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A functional group approach to detecting shifts in macroalgal communities along a disturbance gradient

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A FUNCTIONAL GROUP APPROACH TO DETECTING SHIFTS IN MACROALGAL COMMUNITIES ALONG A DISTURBANCE GRADIENT

BY

J. C. Phillips

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of the Requirements for the Award of
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ABSTRACT

A recently proposed hypothesis argued that morphologically and functionally similar macroalgae could be grouped to study the structure of macroalgal communities. It was argued that these functional groups can be used to predict changes to community composition that result from disturbance. This study examined whether the functional group model held in detecting changes in macroalgal community structure within one bioregion, by applying it to a habitat exposed to different levels of physical disturbance associated with wave exposure. Results obtained using a functional group approach were compared to those obtained using a species level approach. Three parallel reef lines in Marmion Lagoon, Western Australia, were chosen to represent three levels of exposure (high, intermediate and low) to wave-driven physical disturbance. Wave energy measurements taken simultaneously at each reef line confirmed that a gradient of physical disturbance existed. Community structure on each of the three reef lines was measured by determining the biomass and diversity of both functional groups and species at high, intermediate and low disturbance regimes. Comparisons between the two approaches were made using ANOVA of biomass data and derived diversity indices. Multivariate analysis techniques of ordination, Principal Axis Correlation (PCC) and ANOSIM (analysis of similarities) were used to detect patterns of assemblage change. The macroalgal assemblages within the target habitat were found to be highly variable, particularly within exposure levels, when examined at both the species and functional group levels. Overall, however, the functional group approach was less able to detect differences between levels of exposure. In conclusion, the use of the functional group approach is not recommended for communities displaying high spatial heterogeneity without further rigorous testing of the model. Use of the functional group approach resulted in considerable loss of information and did not account for physiological variations between all species in the one functional group. Furthermore, algal functional groups need to be more clearly defined to overcome problems of assigning species to groups that do not easily fit the model.

DECLARATION

I certify that this thesis does not incorporate without acknowledgment any material previously submitted for a degree or diploma in any institution of higher education; and that to the best of my knowledge and belief is does not contain any material previously published or written by another person except where due reference is made in the text.

Signature

Date ..... 8 November 1996 .....

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CHAPTER 1: INTRODUCTION

A recently proposed hypothesis argued that morphologically and functionally similar macroalgae could be grouped to study the structure of macroalgal communities (Steneck and Dethier, 1994). It was argued that these functional groups can be used to predict changes to community composition that result from disturbance (Littler and Littler, 1980; Steneck and Dethier, 1994). This study examined whether the functional group model held in detecting changes in macroalgal community structure within one bioregion, by applying it to a habitat exposed to different levels of physical disturbance associated with wave exposure.

The following sections, starting with an overview of historical approaches to monitoring for changes in community structure, provide information which is necessary in understanding the purpose and nature of this study. A detailed description of macroalgal functional groups follows, with examples of their application in previous studies. Particular reference is made to studies relating functional group responses to disturbance. The chapter then concludes with the rationale and aim of this study, which have evolved from the need to investigate appropriate ways in which to monitor marine environments.

1.1 Background

Human activities are now either directly or indirectly the primary cause of changes to marine biodiversity, (National Research Council, 1995). Growing concern over the magnitude of this change has led to an awareness of the need to protect and manage marine environments (Kenchington, 1990) and, in particular, for some form of monitoring to collect information on the condition of marine ecosystems. Further, it has been recognised that this monitoring

must be conducted at an appropriate scale that distinguishes between changes falling within the range of natural variability (Oliver, *et al*, 1995) of the target ecosystem or community and those which are human-induced.

Traditionally, the study of marine communities has focused at the level of the individual species (Hay, 1994; Steneck and Dethier, 1994). Recently, however, this species-level approach to community ecology has been criticised by several authors (e.g. Sale, 1977; Peters, 1991; Bond *et al.*, 1992; cited in Steneck and Dethier, 1994; p. 476), due to emphasis placed on the uniqueness of species (Steneck and Dethier, 1984). Steneck and Dethier (1994) support this criticism and have put forward a new approach whereby morphologically and functionally similar macroalgae are grouped for the purposes of studying the structure of communities (and forces contributing to that structure). Hay (1994) suggested that such functional groups could be used to illustrate the large ecological forces that change the distribution, abundance and diversity of macroalgal communities. A species-level approach could then be adopted to identify the species-specific differences that determine interactions within functional groups (Hay, 1994).

1.2 Problems Encountered With Species Level Approaches

Identifying assemblages to species level is time-consuming and requires considerable taxonomic expertise. Hillman *et al.* (1994) were unable to identify epiphyte grazers to species level due to resource and time constraints, and were therefore restricted to using broad taxonomic/functional groups. Furthermore, considerable species diversity and taxonomic uncertainty (Simpson and Ottaway, 1987) often prevents identification to species level. The richness of fauna on Panamanian seashores prompted Menge *et al.* (1983) to divide the fauna into functional groups rather than taxonomic groupings. In response to these difficulties, numerous studies have investigated the effect of

identifying to higher taxonomic levels (Ellis, 1985; Warwick *et al.*, 1990; Agard *et al.*, 1993; Warwick and Clarke, 1993; Vanderklift *et al.*, 1996), with these authors concluding that little, if any, information is lost if data are analysed at a level higher than that of species.

A further problem identified with species level approaches is that distributional patterns are often so spatially variable that any species-dependent response to stress may be masked by this variability (Warwick and Clarke, 1993). Natural variability of benthic infauna in coastal waters off Hong Kong failed to reveal any distinct community patterns resulting from natural disturbance, when examined at the species level (Shin, 1989). In local waters, Hillman *et al.* (1994) reported a lack of clear trend in the abundance of epiphyte grazers and periphyton with distance from a sewage outfall. Similarly, in a recent assessment of the impacts of deepwater sewage outfalls, Otway *et al.* (1996) found no clear patterns in the abundances of ichthyoplankton, demersal fish and soft-bottom macro-invertebrates, and suggested that a higher level of spatial and temporal replication was necessary to detect changes. For many studies, however, resource constraints limit the intensity of sampling.

The use of taxonomic classifications in biological monitoring has been recently criticised (Walter and Ikonen, 1989; Faith, 1990). Faith (1990) argues that taxonomic inventories in biological surveillance are limited due to limited taxonomic information available, and as such provide an inadequate ecological summary. Walter and Ikonen (1989) question whether phylogenetic relationships, which indicate shared morphological, physiological and behavioural characteristics, are a sufficient criterion for predicting ecological function. A better summary of community processes can be provided by functional groups (Faith, 1990). Butler (1986) has also suggested that functional groups of sessile invertebrates, based on similar growth forms, are a more adequate monitoring tool as they vary in space more predictably than species of sessile invertebrates.

1.3 Origins of a Macroalgal Functional Group Model

The functional group approach has been in use for some time in terrestrial and freshwater ecological studies. For example, ant community organisation in two Australian national parks were compared at the level of functional groups, according to habitat requirements and competitive interactions (Anderson and Burbidge, 1992). Walter and Ikonen (1989) have also used a functional group approach in the prediction of ecological function in nematophagous arthropods.

The functional group approach to the ecology, physiology and adaptive significance of features of marine algae was developed by Littler (1980) and Littler and Littler (1980) as an improvement on earlier life-form classification schemes (e.g. Funk, 1927; Feldmann, 1938; Katada and Satomi, 1975; Chapman and Chapman, 1976; cited in Littler and Arnold, 1982; p. 307). Their work was instigated by the limitations of the traditional productivity approach to ecological studies; it failed to identify the selective processes that structure communities of primary producers (Littler and Littler, 1980). The early work of Littler (1980) and Littler and Littler (1980) tested the hypothesis that algal morphology, productivity and ecological attributes were interrelated, and examined the adaptive significance of plant morphology relative to these attributes. Many authors have since recognised the clear link between macroalgal form and function, due to their relatively simplistic structure, and argue that predictable patterns of growth forms emerge under given levels of environmental stress or disturbance (e.g., Steneck and Watling, 1982; Littler and Littler, 1984; Dethier, 1994; Steneck and Dethier, 1994).

1.4 Algal Functional Groups

There are several variations in the definition of the functional group model in the literature, depending on the purposes of the researcher, although all are based on the original conceptual model of Littler (1980) and Littler and Littler (1980). This study is based around the functional group model used by Steneck and Dethier (1994) which is based on common morphological and anatomical features of algae, as listed in Table 1.1. Functional groups are ranked according to increasing complexity of these features, and are assigned an algal functional group (FG) number as shown to the left of Table 1.1, along with the trends in increasing size, morphology, toughness and productivity rates (Littler and Arnold, 1982; Steneck and Watling, 1982). The grouping assigned to an alga depends on the part of the thallus examined (e.g. holdfast, stipe or frond), the developmental stage, or the ploidy level of heteromorphic algae (Steneck and Watling, 1982). Many algae have also been observed to be phenotypically plastic (Littler and Arnold, 1980; Taylor and Hay, 1984) and as such will be assigned different algal groupings depending on prevailing environmental conditions. Examples of algae representative of each functional group, with the exception of microalgae, are shown in Plates 1.1 - 1.7.

Table 1.1. Functional groups of algae.

Functional Group		Morphological / Anatomical Characteristics
FG 1	Microalgae	Minute, unicellular and filamentous forms; no holdfasts for attachments; includes spores and zygotes from other algal groups
FG 2	Filamentous Algae	Uniseriate, multiseriate or lightly corticated; filamentous; filaments attached by holdfasts; soft texture
FG 3	Foliose Algae	Thin sheet and tubular; uncorticated; one to several cells thick; soft texture
FG 3.5	Corticated Foliose Algae	Sheet-like; corticated; several cells thick; soft-fleshy texture
FG 4	Corticated Terete Algae	Coarsely branched; upright; terete; morphologically complex; thalli differentiated into outer cortex and inner medulla; fleshy-wiry or tough texture
FG 5	Leathery Macrophytes	Thick blades and branches; more heavily corticated than FG 4; thick-walled cells; morphologically most complex; includes non-calcified crusts; leathery-rubbery texture
FG 6	Articulated Calcareous Algae	Articulated; calcareous; upright; calcified segments connected by flexible joints; stony texture
FG 7	Crustose Algae	Epilithic; prostrate; encrusting; heavily calcified; parallel cell rows; stony or tough texture

The morphological forms of algae are closely related to ecological function. The ranking of algal functional groups corresponds to decreasing productivity rates and grazer susceptibility, and increasing toughness (Littler *et al.*, 1983a; Littler and Littler, 1984). The proportion of photosynthetic volume to structural material also decreases from very high photosynthetic volumes in the filamentous and foliose groups to low volumes in the heavily calcified crustose group (Littler and Littler, 1984). A greater proportion of structural material, however, results in increased light requirements to support such material. The less complex forms (e.g. FG 1 - 3) also show higher surface to

volume ratios (allowing greater nutrient uptake) and more rapid growth rates than more structurally complex forms (e.g. FG 5 - 7) (Littler and Littler, 1980).

Based on the ecological functions described, the algal groups at either end of the continuum show characteristics typical of r- and K-strategists respectively. Selection appears to have linked ecological function to algal morphology (Littler and Littler, 1980; 1984) and therefore a shift in functional groups can be expected across a gradient of selective force such as wave-driven disturbance, which is common in algal habitats.

The functional group approach has since been applied in a limited number of studies of marine macroalgae. Littler and Arnold (1982) extended the functional group approach to predicting primary productivity based on evolutionarily-derived morphological adaptations, and found that ranking of functional groups based on photosynthetic performance supported the functional group hypothesis of Littler (1980) and Littler and Littler (1980), even within widely differing phylogenetic lineages. These authors concluded that the functional group approach was capable of predicting the result of ecological processes that affect productivity of macroalgae, irrespective of biogeographic or phylogenetic boundaries. A similar pattern linking productivity of Caribbean macroalgal communities to functional group was demonstrated by Littler *et al.* (1983b), who also found that predictable patterns of resistance to herbivory, resistance to penetration (toughness) and calorific values of marine macroalgae in a tropical barrier reef system emerged when viewed from a functional group perspective. These authors found further support for their findings, and the generality of the functional group model, in research into algal resistance to herbivory on a Caribbean barrier reef (Littler *et al.*, 1983b).

Other studies supporting the generality of the functional group model include that by Rosenberg *et al.* (1995) into the ability of the model to predict

productivity and growth rates of Brazilian macroalgae, and the examination of functional similarity among isomorphic life-history phases of a red algae by Littler *et al.* (1987). Hanisak *et al.* (1990) recently advocated the application of the functional group model to the culture of seaweeds. They suggest that the productivity aspects of the model would be useful in identifying appropriate species or strains, where the desired product is not species-specific.

1.5 Algal Functional Groups and Disturbance

Previous studies relating algal functional groups more specifically to levels of disturbance include those of Littler and Littler (1984) and Steneck and Dethier (1994). Littler and Littler (1984) found general support for the hypothesis that morphological, physiological and ecological adaptations can be related to the level of disturbance encountered. They concluded that it would be possible to predict community composition based on knowledge of disturbance levels in given environments, or vice versa. Steneck and Dethier (1994) continued research in this direction by attempting to show that algal community composition can be predicted based on productivity potential and disturbance potential. They examined macroalgae in the western North Atlantic, the eastern North Pacific and the Caribbean and concluded that algal communities are more temporally stable and predictable when examined at the functional group level, compared to examination at the species level. Steneck and Dethier (1994) further argued that disturbance and productivity potentials are processes that structure algal communities in a form-specific manner, and that man-made alterations of either or both of these parameters will result in predictable changes to community structure.

Despite the strong conclusions drawn by Steneck and Dethier (1994), there is some concern as to the validity of their research, since comparisons are only valid when similar methodologies, sample sizes and similar habitats are used

(Abele and Walters, 1979; cited in Littler and Littler, 1981; p. 152). Steneck and Dethier's (1994) research was conducted in different habitats and in three biogeographically distinct regions, and disturbance and productivity potentials were determined differently for each location. Furthermore, their study sites were located in areas subject to high levels of wave-driven physical disturbance and, by using a transect sampling method extending from intertidal to deep subtidal waters, they were in fact sampling along a gradient of physical disturbance.

Despite these methodological problems, the studies by Littler and Littler (1984) and Steneck and Dethier (1994) demonstrated clear trends between macroalgal form and physiological function. For this reason, algal functional groups may prove useful in environmental monitoring of disturbance as physiological differences may cause groups to respond differently to a particular disturbance regime.

The two studies mentioned above (Littler and Littler, 1984; Steneck and Dethier, 1994) argue the ability of the functional group approach to predict community structure. However, there has been a lack of research addressing the reciprocal, that is, the ability to detect community changes resulting from disturbance using a functional group approach. In addition, attention has been given to the functional group model elsewhere but has rarely appeared in any published Australian marine macroalgal studies, highlighting the need for research in local waters to further validate the generality of the functional group model for the Australian algal flora. Furthermore, the high level of marine algal species diversity documented for Australian waters (Womersley, 1990; Walker, 1991) may explain why the few species level studies conducted have often failed to separate impact from natural variation (e.g., Hillman *et al.*, 1994), which suggests that a functional group approach may be more appropriate.

1.6 Physical Disturbance

The form of disturbance under examination in this study is the existing physical disturbance regime resulting from wind and oceanic swell waves, which results in press (sustained) rather than pulse (short-term) disturbance (*sensu* Underwood, 1991). The physical disturbance includes associated effects such as abrasion from suspended particles and the brushing or lashing effect (Dayton, 1975) of large leathery macrophytes on more delicate algal forms. Steneck and Dethier (1994) felt that productivity and disturbance potentials are fundamentally important in structuring algal communities. Since physical disturbance can result in a loss of biomass and reduced productivity, it can be regarded as representative of other forms of disturbance (including human-induced) in terms of its effect on the structure of algal communities. In addition, physical disturbance has already been studied by Steneck and Dethier (1994), but over biogeographic zones. In this study, therefore, the same disturbance type will be studied within a biogeographic zone with a view to compare it to their study and see if their conclusions hold.

The levels of disturbance defined in this study are relative to each other depending on the frequency and intensity of disturbance, and are intended to represent points along a gradient rather than absolute measures. High disturbance levels result from high intensity (or severity) oceanic swell and wind waves. Low disturbance levels are characterised by disturbance of considerably lesser intensity due to protection from natural formations. Intermediate disturbance levels represent an intermediate point between high and low levels of disturbance.

