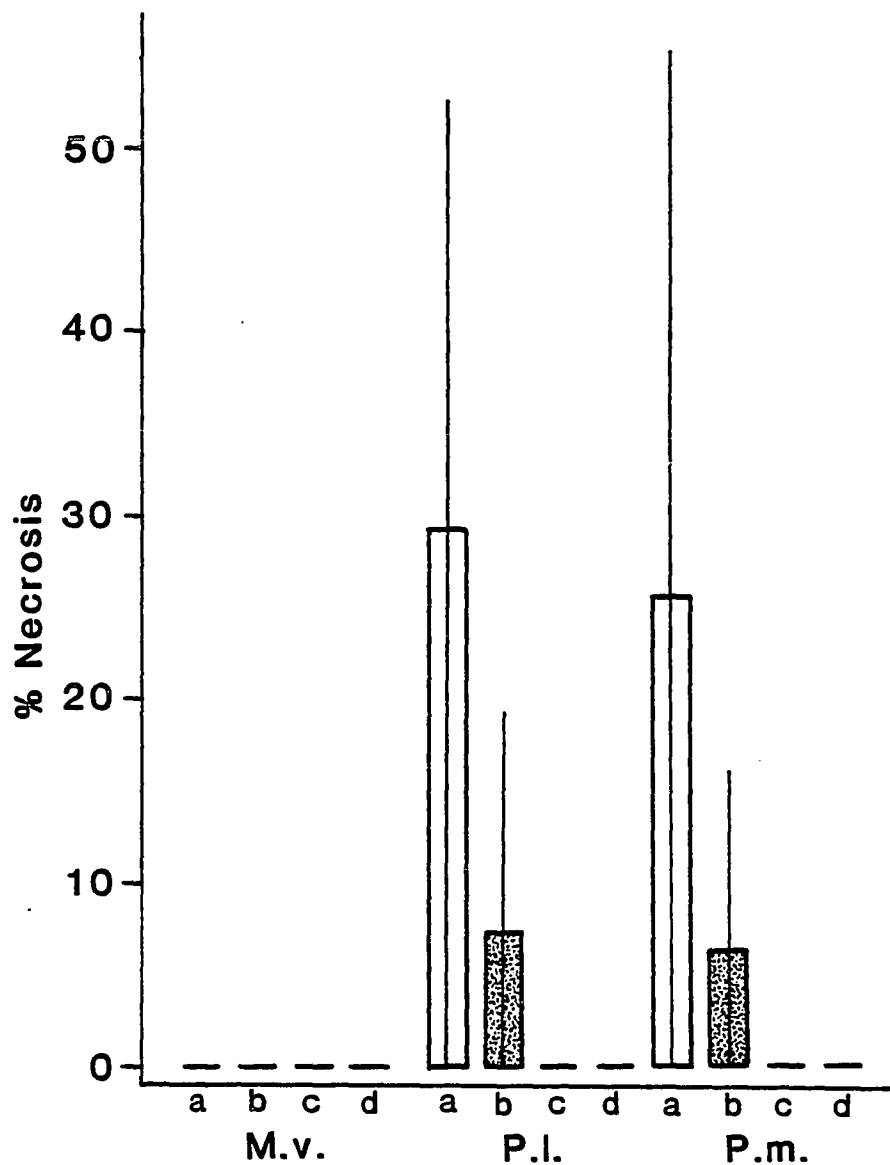


Figure 4.5 Mean percent necrosis of Montipora verrucosa (M.v.), Porites lobata (P.l.), and Pocillopora meandrina (P.m.) colonies (n=30 per treatment) following exposure to combinations of tetracycline and sediment: a = sediment, b = sediment and tetracycline, c = seawater, d = seawater and tetracycline.

treatment were not significantly different from the control (t-test;  $p > 0.05$ ). No test corals were killed by this level of sediment deposition.

Patches of coral tissue necrosis caused by sediment deposition were compared with live healthy tissue using the scanning electron microscope at 20,000 magnification. Many bacteria (rods and cocci) were photographed on all patches but there was no significant difference in number of bacteria between healthy and necrotic tissue (t-test).

### Discussion

Observations of corals subjected to sedimentation in aquaria and the field, as well as previous studies (e.g., Marshall and Orr, 1931; Hubbard and Pocock, 1972; Dyer, 1986) indicate that sediment deposition is affected by physical and biological factors. Physical factors include sediment characteristics, concentration and fall velocity of sediment particles, and geometry of the coral colony surface. In addition, sediment deposits are physically removed by water currents and biological processes described earlier. Clearly, if the deposition rate exceeds the rate of removal, sediment build-up will occur.

Results of sedimentation experiments in the field and in aquaria indicated that a sediment layer was required before tissue necrosis began. That is, no colonies that continuously cleared their surfaces were visibly damaged.

Other potential deleterious effects such as reduced energy levels and reproductive output were not assessed.

The sedimentation experiments provided insight into two questions:

- 1) How does sediment deposition damage corals?
- 2) What coral phenotypes appear to be associated with interspecific differences in sedimentation resistance?

#### Sedimentation, Tissue Necrosis and Microorganisms

Sedimentation experiments with and without tetracycline demonstrated that tetracycline-sensitive microorganisms, presumably bacteria, increased the rate of coral tissue damage and mortality due to sediment deposition. The fact that tissue necrosis only occurred in areas directly underlying sediment deposits and did not occur at the edges of recently broken fragments indicated that initiation of necrosis was dependent on the sediment matrix. This suggests there would be little difference when using colony "fragments" or "whole" colonies for experiments. In addition, since percentage tissue necrosis of Oxypora glabra after 7 days of sedimentation in 1 and 10 mg/l tetracycline treated seawater was not significantly different from 0%, it is possible that sediment deposition in the absence of tetracycline-sensitive microorganisms may not be particularly harmful to some coral species over this time interval.

Although the sequence of deterioration of coral tissue and changes in the sediment layer were indistinguishable in the field and in aquaria, the rate of tissue damage in aquaria was much faster than the field rate. For Oxypora glabra, sedimentation damage in aquaria began after 2 to 5 days and death occurred within 1 week. In contrast, O. glabra colonies in the field began to show damage after 14 weeks and there was no mortality. One explanation for this disparity is that the higher sedimentation rate in aquaria ( $40 \text{ mg/cm}^2/\text{d}$ ) was above the tolerance threshold for this species whereas the field rate ( $20 \text{ mg/cm}^2/\text{d}$ ) was not. Alternatively, it is possible that some factor associated with aquaria enhanced damage rates. One potential cause of an aquarium effect was twice daily stirring which could have distributed bacteria, reduced water quality and increased the rate of infection. Water changes may have been insufficient to counteract these possible effects. Therefore it is not known if the reduced sedimentation damage rate associated with tetracycline treated seawater shown in aquaria would also occur in the field using  $40 \text{ mg/cm}^2/\text{d}$  sedimentation. In the field, wind-induced stirring would presumably move sediments and associated microbes away from the coral.

The results of the tetracycline experiments complement those of Mitchell and Chet (1975) who found that the antibiotics penicillin and streptomycin prevented coral

tissue damage to Platygyra sp. by toxic levels of 3 pollutants: copper, oil and dextrose. Without antibiotics and following addition of the 3 toxic substances, bacterial populations in coral mucus increased rapidly. Low oxidation-reduction potential (100 mV) and zero dissolved oxygen level were measured at the coral surface after 24 h and the corals died within 8 days. Two bacteria associated with coral mucus were Beggiatoa and Desulfovibrio. Although aquarium effects could have altered these results, they suggest that bacteria may kill corals in concert with toxic substances at a rate similar to that found in the sedimentation experiments. In addition, other organisms such as protozoans, viruses, fungi or mycoplasmas could damage corals.

The results using antibiotics generate questions concerning the mechanism of coral necrosis following sedimentation. For example, what is the origin of microorganisms involved? Do bacteria breed rapidly in the sediment matrix using coral mucus as a food source? Does low dissolved oxygen, hydrogen sulfide or some other bacterial product kill the tissue? Is there a sequential succession of microorganisms that take part in the tissue necrosis process? The organisms inhabiting coral mucus and the sediment layer need to be cultured and characterized before these questions can be fully addressed.

Bacteria are ubiquitous in the marine environment and

bacterial production rates on coral reefs have been measured in the water column (Moriarty et al., 1985a), in sediments (Sorokin, 1973, 1978; Burns et al., 1984; Moriarty et al., 1985b) and in coral mucus (Paul et al., 1986). Bacteria involved in coral tissue necrosis following sediment deposition could come from any or all of these sources.

Purified coral mucus is low in caloric value (3.95 - 5.2 cal/mg dry weight) and in Funaria scutaria has a lipid:protein:carbohydrate ratio of approximately 3:35:62, and contains at least 17 amino acids (Krupp, 1982). Ducklow and Mitchell (1979) found that Vibrio alginolyticus comprised 20-30% of the bacterial community residing in Porites astreoides mucus. In addition, Mitchell and Chet (1975), found many gram negative rods in coral mucus, 50% of which showed positive chemotaxis to it. The bacteria could apparently survive using coral mucus as a sole carbon and nitrogen source.

Some evidence suggests that sediment, especially after forming a depositional layer, may stimulate population growth of pathogenic bacteria that are benign at low densities. When bacteria and sediment are mixed in seawater, chemical and physical forces cause microbial adhesion to sediment particles (Egan, 1987). A number of studies have suggested respiration and reproduction increase once microorganisms become attached to sediment

particles (Egan, 1987). When sediment particles have formed a macroscopic deposition layer, rapid microbial population growth leads to development of irreversibly bound biofilms (Egan, 1987). In this way, sediment may provide a substrate for increased activity and population growth that can lead to successful invasion of host tissues.

The physiological response of corals to infection by microorganisms has not been studied in detail. Burkholder and Burkholder (1958), tested antimicrobial activity of gorgonian and scleractinian extracts. Several species of gorgonians showed high antimicrobial activity while none of the scleractinia tested (Acropora palmata, Porites porites, and Montastrea sp. [all Caribbean species]) showed detectable antimicrobial activity.

In the present study, one coral species (Montipora verrucosa) exhibited a high resistance to tissue damage following sediment deposition. During field surveys in Hawaii many M. verrucosa colonies were observed with substantial sediment accumulations that appeared to have remained in place for several weeks, apparently without causing tissue damage. Montipora verrucosa may possess biological resistance to infection by microbes or some other biological or physical factor which prevents tissue damage. In contrast to the conclusions of Hubbard and Pocock (1972), these results imply that sediment clearing



efficiency may play a smaller role in the ability of some corals to resist sedimentation damage; i.e. some corals may rely mainly on cleansing water currents and physiological resistance to infection to survive sedimentation.

An alternative to the hypothesis that tetracycline sensitive bacteria caused tissue damage following sedimentation is that some toxic substance carried by sediment damaged coral tissue, and was followed by bacterial invasion. If the El Nido or Hawaiian sediments contained a toxic substance, the results of antibiotic experiments demonstrated that corals normally damaged by sedimentation survived without damage under a sediment layer for periods of several days when tetracycline was present. This evidence along with that of Mitchell and Chet (1975) is not consistent with the alternative, toxic substance hypothesis. This does not rule out the possibility that toxic substances are involved in sedimentation damage to corals in other areas.

Common toxic substances found in natural soils include heavy metals. A manganese mine has reportedly been planned for the Bacuit Bay drainage basin therefore it is of interest to consider the possible effects of heavy metal pollution on corals. Bacuit Bay sediments from the 3 sites closest to the river mouth (Sites 5, 6 and 7) were tested for one heavy metal, manganese, and it ranged from 24 to 53 ppm (mean 38; S.D. 9).

Evidence suggests that even sediments containing large quantities of heavy metals will not necessarily release them to seawater. For example, sediments collected from Los Angeles Harbor, California contained between 380 and 500 ppm of manganese (Chen et al., 1976), a high contamination level. In laboratory tests of these sediments, release to seawater of copper, iron, chromium, silver, cadmium, manganese, nickel, lead, zinc, and mercury was relatively independent of sediment type and over several days ranged from 0.001 to 0.02 ppm, a million-fold below the level reported to damage corals (Howard and Brown (1984). Metals are usually tightly bound to sediments and physico-chemical equilibria favor stability of those bonds over a wide range of redox potentials and pH (Gambrel et al., 1976).

Uptake of heavy metals by corals exposed to tin-mining and smelting effluent has been studied by Brown and Holley (1982) and Brown and Howard (1985b). They no found difference in skeletal or tissue heavy metal concentrations in corals exposed to effluent versus corals from a pristine environment and concluded that corals appear to regulate and reduce heavy metal uptake. Based on this assessment, it appears that sediments would have to contain unusually high concentrations of loosely bound heavy metals to allow sufficient release in seawater to cause tissue necrosis in corals following sedimentation.

### Sedimentation Resistance Hierarchy

One problem with interpreting comparative data among species is that related species may not be statistically independent due to phylogenetic inertia (shared traits among related taxa; Ridley, 1983) (Clutton-Brock and Harvey, 1984; Felsenstein, 1985). It has been suggested that certain traits may be preserved when interactions among them greatly increase fitness; natural selection should favor harmonious evolution (coadaptation) of those traits (Dobzhansky, 1955; Mayr, 1963; Huey and Bennett, 1987). Felsenstein's (1985) transformation method has been used to account for differences in inter-species distance when phylogenies are known (Sessions and Larson, 1987). When a phylogeny is not known, as is the case with coral species, higher taxonomic levels have been used to reduce the probability of non-independence (Craig, 1987). Two of the coral characters used here (growth form and corallite diameter) are primary taxonomic traits used to distinguish genera, therefore variation in CD and GF within genera should be small compared to variation among genera. Fossil evidence suggests many Indo-Pacific coral genera have shown little phenotypic change for the past several million years (Veron and Kelly, 1988). If coral taxonomy is a true reflection of coral phylogeny then it is likely that the assumption of independence among genera is not violated. The sample size used for the sedimentation tests was too

small to restrict analysis to the generic level, however, 32 of the 50 species were from different genera. For coral community analysis (Chapter 5), a large sample size allowed statistical tests to be performed at the generic level.

Marshall and Orr (1931) conducted sedimentation experiments and concluded that large-polyped species are better at surviving sedimentation than small-polyped species unless the latter are finely branched. The results of the present study are in agreement, and further indicate that large CD, and protrudable polyps are the most resistant phenotypes to sediment damage; corals with small CD, and a low PEA showed a medium to low resistance level.

To assess the effect of unequal sample size on statistical analyses, the number of species of each phenotype combination was listed in Table 4.7. Clearly there are large differences in sample size among phenotype combinations. Although these differences may reflect the abundance distribution of phenotypes in nature, they create problems in interpreting results. For example, Echinopora horrida, the 1 low PEA, medium CD, ramose species was damaged, but all other ramose species tested had low PEA and small CD, therefore it was not possible to separate effects of ramose growth form from the 2 other characters. Only differences between the synergistic effects of each growth form with the low PEA/small CD combination that can be compared. In this comparison among low PEA/small CD

Table 4.7 Number of species with each phenotype combination used in sedimentation experiments. PEA=polyp extensional ability, CD=corallite diameter

PEA/CD	Growth Form				Total
	Ramose	Massive	Phaceloid	Plate	
low/small	11	5	0	9	25
low/medium	1	1	0	3	5
low/large	0	1	0	1	2
hi/small	0	0	0	0	0
hi/medium	0	2	0	1	3
hi/large	0	6	5	4	15
Total	12	15	5	18	50

species, 9 of 11 ramose, 5 of 5 massive and 5 of 9 plate species were damaged.

No data are available on high PEA/small CD species, and data for phaceloid GF are inadequate for comparison except across the high PEA/large CD row. In this comparison there was little difference as 5 of 6 massive, 3 of 5 phaceloid and 4 of 4 plate species were not damaged.

Using 2 massive species (Montastrea cavernosa and M. annularis) Foster (1983) has shown that corallite shape may be independent of colony shape within species. But among species growth form, corallite diameter and polyp size are not necessarily independent. Since 75% of ramose corals are acroporids, most ramose corals have small

corallites and polyps characteristic of the 2 most speciose acroporid genera, Montipora and Acropora. In contrast, most phaceloid species have large corallites and polyps. There are only a few species with both small diameter corallites and polyps with a high extensional ability, e.g. Goniopora spp., and these were not tested.

There is a wide degree of intrageneric and intrafamilial difference in sedimentation resistance which appears to be related in part to variation in phenotype. There is little evidence to support the idea that sedimentation resistance has evolved along supra-specific phylogenetic lineages. For example, within the Family Acroporidae, encrusting, plate, foliaceous, ramose, columnar and massive growth forms are represented. Within the family Poritidae, species of the genera Goniopora and Alveopora have the highest polyp extensional abilities of all Scleractinia, whereas species of the genus Porites have limited polyp extension capabilities.

In cases where there is a similar level of sedimentation resistance along phylogenetic lines, the resistance mechanisms may not be the same. Although 9 out of 10 species of the suborder Astrocoeniina were damaged by sedimentation (refer to Figure 1.2 and Table 4.1), they include a diverse array of phenotypes. In contrast, 4 out of 5 species of the family Agariciidae and 5 of 8 Faviidae were not damaged. Although currently classified in

separate suborders, the latter two families share a common Triassic ancestor in the suborder Fungiina whereas the Astrocoeniina are isolated in a separate lineage. The Agariciidae and Faviidae show a great deal of phenotypic divergence. The former are characterized by plate or foliaceous growth forms and tiny polyps while the Faviidae are generally massive corals with large highly protrusile polyps.

#### Possible Advantages of Certain Phenotypes

The possible advantages of sedimentation resistant phenotypes are now considered. A coral with wide diameter corallites will always have wide diameter polyps. Lateral distension of polyps and tentacles helps to prevent sedimentation damage by physical blocking of the intercalicinal (between polyp) surface and by allowing tentacular movement and polyp expansion to complement other sediment removal mechanisms (Marshall and Orr, 1931). Corals with small polyps and large intercalicinal spaces must rely primarily on ciliary movement for sediment clearing (Yonge, 1930), and this is particularly inefficient for sand-sized particles (Hubbard and Pocock, 1972).

The small polyps and large intercalicinal areas characteristic of Montipora and Acropora species may explain the susceptibility of the ramose species tested to

sedimentation damage. In contrast, several ramose Acropora and Montipora, e.g. M. ramosa and A. pulchra are common on reefs exposed to apparently high sedimentation rates (Hopley and Woessik, 1988; pers. obs.). The ability of these species to withstand sedimentation may depend a great deal on the level of water motion (Parnrong and Chansang, 1986). Interspecific differences in physiological resistance to infection could allow species with poor sediment rejection mechanisms such as Montipora verrucosa in Hawaii to survive.

Corals with protrudable polyps possess an additional clearing mechanism; polyps and tentacles can actively or passively sweep the colony surface, therefore they would be expected to be less susceptible to sedimentation damage than corals without this capability.

#### Exceptions to Phenotype-Sedimentation Hypothesis

Insight may be gained by considering exceptions to the observed pattern of phenotype-sediment damage resistance and the natural history of individual species. The first exceptions considered are those with ostensibly "sediment resistant phenotypes" that suffered mortality during the experiments. For example, Lobophyllia hemprichii is a phaceloid species with very large, protrudable polyps, and yet all colonies were rapidly killed following sedimentation in aquaria while control colonies in aquaria



showed no deleterious effects. Corals such as Lobophyllia spp. have a large amount of tissue which probably has a high absolute oxygen demand. When sediment is added to seawater, oxidation can significantly reduce available dissolved oxygen (DO) depending on the ratio of sediment to seawater (Chen et al., 1976). Although relatively little sediment was added to aquaria, the Lobophyllia colonies used were the largest among all species tested. Oxygen level in aquaria was not monitored, therefore it is not known if low DO was a factor in the rapid demise of L. hemprichii. A phenotypically similar species (L. corymbosa) was not damaged in the field sedimentation experiment. It is not known why another phaceloid species with much longer tentacles, Euphyllia glabrescens, suffered mortality during the field experiment.