1.7 Summary

The recent work by Steneck and Dethier (1994) presents an alternative approach to the study of community structure of marine algae, whereby algal functional groups are used rather than species richness or distribution. These authors claim that the functional group approach can be used to predict community composition based on environmental parameters, or conversely, environmental conditions can be estimated by examining algal communities.

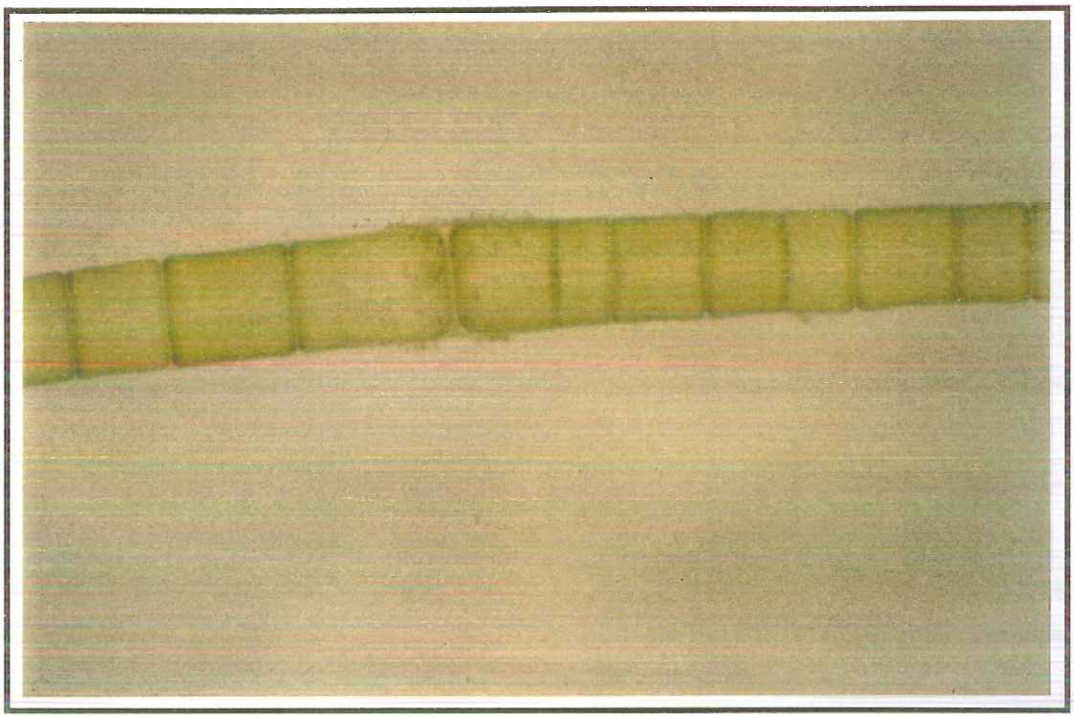
If processes, such as disturbance, impact on marine algae in a form-specific manner (Steneck and Dethier, 1994), it could have major implications for the study of disturbance. If functional groups of algae respond to disturbance in a systematic and predictable manner, the use of a functional group approach may overcome the problems often associated with species level work. As mentioned previously, species level approaches to detecting change in communities have often failed to reveal any discernible trend, due to the variable distribution of species. Alternatively, constraints on the sampling effort in previous species level studies, due to the amount of resources required to identify species, may have reduced the ability to detect changes that actually existed. Problems with the species level approach highlight the importance of investigating alternative methods of detecting change in disturbed environments, at a time when impacts on coastal environments are increasing as a result of human population growth.

As with any new approach, however, rigorous testing of the hypothesis or model is necessary to confirm its validity and generality. If proven to possess better powers of detection and/or prediction, the functional group model may provide a useful alternative to studying the ecological forces that affect the form and function of marine macroalgae, at least in certain circumstances. The benefits of adopting such an approach include a reduction in the taxonomic expertise required by researchers and the considerable amount of time saved

in species identifications. thereby allowing more effort to be directed into sampling.

The aim of this study, therefore, is to test the ability of the functional group model to detect changes to community structure. By restricting hypothesis testing to one habitat type in a localised region, across a gradient of exposure to physical disturbance, conclusions may be drawn about the strength of the functional group approach in detecting change in macroalgal community structure. The findings of this study of the functional group approach can then be used to compare against current models and methods of environmental monitoring in marine macroalgal communities.

a)



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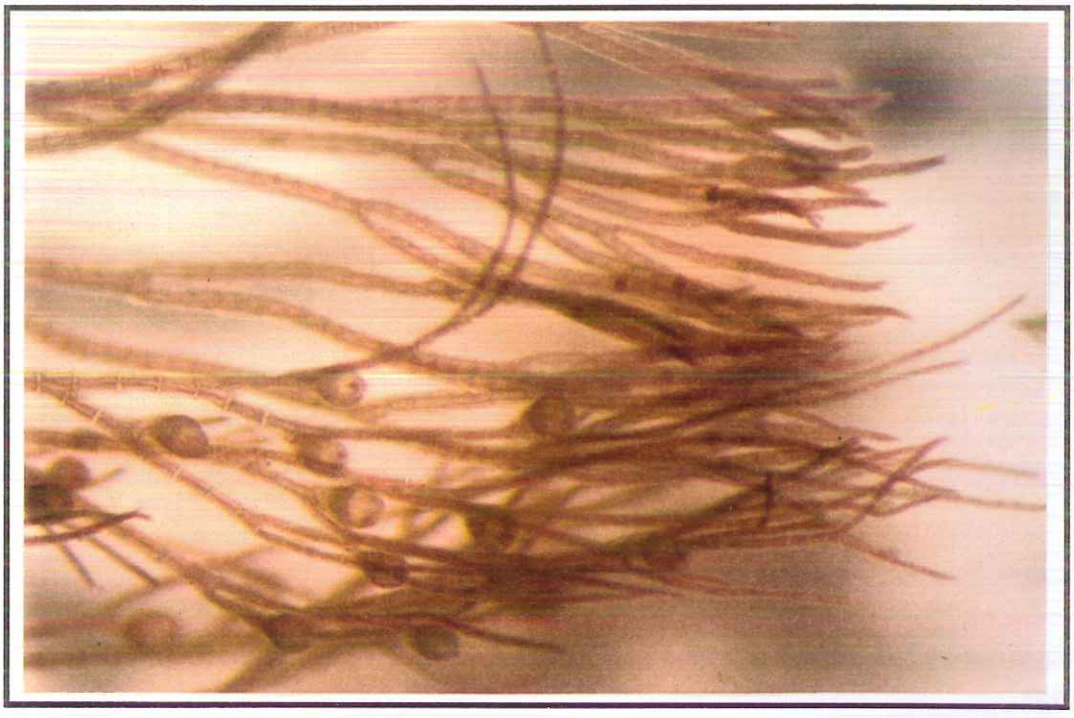


Plate 1.1. Algae representative of the filamentous algae functional group (FG 2). a) *Cladophora* sp. b) *Polysiphonia* sp.

Plate 1.2. *Kallymenia cribrosa,* a representative of the foliose algae functional group (FG 3).

Plate 1.3. *Callophycus* sp., a representative of the corticated foliose algae functional group (FG 3.5).

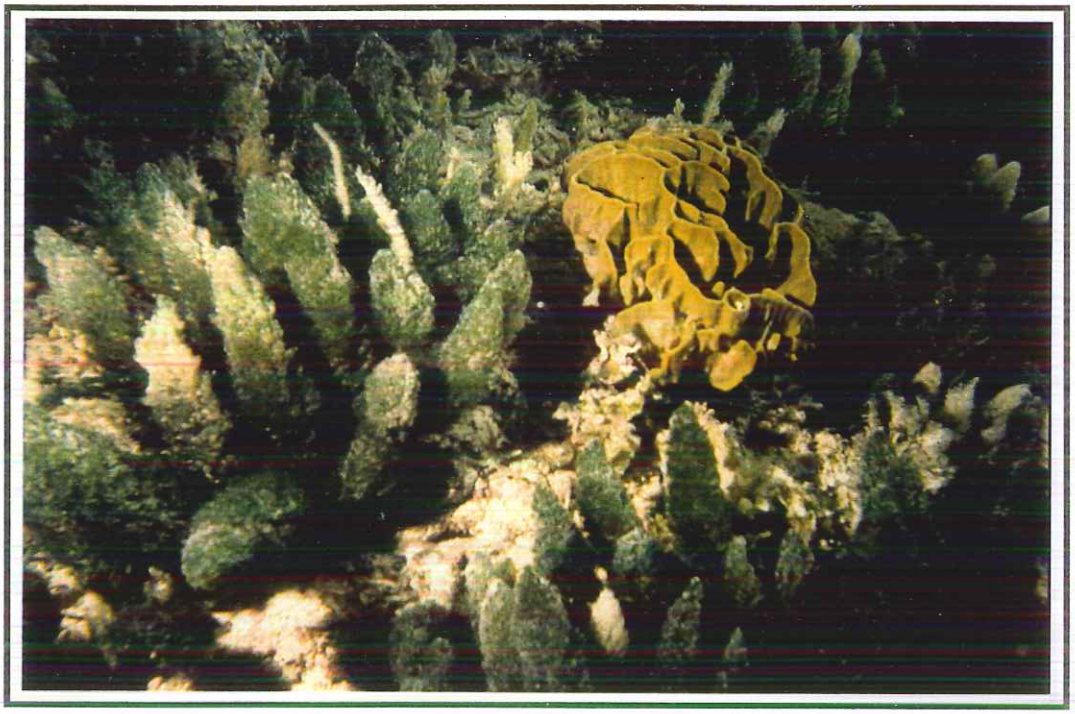


Plate 1.4. *Caulerpa* sp., representing the overall morphology of the corticated terete algae functional group (FG 4). This species does not, however, fit the description for FG 4; refer to Table 2.3 (Chapter 2) for justification for the inclusion of *Caulerpa* in FG 4.

Plate 1.5. *Ecklonia radiata*, a representative of the leathery macrophyte functional group(FG 5). *E. radiata* is the visually dominant algal species on high relief limestone reefs in Marmion Lagoon.

Plate 1.6. *Amphiroa anceps*, a representative of the articulated calcareous algae functional group (FG 6).

Plate 1.7. Encrusting coralline algae growing on reef substrate, representative of the crustose algae functional group (FG 7). Encrusting coralline algae is the dark pink/red algae seen in the upper and lower left, and lower right; paler pink patches are sponge.

CHAPTER 2: METHODS AND MATERIALS

2.1 Study Area

Marmion Lagoon (31°48′18″S, 115°42′11″E) is a shallow (<15m deep) semi-enclosed body of water situated 20km north of Perth, Western Australia, (Hatcher, 1989) (Figure 2.1). Oceanic swells from the west and south-west dominate the local wave climate year round (Searle and Semeniuk, 1985). Locally-generated wind waves, additional to swell waves, have a significant influence close inshore and during storm events (Searle and Semeniuk, 1985). Both types of waves are dampened, diffracted and refracted as they approach the coast, by a series of three parallel limestone reefs formed from submarine relict aeolianite dunes (Seddon, 1972). The dissipation of wave energy as waves encounter each successive reef line was anticipated to produce a gradient of physical disturbance ranging from highly exposed sites (offshore reefs) to sites of low exposure (inshore reefs), and was subsequently shown to be the case in an additional study (see Section 2.4).

The area has approximately 4.35km^2 of high relief reef (Johannes and Hearn, 1985), the habitat type being examined in this study. For the purposes of this study, high relief reef is defined as limestone reef showing considerable change in surface elevation (usually 1-3m). This reef type occurs on all three sets of parallel reef, providing an ideal opportunity to examine the influence of physical disturbance on community structure.

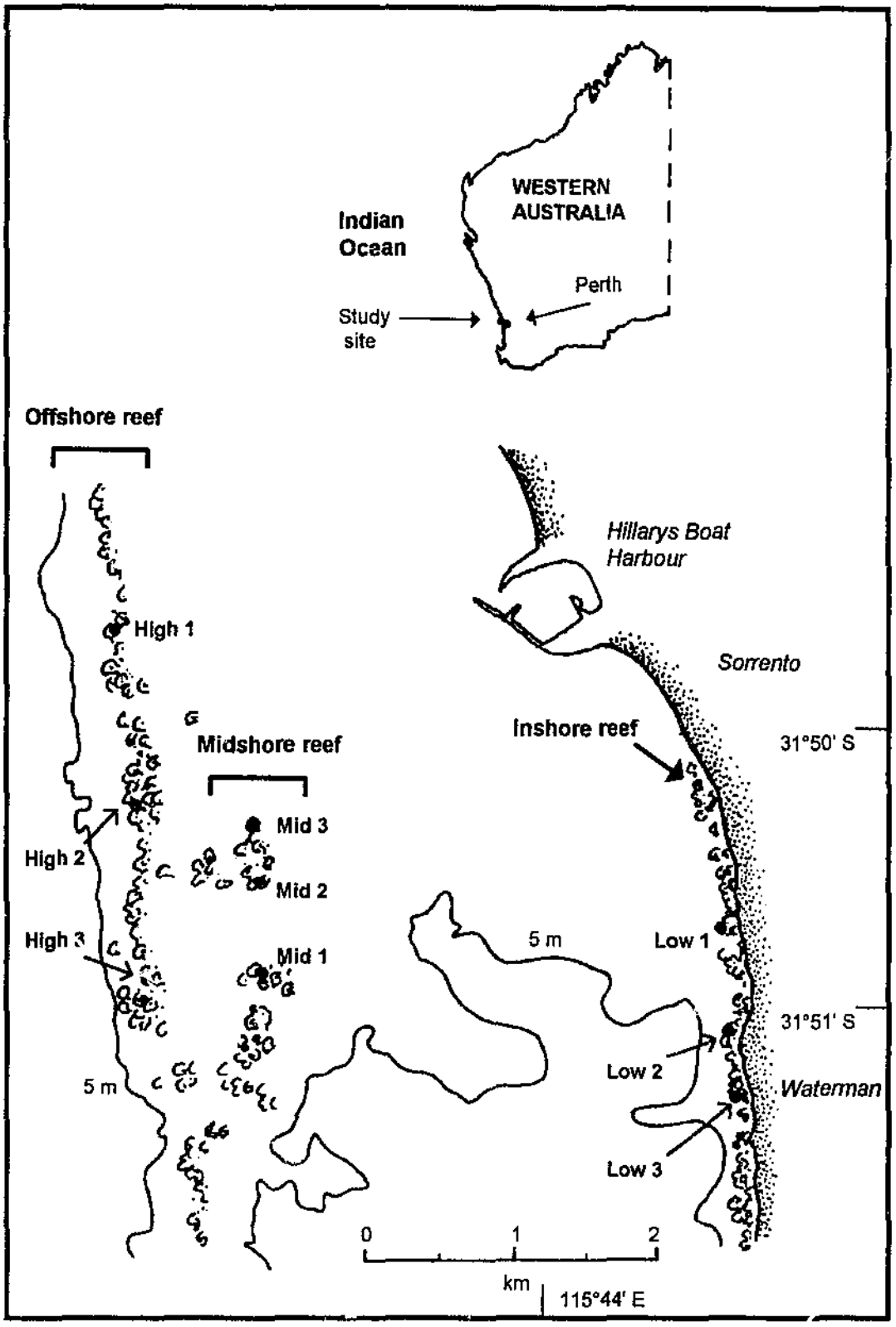


Figure 2.1. Location of Marmion Lagoon. Three parallel reef lines (offshore, midshore, inshore), chosen to represent three levels of physical disturbance, and three sampling sites on each reef (High 1-3, Mid 1-3, Low 1-3) are shown. The solid line represents the 5m depth contour.

2.2 Experimental Design

2.2.1 Two-factorial Nested Design

The biomass of macroalgal communities was sampled on high relief reefs exposed to three levels of physical disturbance. A two-factorial nested sampling design was employed (Table 2.1), whereby sampling of each disturbance level was replicated at three sites, giving a total of nine sampling sites. The two factors considered in this case were disturbance regime and sites within disturbance regimes. At each site, ten replicate macroalgal samples were collected by SCUBA divers using a 0.25m^2 quadrat. Randomisation of replicates was achieved by haphazardly throwing a quadrat within the confines of the target habitat.

In order that the disturbance regime was not confounded by seasonal variation, sampling involved a once-off effort to collect all replicates within a three week period in April-May 1996.

Table 2.1. Two-factorial nested experimental design.

Disturbance Level	High			Intermediate			Low		
Site	1	2	3	1	2	3	1	2	3
Replicates	10	10	10	10	10	10	10	10	10

n = 90

2.2.2 Pilot Study to Determine Optimum Sample Size

Due to the high level of spatial patchiness observed in Perth's limestone reef communities (Hillman *et al.*, 1994), it was necessary to conduct a pilot study to determine the optimum size and number of replicate samples (quadrats). A statistical analysis was conducted early during the project (February 1996),

based on data collected by G. Kendrick and M. Campey in November 1995 (CSIRO Division of Fisheries) and processed that summer.

Kendrick and Campey (pers. comm.) had randomly taken six $1m^2$ replicates from limestone reefs within the low disturbance regime sites at Marmion Lagoon. Each replicate comprised of four $0.25m^2$ quadrats, which allowed analyses of $0.25m^2$, $0.50m^2$ and $0.75m^2$ quadrat sizes. All macroalgae were harvested from within quadrats, species identified and biomass determined (ash-free dry weight). For each quadrat size, the order of the quadrat samples were randomised.

Their data were analysed for optimal quadrat size and sample size using the procedure outlined by Bros and Cowell (1987). This procedure used standard error (SE) as a measure of resolving the statistical power associated with an increasing sample size. The first step was to generate the SE-sample size function (Bros and Cowell, 1987) using a Monte Carlo randomisation procedure. This allowed repeated estimates of the SE for any sample size (2 through to 22 samples) to be made (Bros and Cowell, 1987) as well as the mean, minimum and maximum SE, from which the SE function was estimated for each sample size. This method was repeated for $0.25m^2$, $0.50m^2$ and $0.75m^2$ quadrat sizes at both the species and functional group level, using both biomass data and diversity indices (generated from biomass proportions). In all cases, 250 random draws were made using a customised program in Microsoft Excel. This yielded curves of the SE against increasing numbers of quadrats (sample size) from which it was possible to determine the minimum acceptable sample size beyond the region of maximum change in the slope of the SE function (Bros and Cowell, 1987).

It was then necessary to optimise the sample size by taking into consideration the competing requirements to maximise sample size but minimise cost incurred in collecting samples and the time available to process collected

samples. Cost curves for the collection of increasing numbers of samples of two quadrat sizes (0.25m² and 0.50m²) were generated based on known costs of sampling and equipment, combined with estimates of the number of samples that could be collected in one day. Effort in terms of time required to process increasing numbers of samples of each size was estimated on the basis of the actual time taken to process the preliminary samples collected (G. Kendrick and M. Campey, pers. comm.). Analysis of sample effort-sample size function revealed that in terms of cost, 16 and 10 samples per site (0.25m² and 0.50m² size respectively) were achievable given the funds available, while in terms of time a maximum of 10 and 8 samples per site, respectively, could be processed within the time frame of the project.

To determine differences in actual precision of the various sample sizes (Bros and Cowell, 1987) the minimum detectable difference at the 5% level of significance with 80% power was calculated for sample sizes ranging between 6 - 20 replicates. Minimum detectable difference is the smallest population difference detectable for a given sample size (Zar, 1984). Maximum SE was used for each sample size to give the most conservative estimate of precision (Bros and Cowell, 1987). Minimum detectable differences, for functional groups and selected species, were converted to a percentage of the mean biomass to allow comparison between morphologically different species and groups.

Table 2.2. Comparison of the minimum detectable difference (MDD) calculated as % of the mean biomass for several species and functional group (FG) variables, for two quadrat sizes. Functional group and species diversity MDD is based on Shannon index values derived from biomass data. FG = functional group.

Variable	Quadrat size	MINIMUM DETECTABLE DIFFERENCE (MDD) No. of Replicates							
		6	8	10	12	14	16	18	20
FG diversity	0.25m²	34.06	29.10	26.69	25.95	24.67	23.50	22.93	21.55
	0.50m²	31.12	27.56	25.73	24.29	23.17	22.70	21.57	20.60
Spp. diversity	0.25m²	42.99	37.95	33.97	31.36	29.94	28.83	27.17	26.09
	0.50m²	37.30	33.34	30.23	28.63	27.12	26.25	24.96	24.06
FG 2	0.25m²	78.85	70.32	64.48	58.96	56.71	53.33	50.29	48.58
	0.50m²	57.75	52.54	46.75	44.69	42.64	41.08	38.79	38.06
FG 3	0.25m²	72.63	64.57	58.73	53.02	49.55	46.33	44.27	41.44
	0.50m²	51.84	44.61	40.21	37.97	36.16	34.91	33.17	31.48
FG 3.5	0.25m²	43.97	38.27	34.87	32.71	29.78	28.90	28.08	27.97
	0.50m²	34.21	29.32	27.26	26.20	25.23	23.58	22.36	21.16
FG 4	0.25m²	53.74	44.85	41.70	38.68	36.27	34.34	32.83	31.20
	0.50m²	40.71	35.03	32.21	30.71	29.59	28.04	26.92	25.62
FG 5	0.25m²	38.61	33.97	30.39	28.29	27.11	25.86	24.21	22.95
	0.50m²	31.39	27.88	24.91	23.84	22.33	20.89	19.66	18.61
Callophycus harveyanus	0.25m²	62.48	52.73	46.94	42.03	39.93	38.34	36.32	34.45
	0.50m²	51.21	47.05	42.62	39.84	36.39	34.82	32.92	31.04
Ecklonia radiata	0.25m²	25.40	24.10	22.34	20.81	19.38	18.40	17.37	16.47
	0.50m²	18.62	15.39	14.99	14.09	13.64	12.70	12.12	11.60
Heterodoxia denticulata	0.25m²	96.62	83.90	74.80	68.29	62.85	59.83	56.48	53.02
	0.50m²	71.95	63.02	56.42	50.94	48.82	44.95	42.31	40.68
Jeannerettia pedicellata	0.25m²	76.62	67.93	61.50	58.41	55.33	51.26	48.69	45.62
	0.50m²	42.77	39.30	37.24	34.19	32.26	30.99	29.33	28.03
Lenormandia spectabilis	0.25m²	69.29	60.63	54.81	50.20	47.47	45.37	42.73	40.56
	0.50m²	53.22	48.63	43.25	40.28	38.54	36.26	34.72	33.05
Nitophyllum pulchellum	0.25m²	70.08	58.05	55.95	51.92	48.96	47.70	45.42	43.42
	0.50m²	47.30	40.85	38.59	35.53	34.55	33.52	32.04	31.01
Rhodymenia sonderi	0.25m²	72.90	62.42	56.85	51.49	47.99	45.83	43.48	41.05
	0.50m²	44.01	38.12	35.47	33.02	31.37	29.43	27.82	26.33
Sargassum sp.	0.25m²	101.0	86.62	75.97	71.03	67.33	63.66	60.64	57.48
	0.50m²	56.49	50.69	46.01	43.49	42.52	40.99	38.85	37.40

The final step in determining sample size was to overlay the plot of SE function with a curve of minimum detectable differences, for each functional group and each species considered. Examples for algal functional group 4 are given in Figure 2.2 as they were typical of the trend shown by other functional groups and species analysed.

As time was the greatest limiting factor in this study, a sample size of ten replicates of $0.25m^2$ was selected. This was considered acceptable as no significant gain in resolving power would have been achieved by an increase in replicates, while a significant increase in sampling effort would have been required to reduce the minimum detectable difference. Comparison of quadrat sizes also showed that the minimum detectable difference for ten $0.25m^2$ quadrats was approximately the same as for five $0.5m^2$ quadrats, for all species and functional groups analysed (for FG 4 shown in Figure 2.2 and Table 2.2: 41.70% at $0.25m^2$ and 32.21% at $0.50m^2$). The smaller quadrat size was chosen due to the greater ease of handling underwater and because the amount of material collected per sample was manageable.

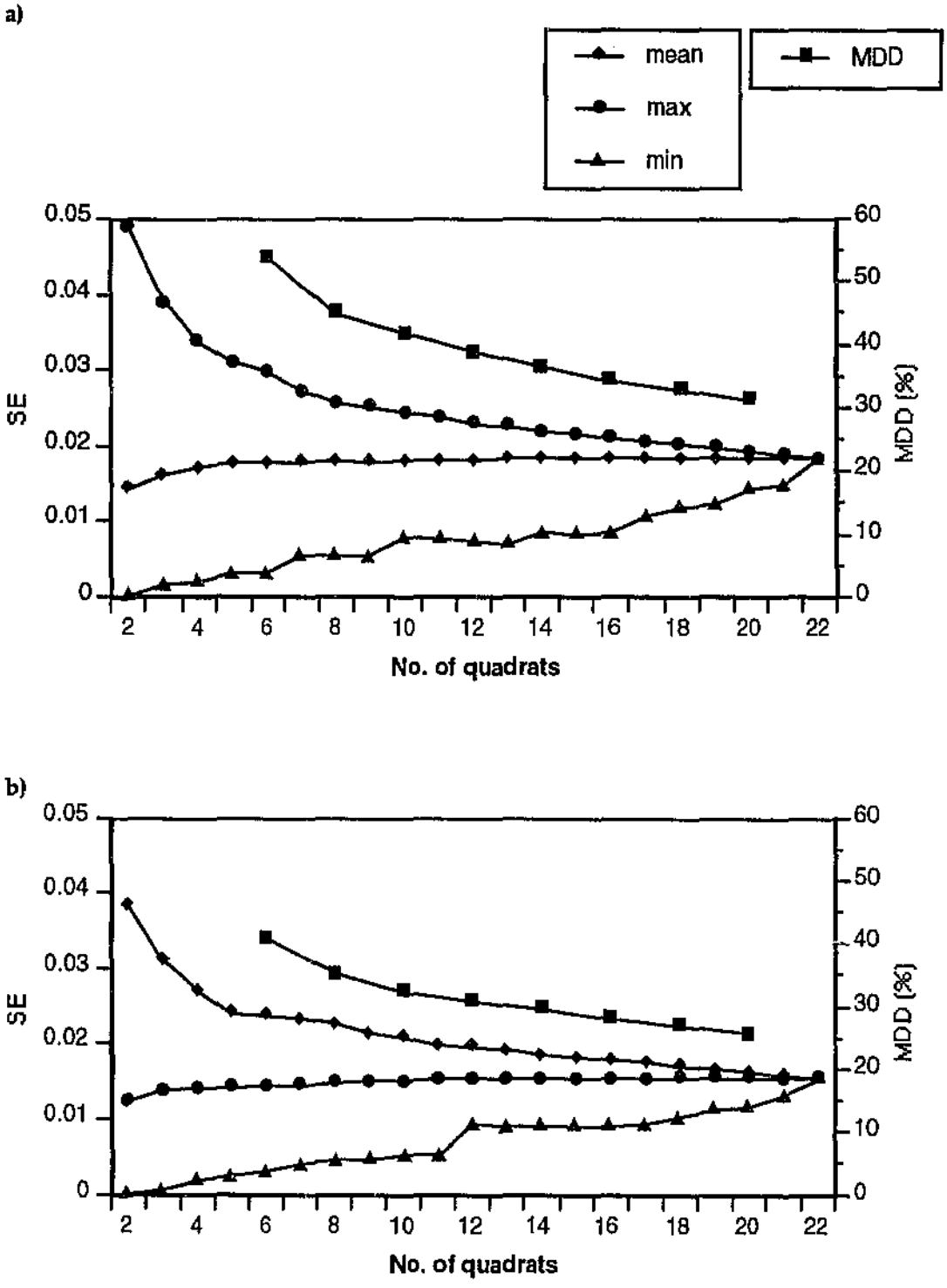


Figure 2.2. Standard error (SE)-sample size function and differences in precision, shown as minimum detectable difference (MDD), based on biomass data collected during pilot study for algal functional group 4 for a range of sample sizes of a) 0.25m² quadrats and b) 0.50m² quadrats.

2.3 Establishing Sampling Sites

Three sites were subjectively chosen on each line of reef (i.e. at the three levels of exposure to physical disturbance) to give a total of nine sites (Figure 2.1). Sites were selected after the navigational chart for the area (Department of Transport, WA 284, 1:25000) was examined to determine degree of protection from oceanic swells, along with a review of swell and wind wave directions (Searle and Semeniuk, 1985) to ensure that replicates of each level of disturbance were likely to be subject to similar disturbance regimes. All sites were selected on the basis of their conforming to a set of key environmental variables that defined the target habitat, namely: height above surrounding substrate (>0.5m); depth of overlying water column (~6m), and; nature of reef substrate (limestone, consistent rugosity between sampling locations). Sites within each level of exposure were located 300-400m apart.

2.4 Quantification of Disturbance Regimes

In order to confirm that the sampling sites located on the three reef lines did in fact represent exposure to different levels of physical disturbance, I quantified the disturbance regime at each location. This was achieved by estimating the total energy (E) per unit area of waves occurring at each location.

2.4.1 Data Collection

The height of waves passing over each reef line were recorded by measuring water depth using Yeo-Kal Submersible Data Loggers (SDLs) (Model 606) anchored at each location on 9th July, 1996. Readings were taken every second for approximately two hours, to a precision of 0.1m, on a day when a swell of 2 - 2.5m was recorded. Simultaneous recordings were obtained at all three locations.

2.4.2 Data Analysis

To account for the effects of the tide and the location of the SDLs at a depth of 6m, a regression analysis was performed on the original water depth data. Using this, the tidal influence was removed and the datum point was adjusted so that all wave cycles oscillated about a mean of zero. The mean value of these adjusted wave heights was then subtracted to account for the method of least squares employed by the simple linear regression. The absolute maximum wave height of each successive wave cycle was then determined using a Fortran computer program specifically written for this purpose, by Dr Ross Sanders of Edith Cowan University. The mean of these maxima was calculated to give a mean wave amplitude for each location. The total energy in joules per square metre of wave was calculated using the formula:

$$E = 1/8\ (\rho g H^2)$$

where ρ is the density of water in kg/m^3 (where sigma value = 25.144, 20°C and 35.5‰, ρ = 1025.144 kg/m^3), g is 9.8 m/s^2 and H is the wave height (double the amplitude) in metres.

2.5 Macroalgal Sampling

2.5.1 Collection and Processing of Samples

For each replicate, all macroalgae were removed by hand, with the exception of encrusting coralline and non-coralline algae. Biomass of these species was calculated using a correlation between percentage cover and ash-free dry weight (see Section 2.5.2). At each sampling location an additional sample of macroalgae species was taken for the purpose of identification. Samples were stored on ice, returned to the laboratory and preserved using 4-5% buffered seawater formalin solution.

Samples processed for biomass measurement were rinsed to remove sediment, salt precipitate, invertebrates, other inorganics and excess formalin. Samples

were separated by species, dried and weighed for dry weight before combusting for 2 hrs at 550°C to determine ash-free dry weight. Due to the logistical problems of ashing large volumes of the kelp *Ecklonia radiata*, only five plants were ashed and the mean loss on ignition (23.96%) was deducted from the dry weights of the remaining plants to convert to ash-free dry weights. Biomass data collected in this study is provided in Appendix 1, as it provides important baseline information on macroalgal assemblages on reefs in Marmion Lagoon.

Species identification prior to ashing was determined using relevant taxonomic keys (Lucas and Perrin, 1947; Fuhrer *et al.*, 1981; Womersley, 1984; 1987; 1994; 1996; Huisman and Walker, 1990) and the assistance of Dr John Huisman (Murdoch University). Functional group numbers were then assigned to each species using the procedure outlined in the following section.

2.5.2 Assigning Functional Groups to Species

Each species identified was assigned the appropriate algal functional group based on the functional group model described in Steneck and Dethier (1994), which is an adaptation of the earlier model presented by Littler (1980) and Littler and Littler (1984). A complete species list along with the functional group assigned to each species is given in Appendix 2.

Some species, however, did not clearly fall into any particular group as the groups defined represent points along a continuum of functional forms rather than discrete entities (Littler and Littler, 1984). In such cases, a judgment was made as to which functional group most closely approximated the functional form of the species in question, taking into consideration morphological and physiological characteristics. The life history stage of some other species collected meant that they were assigned to a functional group that differed from that of typical mature stage plants. Table 2.3 lists these species, the

functional group assigned, and a brief justification for assigning them to the particular functional groups.

Table 2.3. List of species that were difficult to assign functional groups to and justification for final decision made. FG = functional group. Refer to Table 2.1 for description of each group.