The second group of species considered are those with ostensibly "low resistance phenotypes" but which showed no damage during the experiments. Millepora intricata, a common reef-building (and zooxanthellae containing) hydrozoan was one such species. The growth form of M. intricata is composed of slender (2-4 mm), smooth, flat branches. Thin, hair-like polyps (dactylozooids and gastrozooids) extend above the skeletal surface (Boschma, 1956). During the experiments sediment particles easily slid off the smooth branches and never formed the sediment layer apparently necessary for initiation of necrosis.

The results for 4 agariciid species, Pachyseris rugosa, P. gemmea, Pavona cactus and Leptoseris yabae were puzzling. Although both Pachyseris species form thin plates and apparently lack polyps (Veron, 1986), sediment was rapidly removed from their surfaces and neither species was damaged in the experiments. Pavona cactus forms small thin leaves, and Leptoseris yabei forms thick plates with cup-like corallites. Both species have tiny polyps, yet were undamaged in the field experiment. In nature, the 3 plate forming species are often found growing on near-vertical walls where they are not affected by sediment deposition, but they also colonize horizontal surfaces where sediment deposition might be rapid. For these species it appears that ciliary motion is the only active sediment clearing mechanism and yet it is apparently sufficient to clear their relatively smooth surfaces. In the sedimentation experiments, coral plates were oriented in the growth position they were found in. For Pavona, the 45° angle of rest of its thin folia allowed some sediment deposition. A highly efficient ciliary clearing mechanism combined with a smooth surface may partially explain the lack of damage to the 3 other species (Yonge, 1930).

Some foliose corals such as Pectinia spp. and ramose corals such as Pocillopora verrucosa are able to clear sediment by taking in water and expanding their entire epidermis in slow waves, similar to sediment clearing by

Fungia spp. (Abe, 1939; Schuhmacher, 1979), however, the 4 agariciids do not possess this capability. P. verrucosa polyps have a fast retraction mechanism (Yonge, 1930) which may aid in clearing sediment. The two mechanisms help explain the lack of damage to P. verrucosa despite small polyps and a ramose growth form.

#### Previous work

Most previous work cannot be compared directly with these results for the following reasons: only 1 or 2 growth forms or polyp sizes were tested (Mayor, 1924; Kolehmainen, 1974; Rogers, 1977, 1983; Lasker, 1980; Parnrong and Chansang, 1986); an environmentally unrealistic sedimentation rate, especially complete burial, was used (Mayer, 1918; Edmondson, 1928; Marshall and Orr, 1931; Rice, 1985); or experiments focused on the sediment rejection ability of corals rather than measuring damage to coral tissue (Marshall and Orr, 1931; Hubbard and Pocock, 1972; Hubbard, 1973; Bak and Elgershuizen, 1976). Additional complicating factors that prevent a direct comparison with results of sedimentation experiments conducted in the field by Mayor (1924) and Marshall and Orr (1931) are salinities as low as 0.93 ppt in the former case and strong wave action in shallow water in the latter.

Limited data from 4 studies of Caribbean and Indo-Pacific corals were compared with the present results with

reference to corallite size, polyp extensional ability and growth form (Table 4.8). Although the sample size was only 12 species, tests of independence were significant for corallite size ( $p < 0.02$ ) and polyp extensional ability ( $p < 0.02$ ). Although all ramose corals were damaged, the growth form test was not significant ( $p > 0.24$ ). The tests support the hypothesis that large, protrusile polyps are

**Table 4.8** Results of previous sedimentation experiments that are comparable with the present study. Corallite diameter: S = small, M = medium, L = large, Growth form (ma=massive, ra=ramose, pl=plate). D = Damage, and M = colony mortality occurred; D/M = both occurred.

Species	Corallite Diameter (mm)	Growth Form	Extensional Ability	Damage/Mortality
<u>Indo-Pacific</u>				
<i>Porites lutea</i>	S	ma	Low	D/M <sup>1</sup>
<i>Acropora formosa</i>	S	ra	Low	D/M <sup>1</sup>
<i>Pocillopora damicornis</i>	S	ra	Low	D/M <sup>1</sup>
<u>Caribbean</u>				
<i>Agaricia agaricites</i>	S	pl	Low	D/M <sup>2</sup>
<i>Diploria strigosa</i>	L	ma	High	none <sup>3</sup>
<i>Diploria strigosa</i>	L	ma	High	none <sup>5</sup>
<i>Montastrea annularis</i>	M	ma	High	D <sup>3</sup>
<i>Acropora palmata</i>	S	ra	Low	D/M <sup>3</sup>
<i>Acropora cervicornis</i>	S	ra	Low	D <sup>3</sup>
<i>Diploria clivosa</i>	L	ma	High	D <sup>4</sup>
<i>Siderastrea siderea</i>	S	ma	Low	D <sup>5</sup>
<i>Montastrea cavernosa</i>	L	ma	High	none <sup>5</sup>

<sup>1</sup>Parnrong and Chansang, 1986; mud 10 mg/l (8 mg/cm<sup>2</sup>/d) with current, no stirring. <sup>2</sup>Rogers, 1977; mud 5 mm layer, current. <sup>3</sup>Rogers, 1983; coarse calcareous sand, 400 mg/cm<sup>2</sup> applied once, in situ. <sup>4</sup>Rogers, 1983; coarse calcareous sand, 200 mg/cm/day, in situ. <sup>5</sup>Kolehmainen, 1974; mud, 1.5 mm layer.

the most resistant to sediment damage. Of 7 corals with small corallites, all were damaged while only 1 out of 4 corals with large corallites was damaged. High extensional ability was associated with no damage and low extensional ability with damage. These results agree with those from tests of Philippine and Hawaiian corals.

### Partial Mortality

Some reef flat corals survive death of parts of their colony (partial mortality); e.g., upper portions of reef flat corals may be exposed and killed during low tides, forming micro-atolls (Marshall and Orr, 1931). Schuhmacher (1979) reported that following sedimentation damage, some Fungia spp. are capable of forming anthocauli (reproductive buds) from tiny remaining patches of living tissue. The ability to survive partial mortality may be an important competitive life-history strategy (Hughes and Jackson, 1985; Wallace, 1985; Willis and Ayre, 1985) and may alter a coral sedimentation resistance hierarchy. Certain growth forms have been noted for their ability to withstand partial mortality. For example, stands of arborescent Acropora commonly live in areas where the base of each colony is buried under sediment and dies (pers. obs.). It appears that this ability to withstand partial mortality allows arborescent Acropora to survive in areas with deep shifting sediments.

Colony morphology may allow sediment build up in certain areas while gravity keeps the rest of the corallum clean. For example, some foliaceous corals form a bowl shape, open on one side, that only collects sediment inside and at the bottom of the bowl. Like the Acropora, if such species can survive death of their lower regions, sediment clearing ability may be relatively unimportant. Differences in the ability of coral species to withstand partial mortality could reduce the predictive value of a sedimentation resistance hierarchy constructed based on tests of small coral fragments rather than tests using whole colonies in the growth position.

#### Sediment Effects on Larvae

Sediment could potentially affect either adult or larval corals. A factor that may modify the predictive value of a sedimentation resistance hierarchy with respect to community structure is the role larvae play in settlement site selection. Evidence suggests that coral planulae may be able to "assess" the quality of potential settlement sites (Harrigan, 1972). Inhibition of settlement of Pocillopora planulae due to presence of fine sediment, even when bare space was available, could indicate either a direct or indirect response to sediment. A possible direct effect of sediment is that planulae cannot attach to fine grains as suggested by Harrigan (1972). Indirect

alternative causes of settlement inhibition include presence of compounds released by sediment into seawater. Regardless of the specific cause, if planulae of many species behave in a similar fashion, sedimentation at a level that is not directly harmful to adult colonies could have a significant negative impact on larval recruitment by inhibiting settlement. Exceptions may include coral species with larvae that preferentially settle in relatively wave-washed environments. Since water motion reduces sediment deposition, sedimentation may exert little selective pressure on such species and they may lack adaptations for surviving sediment deposition. Results of this study suggest the need to test the effects of sediment on settlement of a wide variety of coral larvae.

### Conclusions

Experimental results indicated that sedimentation caused coral tissue necrosis and that onset of necrosis depended on there being a layer of sediment on coral tissue. Corals exposed to sediment deposition of  $40 \text{ mg/cm}^2/\text{day}$  for 7 days in aquaria or  $20.8 \text{ mg/cm}^2/\text{day}$  for 120 days in the field were categorized based on the level of susceptibility to damage. Of 22 species tested in aquaria, 6 suffered tissue damage and mortality, 7 suffered tissue damage, and 9 did not incur visible damage. Of 36 species tested in the field, 7 suffered tissue damage and

mortality, 12 experienced tissue damage, and 17 were not damaged.

Species that were damaged were ranked according to the rate at which damage occurred and the final outcome. The effect of sedimentation on 6 of 8 species tested both in aquaria and the field was the same in the 2 experiments. The remaining 2 species showed only tissue damage after exposure to the field rate, but suffered mortality in aquarium tests. Based on the appearance in macro-photographs of coral tissue following sediment deposition, the process whereby coral tissue was progressively damaged and eventually killed appeared to be the same in aquaria and in the field, however, damage progressed much more slowly in the field. Minimum time to first mortality in the high sedimentation aquarium tests was 2 days while in lower sedimentation field tests it was 12 days. The accelerated rate of tissue damage in aquaria in comparison to the field rate may have been caused by the higher deposition rate in aquaria or by factors such as poor water quality and increased bacterial populations.

Tetracycline in seawater (1 to 10 mg/l) significantly decreased tissue damage and enhanced survival of corals subjected to sedimentation for up to 10 days in aquaria. Tetracycline-sensitive microbes, presumably bacteria, appear to be a causative factor of coral tissue damage and mortality following sediment deposition in aquaria. The



specific initial cause(s) of tissue necrosis, e.g. reduced oxygen, enzymatic attack by bacteria or hydrogen sulfide poisoning remains unknown.

One coral species (Montipora verrucosa) exhibited a high resistance to tissue damage following sediment deposition, perhaps as a result of physiological resistance to infection by microbes. For species that can survive partial mortality, sediment clearing ability may not always be important.

The extent of sedimentation damage to corals appears to be related to phenotype. Species with large, protrusile polyps were less likely to be damaged by sedimentation than species with small, non-extendable polyps. Colony growth form is important in determining the initial deposition pattern of sediment on the coral surface. In nature, this depends a great deal on the orientation of the colony with respect to gravity and water motion. In calm water, a plate colony growing on a vertical wall will accumulate much less sediment than a plate colony growing over horizontal substrate. But the interaction of certain phenotypes may mask or enhance the effect of others. For example, a coral with tiny polyps and thin branches initially may accumulate less sediment than a plate coral growing horizontally, but might eventually incur greater damage due to a limited ability of the small polyps to remove the sediment. The small sample size of phenotype combinations

such as large CD, ramose GF and high PEA precluded reaching conclusions regarding susceptibility in relation to growth form. Of the phenotypic variables analyzed, polyp extensional ability appeared to be the best and growth form the least accurate predictor of damage from sedimentation. Reevaluation of previous studies on 12 Indo-Pacific and Caribbean corals was in agreement with these results.

Chance and many environmental variables other than sedimentation may affect the evolution of phenotype. Despite these possible influences, a demonstrated association between corallite diameter, polyp extensional ability and sediment tolerance allows predictions to be made concerning what phenotypes and species should be common in high sedimentation environments. There is little evidence to support the idea that sedimentation resistance has evolved along supra-specific phylogenetic lineages.

Settlement of Pocillopora damicornis planulae was reduced by presence of fine sediment even when it covered only half the available substrate. Settlement was completely inhibited by a layer of sediment covering 95% of the bottom. If larvae of many species of corals exhibit a similar settlement inhibition in the presence of sediment, then sediment deposition at a much lower rate than required to damage adult corals might significantly reduce planula settlement and coral recruitment in nature.

## V. SEDIMENTATION AND CORAL COMMUNITY STRUCTURE

The purpose of this chapter is to investigate whether interspecific differences in susceptibility of corals to sedimentation damage are reflected in coral community structure. The working hypothesis was that sediment deposition on some Bacuit Bay reefs in 1986 would be greater than previous exposure levels due to increased sediment discharge resulting from logging of the Bacuit Bay drainage basin. The expected increase in sedimentation was to be measured and used as an experimental treatment at affected sites.

Since there were many potential causes of coral damage and mortality besides sedimentation, it was important to identify them and monitor their effects. High waves are known to physically break down coral reefs (Stoddart, 1974). Low temperature and salinity are other potential causes of coral mortality. The lower limit of temperature tolerance for reef corals has been reported to be 18 °C (Wells, 1956) and 16 °C (Ma, 1959). Only a few of the Pacific or Atlantic species tested can withstand exposure to 16-17 ppt salinity for 24 h (Mayer, 1918; Vaughan, 1916; Edmondson, 1928; Wells, 1957). Four Hawaiian species lived for 3 months in seawater with 22 ppt salinity (Edmondson, 1928). A salinity of about 20 ppt may be near the tolerance threshold for some coral species (Marcus and Thorhaug, 1982). Exposure time may be an important factor.

Verwey (1930, 1931) suggested that light limitation could limit coral growth. In Edmondson's (1928) light exclusion experiments in Hawaii, coral mortality did not begin until between 18 and 45 days depending on the species. Rogers (1977) showed that the compensation point for zooxanthellar production at reefs in Puerto Rico is between 430 to 510 microeinsteins/m<sup>2</sup>-sec. In experiments there, photosynthetically active radiation was completely excluded by covering a reef section with a black plastic channel. Although this treatment also reduced water circulation (a potential deleterious side-effect), 3 weeks passed before the most susceptible corals (Acropora cervicornis) lost zooxanthellae (bleached), and it was 6 weeks until they suffered partial mortality. Palawan is approximately 7° closer to the equator than Puerto Rico so should receive a higher level of solar radiation if each location has a similar cloud cover.

A few coral diseases and a wide variety of coral predators have been described (see reviews by Robertson, 1970; Reese, 1977, 1981; Antonius, 1982 and Brown, 1987). An invertebrate predator that could potentially consume a large amount of coral within one year is the crown-of-thorns starfish (Acanthaster planci) (Randall, 1973; Colgan, 1987). Most invertebrates e.g Drupella spp. characteristically graze on small portions of many colonies rather than continuously grazing on a single colony until

it is killed (Moyer et al., 1982; pers. obs.). Intensive fish predation produces a characteristic "chewed-up" appearance of colonies (Cox, 1986) so can be easily identified.

It is not possible to discount activity of unknown coral diseases in reducing coral cover but the two known coral diseases are visually distinct (Antonius, 1982).

Since there were no quantitative data available on pre-logging sedimentation rates in the bay, the rates measured in 1986 at treatment sites were compared with the rate at a control reef (Site 8). At Site 5, the closest site to the river outlet, sedimentation was significantly higher than at the control site and above the rate shown to damage some corals. Increased sedimentation was predicted to damage and kill susceptible coral colonies resulting in measurable changes in the coral community.

Based on the results of sedimentation experiments (Chapter 4) it was predicted that abundance of corals with a small corallite diameter (CD) and a low polyp extensional ability (PEA) would be reduced on reefs exposed to relatively high levels of sedimentation in comparison to a control reef with a relatively low sedimentation level. The increased sedimentation at Bacuit Bay reefs provided a test of this phenotype-sediment tolerance hypothesis. In order to test this hypothesis, 8 study reefs exposed to different levels of sedimentation in Bacuit Bay, Palawan

were surveyed to assess changes in coral community structure during 1986. Survey methods are presented following a brief review of work in this area.

#### Previous Work: Sedimentation and Community Structure

The results of sedimentation tolerance experiments have been interpreted to indicate that interspecific differences in corals, especially growth form, mediate the effect of sediment on corals (Vaughan, 1916; Edmondson, 1928; Mayer, 1918; Marshall and Orr, 1931; Yonge, 1930). In nature, sedimentation may be chronic, such as the daily, low-level sedimentation found in some atoll lagoons (Roy and Smith, 1971), or acute such as sedimentation resulting from high river discharge events of a few days duration are reported to have killed corals over large areas of reef (Mayor, 1924; Banner, 1968).

Numerous studies have provided observations on the correlation of increased suspended or deposited sediment with reduced coral growth rates, coral species diversity and cover (Roy and Smith, 1971; Maragos, 1972; Loya, 1976; Bak, 1978; Randall and Birkeland, 1978; Liew and Hoare, 1979; Chansang et al., 1982; Aliño, 1983; Cortes and Risk, 1985; Grigg, 1985; Hubbard and Scaturo, 1985; Kuhlman, 1985; Muzik, 1985; Hubbard, 1987). In contrast, Glynn and Stewart (1973) found no correlation between these factors on reefs off the Pacific coast of Panama.

Despite correlative and experimental evidence indicating that sedimentation damages corals, coral reefs can be seen throughout the tropics living in what appears to be turbid water (pers. obs.) with, presumably, high sediment deposition. This suggests that some coral species or possibly certain morphotypes may be adapted to such environments. Perhaps partly because work in highly turbid waters is difficult due to restricted underwater visibility, there have been few studies of reefs exposed to high chronic natural sedimentation such as is reported for reefs off the northeast coast of Australia (Hopley and Woesik, 1988).

The predictive value of most previous work is limited by attempts to infer effects of sedimentation on corals based on limited turbidity or suspended sediment load data and by a lack of accurate measurement of sediment deposition rate over at least one year to account for seasonal variability. In addition, there has been little effort to collect coral community structure data before and after sedimentation for comparison.

#### Turbidity and Sediment Deposition

Turbidity is an optical property. Since fine suspended sediments scatter light and remain in suspension for long periods (Ekern, 1976) the sediment deposition rate in highly turbid waters may be quite low. Unless it is high

enough to significantly block light or reduce salinity, turbidity per se may not damage corals. Roy and Smith (1971) drew attention to the fact that many coral species can and do flourish in water that appears turbid.

#### What Is A High Sedimentation Rate For Corals?

Loya (1976) defined a "high" sedimentation rate as 15 mg/cm<sup>2</sup>/day and a "low" rate as 3 mg/cm<sup>2</sup>/day for reefs in Puerto Rico. Low coral cover and diversity were associated with reefs exposed to the "high" sediment deposition rate. In contrast, a "high" sediment deposition rate on reefs in Guam was defined as 160-200 mg/cm<sup>2</sup>/day and was predicted to limit coral cover and diversity (<10 species, <2% coral cover; Randall and Birkeland, 1978). A "low" rate was defined as 32 mg/cm<sup>2</sup>/day and was predicted to be associated with rich coral communities (>100 species, >12% coral cover). This comparison highlights the relative nature of sedimentation rates; the rate considered "low" in Guam is more than double the "high" rate from Puerto Rico.

There are several reasons for the disparity in definitions of relative sediment deposition rates with respect to reef corals. In addition to a lack of standardized methodology for measuring sediment deposition, it is likely that differences in environmental factors, especially water motion and sediment characteristics, mitigate or enhance the deleterious effects of



sedimentation on coral diversity and cover reported from Guam and Puerto Rico. Direct comparison of the effects on corals of sedimentation rates in the absence of complete information on other important environmental factors could lead to misinterpretation. Clearly, careful definition of both methodology and important environmental parameters is required when reporting sedimentation data.

### Physiological Adaptation

Coral taxonomists have noted that colonies collected from high sedimentation biotopes often have characteristic morphologies (Veron, 1986). For example, in high sedimentation environments ramose species may develop fine branches and plocoid (adjacent corallite walls not joined) species may show greater distance between corallites than in low sedimentation environments. Although no studies have been made, it seems possible that in addition to morphological adaptation, some species may be able to physiologically adapt to different levels of sedimentation. If true, then a species adapted to pristine conditions ( $<1 \text{ mg/cm}^2/\text{day}$ ), might be damaged by a short-term 400% increase in deposition rate to  $4 \text{ mg/cm}^2/\text{day}$ . Colonies of this same hypothetical species that are physiologically adapted; e.g., by enhanced mucus production or increased numbers of cilia, to a "moderate" sedimentation environment, say  $5 \text{ mg/cm}^2/\text{day}$ , might be able

to tolerate a 400% increase to 20 mg/cm<sup>2</sup>/day.

To more accurately define "high" and "low" sedimentation rates it would be useful to consider potential physiological adaptation of corals with respect to their history of exposure to sedimentation. As noted, these are relative terms. The corals found living near river outlets in Guam (Randall and Birkeland, 1978) apparently survived high sediment inputs (>160 mg/cm<sup>2</sup>/day), and are thus resistant to this level of sedimentation. In contrast, many corals considered "sedimentation resistant" at reefs in Puerto Rico, where the "high" rate was only 15 mg/cm<sup>2</sup>/day, would probably be reclassified as "susceptible to sediment damage" if suddenly exposed to the higher Guam rate. But given time and a slow increase in sedimentation, some species might be able to adapt to the higher rate.

#### Potential Damage to Bacuit Bay Corals

Predictions derived from results of sedimentation tolerance tests of 50 coral species provided the basis for evaluating coral community structure in Bacuit Bay with respect to sedimentation levels monitored during 1986.

Clearly it is necessary to quantify what "high" and "low" sedimentation rates were with respect to the 8 reef sites in Bacuit Bay in order to test hypotheses regarding sedimentation effects on corals there. This also allows

comparison of the effects of sedimentation on coral community structure in Bacuit Bay with previous work on this topic in other regions. The lowest sedimentation rate tested that damaged Bacuit Bay corals was the monthly rate measured during the field tests. When calculated on a mean daily basis this rate was  $20 \text{ mg/cm}^2/\text{day}$ . It is not known if rates lower than this would be damaging to some Bacuit Bay corals. For the purpose of the study, any sedimentation rate equal to or greater than  $20 \text{ mg/cm}^2/\text{day}$  was considered to be potentially damaging to Bacuit Bay reef corals.

Although no "treatment" was carried out, Sites 1-7 will be referred to as sedimentation treatment sites to distinguish them from the control site (8). Monthly sedimentation at the control site (8) was similar to that at undisturbed reefs in the Pacific and Caribbean (Hubbard, 1987) and was not affected by sediment plumes in 1986 (Chapter 3). In contrast, a high sedimentation rate was measured at Site 5 and examination of daily peak sediment discharge from the Manlag River revealed that repeated sediment pulses lasting for several days and resulting in high sediment deposition could have occurred at any of the treatment sites (1-7) between October 1 and December 31, 1986 (Chapter 3). It is likely that high sedimentation rates during peak discharge pulses would damage some corals after just a few days.

### Methods

Two surveys, one in January and one in December, 1986, measured changes in the coral community at 8 sites over a 1 year period. Potential wave damage was assessed by observing corals underwater at each site during and after the most severe storm of the year. Two other potential causes of coral mortality, low temperature and salinity, were monitored during high river discharge periods to determine the distribution of river water (Chapter 3). The extent of light reduction underwater by sediment plumes was qualitatively monitored, and predation by vertebrate and invertebrate coralivores was recorded.

Coral reef survey techniques commonly employ quadrats or transects. The technique of surveying multiple transects laid out in parallel across the reef (e.g. Loya, 1972; Ross and Hodgson, 1982) is widely accepted. A primary consideration in transect placement was to control for depth because of the reported effects of depth on sedimentation rate (Wood-Jones, 1912; Vaughan, 1916; Liew and Hoare, 1979; Ohde *et al.*, 1982). In Bacuit Bay, the combination of a steep sedimentation gradient with depth and narrow reefs at Sites 1, 5, 6 and 7 precluded the use of multiple parallel transects.

Preliminary surveys of the study reefs indicated that 3 m was the best depth to place transects in order to obtain the largest sample of living corals at each reef

site. If 2 transects were placed in parallel on either side of the 3 m depth contour and close enough to experience a similar sedimentation regimen, they both passed over the same large colonies. In order to avoid double-counting coral colonies (which would produce non-independent data) and to control for depth, five 10 m transects were placed end-to-end forming one 50 m long line following the 3 m depth contour.

Total transect length was restricted to 50 m due to the short length of reefs at Sites 1 and 5. Colored nylon twine (3 mm diameter) was used as transect line. Five, contiguous, 10 m long transects were tied to the reef substrate parallel to the reef face at each of the 8 sites (refer to Figures 1.4 and 1.5, Chapter 1). The degree of exposure of each reef can be evaluated by referring to wave height data (Chapter 3).

The coral reef transects were first surveyed between December 25, 1985 and January 5, 1986 and then again 1 year later between December 20 and 30, 1986. Using a ruler, each section of substratum underlying a transect line was measured to the nearest centimeter to obtain a "chord-intercept" (Loya, 1972) and identified. Descriptions of the substrate classes used are listed in Table 5.1. The sand, sand/mud and mud categories are qualitative only and do not necessarily correspond to the quantitative categories presented in Chapter 3.

Table 5.1 Definitions of substrate categories

Category name	Definition
<u>Hard Coral</u>	
Live	Living colonies
Recently killed	Bare white skeleton, little or no growth of colonizers.
Old dead	Intact but dead, covered with much algal or other growth, no white skeleton showing.
Coral rubble	Dead coral reduced to fist and finger-sized fragments.
<u>Sediments</u>	
Sand	Individual grains visible to unaided eye predominant.
Sand/Mud	Grains visible to unaided eye $\approx$ 50%.
Mud	Grains visible to unaided eye rare.
<u>Other</u>	
Algae	All macroalgae except coralline algae.
Coralline algae	
Sponge	
Tunicate	
Soft coral	
Sea Anemone	
Gorgonian	

In areas where a transect line became elevated above the substrate, a pointed weight attached to the end of a 2 m long string was dropped to ascertain what substrate was lying directly under the transect. Horizontal measurements (Ross and Hodgson, 1982) were not necessary due to the absence of undercut or overhanging ledges.

If a live coral was encountered, colony length and width were obtained in addition to chord-intercept length (Loya, 1972). Almost all colonies have a tendency to form an oblong or ovoid shape. Colony length was defined as the longest axis of the oval/oblong and width as the axis perpendicular to the length. Colony size (area) was estimated using the equation:  $\pi(\text{length}/2)(\text{width}/2)$ . If an area of living coral was separated completely from surrounding coral tissue by a dead zone (e.g. skeleton), it was considered a separate colony. In large patches of ramose coral, each colony was carefully inspected to assess individuality. The area enclosed by and including each colony's branches was used to obtain colony size measurements.

Axes of dead patches (partial mortality) on individual colonies were also measured with a ruler and the size of each patch was calculated in the same manner as for colony size. Cumulative area of all patches on each affected colony was recorded as a percentage of total surface area.

Each coral measured was identified to species level following the taxonomic interpretations of Veron and Hodgson (in press). For corals with questionable identifications, samples were collected at the end of the study for microscopic examination.

To compare the distribution of colonies among phenotypes, genera were assigned to the GF, CD and PEA classes used in the sedimentation resistance experiments (GF ramose, phaceloid, massive, plate; CD large, medium, small; PEA high, low; Chapter 4). In most cases this classification was clear due to conservation of characters between congeners and could be accomplished based on species' characteristics. For example, although branching pattern is highly variable, all of the approximately 100 Indo-Pacific Acropora species are ramose and have small corallites. Two common genera, Montipora and Porites, are difficult to classify in this manner. Montipora species have a wide range of growth forms. Therefore this genus cannot be placed in a single GF category, but it is easily classified with respect to CD and PEA. Like Acropora, all Montipora have a small CD and low PEA. Porites is another common genus that has both ramose and massive species. On the Bacuit Bay transects, massive Porites spp. such as P. lobata, P. australiaensis and P. lutea made up 81% of Porites cover on reefs, therefore Porites was placed in the "massive" category. Since the one ramose Porites



tested was more resistant than the massive species (Chapter 4), the massive category may be biased slightly towards higher resistance due to this classification.

Species diversity is composed of 2 components; the number of species -- usually called "richness", and the abundance distribution of individuals (or percent cover) among species -- often called "evenness". Two indices were used to quantify species diversity. The Shannon index  $H'$  (Shannon, 1948) was chosen as a simultaneous measure of both diversity components where:

$$H' = \sum -p_i (\ln p_i)$$

$$p_i = n_i/N$$

$H'$  is often calculated using abundance, in which case  $n_i$  = number of individuals of each species and  $N$  = total number of individuals of all species sampled. Due to a large difference in the size of coral colonies, the combined area occupied by all colonies of a particular species may not correspond to the relative abundance of that species. To avoid this problem, a second method of calculating  $H'$  can be used that substitutes the area of each species for abundance ( $H'$ ). For large samples,  $H'$  based on abundance is not significantly different from  $H'$  calculated from cover (Loya, 1972). For the Bacuit Bay case, where many species were rare, it was more accurate to calculate  $H'$  using coral cover where:  $n_i$  = cover of a each species and  $N$  = total cover of all species sampled.

The Fager evenness index, F (Fager, 1972), was chosen to represent the second component of diversity. This index is the standard deviation of the abundance distribution of individuals among species, scaled to sample size. The equations for the Fager index are:

$$F = (\text{maximum S.D.} - \text{observed S.D.}) / \text{maximum S.D.}$$

where maximum S.D. =  $N - S/\sqrt{S}$

N = number of individuals

S = number of species.

### Statistics

Following checks for normality, data were log-transformed if necessary and statistical analyses of coral community changes during 1986 were carried out using 2-way (site X date) analysis of variance (anova). For each parameter, the difference between January and December values was used to test the control Site (8) against the treatment Sites (1-7) as a group (Proc GLM with contrast; SAS, 1985) and individually (Tukey test; SAS, 1985). Unplanned t-tests using Sidak's critical values of Student's t-distribution to limit Type I error to  $p < 0.1$  (Sokal and Rohlf, 1981) were used to test for significance of within-site changes in mean value of coral diversity and cover parameters at each reef site. The mean values of community parameters for 5 transects at each site were used for these statistical comparisons.

## Results

Wide patches of fragile ramose Montipora were common on study reefs, but did not appear to be damaged during the largest storm. Wave energy was probably dissipated when waves broke at the reef front where more sturdy corals predominated. After the storm no piles of coral rubble and freshly broken fragments normally associated with damaging wave action (Orme, 1977; pers. obs.) were seen. No wave damaged corals were observed.

Temperature reduction (minimum 26 °C; Chapter 3) was not low enough to damage corals because this was within the seasonal range for Bacuit Bay (26-32 °C). Periods of low salinity (19 - 25 ppt) measured at Sites 3, 4 and 7 during high river discharge events could have injured some corals living near the surface if exposed for several hours. Low salinity measured near the surface (Chapter 3) may not have reached corals at 3 m where the transects were located. Frequent underwater observations made during high river discharge periods indicated that the line of visible refractive difference associated with low salinity water did not extend beneath 1 m depth. Occasional tests of salinity below 1 m confirmed that salinity reduction was not detectable there. In addition, rainstorms that caused high river discharge were usually associated with windy weather conditions. These conditions caused mixing of plume water with bay water such that reduced salinity at

the surface was not detectable after a few hours.

Since light levels were not measured underwater at reefs in Bacuit Bay, it is not known if high turbidity plumes reduced photosynthetically active radiation below the zooxanthellar compensation point. Observations of surface sediment plume dynamics in 1986 indicated that they did not remain intact for more than a few days at Site 5, the site most exposed to sediment plumes because of its proximity to the Manlag River outlet. Surface plumes remained intact for less time at other sites.

Although common in some parts of the Philippines (pers. obs.), only 2 Acanthaster sea stars were seen in Bacuit Bay in 1986 and neither were near the study sites. Although colonies showing evidence of fish predation (e.g. missing branch tips and scrape marks) were common, heavily damaged colonies were not observed. Other invertebrate and vertebrate predators were active at Bacuit Bay reefs but did not produce any large scale damage. The two known coral diseases were not common in Bacuit Bay in 1986.

#### Changes in substrate composition

The composition of reef substrate at 3 m depth at each site in January and December 1986 is shown in Figure 5.1. With the exception of soft coral, all members of the "other" substrate category (see Table 5.1 for substrate definitions) were pooled for analysis since none

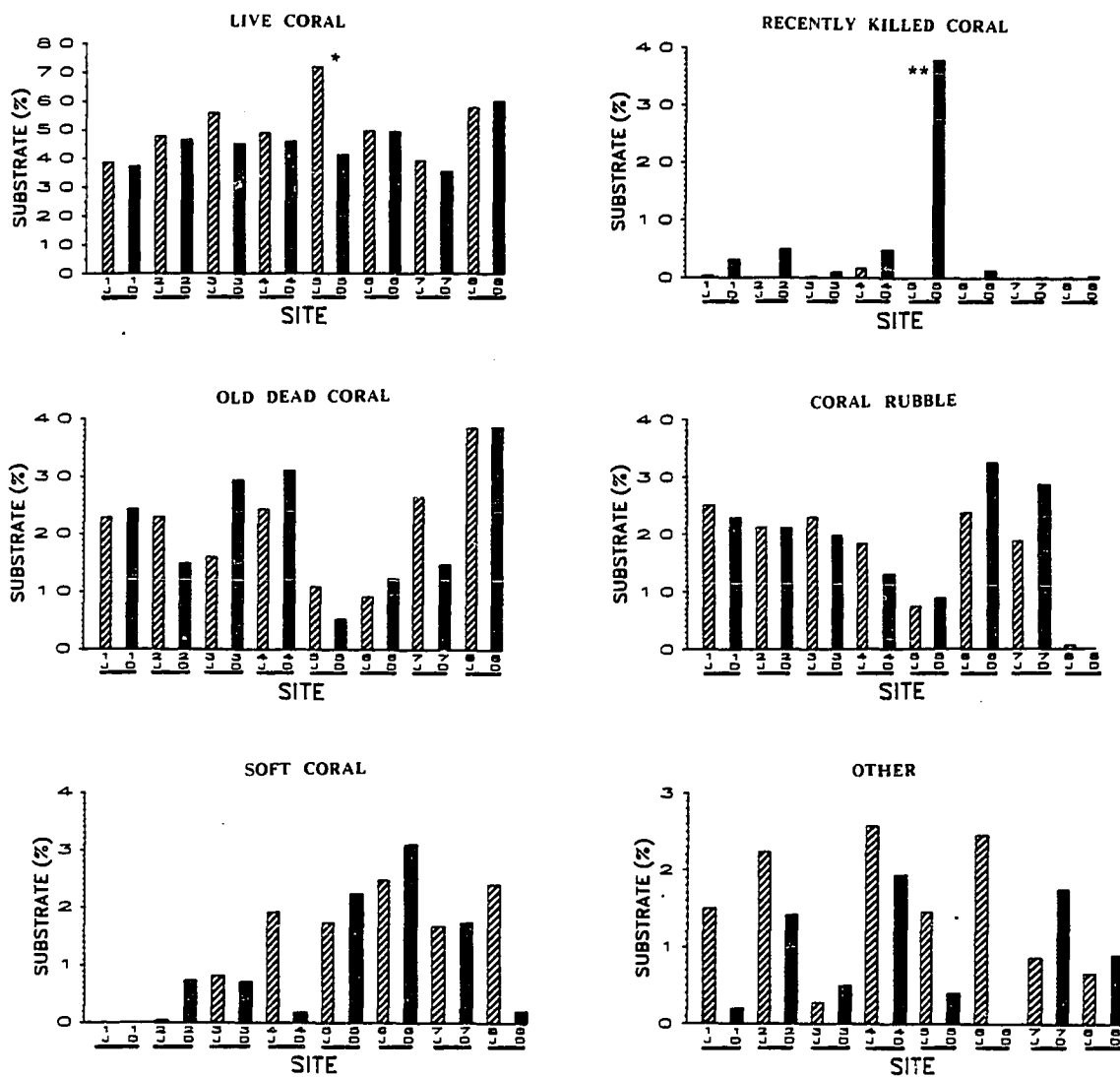
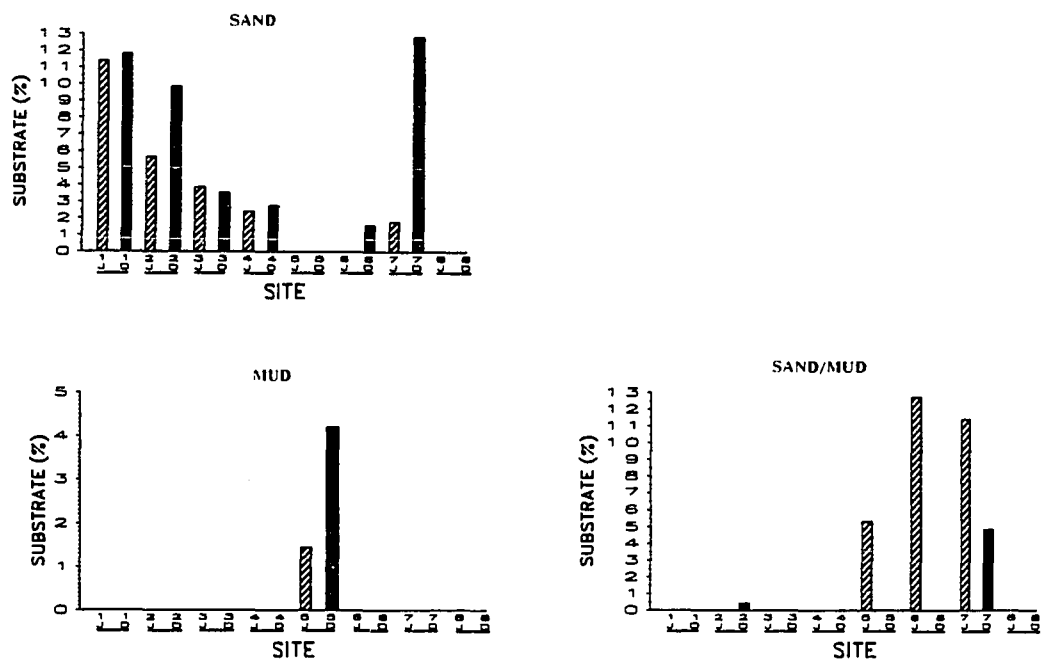


Figure 5.1 Mean percentage cover of each substrate category at each site (n=5, 10 m transects). 1J=Site 1 in January, 1D=Site 1 in December, etc. Several growth form categories were combined to form the "other" category. Significant differences between January and December (\* $p < 0.05$ , \*\* $p < 0.01$ ). Note different scales of Y axes.



**Figure 5.1 (continued)** Mean percentage of each substrate category at Sites 1-8 (n=5, 10 m transects). 1J=Site 1 in January, 1D=Site 1 in December, etc. Note different scales of Y axes.

individually exceeded 2% of the substrate at any site. For standard deviations see Table E.1, Appendix E.