Species	FG	Justification
Dictyota sp.	3	Similar to FG 3.5 (corticated foliose algae) yet only a few cells thick and lacking cortication.
Lobophora variegata	3	As for *Dictyota* sp.
Zonaria turneriana	3	As for *Dictyota* sp.
Tylotus obtusatus	3.5	Mature plants are thickened and leathery, characteristic of the leathery macrophytes (FG 5), yet specimen collected during sampling was young plant with relatively little thickening; structurally more similar to corticated foliose algae (FG 3.5).
Caulerpa distichophylla	3.5	As for all *Caulerpa* spp., this alga is coenocytic (thallus is a single multinucleate siphon lacking cortication) and unlike any FG. Assigned to FG 3.5 (corticated foliose algae) as it most closely resembles its overall morphology and ecological function.
Caulerpa brownii	4	Also coenocytic; overall morphology resembling large corticated terete algae (FG 4).
Caulerpa cactoides	4	As for *Caulerpa brownii.*
Codium cf. *harveyi*	4	Also coenocytic, therefore as for *Caulerpa brownii.*
Laurencia elata	4	Slightly compressed thallus but physiology same as for other *Laurencia* spp. in FG 4.
Champia viridis	4	Thallus constructed of regular hollow sections and hence lacking the differentiation into outer cortex and inner medulla characteristic of corticated foliose algae (FG 4); assigned FG 4 based on overall morphology.
Gloiosaccion brownii	4	As for *Champia viridis.*
Webervanbossea splachnoides	4	As for *Champia viridis.*
Callophycus oppositifolius	5	Specimen collected differed from other *Callophycus* spp. collected as it had a noticeably thicker, denser medulla giving it a tough leathery texture.
Metamastophora flabellata	6	A calcified alga which although lacking genicula (uncalcified joints) is otherwise analogous to articulated calcareous algae (FG 6).

2.5.3 Percentage Cover-Biomass Correlation of Crustose Algae

Due to the logistical problems involving the complete removal and collection of crustose algae (encrusting coralline and non-coralline algae), a correlation was determined between the percentage cover and biomass of species for these functional groups. Using a gridded 0.25m² quadrat (divided into 5cm x 5cm squares giving a total of 81 intercept points), all crustose algae from a known area were collected. A total of five samples were collected for the regression. This is less than originally intended, however logistical constraints prevented the collection of a larger sample size. These samples were processed to ash-free dry weight and a regression analysis was performed on the results. The regression of biomass on percentage cover of crustose algae was significant ($y = 0.0769x$, $R^2 = 0.8674$, $n = 5$, $P = 0.017$) (Figure 2.3). It is unfortunate that none of the data points fell in the lower range of percentage cover, however the regression was extrapolated into this region by forcing it through the origin, as when there is zero percent cover of crustose algae there would be zero biomass.

The results of the regression analysis were then applied to the percentage cover of crustose algae recorded for each replicate (% cover was estimated using the point-intercept method) to give an estimate of the biomass.

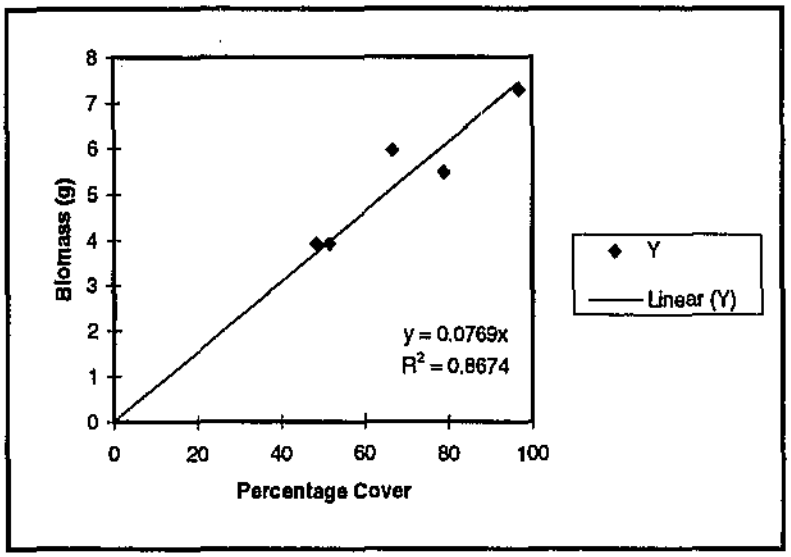


Figure 2.3. Regression of biomass on percentage cover of encrusting coralline and non-coralline algae.

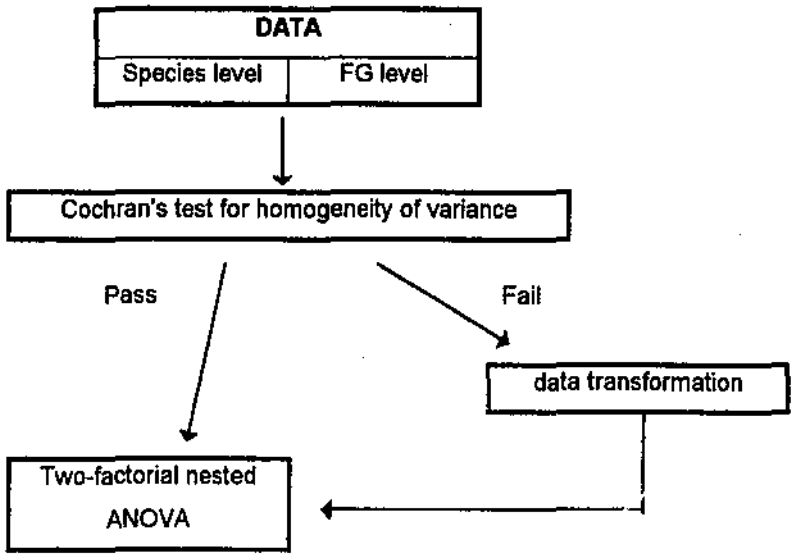
2.6 Data Analysis

Data were analysed to see whether shifts in macroalgal communities along a physical disturbance gradient could be detected at a) the species level and b) the functional group level. Specifically, the questions addressed were whether differences in macroalgal community structure resulting from exposure to different levels of physical disturbance were evident using a species level approach and, alternatively, using a functional group level approach. The two approaches were then compared to determine if they differed in sensitivity to detecting shifts in community composition. Analyses were directed at detecting within-exposure differences and between-exposure differences. Two measures of community structure were chosen to investigate differences in macroalgal communities, namely biomass and diversity. Biomass provides a simple community measure in terms of the absolute organic weight of species, while many diversity measures incorporate how equally abundant the species are ('equitability') with the number of species (species richness) (Magurran,

1988). Ecological diversity, therefore, is a more complex concept and is often used to explore many fundamental questions in theoretical and applied ecology (Magurran, 1988) such as the relationship of a community's diversity to the environmental conditions that the community is exposed to (Pielou, 1975). It was therefore relevant in this study to use diversity indices to detect shifts in macroalgal assemblages along a gradient of physical disturbance. Between-exposure differences were explored using several multivariate techniques based on (dis)similarity coefficients derived from biomass data matrices, at both species and functional group levels.

Due to the relative complexity of analyses, flow diagrams summarising the univariate and multivariate analyses that were conducted are provided (Figure 2.4). Each analysis procedure is then detailed in the following sections.

a) Univariate analyses



b) Multivariate analyses

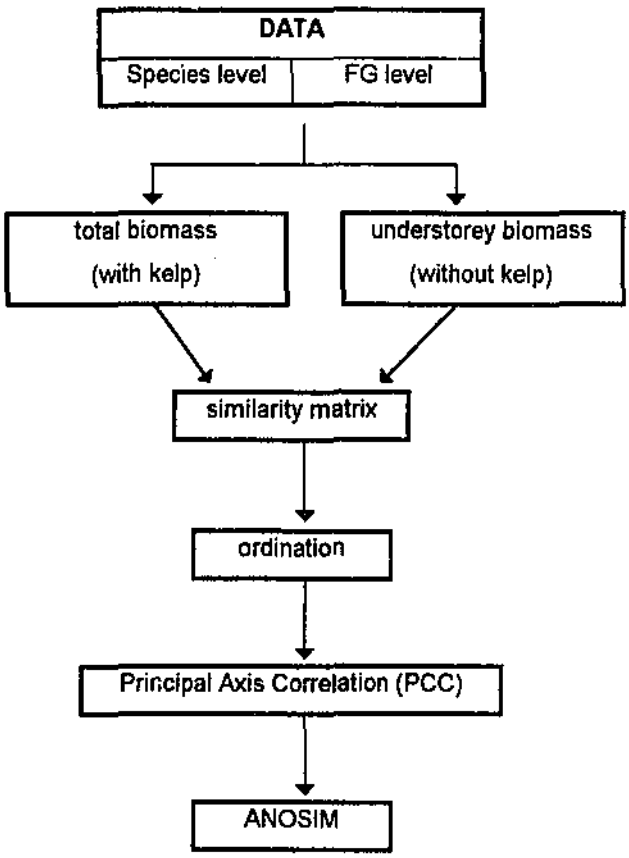


Figure 2.4. Flow diagrams summarising analyses conducted at a) univariate level, and b) multivariate level. Arrows indicate progression to the next stage of analysis. FG = functional group.

2.6.1 Comparison of Biomass at Species and Functional Group Levels

To test for differences between sites, the mean abundance (biomass) of each site was compared using a two-factorial nested ANOVA model in the software package SuperANOVA™ (Abacus Concepts, Inc.). The biomass of each site was divided into three categories: total biomass (all species combined); biomass of understorey species only, and; biomass of the canopy species, *Ecklonia radiata*, which is the visually dominant organism in this habitat. Since the kelp *E. radiata* has a high biomass compared to all other species (in most cases several orders of magnitude greater), it was felt that by splitting the biomass into understorey only and canopy only, differences between sites within an exposure might be revealed that were otherwise concealed by the dominance of the kelp biomass. Furthermore, as the habitat under investigation was essentially a kelp forest, the response of *E. radiata* to exposure to different levels of physical disturbance was of interest. At the functional group level, differences within an exposure were examined by comparing the biomass of each functional separately for each site. Post-hoc comparisons were not possible due to the two-factorial nested design where sites were nested within exposure levels.

Prior to ANOVAs being conducted, Cochran's test (Winer *et al.*, 1991) was used to test for homogeneity of variance. Where heterogeneity in variances was still present, data were rank transformed following the procedure outlined in Fowler and Cohen (1990) for assigning ranks. This allowed two-factorial nested ANOVAs to be performed on all data sets.

2.6.2 Comparison of Biomass Variability

Levene's test was used to assess whether the variability of certain species and functional group level variables differed within and between levels of exposure. Following Van Valen (1978), Levene's test was calculated as the absolute value of the replicate minus the mean, all divided by the mean, using

untransformed biomass data. This provided the mean-standardised proportional deviation from the mean for each replicate at each site.

Levene's tests were not performed on data sets that contained large numbers of zero values, recorded when a species or functional group was absent, as this would have resulted in potential misinterpretation of the variability of the distribution of such species or functional groups. The data sets that were used in Levene's tests were kelp biomass, total biomass, understorey biomass and the biomass of functional groups 3.5, 5 and 7. The calculated Levene's values were tested for homogeneity of variance using Cochran's test (Winer *et al.*, 1991), and were subsequently square-root transformed for all data sets to stabilise variance. Transformed Levene's values were compared in a two-factorial nested ANOVA using the SuperANOVA™ software package (Abacus Concepts, Inc.).

2.6.3 Comparison Using Diversity Indices

Three measures of diversity were selected for their varying degrees of sensitivity to species richness and species dominance, and for the purposes of comparing the utility of different diversity measures at both the species and functional group levels. The simplest measure used was species richness *S*, where *S* is the number of species (or functional groups) in a sample, and was chosen because algal distribution patterns in response to environmental variables are often evident at the species richness level (Kendrick *et al.*, 1988). Two other diversity measures (Margalef's and Berger-Parker) were also calculated for each sample, giving a mean value for each site. To calculate diversity, biomass data for species and for functional groups was used. Margalef's diversity index is a species richness measure which is derived using

a combination of S and N (the total biomass summed over all S species) (Magurran, 1988) and is calculated as

$$D = (S - 1)/\ln N$$

and therefore is responsive to slight changes in species richness provided an adequate sample size and sampling intensity is employed (Magurran, 1988).

The Berger-Parker diversity index, a dominance measure, is weighted towards the abundance of the most common species rather than providing a measure of species richness (Magurran, 1988). This index was selected to investigate how the dominance of the visually dominant species (*E. radiata*) and its corresponding functional group (FG 5) varied within and between exposure levels. The reciprocal of the Berger-Parker index, N_∞ was adopted so that an increase in the value of the index accompanied an increase in diversity and a reduction in dominance (Magurran, 1988) and was calculated as

$$N_\infty = 1/(N_{max}/N)$$

where N_{max} is the biomass of the most abundant species and N is the total biomass of the site.

Variances of all diversity index data sets were tested for homogeneity of variance using Cochran's test (Winer *et al.*, 1991). As some data sets displayed heterogeneous variances, all data sets were rank transformed prior to two-factorial nested ANOVAs being conducted using SuperANOVA™ (Abacus Concepts, Inc.). This allowed for direct comparisons to be made as to the utility of the different indices at both species and functional group levels.

2.6.4 Patterns of Assemblage Change

Multivariate statistical analyses were conducted to explore patterns in macroalgal assemblages due to exposure to different levels of physical disturbance. Summed species biomass and functional group biomass data matrices recorded for each site were used. Analyses were only conducted at the site level as it would be too difficult to interpret graphical representations of the ecological distance between all 90 replicates. All data sets were transformed prior to analyses using log(n+1) transformation to account for the large number of zero counts.

2.6.4.1 Ordination

The multivariate statistical analysis package PATN (Belbin, 1993) was used to conduct ordination of sites. To calculate the dissimilarity between sites, data were first associated using the Bray-Curtis association measure. This is a robust measure and is the most accepted measure used for ecological data (Faith *et al.*, 1987). Ordinations performed on the association matrix were 2-dimensional non-metric multidimensional scaling (MDS) ordinations, produced by selecting an association cut value of 0.

2.6.4.2 Principal Axis Correlation (PCC)

To investigate whether the species or functional groups were responding to the level of exposure to disturbance, the Principal Axis Correlation (PCC) program in PATN was performed against the ordinations produced for each data set. PCC is a multiple-linear regression program that determines the direction of best fit and the correlation coefficient of that fit for each species or functional group in the ordination space (Belbin, 1993). The correlation coefficient was used as a rough indicator of the significance of each species or functional group (Belbin, 1993). Those species or functional groups with a correlation coefficient greater than 0.8 were considered to be significantly influencing the ordination pattern.

2.6.4.3 Analysis of Similarities

To test for differences between exposure levels and between sites within exposure levels, two-way nested ANOSIM (analysis of similarities) was conducted using the PRIMER (Plymouth Routines In Multivariate Ecological Research) analysis package. ANOSIM is a non-parametric permutation procedure that is applied to the (rank) similarity matrix underlying the ordination of sites (Clarke and Warwick, 1994). The ANOSIM procedure, as outlined by Clarke (1993) and Clarke and Warwick (1994), tested the null hypothesis of no difference between sites within exposure levels and, then, tested for differences between exposure levels.

Data used was log(n+1) transformed total biomass and understorey biomass, at both the species level and functional group level. The Bray-Curtis association measure was again used, to be consistent with other multivariate analyses performed. Using the association values, ANOSIM calculated a global *R* statistic which is the average of ranked similarity values of pairs of replicates (Clarke, 1993). The *R* statistic was then recalculated for all possible permutations of the replicates, and the distribution of permuted *R* values compared to the original *R* value to give a significance value (Clarke and Warwick, 1994). The significance value, shown as a percentage, indicates the number of times a better assemblage pattern was obtained from random rearrangement of the association matrix, compared to the original pattern shown in the data (Clarke and Warwick, 1994). As an example, if 3% of the random permutations result in a better pattern than the original sample groups, the null hypothesis is rejected and it is concluded that there is a significant difference ($p = 0.03$). In providing an indication of the significance of the observed pattern, ANOSIM overcomes the subjective analysis of ordination plots.

CHAPTER 3: RESULTS

3.1 Disturbance Regimes

A gradient of exposure to wave-driven physical disturbance (mean wave energy) was observed between three lines of reef. Mean wave energy at the offshore (high exposure) reef was more than three times the energy at the inshore (low exposure) reef (Figure 3.1). There was a decrease in wave energy from the offshore site to the inshore site (Figure 3.1), corresponding to the dissipation of swell and wind waves as they approached the shore.

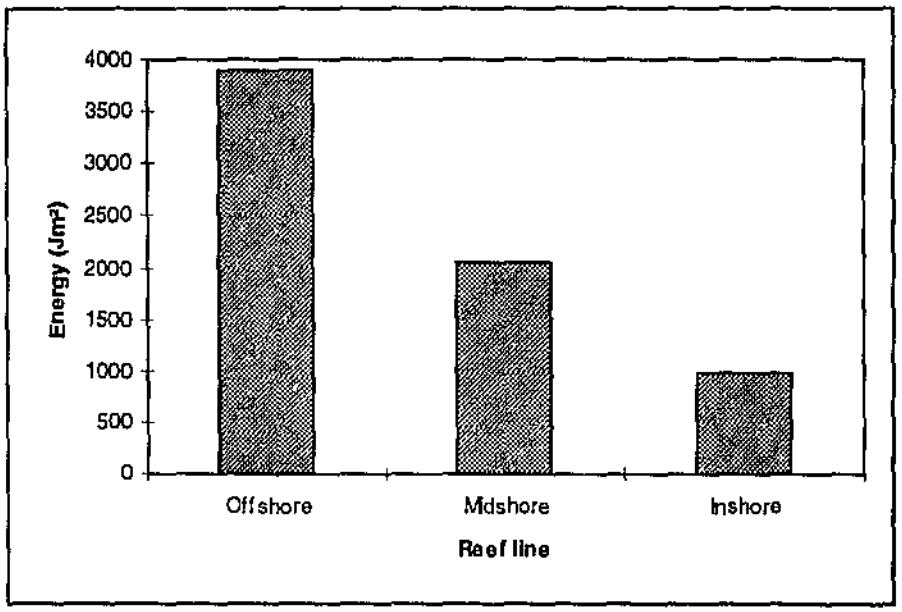


Figure 3.1. Mean wave energy recorded simultaneously over two hours at three lines of reef in Marmion Lagoon on 9th July, 1996.

3.2 Macroalgal Sampling

A total of 82 species were recorded during the macroalgal sampling (Table 3.1). These species were unevenly distributed across the seven algal functional groups, with over 40% of all taxa belonging to FG 3.5 (corticated foliose algae). Functional group 4 was also species-rich (22% of all taxa). The least species-rich group (excluding FG 7 for which species were not identified) was FG 2 (filamentous algae) (Table 3.1). A full list of all species recorded during this study, along with the functional group to which they were assigned, is given in Appendix 2.

Table 3.1. Number of taxa and percentage of total taxa recorded for each functional group (FG).

Functional Group		No. of taxa recorded	% of total taxa
FG 2	filamentous algae	3	3.7
FG 3	foliose algae	7	8.5
FG 3.5	corticated foliose algae	33	40.2
FG 4	corticated terete algae	18	22.0
FG 5	leathery macrophytes	14	17.1
FG 6	articulated calcareous algae	6	7.3
FG 7	crustose algae	1	1.2
	Total	**82**	**100.0%**

The number of species specific to each pair of exposure levels gave an indication of the degree of similarity in assemblage composition between reef lines. The High, Mid and Low sites had 22, 9 and 15 species which were unique to those regions respectively (Figure 3.2). In addition to these site-specific species, 16 species were common to all three exposure levels (Figure 3.2). An additional seven species were common to both High and Mid

3.2). An additional seven species were common to both High and Mid exposure sites, and an additional four were common to both Mid and Low (Figure 3.2). This indicated that the midshore reef line was more similar to the offshore than to the inshore reef line. Overall, however, species composition was more similar between High and Low exposure levels, with nine species in common that were not recorded at the midshore reef line (Figure 3.2).

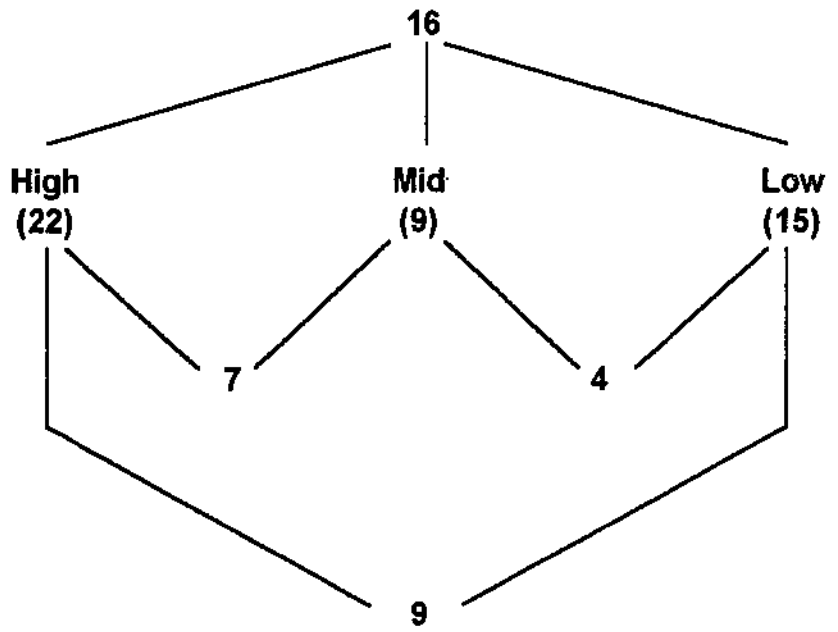


Figure 3.2. Similarity of species composition across the disturbance gradient. Lines joining exposure levels indicate number of species found only at those exposures (e.g. 16 species found at all exposure levels, 7 species found only at High and Mid exposures, 9 species found only at High and Low exposures). Numbers in parentheses indicate number of species unique to each exposure level.

3.3 Overall Patterns in Species and Functional Group Analyses

With only a few exceptions, there were no clear trends shown in the response of individual species or functional group components. The absence of clear trends was supported by a consistent degree of variability, in terms of biomass, across all levels of exposure for selected species and functional group components. The use of certain diversity indices did, however, show differences in the sensitivity of species and functional group level approaches, with differences between sites generally more pronounced at the species level. All multivariate techniques used to investigate patterns in the assemblages as a whole revealed stronger trends evident at the species level. Several sets of analyses will be presented in the following sections, each of which reveal overall trends outlined above.

3.4 Biomass Comparisons

3.4.1 Species Level Comparisons

Between exposure levels there were no significant differences in the biomass of kelp (*Ecklonia radiata*), the total biomass of understorey species, or the total biomass of all species (Table 3.2). This indicated that there was little variation in these components between reef lines. The mean biomass of kelp at each site, however, showed that there was considerably less kelp at the inshore sites (Low 1-3) compared to the midshore and offshore sites (Mid 1-3 and High 1-3 respectively) (Figure 3.3), but this was not significantly different from other reef lines due to the high level of variability within reef lines. A very similar trend was shown in the total biomass, as kelp accounted for nearly all the biomass recorded for each site (Figure 3.4).

Differences between sites within exposure levels were more apparent, although only understorey biomass was statistically significant (Table 3.2).

Biomass of understorey species was highly variable within exposure levels (Figure 3.4) resulting in a significant difference between sites within exposures (Table 3.2).

Table 3.2. Results of two-factorial nested analysis of variance (ANOVA) tests for differences in the biomass of three species-level components. Data used were untransformed in all cases. Understorey biomass is the total biomass less the kelp biomass for each site.

VARIABLE	TWO-FACTORIAL NESTED ANOVA			
	Between Exposure Levels			
	d.f.	Mean Square	*F*-value	*P*-value
Kelp biomass	2	22678.372	1.785	0.3086 NS
Understorey biomass	2	450.280	1.322	0.3876 NS
Total biomass	2	16759.126	1.577	0.3404 NS
	Between Sites Within Exposure Levels			
	d.f.	Mean Square	*F*-value	*P*-value
Kelp biomass	6	12.707.048	2.083	0.1085 NS
Understorey biomass	6	340.693	2.796	0.0452 *
Total biomass	6	10629.053	1.803	0.1529 NS

KEY:

NS Not statistically significant
* Statistically significant ($p < 0.05$)

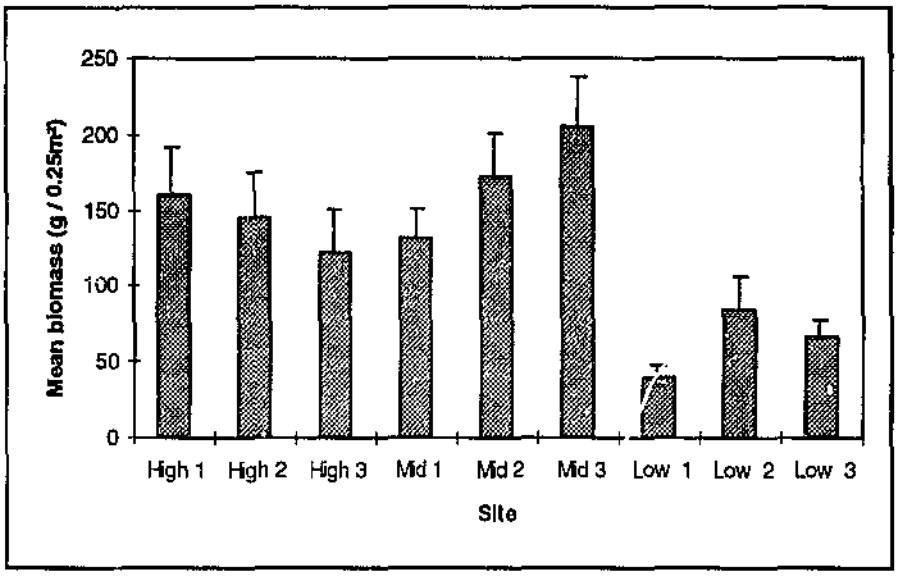


Figure 3.3. Mean biomass (+ SE, n = 10) of the canopy-forming kelp (*Ecklonia radiata*) recorded at three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

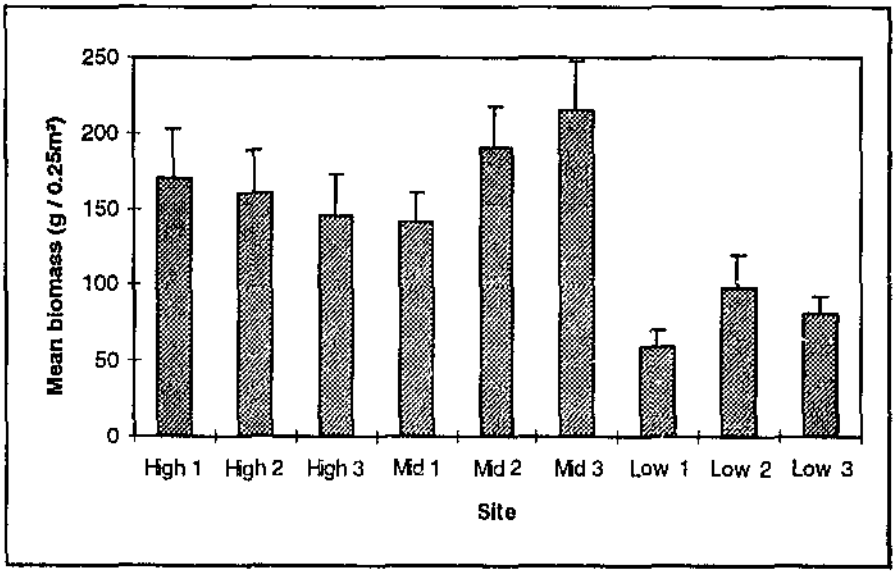


Figure 3.4. Mean total biomass (+ SE, n = 10) of macroalgae recorded at three sampling sites (1, 2, 3) within each level of exposure (High, Low, Mid).

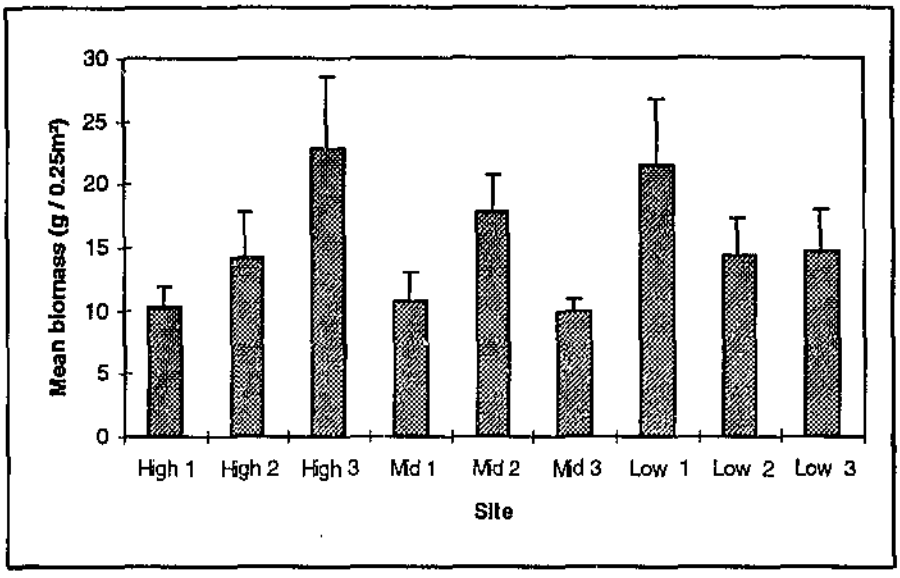


Figure 3.5. Mean total biomass (+ SE, n = 10) of all understorey macroalgae recorded at three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

3.4.2 Functional Group Level Comparisons

None of the seven functional groups showed significant differences in mean biomass along the exposure gradient (Table 3.3). Only two functional groups, (FG 6 and FG 7) were significantly different in mean biomass between sites within exposure levels (Table 3.3). The remaining functional groups, while not statistically significant, showed greater differences within exposure levels than between exposure levels (Table 3.3). These trends are reflected in the plots of mean biomass for each functional group (Figures 3.6 - 3.12). The overall trend, therefore, was variability in mean biomass within reef lines but no evidence of differences along the exposure gradient.

Table 3.3. Results of two-factorial nested analysis of variance (ANOVA) tests for differences in functional group biomass between the nine sampling sites within exposure levels. Rank transformed data were used in all cases.

VARIABLE	TWO-FACTORIAL NESTED ANOVA			
	Between Exposure Levels			
	d.f.	Mean Square	*F*-value	*P*-value
FG 2	2	827.465	1.084	0.4422 NS
FG 3	2	153.025	0.302	0.7593 NS
FG 3.5	2	3135.519	2.972	0.1943 NS
FG 4	2	1285.719	1.959	0.2856 NS
FG 5	2	2498.662	3.104	0.1860 NS
FG 6	2	311.490	0.186	0.8394 NS
FG 7	2	678.425	0.409	0.6967 NS
	Between Sites Within Exposure Levels			
	d.f.	Mean Square	*F*-value	*P*-value
FG 2	6	763.171	2.151	0.1000 NS
FG 3	6	506.312	1.392	0.2509 NS
FG 3.5	6	1055.000	1.752	0.1627 NS
FG 4	6	656.350	1.236	0.3017 NS
FG 5	6	805.008	1.697	0.1738 NS
FG 6	6	1676.950	8.229	0.0001 **
FG 7	6	1660.512	2.949	0.0374 *

KEY:

FG Functional Group (refer to Table 1.1 for description of each group)
NS Not statistically significant
* Statistically significant ($p < 0.05$)
** Highly statistically significant ($p < 0.01$)

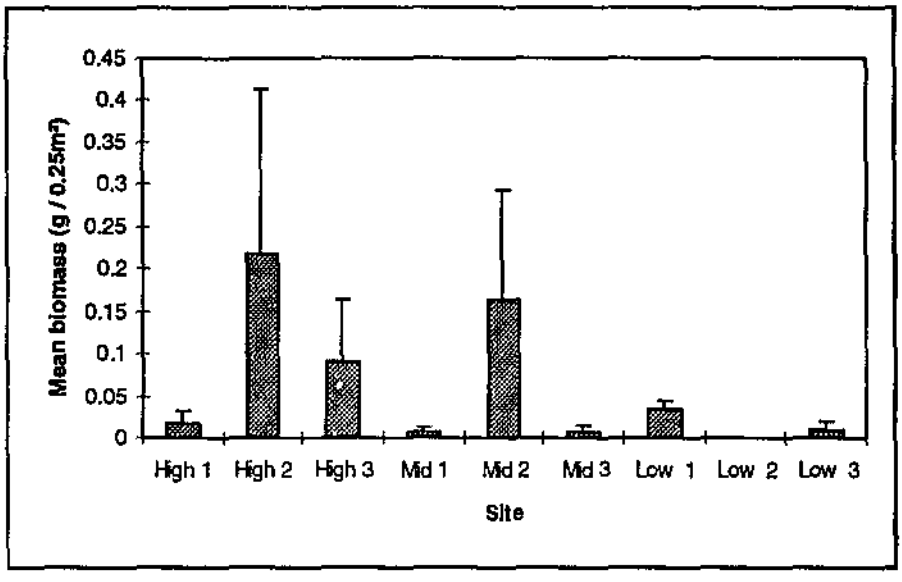


Figure 3.6. Mean biomass (+ SE, n = 10) of filamentous algae (FG 2) recorded at three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