Two-way anovas (date X site) for each substrate type (Table 5.2) show that between January and December, 1986 live coral cover was significantly reduced and there was a significant difference in live cover among sites. Old dead coral significantly increased between January and December and there was a significant difference among sites. The increase in old dead coral between January and December occurred at 3 sites only. Sand substrate was present at all sites except 5 and 8 and increased significantly between January and December; there was a significant difference among sites. There were no interactions between sites and dates for any substrate category.

Within-site comparisons of change in percent cover for each substrate type between January and December, were significant only for a decrease in live coral cover ( $t = 4.08$ ,  $p < 0.02$ ) and an increase in recently killed coral cover ( $t = 4.11$ ;  $p < 0.01$ ), and these only at Site 5 (Sidak's critical values for a Type I experimentwise error rate of  $p < 0.1$ , with 8 degrees of freedom and 8 unplanned comparisons; Sokal and Rohlf, 1981). Live cover loss at Site 5 was also significantly greater than cover loss at all other sites except Site 3 ( $p < 0.05$ , Tukey test). Increased cover of recently killed coral at Site 5 was significantly greater than the increase at the control

Table 5.2 Two-way anovas of mean line-length (cm) of live coral, recently killed coral, old dead coral, coral rubble, soft coral, "other", sand and sand/mud substrate between dates (January and December, 1986) and among sites (1-8); n = 5 transects per site.

Source of variation	DF	SS	F VALUE	P<
<u>LIVE CORAL</u>				
DATE	1	2691.45	12.30	.0005
SITE	7	6351.26	4.15	.0002
SITE*DATE	7	298.31	0.19	NS
ERROR	3107	680096.30		
TOTAL	3122	689437.33		
<u>RECENTLY KILLED CORAL</u>				
DATE	1	14117.74	2.40	NS
SITE	7	50305.51	1.22	NS
SITE*DATE	7	0.00	0.00	NS
ERROR	56	329665.80		
TOTAL	71	391842.61		
<u>OLD DEAD CORAL</u>				
DATE	1	6813.95	21.47	.0001
SITE	7	17821.67	8.02	.0001
SITE*DATE	7	2041.30	0.92	NS
ERROR	915	290418.32		
TOTAL	930	317095.24		
<u>CORAL RUBBLE</u>				
DATE	1	3591.21	3.00	NS
SITE	7	15186.90	1.81	NS
SITE*DATE	7	7974.71	0.95	NS
ERROR	397	474739.41		
TOTAL	412	501492.24		



Table 5.2 (Continued) Two-way anova of mean line-length of sand and sand/mud between dates (January and December, 1986) and among sites (1-8); n = 5 transects per site.

Source of variation	DF	SS	F VALUE	P<
<u>SOFT CORAL</u>				
DATE	1	163.59	0.32	NS
SITE	6	1174.14	0.38	NS
SITE*DATE	6	1331.02	0.43	NS
ERROR	31	15867.02		
TOTAL	44	18535.78		
<u>OTHER</u>				
DATE	1	45.22	0.36	NS
SITE	7	760.70	0.86	NS
SITE*DATE	6	628.11	0.83	NS
ERROR	31	8495.71		
TOTAL	44	9929.75		
<u>SAND</u>				
DATE	1	6497.07	12.70	.0005
SITE	5	14484.73	5.66	.0001
SITE*DATE	5	1437.69	0.56	NS
ERROR	118	60367.30		
TOTAL	129	82786.81		
<u>SAND/MUD</u>				
DATE	1	504.38	0.40	NS
SITE	3	3610.13	0.95	NS
SITE*DATE	5	1407.01	0.37	NS
ERROR	50	63233.37		
TOTAL	57	68754.56		

reef (Site 8;  $p < 0.05$ , Tukey test). The mud category was only recorded at Site 5 and although mud cover increased 300%, this was not significant because 2 of the 5 transects did not experience large increases in mud cover.

There was a significant positive relationship between loss of coral cover at each site and mean sediment deposition (natural logarithm transformed) ( $p < 0.02$ ,  $r^2 = 0.62$ ;  $y = 6.28x + 1.3$ ) (Figure 5.2). Similar relationships were found between cover loss and deposition of each particle size fraction (clay,  $p < 0.04$ ,  $r^2 = 0.55$ ; silt,  $p < 0.03$ ,  $r^2 = 0.59$ ; sand,  $p < 0.02$ ,  $r^2 = 0.65$ ).

#### Changes in coral diversity

Of 194 reef building species identified from 8 transect sites, there were 189 scleractinian corals, 3 species of fire coral, Millepora spp. (Class Hydrozoa, Order Hydrocorallia, Family Milleporidae), organ pipe coral, Tubipora musica (Class Anthozoa, Order Stolonifera, Family Tubiporidae) and blue coral, Helipora coerulea (Class Anthozoa, Order Coenothecalia, Family Helioporidae). The 189 scleractinian species account for almost 40% of the scleractinian fauna known from the Philippines, many of which are rare (Veron and Hodgson, in press). The species list for each site is given in Table E-2, Appendix E.

Mean (and standard deviation) coral cover, colony size and diversity values for the 5, 10 m transects at each

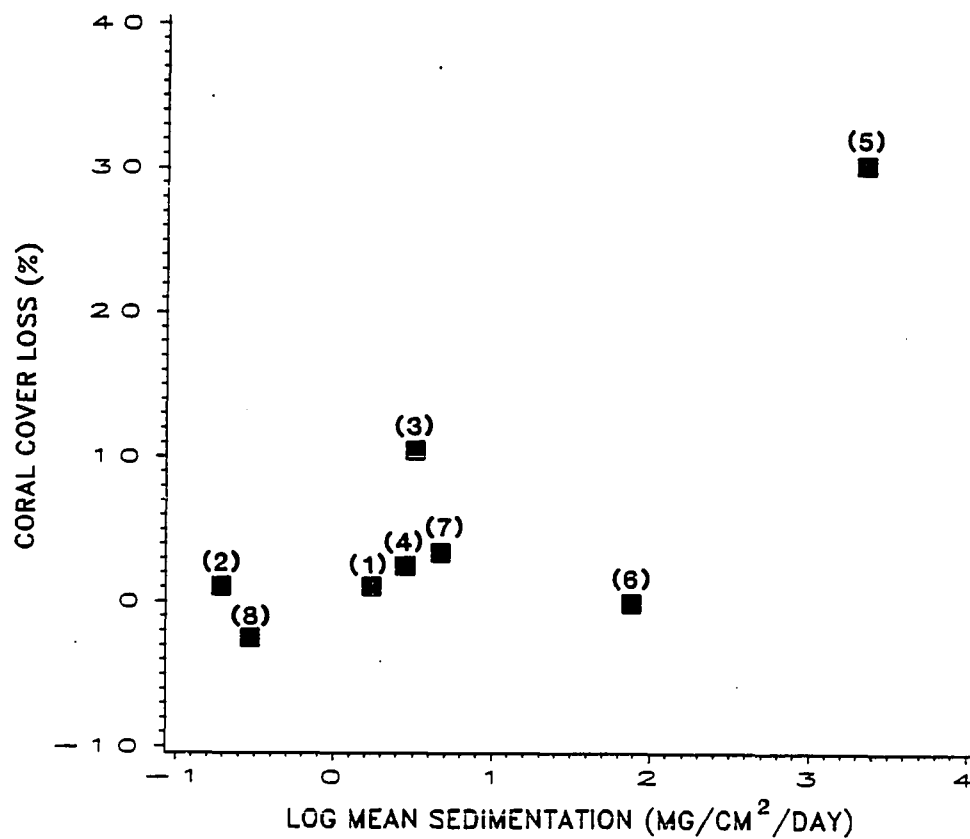
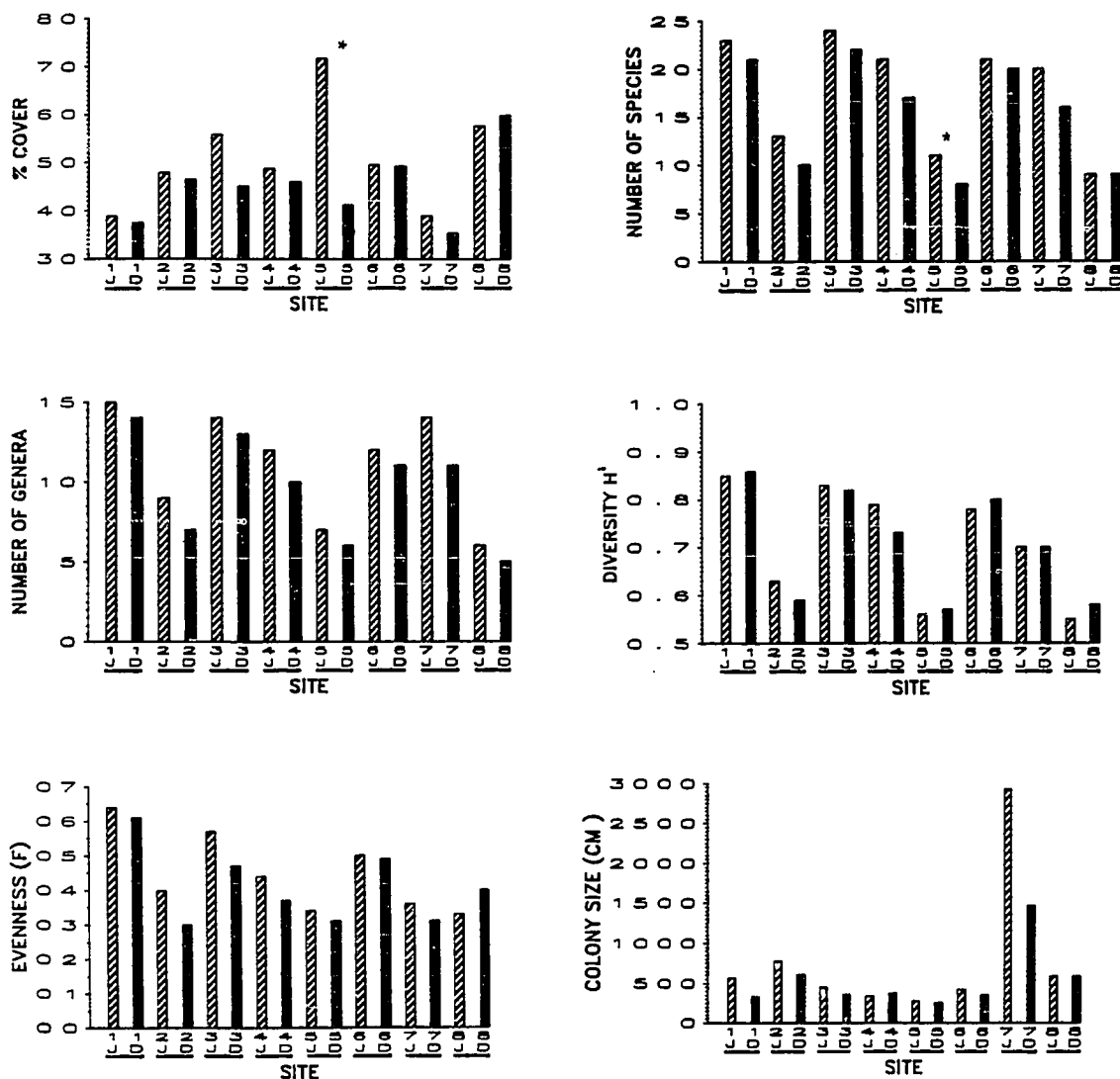


Figure 5.2 Plot of coral cover loss at each transect site (1-8) versus mean annual sediment deposition (natural logarithm transformed). Linear regression ( $p < 0.02$ ,  $r^2 = 0.62$ )

site in January and December 1986 are listed in Table E.3 (Appendix E) and plotted (means only) in Figure 5.3. The results for live cover are repeated in Figure 5.3 for reference and have already been discussed. Two-way anovas (Table 5.3) show that between sample dates, there was a significant reduction in number of species and number of genera at the study reefs. There was also significant interaction between sites and dates for number of species, apparently due to the relatively small absolute reductions in number of species at Sites 6 and 8. Although there was a trend in reduction in evenness, and colony size between dates, this was not significant. Among sites there was a significant difference in number of species, number of genera, diversity ( $H'$ ), and evenness ( $F$ ) indicating that the sites differ in coral community structure.

Within-site comparisons of changes in coral diversity parameters and colony size between January and December 1986 showed significant reduction only of number of species, and then only at Site 5, the closest to the Manlag River outlet, (t-test;  $t=3.2$ ,  $df=8$ ,  $p<0.02$  using Sidak's critical values for a Type I experimentwise error rate of  $p<0.1$ , with 8 degrees of freedom and 8 unplanned comparisons). However, this reduction was not significantly greater than that at the control site (Tukey test). Changes in community parameters in 1986 showed a high variance among sites and among the 5 transects at each



**Figure 5.3** Mean values of coral cover, number of species, number of genera, diversity  $H'$ , evenness  $F$ , and colony size ( $\text{cm}^2$ ) at all 8 sites in January and December ( $n=5$ , 10 m transects). 1J = Site 1 January, 1D = Site 1 December, etc. Significant differences between dates (\* =  $p<0.05$ ).

Table 5.3 Two-way anovas of mean diversity values and colony size (cm<sup>2</sup>) between dates (January and December, 1986) and among Sites (1-8); n = 5 transects per site.

Source of variation	DF	SS	F VALUE	P<
<u>NUMBER OF SPECIES</u>				
DATE	1	2289.80	20.06	.0001
SITE	7	6729.20	8.42	.0001
DATE*SITE	7	2113.80	2.65	.02
ERROR	64	7305.20		
TOTAL	79	18438.00		
<u>NUMBER OF GENERA</u>				
DATE	1	43.51	4.04	.05
SITE	7	781.09	10.35	.0001
DATE*SITE	7	8.39	0.11	NS
ERROR	64	690.00		
TOTAL	79	1522.99		
<u>DIVERSITY H'</u>				
DATE	1	0.0005	0.02	NS
SITE	7	0.9041	6.11	.0001
DATE*SITE	7	0.0172	0.12	NS
ERROR	64	1.3535		
TOTAL	79	2.2754		
<u>EVENNESS F</u>				
DATE	1	0.0278	1.14	NS
SITE	7	0.7655	4.45	.0004
DATE*SITE	7	0.0587	0.34	NS
ERROR	64	1.5722		
TOTAL	79	2.4244		
<u>COLONY SIZE (cm)</u>				
DATE	1	3119576.13	0.69	NS
SITE	7	45771440.55	1.44	NS
DATE*SITE	7	12358342.04	0.34	NS
ERROR	64	290708730.92		
TOTAL	79	351958089.65		

site. Some of this variance was probably caused by the patchy distribution of coral cover on reefs and the relationship between transect length and patch size. This variation apparently overwhelmed a weak sedimentation effect.

Mean size of areas of dead tissue (partial mortality) significantly increased between January and December and differed significantly among sites (Table 5.4); there was significant interaction between sites and dates probably due to the large increases at Sites 5 and 6 compared to the other sites. In within-site comparisons, increased patch size was significant only at Site 5 (t-test;  $t = 4.72$ ,  $p < 0.0001$ ; Type I experimentwise error rate  $p < 0.1$ , 40 degrees of freedom and 8 unplanned comparisons) and this increase was greater than that at all other sites ( $p < 0.05$ ; Tukey test).

Regression of increases in partial mortality on sediment deposition at each Site (1-8) between January and December, 1986 was highly significant (Figure 5.4;  $p < 0.0001$ ;  $r^2 = 0.98$ ).

The difference between January and December values for live coral cover, number of species, number of genera,  $H'$ ,  $F$ , recently killed coral and partial mortality at treatment Sites 1-7 (as a group) was tested by one-way anova against the change in these parameters over this period at Site 8. None of these tests was significant, probably because

**Table 5.4** Two-way anova of mean partial mortality between dates (January and December, 1986) and among Sites (1-8).

Source of variation	DF	SS	F VALUE	P<
DATE	1	4321.51	11.73	.0007
SITE	7	5780.54	2.24	.04
DATE*SITE	6	5761.45	2.61	.02
ERROR	196	72195.06		
TOTAL	15	88058.56		

Partial mortality in January and December 1986. Mean percent of the surface area affected and standard deviation. N=number of colonies affected, NS=no significant difference between Jan and Dec means.

Percentage Partial Mortality					
Site		N	Mean	SD	t-test
1	Jan	18	21.67	11.88	NS
1	Dec	20	23.89	13.98	
2	Jan	13	12.69	8.32	NS
2	Dec	15	16.80	8.94	
3	Jan	3	15.00	5.00	NS
3	Dec	4	20.00	8.16	
4	Jan	11	26.57	16.41	NS
4	Dec	19	28.18	23.05	
5	Jan	26	20.65	15.21	p<0.0001
5	Dec	16	50.00	20.65	
6	Jan	14	20.21	16.95	NS
6	Dec	24	31.25	21.33	
7	Jan	20	24.35	26.82	NS
7	Dec	20	29.50	24.11	
8	Jan	2	22.50	3.53	NS
8	Dec	6	27.17	35.52	



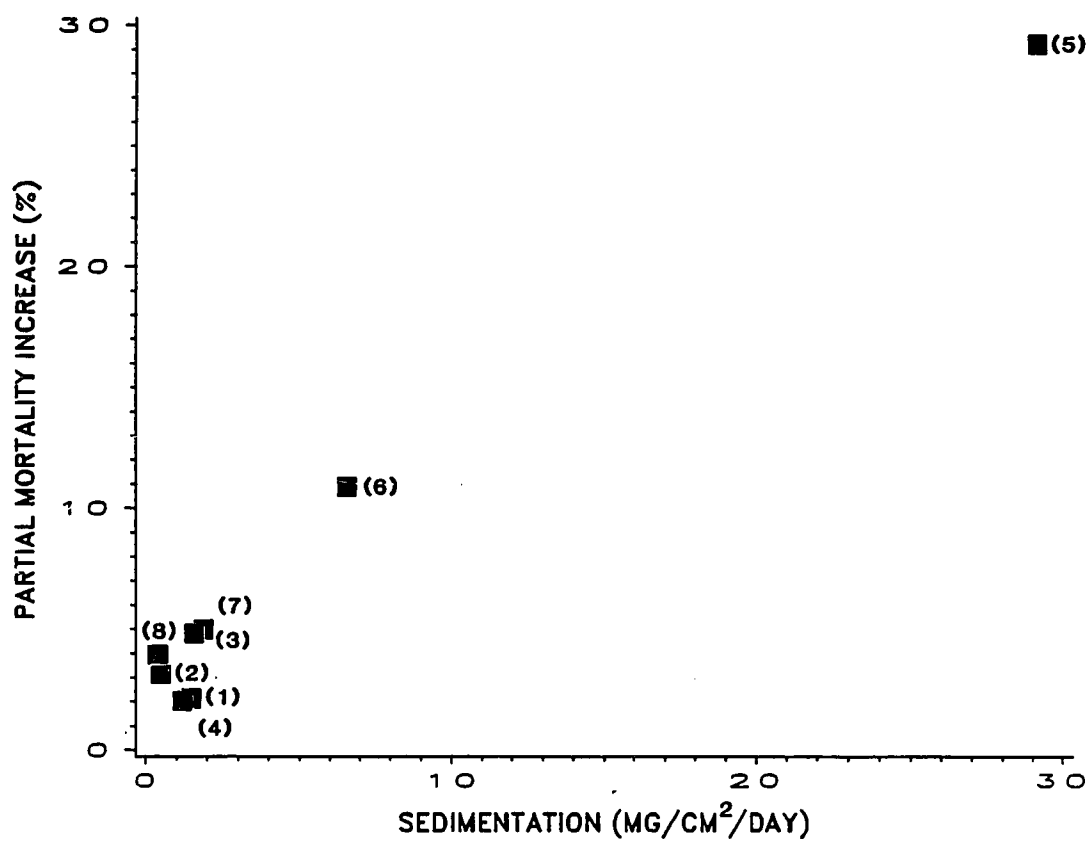


Figure 5.4 Plot of December minus January mean partial mortality versus mean sediment deposition at each site (1-8). Linear regression is significant ( $p < 0.0001$ ;  $r^2 = 0.98$ ).

changes at Site 5 were much more extreme or in a different direction than the changes at the other treatment sites.