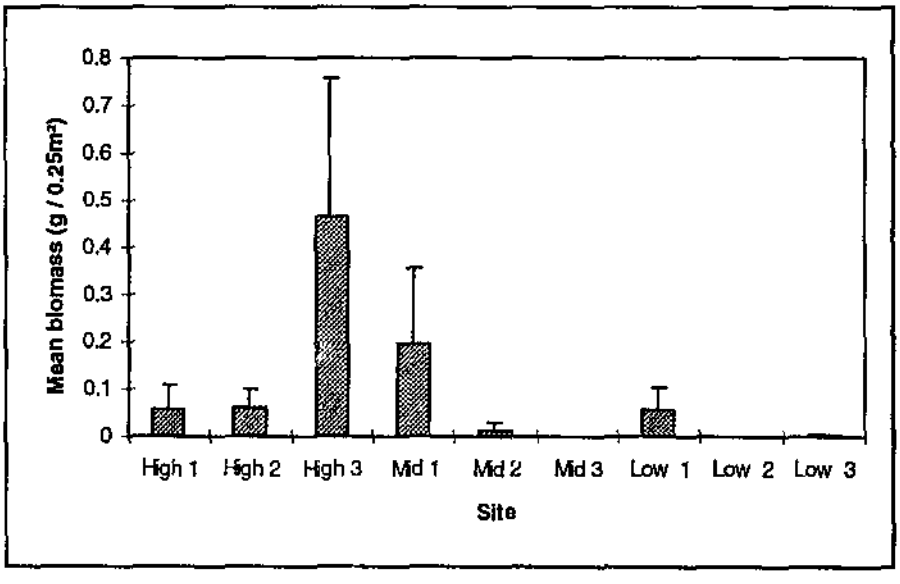


Figure 3.7. Mean biomass (+ SE, n = 10) of foliose algae (FG 3) recorded at three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

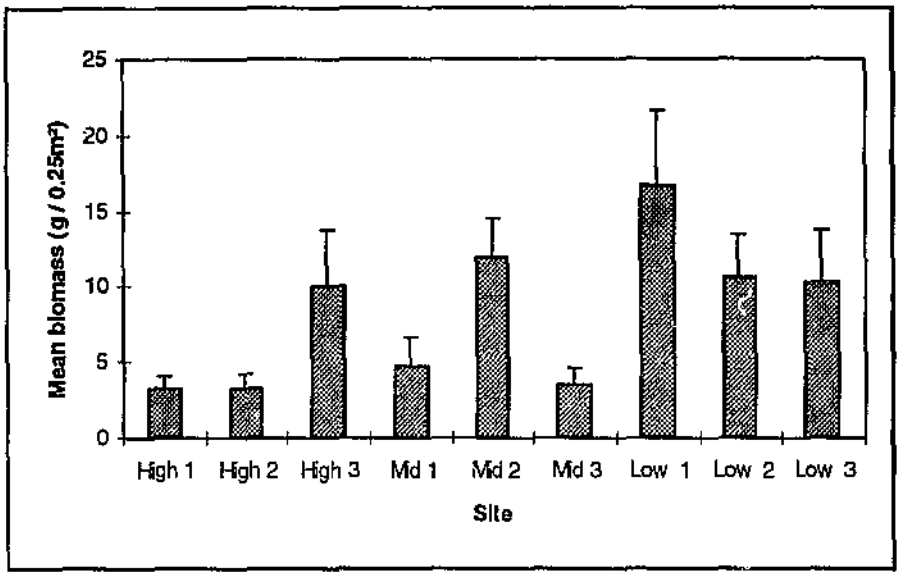


Figure 3.8. Mean biomass (+ SE, n = 10) of corticated foliose algae (FG 3.5) recorded at three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

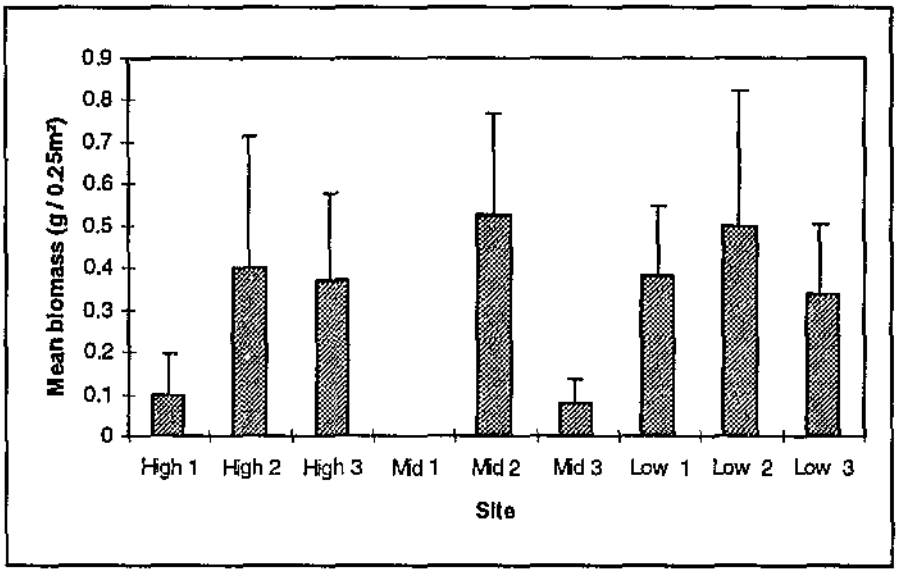


Figure 3.9. Mean biomass (+ SE, n = 10) of corticated terete algae (FG 4) recorded at three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

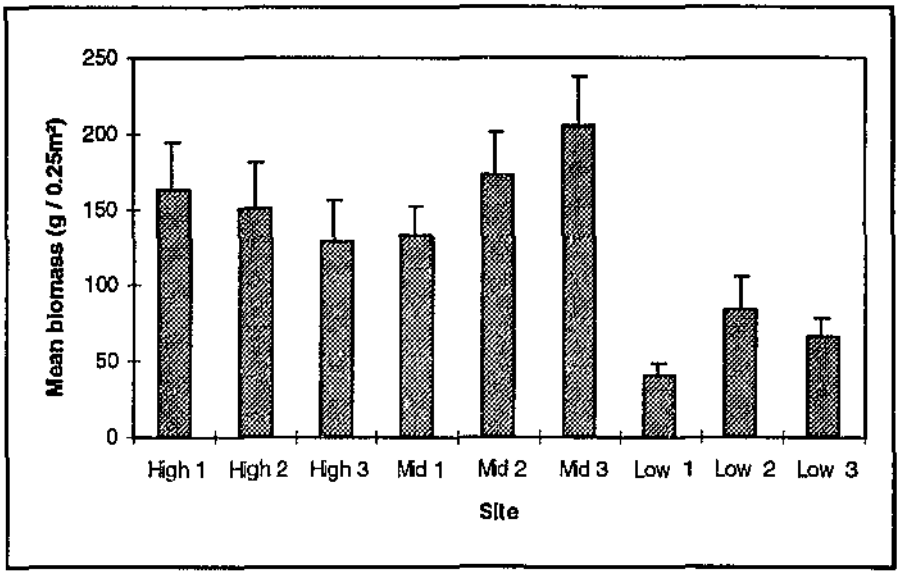


Figure 3.10. Mean biomass (+ SE, n = 10) of leathery macrophytes (FG 5) recorded at three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

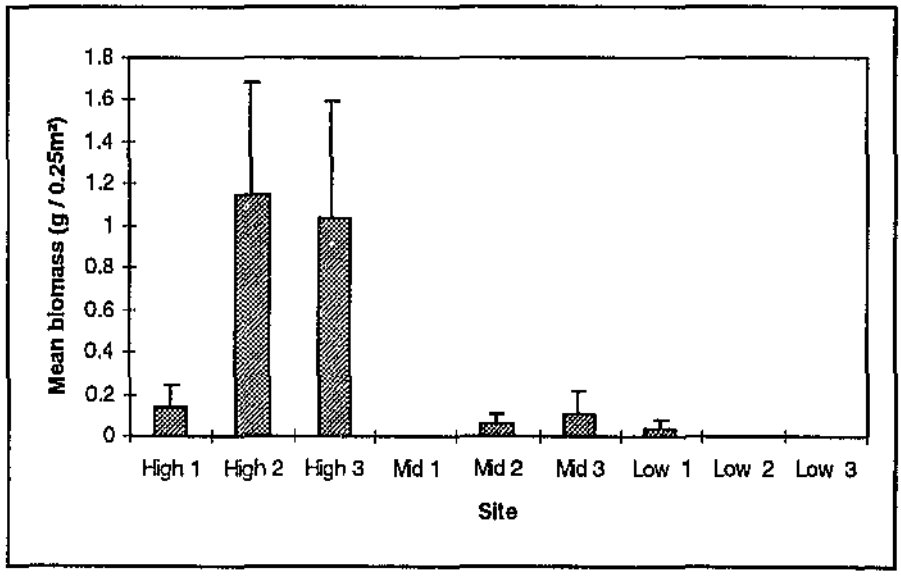


Figure 3.11. Mean biomass (+ SE, n = 10) of articulated calcareous algae (FG 6) recorded at three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

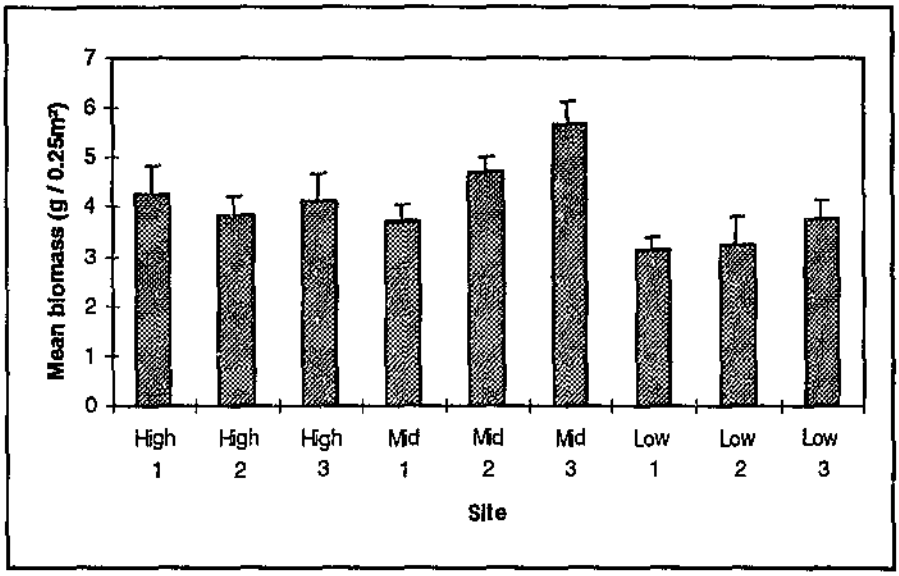


Figure 3.12. Mean biomass (+ SE, n = 10) of crustose algae (FG 7) recorded at three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

3.4.3 Variability of Biomass

The absence of significant differences in the biomass comparisons that have just been described suggested that there were similar levels of variability for the components measured, at both spatial scales (i.e. between and within exposure levels). To confirm this, Levene's tests were conducted to examine the proportional deviation of biomass from the mean, and comparisons between sites and exposure levels were made using ANOVA. As mentioned previously, Levene's tests were not performed on data sets that contained large numbers of zero values, due to the potential for misinterpretation. This restricted the possible analyses to kelp, understorey and total biomass, and functional groups 3.5, 5 and 7 (corticated foliose, leathery macrophytes and crustose algae, respectively).

No significant differences were found for any of the variables tested at either the exposure or site within exposure level (Table 3.4). This result clearly showed that the assemblages sampled on all three reef lines displayed the same degree of spatial patchiness for the population variables measured. For all variables, with the exception of understorey biomass, differences were more significant between exposures than between sites within exposures (Table 3.4), in other words there was greater variability between reef lines than within. This trend was evident in the plots of the mean Levene's test values (untransformed) for each site, shown in Figures 3.13 and 3.15 - 3.18. For understorey biomass (Figure 3.14) differences in variability were greater within exposure levels than between exposure levels.

Table 3.4. Results of two-factorial nested analysis of variance (ANOVA) tests for differences in Levene's test values of the mean biomass at species and functional group levels. Data were square-root transformed Levene's values in all cases. Understorey biomass is the total biomass less the kelp biomass for each site.

VARIABLE	TWO-FACTORIAL NESTED ANOVA			
	Between Exposure Levels			
	d.f.	Mean Square	*F*-value	*P*-value
Species level				
Kelp biomass	2	0.035	0.990	0.4675 NS
Understorey biomass	2	0.032	0.660	0.5787 NS
Total biomass	2	0.044	2.484	0.2310 NS
FG level				
FG 3.5	2	0.059	1.706	0.3201 NS
FG 5	2	0.027	1.328	0.3862 NS
FG 7	2	0.042	3.361	0.1714 NS
	Between Sites Within Exposure Levels			
	d.f.	Mean Square	*F*-value	*P*-value
Species level				
Kelp biomass	6	0.036	0.534	0.6605 NS
Understorey biomass	6	0.049	0.736	0.5335 NS
Total biomass	6	0.018	0.349	0.7899 NS
FG level				
FG 3.5	6	0.034	0.259	0.8545 NS
FG 5	6	0.020	0.325	0.8073 NS
FG 7	6	0.012	0.371	0.7739 NS

KEY:

FG Functional Group
NS Not statistically significant

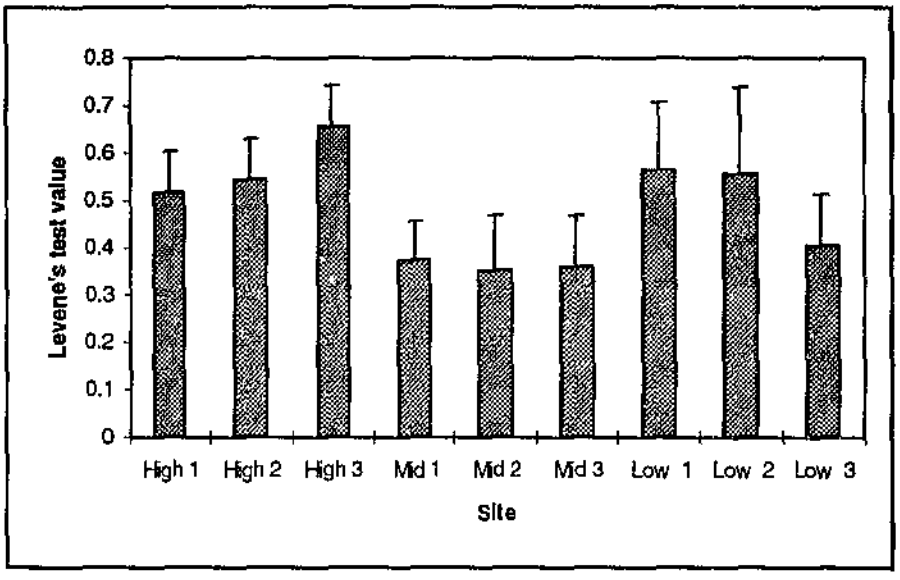


Figure 3.13. Mean untransformed Levene's test values (+ SE, n = 10) of the proportion of deviation from the mean, based on kelp biomass at three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

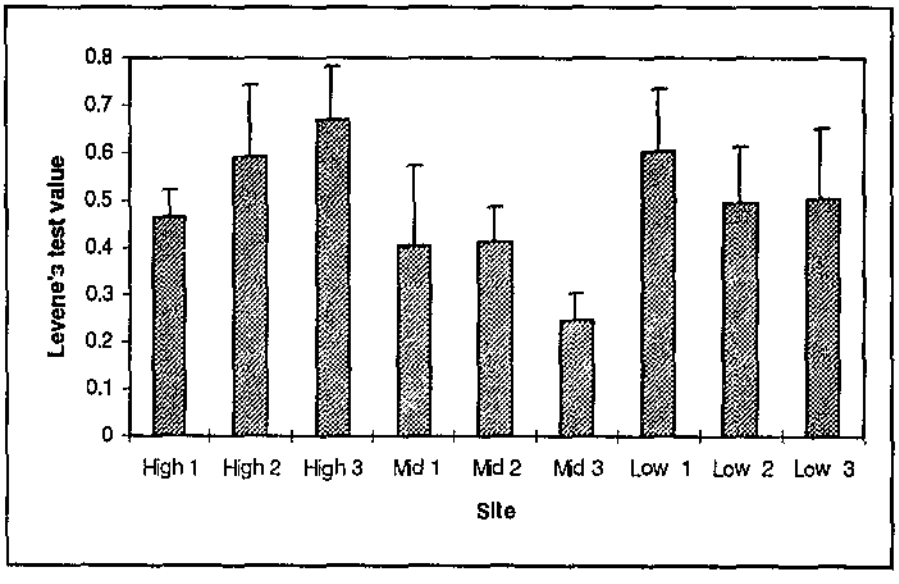


Figure 3.14. Mean untransformed Levene's test values (+ SE, n = 10) of the proportion of deviation from the mean, based on understorey biomass at three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

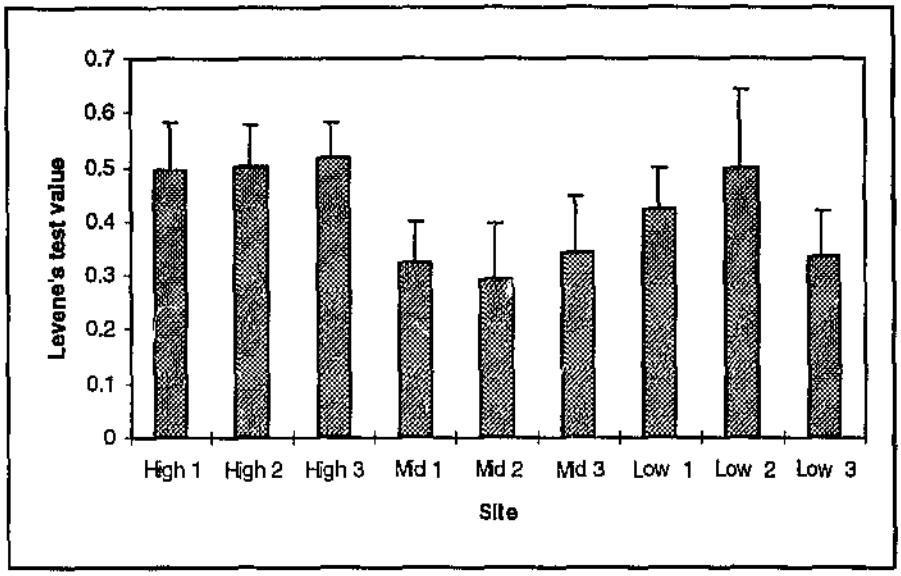


Figure 3.15. Mean untransformed Levene's test values (+ SE, n = 10) of the proportion of deviation from the mean, based on total biomass at three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

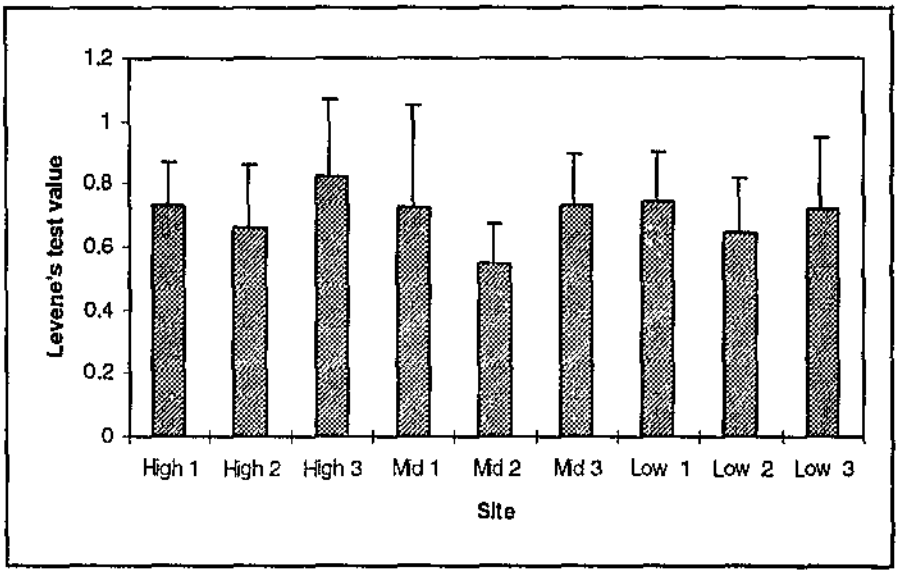


Figure 3.16. Mean untransformed Levene's test values (+ SE, n = 10) of the proportion of deviation from the mean, based on biomass of corticated foliose algae (FG 3.5) at three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

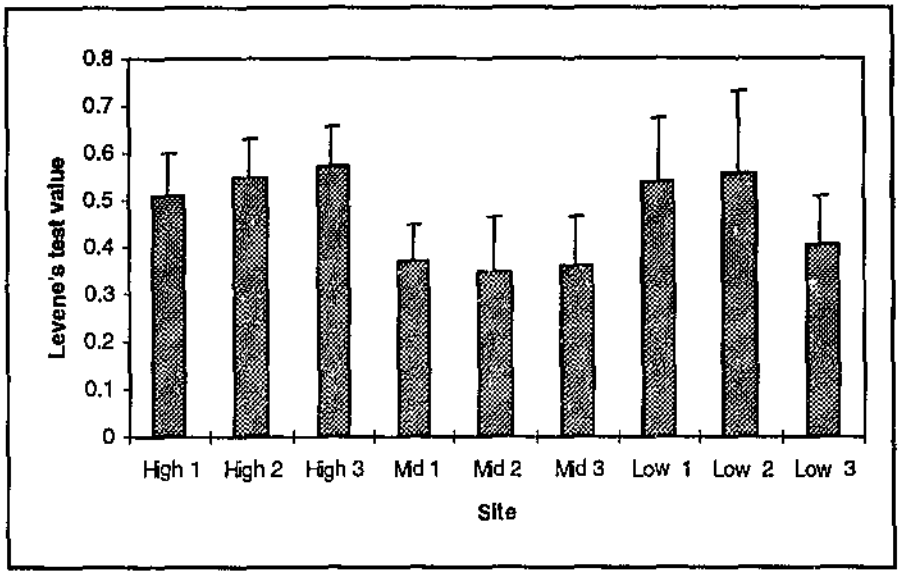


Figure 3.17. Mean untransformed Levene's test values (+ SE, n = 10) of the proportion of deviation from the mean, based on biomass of leathery macrophytes (FG 5) at three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

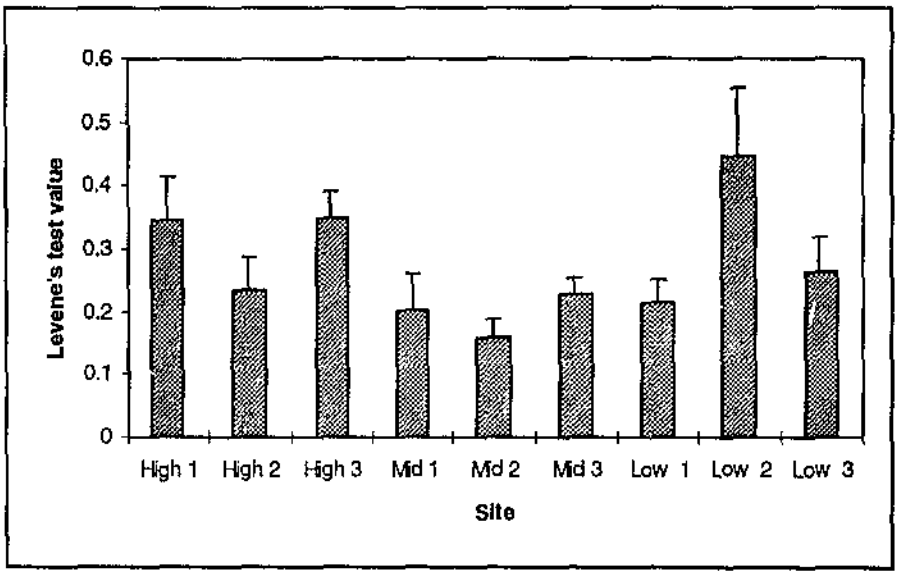


Figure 3.18. Mean untransformed Levene's test values (+ SE, n = 10) of the proportion of deviation from the mean, based on biomass of crustose algae (FG 7) at three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

3.5 Diversity Indices Comparisons

The use of several measures of diversity provided an indication of the utility of different indices at both the species and functional groups levels. Three indices were selected; Margalef's, Berger-Parker and species richness. In all cases, the trend in differences between sites was the same for both species and functional group approaches, although indices were almost always proportionally higher at the species level due to the loss of information when species are pooled into functional groups. Correspondingly, the changes in diversity were more pronounced at the species level.

Margalef's index, which is standardised by the amount of biomass collected, indicated that the most diverse site was in the Low exposure region, but that very high diversity was also noted at some High exposure sites (Figure 3.19). The midshore reef sites (Mid 1-3) showed the lowest diversity as well as the least amount of variation between sites.

Variation among sites at the three exposure levels was less evident from the Berger-Parker index (Figure 3.20), which measured dominance. Since the reciprocal form of the Berger-Parker index was adopted, an increase in the value of the index represented an increase in diversity and a reduction in dominance (Magurran, 1988). Sites at the low level of exposure (Low 1-3) showed relatively high levels of diversity (Figure 3.20). This corresponds to the reduction in dominance of kelp at these sites compared to sites within higher levels of exposure which was noted previously (Figure 3.3). The large biomass of understorey species resulted in the relatively high diversity at the High 3 site (Figure 3.5 and 3.20). Differences between species level and functional group diversity was not as pronounced for the Berger-Parker index due to the dominance of kelp at both levels.

Variability between sites was high for species richness measured at the species level (Figure 3.21). Highest species richness (at the species level) was recorded at the High 3 site although both Low 1 and High 2 sites were also relatively species-rich (Figure 3.21). Sites within the mid level of exposure showed the lowest species richness in general (Figure 3.21). Although the underlying trend was reflected at the functional group level, differences were less evident due to the reduced range of possible richness values (Figure 3.21).

Analysis of variance of the differences in each diversity index revealed no significant differences between exposure levels at either the species or functional group levels (Table 3.5). Sites within exposure levels were more variable, and both Margalef's index and species richness showed significant differences at both the species and functional group levels (Table 3.5). In both cases, the species level approach was more sensitive to differences (Table 3.5). The Berger-Parker index, although not statistically significantly different between sites within exposures, again showed a greater level of significance at the species level (Table 3.5).

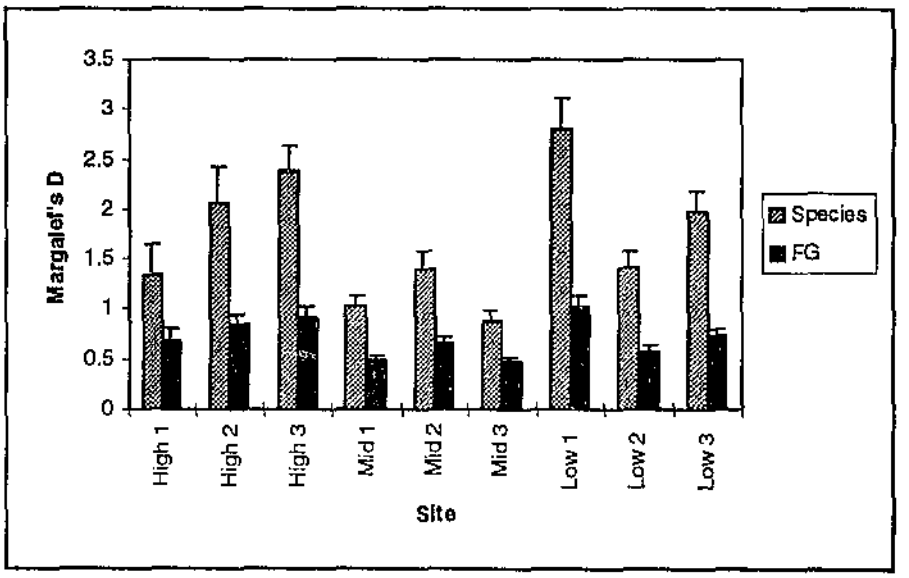


Figure 3.19. Mean Margalef's D diversity index (+ SE, n = 10) calculated at the species level and functional group (FG) level biomass data for three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

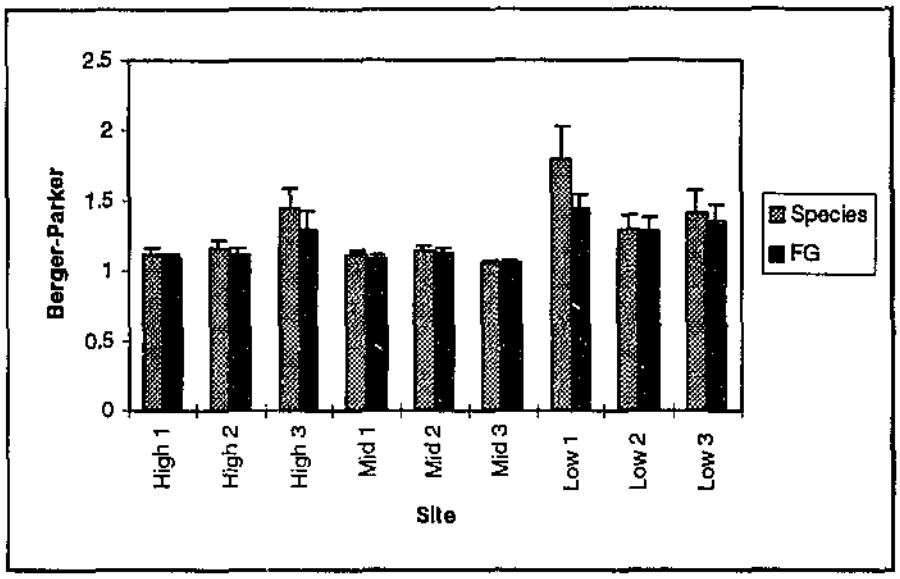


Figure 3.20. Mean Berger-Parker diversity index (+ SE, n = 10) calculated for species level and functional group (FG) level biomass data for three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

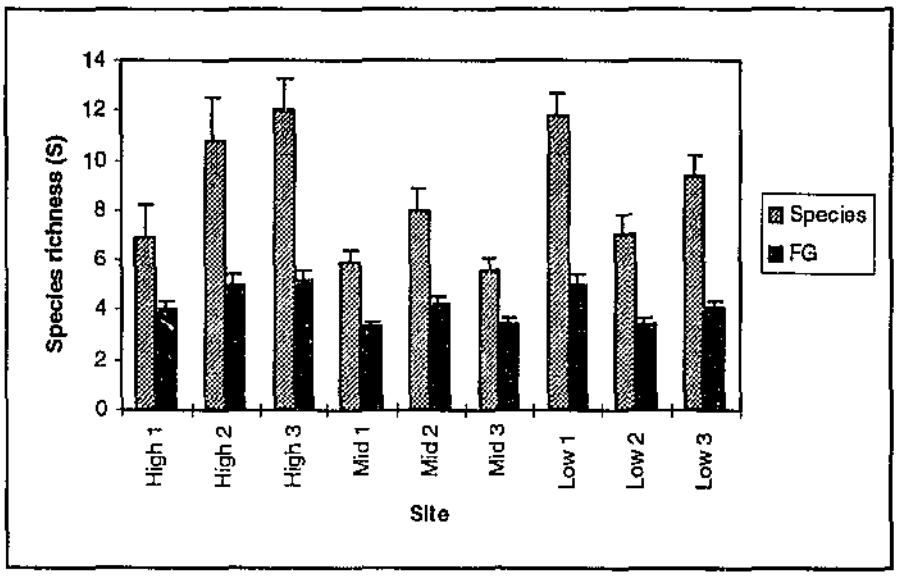


Figure 3.21. Mean species richness (+ SE, n = 10) at the species level and functional group (FG) level for three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

Table 3.5. Results of two-factorial nested analysis of variance (ANOVA) tests for differences in diversity using three indices (Margalef's, Berger-Parker, species richness) at species and functional group levels. Rank transformed data were used in all cases.