#### Coral Cover Changes and Phenotype

According to the phenotype-sediment tolerance hypothesis, corals with a large CD and a high PEA should be more resistant to sedimentation damage than species with other phenotypes. These predictions were tested using data from Site 5 where mean monthly sedimentation was high and significantly greater than at the control site. In addition, since it is possible that pulses of high sedimentation could have reached any treatment site (1-7) (Chapter 3), cover loss between January and December at all treatment sites was examined with respect to the predictions.

The transect data show that the number of species with each phenotype combination was unequal (Table 5.5). Given the large size of the total sample and wide distribution of transect sites, the sample sizes for phenotype combinations are believed to accurately reflect the composition of the coral community at 3 m in Bacuit Bay. The high abundance of the ramose/low PEA/small CD phenotype combination (35% of all colonies) was due to the abundance of Acropora species, all of which share this phenotype combination. This "linkage" of phenotypes (Chapter 4) and the lack of species for all but 1 other ramose phenotype

combination complicated interpretation of the statistical analysis.

**Table 5.5** Number of species with each phenotype combination sampled along transects in Bacuit Bay. PEA=polyp extensional ability, CD=corallite diameter

PEA/CD	Growth Form				Total
	Ramose	Massive	Phaceloid	Plate	
low/small	69	20	0	24	113
low/medium	0	6	0	5	11
low/large	0	6	0	3	9
hi/small	0	0	0	0	0
hi/medium	0	12	0	2	14
hi/large	3	18	7	19	47
Total	72	62	7	53	194

Three-way anovas were used to compare mean number of colonies among sites, among phenotype classes and between dates for each character (Table 5.6). The anovas indicated that there was a significant difference in number of colonies among sites and among phenotype classes for all 3 characters (PEA, CD, GF). For GF and CD the significant interactions between site and phenotype class suggest that differences between sites affected the number of colonies of each phenotype (ramose, phaceloid, massive, and plate GF, and large, medium and small CD). The 3-way interaction for GF indicates that the mean number of colonies of each growth form depended on both the site and date.

Table 5.6 Three-way anovas of mean number of colonies among sites, phenotype classes and between dates. The results are from 3 anovas, 1 each for CD = corallite diameter, GF = growth form, and PEA = polyp extensional ability.

Source of variation	DF	SS	F VALUE	P<
<u>Corallite Diameter</u>				
CD	2	8054.90	43.08	.0001
SITE	7	4756.54	7.27	.0001
DATE	1	186.77	2.00	NS
SITE*DATE	7	576.77	0.55	NS
SITE*CD	14	4294.77	3.28	.0001
DATE*CD	2	322.81	1.73	NS
SITE*DATE*CD	14	719.49	0.55	NS
ERROR	447	41793.61		
TOTAL	494	60705.68		
<u>Growth Form</u>				
GF	3	26120.79	251.58	.0001
SITE	7	3820.77	15.77	.0001
DATE	1	185.52	5.36	.02
SITE*DATE	7	530.78	2.19	.03
SITE*GF	19	12349.18	18.78	.0001
DATE*GF	3	805.32	7.76	.0001
SITE*DATE*GF	18	1829.67	2.94	.0001
ERROR	432	14950.83		
TOTAL	490	60592.88		
<u>Polyp Extensional Ability</u>				
PEA	1	3441.68	31.77	.0001
SITE	7	4759.01	6.28	.0001
DATE	1	118.36	1.09	NS
SITE*DATE	7	456.96	0.60	NS
SITE*PEA	7	1391.44	1.83	NS
DATE*PEA	1	93.99	0.87	NS
SITE*DATE*PEA	7	342.61	0.45	NS
ERROR	462	50054.35		
TOTAL	493	60658.45		

Two-way anovas were used to compare mean number of colonies among sites and between dates for each phenotype class (Table 5.7; Type I experimentwise error was restricted to  $p < 0.1$ ). There was a significant reduction in number of colonies between dates for small CD, ramose GF, and low PEA. There was a significant difference among sites for all phenotypes except medium CD and phaceloid GF. These exceptions may be due to the small sample sizes for these phenotypes. There was a significant interaction between site and date only for phaceloid GF.

The difference between January and December abundance of each phenotype at treatment Sites 1-7 (as a group) was tested by anova against the control Site (8). Only low PEA was significant ( $p < 0.009$ ) due to a large variance among treatment sites for other phenotypes.

For each site, within-site unplanned paired t-tests with a limit on Type I error were used to compare the loss or gain of colonies with respect to phenotypes (GF, CD and PEA classes) between January and December. Type I experimentwise error was limited to  $p < 0.1$  with 8 degrees of freedom for 8 unplanned comparisons. The data set was the mean difference ( $n=5$  transects per site) in number of colonies of each genus between January and December at each site; this is the difference between the pairs of vertical bars for each site in Figures 5.5 (PEA), 5.6 (GF) and 5.7 (CD). For standard deviations see Table E.4, Appendix E.

**Table 5.7** Two-way anovas of mean number of colonies for each of 9 phenotypes, among sites and between dates.

Source of variation	DF	SS	F VALUE	P<
<u>Corallite Diameter=Small</u>				
SITE	7	10003.28	10.22	.0008
DATE	1	1739.11	12.43	.0001
SITE*DATE	7	1940.98	1.98	NS
ERROR	64	8952.80		
TOTAL	79	22636.19		
<u>Corallite Diameter=Medium</u>				
SITE	7	532.14	1.82	NS
DATE	1	0.30	0.01	NS
SITE*DATE	7	38.68	0.13	NS
ERROR	46	1921.96		
TOTAL	61	2493.09		
<u>Corallite Diameter=Large</u>				
SITE	7	548.24	5.52	.0001
DATE	1	4.50	0.32	NS
SITE*DATE	7	28.11	0.28	NS
ERROR	56	795.13		
TOTAL	71	1376.00		
<u>Growth Form=Massive</u>				
SITE	7	1259.08	4.42	.0005
DATE	1	47.07	1.16	NS
SITE*DATE	7	70.74	0.25	NS
ERROR	59	2401.28		
TOTAL	74	3778.18		
<u>Growth Form=Phaceloid</u>				
SITE	5	0.60	1.62	NS
DATE	1	0.19	2.68	NS
SITE*DATE	4	3.08	0.25	.002
ERROR	9	0.66		
TOTAL	19	4.55		

**Table 5.7 (continued) Two-way anovas of mean number of colonies for each of 9 phenotypes, among sites and between dates.**

Source of variation	DF	SS	F VALUE	P<
<u>Growth Form=Plate</u>				
SITE	7	305.60	2.53	.03
DATE	1	10.15	0.59	NS
SITE*DATE	7	12.28	0.10	NS
ERROR	53	915.11		
TOTAL	68	1243.15		
<u>Growth Form=Ramose</u>				
SITE	7	13917.88	14.45	.0001
DATE	1	1436.51	10.44	.002
SITE*DATE	7	2025.98	2.10	NS
ERROR	64	8803.60		
TOTAL	79	26283.98		
<u>Polyp Extensional Ability=High</u>				
SITE	7	695.82	2.62	.02
DATE	1	21.62	0.57	NS
SITE*DATE	7	30.36	0.11	NS
ERROR	58	2204.56		
TOTAL	73	2952.37		
<u>Polyp Extensional Ability=Low</u>				
SITE	7	7561.75	7.57	.0001
DATE	1	1881.80	13.18	.0006
SITE*DATE	7	1858.00	1.86	NS
ERROR	64	9134.40		
TOTAL	79	20435.95		

**Figure 5.5** Mean number of colonies of each PEA (polyp extensional ability category; high or low) at each site in January and December 1986 (n = 5, 10 m transects). 1J = Site 1 January, 1D = Site 1 December, etc. Significant differences (\* =  $p < 0.05$ ).



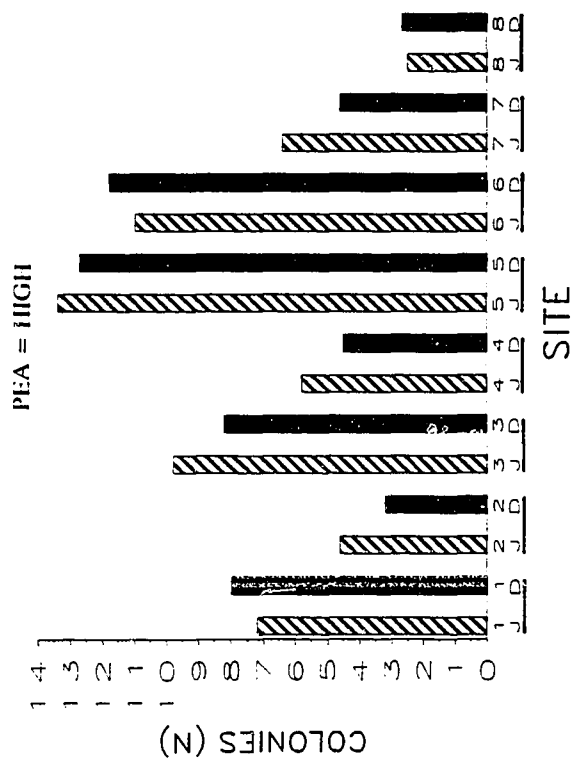
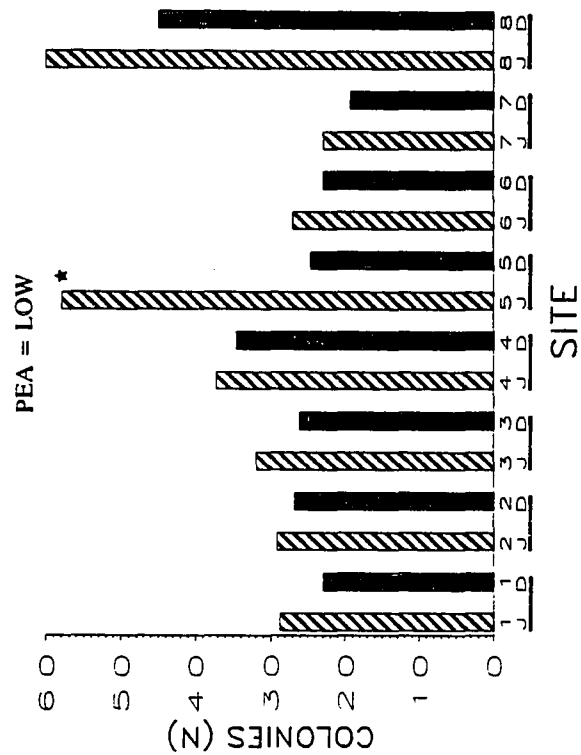
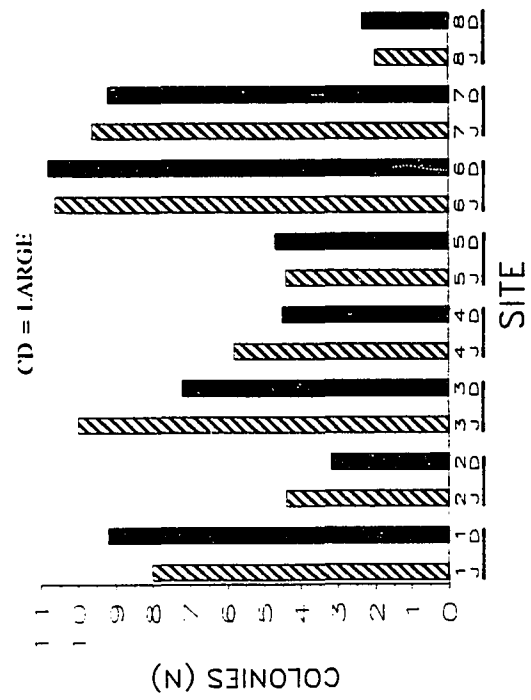
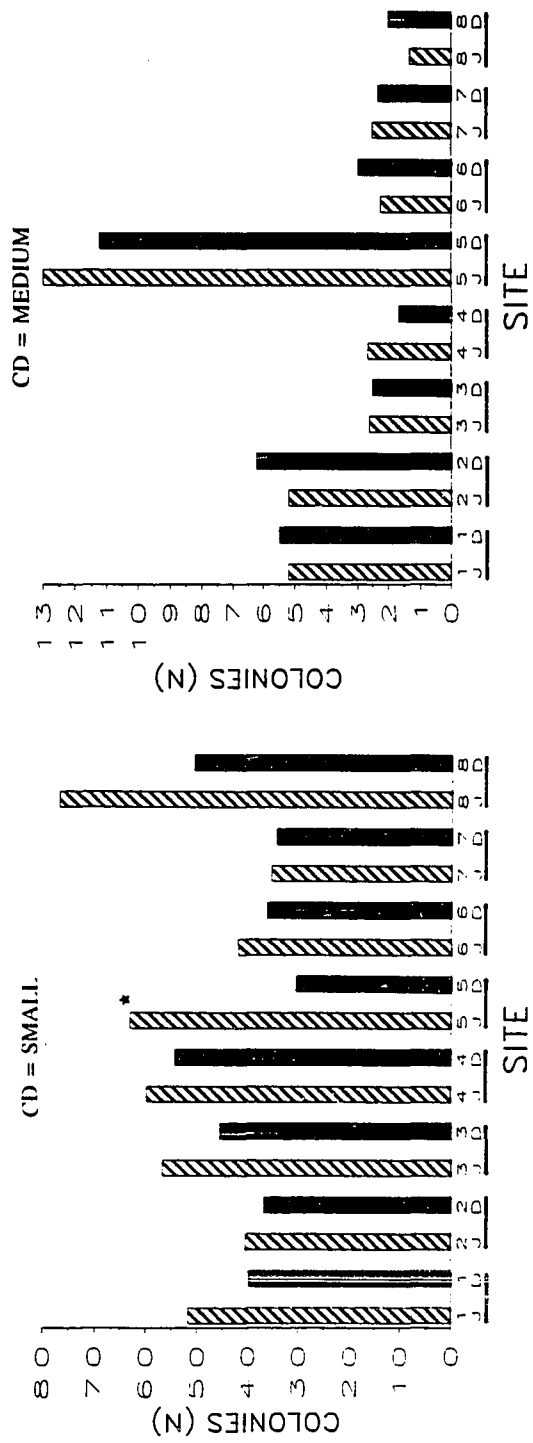
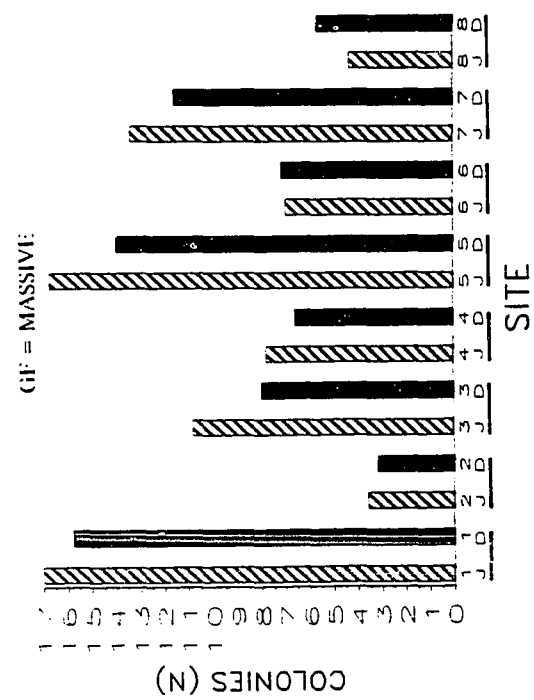
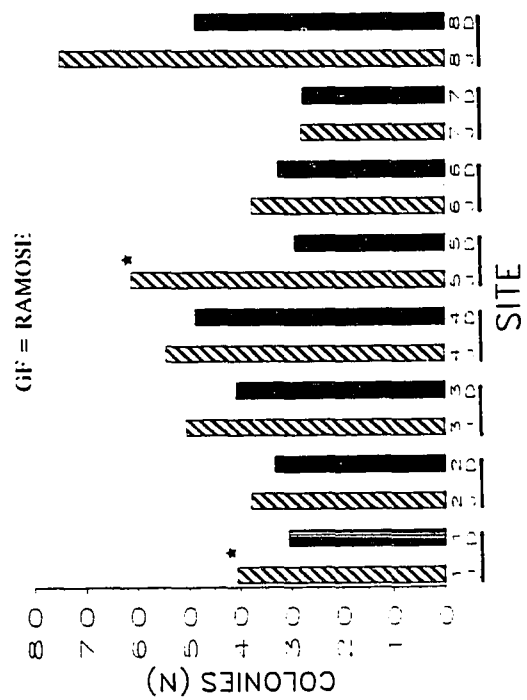
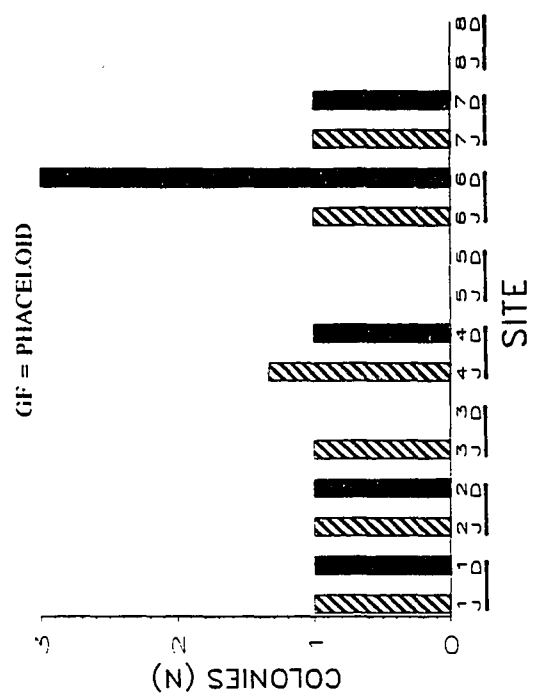
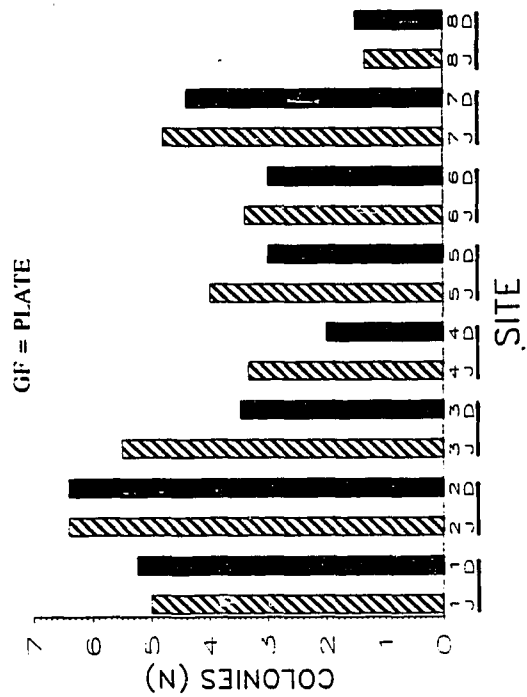


Figure 5.6 Mean number of colonies of each CD (corallite size category; small, medium, large) at each site in January and December (n = 5, 10 m transects). 1J = Site 1 January, 1D = Site 1 December, etc. Significant differences (\* =  $p < 0.05$ ).



**Figure 5.7** Mean number of colonies of each GF (growth form; massive, phaceloid, ramose, plate) at each site in January and December (n = 5, 10 m transects). 1J = Site 1 January, 1D = Site 1 December, etc. Significant differences (\* =  $p < 0.05$ ).



Although there was a trend in reduced numbers of phenotypes predicted to be susceptible to sedimentation (low PEA, small CD and ramose GF), most within-site changes were not significant. At Site 5 there was a significant reduction in number of ramose colonies ( $p < 0.03$ ,  $t = 3.45$ ), colonies with low PEA ( $p < 0.03$ ;  $t = 3.49$ ), and colonies with small CD ( $p < 0.02$ ;  $t = 3.59$ ). These reductions were significantly greater than those at all other sites individually ( $p < 0.05$ ; Tukey test). Ramose colonies were also reduced at Site 1 ( $p < 0.03$ ,  $t = 3.43$ ), but this was not significantly different from the reduction at the control site (8).

A matrix showing the January and December composition of the Site 5 reef is given in Table 5.8. All of the 47% reduction in live coral cover was due to significant losses from the low PEA/ramose GF/small CD category, primarily Acropora spp. The linkage of these phenotypic characters due to the abundance of Acropora makes it difficult to determine the importance of each separately. The massive GF/medium CD combination showed the greatest relative gain during this period.

Change in coral cover at all Sites (1-8) between January and December with respect to CD was analyzed by regression (Proc GLM; SAS, 1985), using corallite diameter as a continuous variable. First, all genera were divided into two groups, those that gained and those that lost cover during 1986. Genera that remained the same were not

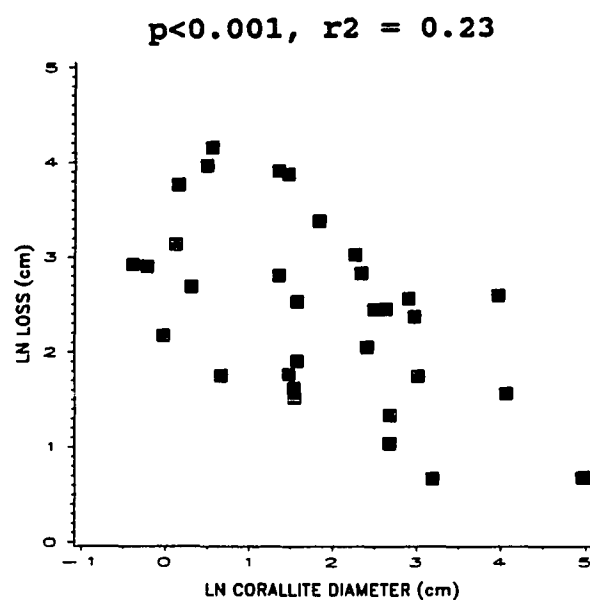
**Table 5.8** Distribution of live coral cover among 4 growth forms at Site 5 in January and December 1986 (first 2 columns). Change in coral cover composition (December minus January values) for each growth form/corallite size combination (last 3 columns).

Growth Form	<u>Composition</u>		<u>Corallite Diameter</u>		
	Jan	Dec	Large	Medium	Small
	%	%	% Change	% Change	% Change
Free living	2	2	0	0	0
Massive	16	36	1	18	1
Plate	2	2	0	0	0
Ramose	80	60	0	0	-20
Total	100	100			

included in the analysis. All data were natural logarithm-transformed, and then for each group, mean CD was regressed on mean transect length lost (or gained) per genus.

For the cover loss group of genera (n=30), there was a negative relationship between CD and cover loss ( $p < 0.001$ ,  $r^2 = 0.23$ ;  $y = -0.35x + 3.13$ ) while for the gain group (n=18), the regression was not significant ( $p < 0.3$ ,  $r^2 = 0.02$ ), and the data points were widely scattered (Figure 5.8). One explanation for these results is that increasing CD may impart increasing sedimentation tolerance only for corals susceptible to sedimentation damage. For resistant corals, a variety of resistance mechanisms could alter the relationship between CD and sedimentation resistance as measured by cover increase.

A



B

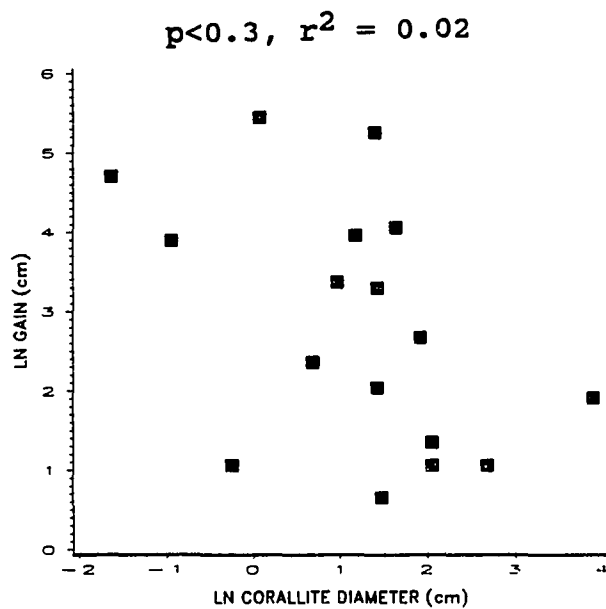


Figure 5.8 Plot of mean corallite diameter versus cover loss (transect length) (A) or gain (B) for each genus between January and December, 1986. All data log-transformed.



## Discussion

### Causal Hypotheses

Potential causes of coral mortality at Bacuit Bay reefs in 1986 included physical factors such as light reduction, or temperature, salinity, sedimentation and wave action at levels above the threshold of coral tolerance, as well as biological factors such as disease and predation.

It appears unlikely that seawater temperatures were low enough or fell quickly enough to damage Bacuit Bay corals in 1986. Corals living along the Pacific coast of Panama are known to experience temperature changes of up to 6.4 °C in 2 hours (Glynn and Stewart, 1973).

Because of the location of the transects at 3 m and the relatively rapid mixing of plume water with seawater, it is not likely that low salinity had a deleterious effect on corals living along transect lines in 1986. However, this factor cannot be ruled out for corals living closer to the surface, and low salinity occurring during seasonal low tides and calm wind conditions might cause damage. Reduced salinity due to high runoff is believed to have killed corals living in shallow water in Kaneohe Bay, Hawaii in May, 1965 (Banner, 1968) and January, 1988 (pers. obs.). Since logging significantly increases runoff and peak stream flow (Hamilton, 1985), the potential for low salinity damage of corals may be increased by further logging of the Bacuit Bay drainage basin.

Unless the Acropora species at Site 5 were damaged much more rapidly by light reduction than Hawaiian and Caribbean species, the limited duration of individual high turbidity events compared to the time required to damage susceptible corals suggests that light reduction due to high turbidity did not damage Bacuit Bay corals in 1986.

It is highly unlikely that Acanthaster predation caused the live coral cover losses documented during the study period. Few predators could cause such a dramatic loss of coral cover as occurred at Site 5.

There is little evidence to support the hypotheses that low temperature, light, or salinity, or predation, wave damage or unknown diseases significantly reduced coral cover at Site 5 compared with the control site, in 1986.

The hypothesis that coral cover reduction measured in 1986 was caused by sedimentation appears to have the strongest support. The significant positive linear relationship between silt content of trapped sediment and distance from the Manlag River mouth (Chapter 3) suggested that it was the silt fraction, rather than the rate of total sediment deposition that was associated with damage to corals. However, all 3 sediment fractions (sand, silt, clay) were linearly related to coral cover loss, so none could be ruled out as potential causative factors. A discussion of sedimentation damage to coral reefs in Bacuit Bay follows.

### Coral Community Changes (January to December, 1986)

Although analysis of variance showed that coral cover was significantly reduced at Bacuit Bay study reefs between January and December 1986, changes at individual sites in parameters such as reduced coral cover, increased cover of recently killed coral and partial mortality were significantly different from the control site (8) only at Site 5, the site with the highest sedimentation rate due to proximity to the river outlet. The significant linear relationship between sediment deposition and cover loss may be due in part to sedimentation pulses associated with high discharge plumes.

The large, but non-significant increase in mud substratum at Site 5 was consistent with the increased discharge of fine suspended sediments documented previously. Since larvae of one coral species were inhibited from settling on substrate covered by fine sediment (Chapter 4) another important effect of increased cover of mud could be a reduction in coral larval recruitment. Given the slow growth of many corals, the effect of reduced larval recruitment on coral community structure might not be detectable for several years.

The significant increase in partial mortality between January and December parallels effects of sedimentation on corals observed during field experiments. The positive relationship between partial mortality and sediment

deposition could result from the following process. As sediment deposition increases, sediment clearing mechanisms may become overloaded and tissue necrosis may begin (as described in Chapter 4). Once a patch of coral surface tissue has died, sediment can build up there since biological cleaning mechanisms can no longer reach that area (except for species with very long tentacles). Polyps located along the border between living and dead tissue have no protection from sediment that builds up over the dead patch and such polyps may be buried on one side, perhaps increasing their susceptibility to microbial attack. Border polyps should have a higher rate of mortality than polyps surrounded by healthy tissue. Progressive mortality of polyps around the edge of dead patches was observed in field experiments. The significant positive regression of partial mortality on sediment deposition at each site may indicate a causal relationship, but this should be tested at other locations to rule out alternative explanations. The relationship might be expected to vary with respect to timing and intensity of individual sedimentation events. In addition, different species may be able to repair damaged areas more quickly than others (Kobayashi, 1984).

### Diversity

The significant loss of species and genera between January and December is consistent with the finding that certain species are more sensitive to sedimentation damage than others. Less tolerant species would be expected to be killed first.

The fact that the diversity indices differed significantly among sites may suggest that each site is exposed to a unique set of environmental variables. The lack of significant change in diversity index values between January and December is due in part to the small loss in cover at all sites except 3 and 5. At Sites 3 and 5, the lack of significant reduction in diversity and evenness index values may be due to compensatory mortality (Connell, 1978). That is, if common species suffer proportionately greater losses than rare species, the increase in  $H'$  due to evenning of the abundance distribution is balanced by a reduction in  $H'$  due to loss of some rare species therefore the index values change little despite a loss of coral abundance. Clearly this was the case at Site 5 where a high percentage of cover loss was from the common Acropora species, but some rare species were also lost.

### Community Changes and Phenotype

If sedimentation caused most cover loss at Bacuit Bay transects, the significant negative relationship between CD and cover loss for susceptible genera is in agreement with one of the predictions of the phenotype-sediment tolerance hypothesis. The lack of a similar relationship for resistant genera indicates that the predictions of the hypothesis may be require adjustment to account for individual thresholds of various morphotypes. The results confirm the predictions for Site 5 where all loss was from low PEA, small CD phenotypes. Although all loss at Site 5 was also composed of ramose species, the linkage of low PEA, small CD and ramose GF by the predominant Acropora spp. makes it is difficult to determine if ramose corals were more susceptible than other growth forms to sedimentation damage. Significant losses of small CD and low PEA phenotypes are also in agreement with the predictions.

For all 7 treatment sites, measurements of both physical and biological parameters showed wide variation and the existence of a gradient with respect to sedimentation. This gradient and variation in other physical parameters were probably responsible for the lack of significant differences between the control site (8) and treatment Sites (1-7), as a group, for change in biological parameters between January and December, 1986.

### Historical Factors

Since some sensitive coral species could have been prevented from colonizing reefs or eliminated by pre-1986 sedimentation, changes in community structure believed to be due to sedimentation in 1986 should be considered in light of pre-1986 sedimentation history at each site. For example, it is likely that Site 5 has always had a higher sedimentation rate than Site 3 since Site 5 is 2 km closer to the river mouth. In 1986, 57% of coral cover loss at Site 3 was from 5 Acropora species, and 2 species (Acropora nasuta and A. palifera) accounted for 54%. In sedimentation experiments 3 Acropora species (including A. palifera) were damaged. In January 1986, although Acropora made up nearly 70% of the corals at Site 5, neither A. nasuta nor A. palifera were recorded there. It is possible that this is due to chance; or it may be that A. palifera and A. nasuta (and perhaps other species) may be relatively sensitive to sedimentation and so are not commonly found on reefs exposed to moderate sedimentation such as near river mouths. Following exposure to elevated sediment deposition rates, a reef primarily composed of sensitive species would be expected to show a higher level of coral cover loss than one composed of relatively resistant coral species. Differences in sedimentation history could explain the greater live coral cover loss at

Site 3 (mean sedimentation 1.8 mg/cm<sup>2</sup>/day) than at Site 6 (mean sedimentation 6.8 mg/cm<sup>2</sup>/day).

#### Unrelated and Linked Characters

It is possible that the phenotypes considered so far do not affect the extent of sedimentation damage, but that unrelated characters, e.g. mucus production or ciliary action mediate differential losses of live cover that merely appear to be associated with GF, CD and PEA. None of the statistical tests used can detect such spurious correlations.

Character linkage is another potential difficulty. Members of the Family Acroporidae made up about 40% of all species sampled. At some sites, especially Sites 5 and 8, acroporids also accounted for a high percentage of the total live cover. With the exception of non-ramose Montipora species, all Montipora and Acropora have the same phenotype combination (small CD, low PEA, and ramose GF) causing the problem of "linked" phenotypes. Even if only 1 of the 3 phenotypic characters was the cause of susceptibility to sedimentation damage, analysis of distributions would implicate all 3. The reasonable sample size of non-ramose species with small CD and low PEA, makes it possible to assess the effect of the latter 2 phenotypes on sedimentation resistance, but the lack of medium and large CD/low PEA ramose species makes it difficult to rank



the ramose growth form with respect to sedimentation damage. Further experiments will be necessary to separate these linked characters. Since one large coral colony may exhibit several growth forms in different parts of the colony, it may be possible to expose each form to sedimentation and compare the damage.

### Physiological Adaptation

Phenotypic plasticity of coral growth form in response to environmental variation is well-known to coral taxonomists (e.g., Veron and Pichon, 1976; Veron, 1986). Studies of GF variation suggest that massive corals tend to flatten out in response to lowered light levels (Schoffin, 1979; Grigg, 1982). If chronic turbidity lowers light levels such that massive corals grow into plate-like forms, they may increase the surface area exposed to sedimentation, resulting in greater damage. In contrast, in turbid, reduced light environments, columnar forms tend to form thinner columns and branches of ramose forms tend to become finer (Veron and Pichon, 1976; Hodgson and Ross, 1982). Although the cause of narrowed branch growth in low light has not been established, it reduces the surface area exposed to sediment deposition. Coral reefs composed of ramose GFs that are subjected to a slow steady increase in chronic sedimentation might be able to respond by GF changes that have adaptive value.

Several coral species, especially Porites spp. rely on production of mucus webs to trap sediments. The risk of this system is that the coral cannot clear off the mucus web and depends on water motion to do this (Parnrong and Chansang, 1986). Therefore, during periods of low wave action or when water currents are absent, mucus webs may trap sediments, allowing rapid bacterial colonization that can kill the coral (Parnrong and Chansang, 1986). This is one explanation for the fairly large losses of massive Porites lutea, at several Bacuit Bay sites.

#### Evolutionary Implications

If it is assumed, as was proposed in the introduction, that the range of environments found in tropical oceans today is not much different from that which existed during the evolution of the Scleractinia, then high sedimentation environments would have existed in places such as near river mouths, or eroding coastlines. The geographic extent of such environments may have been large. For example, high sedimentation environments now exist along thousands of kilometers of the Indian and south China coastlines where corals are also found (IUCN, 1988). Although it is possible that all corals were completely excluded from such environments due to inhibition of larval settlement or mortality of adult colonies, it seems more likely that some coral species survived and may have become

specialized to endure elevated sedimentation.

Specialization would be expected to reduce competitive ability outside high sedimentation areas. Yonge (1930) noted that ability to remove sediment by ciliary currents might interfere with feeding ability unless the ciliary motion can be reversed. He found that not all species were able to reverse the direction of their cilia, and for those that can, only certain cilia were involved. Other specializations might increase fitness for several reasons. High PEA might be an advantage for feeding, increasing surface area for light-dependent zooxanthellar production, and for defense. Several genera, especially Alveopora and Goniopora (Poritidae), Euphyllia and Catalophyllia (Caryophyllidae) and Heliofungia (Fungiidae) have developed this character to the extreme, with polyps extending 10 to 20 cm. A potential drawback of highly protrusile polyps might be that when extended beyond the protective skeleton, predators might have better access to coral tissue.

Many environmental variables might act on the evolution of CD. A wide skeletal cup can support a large polyp which should be able to capture larger prey, however, any advantage would depend on prey size distribution. Montrastrea cavernosa, a large-polyped Caribbean species has a catholic diet and exploits zooplankton over a wide size range (Porter, 1974). In contrast, Porites has tiny corallites and polyps, but based on abundance and

geographic distribution, it is an evolutionarily successful genus with columnar, ramose, encrusting and massive GFs.

The 3 species of Acropora subjected to sedimentation experiments were damaged and a large percentage of cover loss at several sites was composed of Acropora. Although high sedimentation environments are assumed to have existed throughout the evolution of Acropora, perhaps only a few (and as yet untested) species are adapted to those environments. Acropora pulchra is common in a high sedimentation environment at Magnetic Island, Australia (Hopley and Woesik, 1988). The competitive ability of many Acropora species may be low in high sedimentation environments. But in low sedimentation environments other characteristics, especially the ability to reproduce prolifically by asexual fragmentation, the ability to survive partial mortality of the colony base and to grow above loose sediments may give them a competitive advantage over other corals.

Evidence suggests that one species of the acroporid genus Montipora may have developed physiological resistance to infection due to sediment deposition. This may explain why certain species of Montipora, e.g., M. ramosa are numerically dominant in high sedimentation environments such as at reefs off Magnetic Island, Australia (Hopley and Woesik, 1988).

During the evolution of corals, chance, interspecific competition, predation and physical disturbances on coral reefs might have excluded certain species from low sedimentation environments. If these species were able to adapt to high sedimentation conditions, they would have persisted in this high sedimentation refuge. It was not the purpose of this work to determine which (if any) corals are "high sedimentation refuge species". Nevertheless, insight into the evolutionary process may be gained by listing corals subjectively judged to be abundant on reefs exposed to high levels of turbidity and sedimentation, based on observations of coral distributions in the Philippines (Hodgson and Ross, 1982; Veron and Hodgson, in press). These corals include: Oulastrea crispata, Pocillopora verrucosa, Trachyphyllia geoffroyi, Plerogyra turbida, and nearly all species in the genera Euphyllia, Pectinia, Alveopora, Goniopora, Turbinaria, Fungia, Galaxea, Symphyllia, and Lobophyllia. The corals in this list cover a wide taxonomic range and exhibit a variety of adaptations that apparently allow them to survive high sedimentation. Most importantly, with the exception of Plerogyra turbida (= Nemenezophyllia turbida, Hodgson and Ross, 1982) which has only been observed growing in turbid water, on muddy substrate, all these corals are found in both high and low sedimentation environments (Ross and Hodgson, 1982; Veron, 1986). This may indicate that

despite the existence of high sedimentation marine environments throughout history, enough space in low sedimentation environments has been available to allow nearly all species to coexist there. Storms (Stoddart, 1974) and predation (Colgan, 1987), are common disturbances that create space on reefs for potential colonization and recolonization by corals (Connell, 1978; Hughes and Jackson, 1985).

If larvae of many species behave similarly, the apparent inability of Pocillopora damicornis larvae to settle on fine sediment may indicate a history of strong selection against settling in high sedimentation environments.

Such a scenerio for coral evolution implies that:

- 1) many apparent adaptations to sedimentation may be the result of chance or of selection by factors other than sedimentation
- 2) many corals should be adapted to short-term sedimentation such as occurs at "pristine" reefs, but few should be adapted to high, chronic sedimentation
- 3) corals observed living in apparently high sedimentation environments may have settled there when sedimentation was low (a seasonal occurrence in many areas)
- 4) if larval settlement is inhibited by a sediment, a high percentage of coral reproduction at reefs

affected by chronic, long-term, high sedimentation should be due to fragmentation, therefore genetic diversity at such reefs should be lower than at reefs exposed to less sedimentation.

All corals show some degree of sedimentation resistance as all corals, even those living at reefs considered to be pristine have been exposed to periodic sedimentation events, but it appears unlikely that many high sedimentation refuge species will be discovered.

### Conclusions

Coral surveys at 8 reef sites between January and December, 1986 showed that the greatest change in community parameters occurred at Site 5, the closest site to the Manlag River mouth. High sedimentation at Site 5 was concluded to have caused a significant reduction in coral cover and number of species and a significant increase in partial mortality when compared with the control site (8).

Pulses of high sediment deposition during high Manlag River discharge periods may have reduced coral cover, number of genera and species and increased partial mortality at treatment sites (1-7). A linear relationship between sediment deposition and coral cover loss, and reduced abundance of phenotypes predicted to be susceptible to sediment damage (low PEA, small CD) support this idea. The positive relationship between size of damaged tissue

patches and sedimentation rate, and the negative relationship between cover loss and corallite diameter for corals that were damaged provide additional support.

Although all coral species are expected to show some resistance to sedimentation, few species appear to be exclusively adapted to existence in high sedimentation environments. One conclusion drawn from the small number of refuge species found only in high sedimentation environments is that space on reefs has not been limited, i.e. there has been little exclusion of species due to competition for space. Therefore few species have been restricted to sub-optimal, high sedimentation environments where adaptations to high sediment deposition could have evolved. It appears likely that the frequency and intensity of disturbance on coral reefs has limited the potential for competition for space. Many apparent adaptations to sedimentation resistance may be due to chance or to selection by other factors.

Despite the relatively small proportion (11.5%) of commercial forest affected by logging in 1986 and the short period of accelerated sedimentation, damage was readily detectable by standard ecological measures of coral community parameters. It appears likely that increased logging and erosion within the Bacuit Bay drainage basin will result in increased extent and degree of deleterious effects (reduced coral cover and diversity and possibly



lowered larval recruitment). The potential direct and indirect effects of these changes on economically important marine resources have been considered by Hodgson and Dixon (1988). Over a 10 year period, economic losses of marine resources were predicted to be greater than gains from sales of wood products from logging.

Sedimentation appears to be one of many environmental variables that can affect coral community structure, and at high levels it may limit which species are found at a given site. This limitation will depend on the interaction of physical parameters, especially water motion, with biological parameters including corallite diameter, polyp extensional ability, colony growth form and active resistance mechanisms. It is likely that the synergistic effects of site-specific environmental variables can alter the hierarchy of sedimentation resistance.

## APPENDIX A. SOIL ANALYSIS

### Particle Size Distribution

The particle size distribution for the portion of the soil with particle sizes larger than 0.05 mm is determined by wet sieving, drying and weighing each of 5 fractions (2-1mm, 1-0.5 mm, 0.5-.25 mm, 0.25-0.10 mm, 0.10-0.05mm). The procedure for determining the particle size distribution of the finer soil is based on the differential fall velocity of different sized particles in water predicted by Stoke's Law. This "pipette method" is modified from a pipette method of Guy (1969; p. 23) as follows: A soil sample of 15 g is mixed with 50 ml distilled water and 5-10 ml, 30% H<sub>2</sub>O<sub>2</sub> in a 400 ml beaker and warmed on a hot plate. Hydrogen peroxide is added until effervescence stops. The soil is then dried at 105°C to constant weight. Twenty ml sodium hexametaphosphate dispersing solution is added to sample and allowed to stand overnight. The sample is transferred to a 1000 ml graduated cylinder to which distilled water is added until full, and then stirred with a plunger. At time intervals specified by Stoke's Law for silt (0.05 mm-0.002 mm) and clay (<0.002 mm), 20 ml of solution are pipetted out from a depth of 10 cm. The aliquots are emptied into tared drying tins and dried at 105°C overnight, and then weighed. The weight of the dispersing solution residue is subtracted to obtain the soil weight.

### Calcium Carbonate Determination

The calcium carbonate determination is a dilute acid leach technique with back titration modified from Black (1965) as follows:

Five grams of soil are placed in a 250 ml flask and then 100 ml, 0.5 N HCl are slowly added and the mixture is allowed to stand with occasional stirring. After 1 h, 20 ml of supernatant are pipetted into a flask for titration with 0.25 N NaOH using 6 drops, 1% phenolphthalein indicator solution. This is compared with a titration of 20 ml, 0.5 N, HCl.

### Organic Carbon Determination

The organic carbon determination is a colorimetric technique using sucrose standards, sulfuric acid and potassium dichromate. Dry AR sucrose is used to prepare 0.5, 1, 1.5, 2, 2.5 mg C/ml standard solutions. Two ml distilled water, 1 ml 10% dichromate and 5 ml sulfuric acid are added to each test tube. After cooling, 19 ml water is added and % transmittance is measured at 627 mu. Soil samples are treated the same except that 21 ml of water are added. Percent transmittance of known standards are compared to those of samples to obtain % C of samples.

## APPENDIX B. TERRESTRIAL DATA

**Table B.1** Monthly rainfall (mm) and number of rainy days at each rain gage site. S.D. = standard deviation.

Month	Rainfall (mm)				Rain days (#)
	El Nido	Manlag	Cut	Uncut	Manlag
January	49	51	63	53	2
February	11	13	11	12	3
March	9	10	7	9	1
April	18	18	20	19	3
May	254	188	155	186	10
June	306	391	379	364	18
July	405	629	501	596	13
August	632	633	544	548	16
September	358	397	442	446	13
October	322	444	425	468	8
November	343	587	636	591	6
December	106	137	131	90	7
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Mean	234	291	276	282	8
S.D.	(197)	(250)	(234)	(243)	(6)
Total	2,813	3,496	3,313	3,384	100

Anova and Tukey test of means are not significant.

Table B.2 Mean weekly runoff (liters) from the 3 erosion plots (Cut Forest, Uncut Forest and Road) for each month of 1986. Total runoff for 1986 was Cut (1557 l), Uncut (196 l) and Road (4268 l). Standard deviations given in parentheses. Divide by 8 to obtain runoff/m<sup>2</sup>.

Month	Cut	Uncut	Road
January	0	0	0
February	0	0	0
March	0	0	0
April	0	0	0
May	0	0	147 (35)
June	10 (9)	7 (7)	173 (0)
July	36 (26)	5 (5)	169 (3)
August	48 (44)	4 (4)	163 (19)
September	53 (46)	2 (2)	164 (19)
October	69 (70)	3 (4)	171 (4)
November	144 (53)	22 (23)	170 (20)
December	44 (43)	11 (10)	112 (49)
-----			
Mean	34	4	107
(S.E.)	(43)	(7)	(80)

Table B.3 Mean weekly erosion ( $\text{g/m}^2$ ) and (S.D.) from the 3 erosion plots (Cut forest, Uncut forest and Road) for each month of 1986. Total erosion for 1986 was Cut (64), Uncut (26) and Road (3,215  $\text{g/m}^2$ ).<sup>1</sup>

Month	Cut	Uncut	Road
January	0	0	0
February	0	0	0
March	0	0	0
April	0	0	0
May	0	0	347 (162)
June	2 (1)	1 (1)	585 (23)
July	4 (3)	1 (1)	196 (77)
August	2 (2)	1 (0)	93 (66)
September	1 (1)	1 (0)	41 (16)
October	3 (2)	1 (0)	26 (12)
November	2 (0)	1 (1)	19 (3)
December	1 (2)	1 (0)	11 (6)
Mean	2	1	110
(S.E.)	(1)	(>1)	(183)

<sup>1</sup> Due to rounding of means, total erosion is not equal to the annual sum of 4 times the mean weekly rate.

**Table B.4** Mean daily Manlag River water discharge, suspended sediment load and flood stage for each month in 1986. Standard deviations are in parentheses.

Month	Water Discharge (1000 m <sup>3</sup> /d)		Sediment Discharge (mt/d)		Flood Stage (m)	
January	14	(2)	75	(27)	0.63	(0.06)
February	9	(2)	15	(25)	0.49	(0.06)
March	10	(2)	26	(18)	0.52	(0.04)
April	108	(2)	37	(25)	0.54	(0.06)
May	97	(15)	53	(49)	0.59	(0.06)
June	236	(22)	156	(200)	0.95	(0.44)
July	119	(59)	116	(379)	0.58	(0.18)
August	179	(243)	49	(164)	0.63	(0.32)
September	172	(335)	59	(236)	0.54	(0.41)
October	155	(272)	176	(922)	0.62	(0.48)
November	158	(263)	91	(470)	0.57	(0.34)
December	184	(378)	412	(1,160)	0.64	(0.82)
Mean	120		105		0.61	
(S.E.)	(75)		(108)		(0.12)	

# APPENDIX C. MARINE DATA

Table C.1 Mean seawater temperatures (°C) at each site (n=2).

Month	Site							
	1	2	3	4	5	6	7	8
January	28	27	27	28	28	28	28	28
February	27	27	27	27	27	27	27	27
March	28	27	27	27	27	28	27	28
April	29	29	28	29	28	29	29	28
May	29	29	29	29	29	29	29	29
June	32	32	31	32	32	32	32	31
July	29	29	30	30	29	29	30	29
August	28	28	27	27	28	28	28	28
September	29	29	29	29	29	29	29	28
October	30	30	30	30	30	30	30	29
November	28	28	28	28	29	29	29	28
December	28	28	28	28	28	28	28	28
Mean	29	28	28	29	29	29	29	28
(S.E.)	(1)	(2)	(2)	(2)	(1)	(2)	(1)	(1)



**Table C.2 Mean salinity (ppt) at each site (n=2).**

Month	Site							
	1	2	3	4	5	6	7	8
January	35	35	34	35	34	35	34	34
February	34	35	35	34	30	30	32	34
March	35	34	34	34	34	35	34	35
April	34	35	34	34	35	35	35	34
May	35	34	35	35	35	35	36	35
June	34	34	35	35	34	34	35	34
July	33	32	34	34	32	33	34	32
August	33	29	25	24	31	31	26	33
September	33	33	33	33	32	33	32	34
October	34	34	34	33	34	34	34	34
November	34	32	33	33	33	33	29	34
December	34	34	33	33	34	34	33	33
Mean	34	33	33	33	33	33	33	34
(S.E.)	(1)	(2)	(3)	(3)	(2)	(2)	(3)	(1)

**Table C.3** Mean wind speed (m/s), standard errors and direction (n=2 days, 5 replicates at 1 minute intervals).

Month	Speed (m/s)	S.E.	Compass Bearing
January	2.5	(1.5)	65-85
February	3.9	(2.6)	95-100
March	2.7	(0.7)	90-120
April	2.4	(0.3)	280-320
May	1.7	(1.3)	100-260
June	1.5	(1.0)	235-260
July	1.7	(0.9)	200
August	4.8	(1.6)	210-240
September	4.1	(2.2)	220-240
October	1.1	(0.9)	315
November	1.9	(0.1)	180
December	3.9	(1.6)	45-60
<hr/>			
Mean	2.7	(1.2)	

**Table C.4** Mean marine sediment deposition ( $\text{mg}/\text{cm}^2/\text{d}$ ) at 8 sites in Bacuit Bay (includes  $\text{CaCO}_3$ ;  $n=4$ ). Refer to Figure 1.2 for location of sites.

Month	Site							
	1	2	3	4	5	6	7	8
January	1.1	0.6	2.0	3.0	56.2	lost	1.8	0.5
February	1.6	1.5	4.0	2.8	34.6	21.5	2.1	1.0
March	0.3	0.3	0.8	0.7	3.5	1.3	0.8	0.3
April	0.5	0.2	0.7	0.6	5.3	1.4	1.8	0.1
May	3.1	0.3	2.0	2.5	30.5	12.8	0.1	0.5
June	2.1	0.3	1.5	1.7	26.2	8.5	0.7	0.4
July	0.9	0.3	0.9	0.9	20.2	3.6	1.3	0.3
August	1.6	0.4	1.1	1.4	35.6	6.4	3.1	0.4
September	1.5	0.5	0.7	1.2	23.3	5.0	2.3	0.4
October	0.5	0.8	1.3	1.5	45.1	6.3	4.6	0.6
November	1.6	0.3	2.7	1.2	29.0	3.7	2.7	1.4
December	2.0	0.8	3.5	3.0	69.5	4.5	3.3	1.4
Mean	1.4	0.5	1.8	1.7	31.6*	6.8	2.1	0.6
S.D.	(0.8)	(0.4)	(1.1)	(0.9)	(19.0)	(5.9)	(1.3)	(0.4)

\* Significantly greater ( $p<0.05$ ) than all others; Tukey test.

**Table C.5** Mean deposition rate of non-carbonate sediments assumed to be of terrestrial origin (mg/cm<sup>2</sup>/d) at 8 sites in Bacuit Bay (n=4).

Month	Site							
	1	2	3	4	5	6	7	8
January	0.5	0.3	1.6	1.8	48.2	lost	1.4	0.2
February	0.7	0.6	1.6	1.7	5.9	16.5	1.4	0.4
March	0.1	0.2	0.5	0.5	3.2	1.1	0.7	0.2
April	0.2	0.1	0.4	0.4	4.8	1.1	1.4	0.1
May	2.9	0.2	1.3	1.9	26.7	9.5	0.1	0.2
June	1.5	0.2	0.9	1.3	22.9	6.2	0.5	0.2
July	0.5	0.2	0.5	0.6	17.7	2.6	0.9	0.2
August	0.9	0.2	0.7	0.9	31.4	4.3	2.4	0.1
September	0.8	0.3	0.3	0.8	20.8	3.8	1.8	0.2
October	0.2	0.4	0.5	0.9	39.4	4.7	3.8	0.2
November	0.8	0.2	1.4	0.8	25.7	2.9	2.1	1.0
December	1.0	0.3	2.3	1.9	60.5	3.7	2.6	1.0
Mean	0.8	0.3	1.0	1.1	25.6*	5.1	1.7	0.3
S.E.	(0.8)	(0.1)	(0.6)	(0.6)	(17.5)	(4.4)	(1.0)	(0.3)

\* Significantly greater ( $p < 0.05$ ) than all others; Tukey test.

# APPENDIX D. CORAL PARAMETERS

Table D.1 Mean corallite size and polyp extension length (fully extended) of Indo-Pacific corals. Data from taxonomic publications listed in text. Polyp extension lengths not listed here were estimated: L <5 mm, H >5 mm

	Corallite Size (mm)	Polyp Extension (mm)
Acropora C	2.00	2.0
Acropora D	2.00	L
Acropora E	2.00	L
Acropora aculeus	1.25	L
Acropora acuminata	2.00	L
Acropora anthoceris	2.00	L
Acropora arbuscula	2.00	L
Acropora austera	1.90	L
Acropora brueggemanni	1.75	L
Acropora cerealis	1.50	L
Acropora digitata	--	L
Acropora digitifera	1.50	L
Acropora dispar	1.75	L
Acropora florida	1.50	2.0
Acropora formosa	2.00	L
Acropora grandis	1.75	L
Acropora horrida	1.50	2.0
Acropora humilis	2.20	1.5
Acropora loripes	2.25	L
Acropora microclados	1.80	L
Acropora microphthalma	1.50	L
Acropora millepora	1.75	L
Acropora nasuta	1.50	2.0
Acropora nobilis	2.60	L
Acropora palifera	2.00	L
Acropora paniculata	1.70	2.0
Acropora patula	2.50	L
Acropora samoensis	2.40	1.0
Acropora selago	1.45	L
Acropora subulata	1.50	L
Acropora valenciennesi	1.20	L
Acropora valida	1.45	2.0
Acropora varia	1.40	L
Acropora vauhani	1.10	L
Acropora willisae	2.00	2.0
Alveopora allingi	4.00	70.0
Anacropora puertogalerae	0.45	1.0
Astreopora culcullata	2.30	L

**Table D.1 (Continued)**  
**Corallite size and polyp extension**

	Corallite Size (mm)	Polyp Extension (mm)
<i>Astreopora gracilis</i>	1.80	L
<i>Astreopora myriophthalma</i>	2.50	L
<i>Astreopora suggesta</i>	--	L
<i>Barbattoia amicum</i>	8.00	H
<i>Caulastrea echinulata</i>	12.00	H
<i>Caulastrea furcata</i>	9.50	H
<i>Caulastrea tumida</i>	12.50	H
<i>Coeloseris mayeri</i>	4.50	L
<i>Cycloseris dodderleini</i>	55.00	25.0
<i>Cycloseris marginata</i>	55.00	H
<i>Cycloseris sinensis</i>	67.50	H
<i>Cycloseris vauhani</i>	55.00	H
<i>Cynarina lacrymalis</i>	60.00	25.0
<i>Cyphastrea chalcidicum</i>	2.00	L
<i>Cyphastrea microphthalma</i>	1.85	L
<i>Cyphastrea serailia</i>	2.30	L
<i>Diploastrea heliopora</i>	10.00	H
<i>Echinophyllia aspera</i>	12.00	L
<i>Echinophyllia orpheensis</i>	17.00	L
<i>Echinopora horrida</i>	4.50	L
<i>Echinopora lamellosa</i>	4.25	L
<i>Echinopora mammiformis</i>	4.25	L
<i>Euphyllia ancora</i>	12.50	20.0
<i>Favia fava</i>	11.00	H
<i>Favia lizardensis</i>	11.50	H
<i>Favia pallida</i>	12.00	H
<i>Favia speciosa</i>	9.50	H
<i>Favites abdita</i>	8.00	L
<i>Fungia concinna</i>	117.50	H
<i>Funiga echinata</i>	206.50	15.0
<i>Funiga fralinae</i>	75.00	H
<i>Funiga fungites</i>	160.00	15.0
<i>Funiga mollucensis</i>	125.00	H
<i>Funiga paumotensis</i>	141.50	H
<i>Funiga repanda</i>	200.00	H
<i>Funiga scabra</i>	100.00	H
<i>Galaxea fascicularis</i>	7.00	H
<i>Goniastrea australiensis</i>	7.50	H
<i>Goniastrea edwardsii</i>	4.75	L
<i>Goniastrea favulus</i>	3.00	8.0
<i>Goniastrea palauensis</i>	10.50	H
<i>Goniastrea pectinata</i>	4.00	L

**Table D.1 (Continued)**  
**Corallite size and polyp extension**

	Corallite Size (mm)	Polyp Extension (mm)
<i>Goniastrea retiformis</i>	3.50	L
<i>Goniopora columna</i>	4.25	70.0
<i>Goniopora fruticosa</i>	2.40	10.0
<i>Goniopora lobata</i>	4.50	70.0
<i>Goniopora palmensis</i>	3.50	20.0
<i>Goniopora pandoraensis</i>	4.25	20.0
<i>Goniopora somaliensis</i>	4.75	10.0
<i>Goniopora stokesi</i>	5.50	H
<i>Goniopora tenuidens</i>	4.00	15.0
<i>Heliofungia actiniformis</i>	15.00	80.0
<i>Heliopora coerulea</i>	--	L
<i>Herpetoglossa simplex</i>	25.00	H
<i>Hydnophora exesa</i>	4.50	1.0
<i>Hydnophora ridgida</i>	6.00	2.0
<i>Leptastrea pruinosa</i>	3.50	H
<i>Leptastrea purpurea</i>	6.50	4.0
<i>Leptoria phrygia</i>	4.50	H
<i>Leptoseris explanata</i>	5.00	L
<i>Leptoseris scabra</i>	6.00	L
<i>Lobophyllia corymbosa</i>	22.50	25.0
<i>Lobophyllia hataii</i>	22.50	H
<i>Lobophyllia hemprichii</i>	20.00	H
<i>Merulina ampliata</i>	4.25	L
<i>Merulina scabricula</i>	4.25	L
<i>Millepora exesa</i>	--	L
<i>Millepora foveolata</i>	--	L
<i>Millepora intricata</i>	--	2.0
<i>Millepora platyphylla</i>	--	L
<i>Montastrea magnistellata</i>	11.00	H
<i>Montastrea valenciennesi</i>	11.50	L
<i>Montipora A</i>	1.25	L
<i>Montipora aequituberculata</i>	0.75	L
<i>Montipora angusta</i>	0.75	L
<i>Montipora cactus</i>	0.75	L
<i>Montipora confusa</i>	1.00	L
<i>Montipora corbettensis</i>	0.65	L
<i>Montipora danae</i>	0.70	L
<i>Montipora efflorescens</i>	0.75	L
<i>Montipora erythraea</i>	0.75	1.0
<i>Montipora florida</i>	0.60	L
<i>Montipora floweri</i>	0.75	L
<i>Montipora foliosa</i>	0.75	1.5

**Table D.1 (Continued)**  
**Corallite size and polyp extension**

	Corallite Size (mm)	Polyp Extension (mm)
Montipora foveolata	1.70	L
Montipora fragilis	0.80	L
Montipora gaimardi	0.80	L
Montipora grisea	0.80	L
Montipora hispida	0.80	L
Montipora informis	0.60	L
Montipora libera	0.80	L
Montipora millepora	0.60	L
Montipora monasteriata	0.75	L
Montipora nodulosa	0.75	L
Montipora peltiformis	0.75	L
Montipora pilosa	0.65	L
Montipora plateformis	0.80	L
Montipora spumosa	0.80	L
Montipora stellata	0.75	1.5
Montipora turgescens	0.90	1.5
Montipora turtlensis	0.75	L
Montipora undata	0.60	L
Montipora venosa	1.20	1.0
Montipora verrucosa	1.25	L
Mycedium elephantotus	14.00	L
Oxypora glabra	6.50	L
Oxypora lacera	6.50	L
Pachyseris rugosa	0.20	0.0
Pachyseris speciosa	0.20	0.0
Pavona cactus	4.00	L
Pavona decussata	2.00	1.0
Pavona explanulata	5.00	2.0
Pavona varians	1.00	L
Pavona venosa	1.50	L
Pectinia alcicornis	85.00	H
Pectinia lactuca	35.00	H
Pectinia paeoni	30.00	H
Physogyra lichtensteini	15.00	15.0
Platygyra daedalea	6.50	8.0
Platygyra lamellina	6.50	H
Platygyra pini	3.50	H
Plerogyra eurysepta	15.00	40.0
Pocillopora damicornis	1.20	2.5
Pocillopora verrucosa	1.00	1.0
Porites A	--	L
Porites annae	1.25	L



**Table D.1 (Continued)**  
**Corallite size and polyp extension**

	Corallite Size (mm)	Polyp Extension (mm)
Porites australiensis	1.30	L
Porites compressa	1.10	L
Porites cylindrica	1.25	1.0
Porites deformis	1.25	L
Porites latistellata	1.00	L
Porites lichen	1.15	L
Porites lobata	1.50	L
Porites lutea	1.25	2.0
Porites mayeri	0.95	L
Porites murrayensis	0.90	L
Porites nigrescens	1.15	L
Porites rus	0.60	L
Porites sillimaniana	1.15	L
Porites solida	1.75	L
Porites stephensoni	1.00	L
Psammacora superficialis	2.00	1.5
Sandolitha robusta	4.50	8.0
Seriatopora caliendrum	0.70	1.0
Seriatopora hystrix	0.60	1.0
Stylophora pistillata	1.00	1.0
Symphyllia radians	20.00	15.0
Symphyllia recta	17.50	H
Trachyphyllia geoffroyi	21.00	25.0
Turbinaria peltata	6.50	15.0

## APPENDIX E. COMMUNITY PARAMETERS

**Table E.1** Standard deviations for Figure 5.1; all substrate types.

	Site							
	1	2	3	4	5	6	7	8
<u>Live Coral</u>								
Jan	98.3	200.2	65.3	87.1	103.5	219.8	118.6	156.3
Dec	71.8	204.6	65.8	48.4	131.5	217.4	127.4	128.7
<u>Recently Killed Coral</u>								
Jan	18.1	77.8	50.0	65.1	283.5	32.5	4.4	8.8
Dec	16.0	0.0	10.0	55.1	0.0	0.0	0.0	2.1
<u>Old Dead Coral</u>								
Jan	105.5	49.9	152.9	106.8	61.2	88.9	72.3	145.6
Dec	91.7	134.4	67.7	124.8	99.7	54.2	112.9	123.8
<u>Coral Rubble</u>								
Jan	159.0	198.6	114.6	92.8	99.1	219.0	121.2	0.0
Dec	32.8	98.8	107.7	129.4	77.5	167.7	113.1	13.4
<u>Soft Coral</u>								
Jan	0.0	2.0	3.3	10.8	39.7	19.8	3.3	11.1
Dec	0.0	9.1	36.8	8.7	43.8	48.1	66.5	0.0
<u>Other</u>								
Jan	3.3	18.6	12.5	16.7	6.8	0.0	17.6	16.1
Dec	15.6	31.3	4.3	51.9	17.0	0.0	6.4	8.2

**Table E.1 (continued)**

	<b>Site</b>							
	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>5</b>	<b>6</b>	<b>7</b>	<b>8</b>
	<b><u>Sand</u></b>							
<b>Jan</b>	<b>77.6</b>	<b>74.8</b>	<b>21.9</b>	<b>26.8</b>	<b>0.0</b>	<b>34.4</b>	<b>121.2</b>	<b>11.6</b>
<b>Dec</b>	<b>80.7</b>	<b>58.3</b>	<b>25.3</b>	<b>8.0</b>	<b>0.0</b>	<b>0.0</b>	<b>40.2</b>	<b>0.4</b>
	<b><u>Sand/Mud</u></b>							
<b>Jan</b>	<b>0.0</b>	<b>3.8</b>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>85.6</b>	<b>0.0</b>
<b>Dec</b>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>68.3</b>	<b>232.6</b>	<b>59.4</b>	<b>0.0</b>
	<b><u>Mud</u></b>							
<b>Jan</b>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>61.7</b>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>
<b>Dec</b>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>	<b>32.2</b>	<b>0.0</b>	<b>0.0</b>	<b>0.0</b>

Table E.2 Species list for 3 m depth.

Species	Site							
	1	2	3	4	5	6	7	8
Acropora C						x		
Acropora D		x						
Acropora E				x				
Acropora aculeus		x	x			x		
Acropora acuminata	x			x				x
Acropora anthoceris			x					
Acropora arbuscula				x				
Acropora austera				x				x
Acropora brueggemanni			x					
Acropora cerealis				x		x		
Acropora digitata	x	x		x			x	
Acropora digitifera	x		x					x
Acropora florida	x	x	x	x		x	x	
Acropora formosa			x	x	x			x
Acropora grandis				x	x			x
Acropora horrida					x			
Acropora humilis				x		x		x
Acropora latistella			x					
Acropora loripes	x					x	x	
Acropora microclados			x	x				
Acropora microphthalma			x	x		x	x	
Acropora millepora				x		x		
Acropora nasuta			x			x	x	
Acropora nobilis								x
Acropora palifera		x	x			x		
Acropora paniculata						x		
Acropora samoensis							x	
Acropora selago				x		x		
Acropora solitaryensis							x	
Acropora subulata	x			x				
Acropora valenciennesi			x					
Acropora valida			x	x	x	x		
Acropora vauhani					x			
Acropora willisae				x				x
Alveopora allingi							x	
Anacropora puertogalerae		x			x			
Anacroproa spinosa						x		
Astreopora culcullata				x				
Astreopora gracilis	x	x	x			x	x	
Astreopora myriophthalma						x		
Astreopora suggesta	x					x		

**Table E.2 (Continued)**  
**Species list for 3 m depth**

Species	Site							
	1	2	3	4	5	6	7	8
Barbattoia amicornum	x		x				x	
Caulastrea echinulata		x						
Caulastrea furcata			x					
Caulastrea tumida		x						
Coeloseris mayeri	x	x	x				x	x
Cycloseris costulata				x				
Cycloseris marginata		x						
Cycloseris sinensis			x					
Cycloseris vaughani	x			x	x	x		
Cyphastrea chalcidicum	x	x	x					
Cyphas. microphthalma	x	x	x	x		x	x	x
Cyphastrea serailia					x			
Cynarina lacrymalis							x	
Diploastrea heliopora			x	x				
Echinophyllia aspera					x			
Echinophyllia orpheensis		x						
Echinopora gemmae	x							x
Echinopora horrida			x					
Echinopora lammellosa			x			x		
Echinopora mammiformis		x		x				
Euphyllia ancora				x				
Favia favius	x	x	x		x	x		
Favia lizardensis			x					
Favia pallida		x				x		x
Favia speciosa	x			x			x	
Favites abdita	x		x	x		x	x	
Fungia concinna	x	x	x			x	x	
Funiga echinata		x	x	x		x		
Fungia fralinae	x							
Fungia fungites	x	x	x	x	x	x	x	
Fungia mollucensis						x	x	
Fungia paumotensis	x	x	x	x	x	x	x	
Fungia repanda	x	x	x		x	x	x	
Fungia scabra				x				
Galaxea fascicularis	x		x	x	x	x	x	x
Gonias. australiensis	x							
Goniastrea edwardsii	x							
Goniastrea favulus	x							
Goniastrea palauensis		x						
Goniastrea pectinata	x	x	x	x		x	x	x
Goniastrea retiformis		x						
Goniopora columna					x			
Goniopora fruticosa					x			
Goniopora lobata					x			

**Table E.2 (Continued)**  
**Species list for 3 m depth**

Species	1	2	3	Site 4	5	6	7	8
Goniopora palmensis							x	
Goniopora pandoraensis					x	x	x	x
Goniopora somaliensis		x						
Goniopora stokesi			x					
Goniopora tenuidens			x	x		x	x	
Halomitra pileus			x					
Heliofungia								
actiniformis	x							
Heliopora coerulea							x	x
Herpetoglossa simplex			x					
Hydnophora exesa	x			x	x			
Hydnophora ridgida	x			x		x		
Leptastrea pruinosa	x	x	x	x	x		x	
Leptastrea purpurea				x	x	x		
Leptoria phrygia			x			x		
Leptoseris explanata							x	
Leptoseris scabra						x		
Lobophyllia corymbosa						x		
Lobophyllia hataii						x		
Lobophyllia hemprichii	x	x				x	x	
Merulina ampliata	x	x					x	
Merulina scabricula	x		x	x		x	x	x
Millepora exesa				x				
Millepora foveolata			x					
Millepora intricata	x				x		x	
Millepora platyphylla				x			x	
Montastrea								
magnistellata	x							
Montast. valenciennesi			x	x	x	x	x	
Montipora A						x		
Montip. aequituberculata				x	x	x		
Montipora angulata						x		
Montipora cactus					x			
Montipora confusa			x					
Montipora corbettensis							x	
Montipora danae		x	x					
Montipora efflorescens								x
Montipora erythraea			x					
Montipora florida						x		
Montipora floweri	x							
Montipora foliosa			x	x	x	x	x	
Montipora foveolata	x							
Montipora fragilis						x	x	
Montipora friabilis							x	

**Table E.2 (Continued)**  
**Species list for 3 m depth**

Species	1	2	3	Site 4	5	6	7	8
Montipora gaimardi				x				
Montipora grisea	x		x	x			x	
Montipora hispida	x		x	x	x	x		
Montipora informis	x							
Montipora malampaya							x	
Montipora millepora				x		x		
Montipora monasteriata	x		x					
Montipora peltiformis			x	x			x	
Montipora pilosa				x			x	
Montipora stellata	x		x	x	x	x		
Montipora spumosa	x	x	x	x		x	x	
Montipora turgescens	x	x		x		x		
Montipora turtlensis							x	
Montipora undata							x	
Montipora venosa				x				
Montipora verrucosa			x					
Mycedium elephantotus		x		x		x		
Oxypora glabra					x	x		
Oxypora lacera	x							
Pachyseris rugosa	x		x	x				x
Pachyseris speciosa							x	
Pavona cactus	x	x	x					
Pavona decussata		x		x	x		x	
Pavona explanulata		x		x		x		
Pavona varians		x						x
Pavona venosa					x		x	x
Pectinia alcicornis	x						x	
Pectinia lactuca	x		x			x		
Pectinia paeoni	x	x	x	x	x	x	x	
Physogyra lichtensteini				x			x	
Platygyra daedalea	x		x					x
Platygyra lamellina	x		x	x			x	x
Platygyra pini	x		x					
Platygyra sinensis			x					
Plerogyra eurysepta							x	
Pocillopora damicornis				x			x	
Pocillopora verrucosa			x	x	x	x		
Porites A						x		
Porites annae					x	x		
Porites australiensis	x					x		
Porites compressa	x			x		x	x	
Porites cylindrica	x	x		x		x	x	
Porites deformis	x					x	x	

**Table E.2 (Continued)**  
**Species list for 3 m depth**

Species	1	2	3	Site 4	5	6	7	8
Porites latistella						x		x
Porites lichen	x		x				x	
Porites lobata	x			x	x	x	x	
Porites lutea	x	x	x	x		x	x	x
Porites mayeri	x		x					
Porites murrayensis			x					
Porites nigrescens		x	x	x				
Porites palmata	x							
Porites rus	x	x	x					
Porites sillimaniana			x			x		x
Porites solida						x		
Porites stephensoni	x			x		x	x	
Psammacora superficialis				x				
Sandolitha robusta		x	x					
Seriatopora hystrix			x	x	x	x		x
Seriatopora caliendrum	x		x			x	x	
Stylophora pistillata	x		x				x	
Symphyllia radians						x		
Symphyllia recta	x			x				
Trachyphyllia geoffroyi			x					



Table E.3 Mean and (standard deviation) of coral cover, diversity values and colony size at each site (1-8) in Bacuit Bay at the beginning (Jan) and end (Dec) of 1986. N=5, 10 m transects per site.

Site/Date	Cover %	Number of species	Number of genera	Diversity H'	Evenness F	Colony size (cm <sup>2</sup> )
1 Jan	38.86 (71.85)	23 (5)	15 (2)	0.85 (0.13)	0.64 (0.04)	565 (683)
1 Dec	37.50 (98.39)	21 (2)	14 (2)	0.86 (0.16)	0.61 (0.05)	333 (173)
2 Jan	47.90 (20.46)	13 (3)	9 (1)	0.63 (0.19)	0.40 (0.14)	782 (178)
2 Dec	46.54 (20.02)	10 (3)	7 (2)	0.59 (0.11)	0.30 (0.18)	611 (683)
3 Jan	55.86 (65.86)	24 (7)	14 (5)	0.83 (0.08)	0.57 (0.10)	451 (162)
3 Dec	45.12 (65.28)	22 (3)	13 (1)	0.82 (0.08)	0.47 (0.13)	364 (93)
4 Jan	48.80 (48.44)	21 (8)	12 (5)	0.79 (0.13)	0.44 (0.13)	338 (244)
4 Dec	46.08 (87.14)	17 (6)	10 (4)	0.73 (0.11)	0.37 (0.09)	380 (129)
5 Jan	71.76 (20.50)	11 (8)	7 (6)	0.56 (0.06)	0.34 (0.20)	276 (78)
5 Dec	41.24 (24.14)	8 (5)	6 (3)	0.57 (0.26)	0.31 (0.12)	257 (125)
6 Jan	49.54 (21.73)	21 (5)	12 (1)	0.78 (0.25)	0.50 (0.15)	421 (242)
6 Dec	49.32 (21.98)	20 (3)	11 (2)	0.80 (0.24)	0.49 (0.18)	352 (175)
7 Jan	39.06 (12.74)	20 (8)	14 (4)	0.70 (0.20)	0.36 (0.26)	2,933 (4,374)
7 Dec	35.40 (11.86)	16 (4)	11 (3)	0.70 (0.11)	0.31 (0.21)	1,470 (2,286)
8 Jan	57.56 (12.87)	9 (6)	6 (3)	0.55 (0.07)	0.33 (0.13)	590 (279)
8 Dec	59.76 (15.63)	9 (4)	5 (3)	0.58 (0.11)	0.40 (0.11)	416 (187)

**Table E.4** Standard deviations for Figures 5.5 - 5.7; number of colonies of each phenotype in January and December.

	Site							
	1	2	3	4	5	6	7	8
<u>High PEA</u>								
Jan	4.5	2.6	3.5	2.6	10.1	3.8	3.2	1.5
Dec	2.7	1.5	2.8	1.4	17.4	4.6	1.6	1.5
<u>Low PEA</u>								
Jan	6.5	21.4	8.4	6.5	18.5	19.5	11.5	13.8
Dec	8.4	21.5	6.9	8.0	16.5	22.5	12.8	15.4
<u>Small CD</u>								
Jan	6.9	12.5	10.9	8.0	21.0	19.2	13.6	13.7
Dec	11.5	15.5	7.0	7.7	16.8	23.8	5.5	15.0
<u>Medium CD</u>								
Jan	1.5	17.4	3.0	1.3	12.5	1.0	1.0	1.1
Dec	3.1	21.4	1.1	1.2	18.0	1.6	1.1	2.3
<u>Large CD</u>								
Jan	4.4	2.3	4.2	3.6	2.5	4.3	3.6	3.2
Dec	1.8	1.5	3.1	0.8	1.7	4.4	3.8	1.2
<u>Ramose GF</u>								
Jan	7.2	14.0	10.9	10.2	22.3	19.1	5.8	15.5
Dec	5.0	8.7	6.6	12.5	16.9	21.6	2.6	15.3
<u>Plate GF</u>								
Jan	4.3	16.5	3.8	2.4	2.2	7.9	5.4	5.6
Dec	4.5	20.3	3.0	1.5	6.9	6.4	5.6	5.4

**Table E.4 (continued) Standard deviations for Figures 5.5 - 5.7; number of colonies of each phenotype in January and December.**

<hr/>								
Site								
	1	2	3	4	5	6	7	8
<hr/>								
<u>Massive GF</u>								
Jan	10.5	3.6	6.5	3.9	15.0	4.2	16.0	5.4
Dec	3.7	5.4	1.1	4.3	17.1	3.8	15.5	5.7
<hr/>								
<u>Phaceloid GF</u>								
Jan	5.5	0.0	5.6	4.4	0.0	2.5	6.3	0.0
Dec	5.3	0.0	4.5	2.5	0.0	2.3	2.3	0.0
<hr/>								

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