VARIABLE	TWO-FACTORIAL NESTED ANOVA			
	Between Exposure Levels			
	d.f.	Mean Square	*F*-value	*P*-value
Species level				
Margalef's	2	4.823	1.644	0.3296 NS
Berger-Parker	2	3265.033	2.482	0.2312 NS
Species richness	2	2771.037	1.183	0.4179 NS
FG level				
Margalef's	2	0.363	1.518	0.3503 NS
Berger-Parker	2	3679.033	3.450	0.1668 NS
FG richness	2	1363.557	0.865	0.5050 NS
	Between Sites Within Exposure Levels			
	d.f.	Mean Square	*F*-value	*P*-value
Species level				
Margalef's	6	2.934	4.339	0.0068 **
Berger-Parker	6	1315.483	2.470	0.0675 NS
Species richness	6	2341.633	4.471	0.0058 **
FG level				
Margalef's	6	0.239	3.169	0.0285 *
Berger-Parker	6	1066.333	2.087	0.1081 NS
FG richness	6	1575.833	2.934	0.0381 *

KEY:

FG Functional Group
NS Not statistically significant
* Statistically significant ($p < 0.05$)
** Highly statistically significant ($p < 0.01$)

3.6 Patterns of Assemblage Change

3.6.1 Ordination

Patterns in assemblage changes were also analysed by ordinating sites based on species and functional group biomass data. The results of ordinations on total biomass and only understorey biomass, at both the species and functional group levels, are shown in Figure 3.22. This figure indicates that shifts in assemblages were more strongly displayed at the species level.

At the functional group level, all sites from the low exposure level (Low 1-3) formed a tight cluster (Figure 3.22a). High 2 and 3 sites grouped close together but the remaining High site was not separated from the Mid sites (Figure 3.22a). When total biomass data at the species level was used to ordinate sites, the gradient from sites at a low level of exposure through to sites at a high level was more evident (Figure 3.22b) although the Low 1-3 sites were not as tightly clustered as in Figure 3.22a. There was also a rotation of the ordination pattern so the differences between Low and High sites occurred on the second axis.

The ordination of sites based on understorey biomass at the functional group level (Figure 3.22c) showed a similar pattern to that shown for total biomass (Figure 3.22a), although Low sites were not as tightly clustered. The removal of kelp biomass did, however, rotate the position of sites along the axes. Similarly, the species level ordination (Figure 3.22d) showed close to a mirror image of Figure 3.22b, with sites having been switched from left to right after the removal of kelp biomass. This indicates that kelp was having a similar influence on assemblage composition across sites.

The stress values of both species level ordinations, that is, based on total biomass and understorey biomass, were lower than the corresponding

functional group analyses. Species level ordinations, therefore, provided better representation of the assemblage patterns.

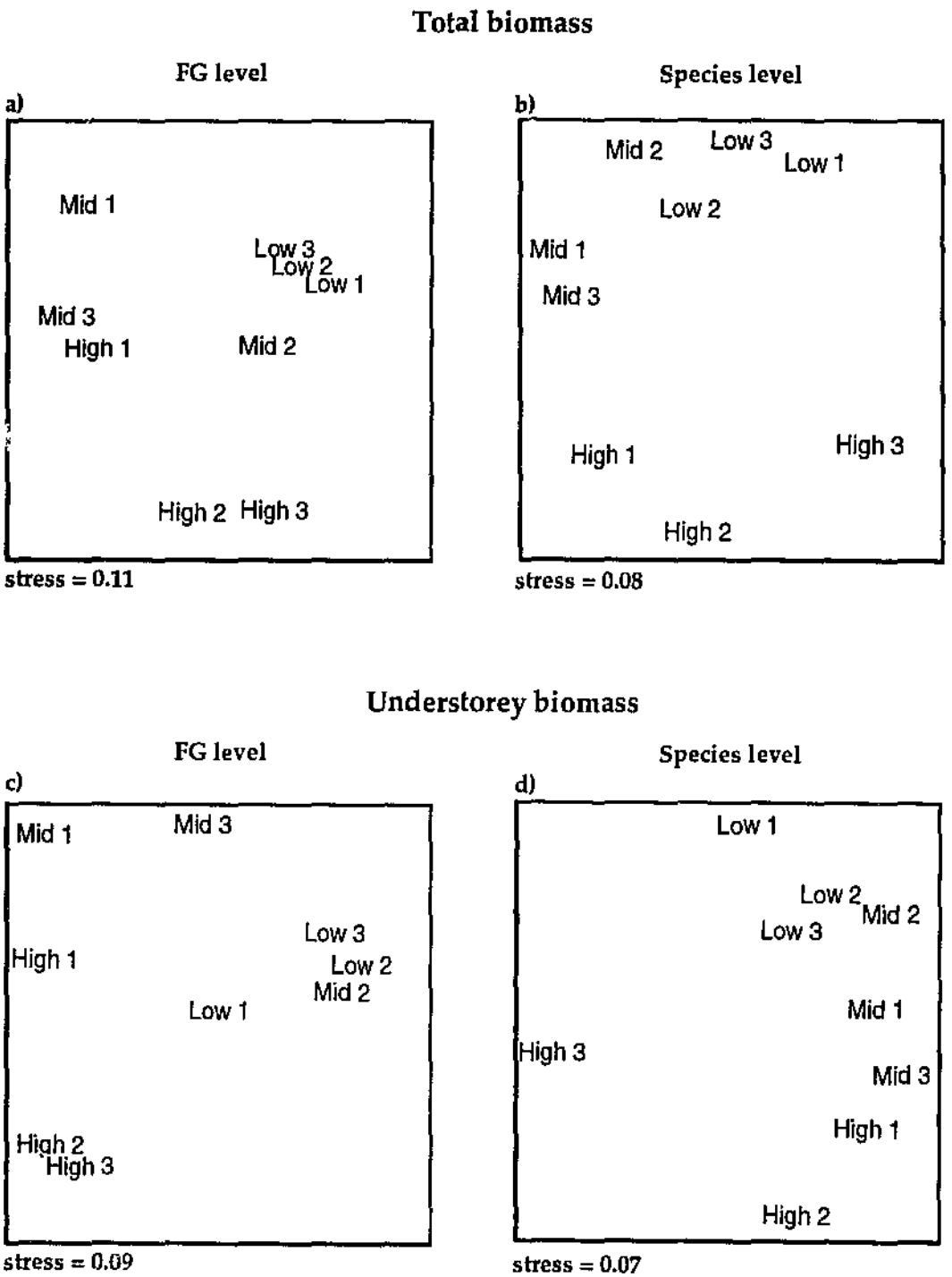


Figure 3.22. Two-dimensional non-metric MDS ordinations of the nine sampling sites, using log (n+1) transformed biomass data in all cases. a) Total biomass at the functional group (FG) level. b) Total biomass at the species level. c) Understorey biomass at the functional (FG) group level. d) Understorey biomass at the species level.

3.6.2 Principal Axis Correlation (PCC)

To investigate which species or functional groups were responding in a systematic way to the disturbance gradient, and therefore driving the ordination patterns, Principal Axis Correlations (PCC) (Belbin, 1993) were performed against each of the ordinations shown in Figure 3.22. As the correlation coefficient calculated by PCC was used as a rough indicator of the significance of each species and functional group in the ordination patterns shown, those with a correlation coefficient greater than 0.8 were considered highly significant and are presented here. The full results of all four PCCs conducted are listed in Appendix 3.

Four functional groups were shown to be significantly influencing the ordination pattern based on total biomass (Table 3.6). The strongest correlation was for FG 6, the articulated calcareous algae, which in Figure 3.11 showed high relative abundance (biomass) at the high level of exposure yet was virtually absent at the low level sites. Functional groups 3.5 and 4 also had high correlation coefficients (Table 3.6), which for FG 3.5 was due to its high relative abundance at all low sites compared to high and mid level exposure sites (Figure 3.8). The distribution of FG 4 across sites within exposures was more variable although considerably less variation was seen between sites at the low level of exposure (Figure 3.9). The lowest correlation coefficient shown in Table 3.6 was for FG 5, which consisted predominantly of kelp biomass. The important trend in the abundance of this functional group was the considerably lower amount of biomass collected at all low exposure sites (Figure 3.10). All four groups mentioned above showed the most pronounced biomass differences between the low level of exposure and the other two levels, which explains the tight clustering of all low sites in Figure 3.22a.

Table 3.6. Functional groups with a correlation coefficient > 0.8 following PCC against non-metric ordination of sampling sites based on total biomass at the functional group level, as shown in Figure 3.22a.

Functional Group	Response to Increased Disturbance	Correlation Coefficient
FG 3.5 (corticated foliose)	– ve	0.9403
FG 4 (corticated terete)	– ve	0.9208
FG 5 (leathery macrophytes)	+ ve	0.8464
FG 6 (articulated calcareous)	+ ve	0.9787

KEY:

+ ve indicates overall trend of increased biomass with increased disturbance
– ve indicates overall trend of decreased biomass with increased disturbance

At the species level, 17 species were significantly influencing the ordination pattern based on total species biomass in Figure 3.22b (Table 3.7). The first three species shown, *Amphiroa anceps*, *Haliptilon roseum* and *Sargassum* cf. *spinuligerum*, occurred almost exclusively at high exposure sites (Figures 3.23 - 3.25). *Dictymenia sonderi* (Figure 3.26) was collected at all exposure levels, but not all sites, and was most abundant on all sites within the low level of exposure. *Pterocladia lucida* was collected at all nine sites and although variation between sites was high, there was a trend toward increasing biomass at the low level of exposure (Figure 3.27).

It is worth noting that kelp (*Ecklonia radiata*), the dominant species visually and in terms of biomass, was not having a significant influence on the ordination pattern of sites based on total species biomass. The correlation coefficient for kelp was 0.7616 which, although relatively high, was not as significant as the coefficients for species in Table 3.7. This supports the theory that kelp was having a similar influence on assemblage composition across sites.

A second noteworthy point is that while the corticated foliose group (FG 3.5) generally responded negatively to increased disturbance (Table 3.6), there were some species within that functional group which responded positively (e.g *Callophycus dorsiferus, Plocamium preissianum;* Table 3.7).

Table 3.7. Species with a correlation coefficient > 0.8 following PCC against non-metric ordination of sampling sites based on total biomass at the species level, as shown in Figure 3.22b.

Species	FG	Response to Increased Disturbance	Correlation Coefficient
Amphiroa anceps	6	+ ve	0.9421
Callophycus dorsiferus	3.5	+ ve	0.8234
Chauviniella coriifolia	3.5	+ ve	0.9630
Dictymenia sonderi	3.5	– ve	0.8988
Erythrymenia minuta	3.5	+ ve	0.8692
Euptilota articulata	4	– ve	0.8020
Haliptilon roseum	6	+ ve	0.8964
Jeannerettia pedicellata	3.5	– ve	0.8583
Lobophora variegata	3	+ ve	0.8061
Metagoniolithon radiatum	6	+ ve	0.8276
Plocamium preissianum	3.5	+ ve	0.8584
Pterocladia lucida	3.5	– ve	0.8782
Rhodopeltis borealis	6	+ ve	0.8578
Rhodymenia sonderi	3.5	– ve	0.8113
Sargassum cf. *spinuligerum*	5	+ ve	0.9459
Sargassum recruits	3.5	+ ve	0.8353
Sargassum subg. *Phyllotrichia*	5	+ ve	0.8290

KEY:

FG Functional Group
+ ve indicates overall trend of increased biomass with increased disturbance
– ve indicates overall trend of decreased biomass with increased disturbance

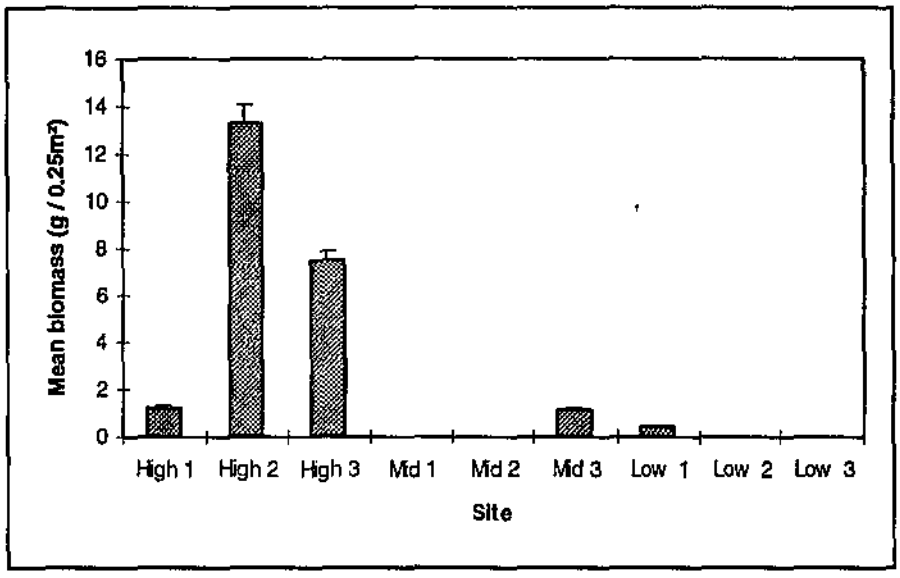


Figure 3.23. Mean biomass (+ SE, n = 10) of *Amphiroa anceps* recorded at three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

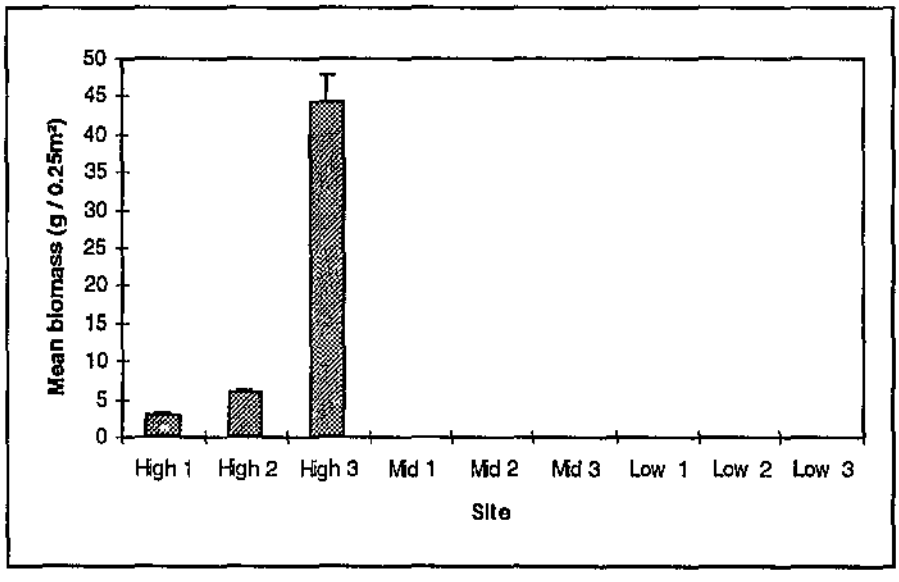


Figure 3.24. Mean biomass (+ SE, n = 10) of *Haliptilon roseum* recorded at three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

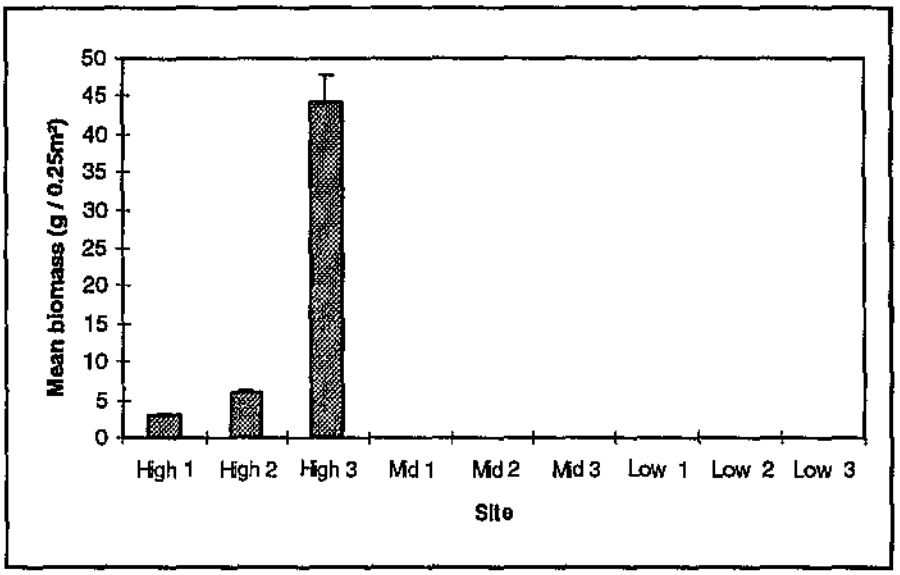


Figure 3.25. Mean biomass (+ SE, n = 10) of *Sargassum* cf. *spinuligerum* recorded at three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

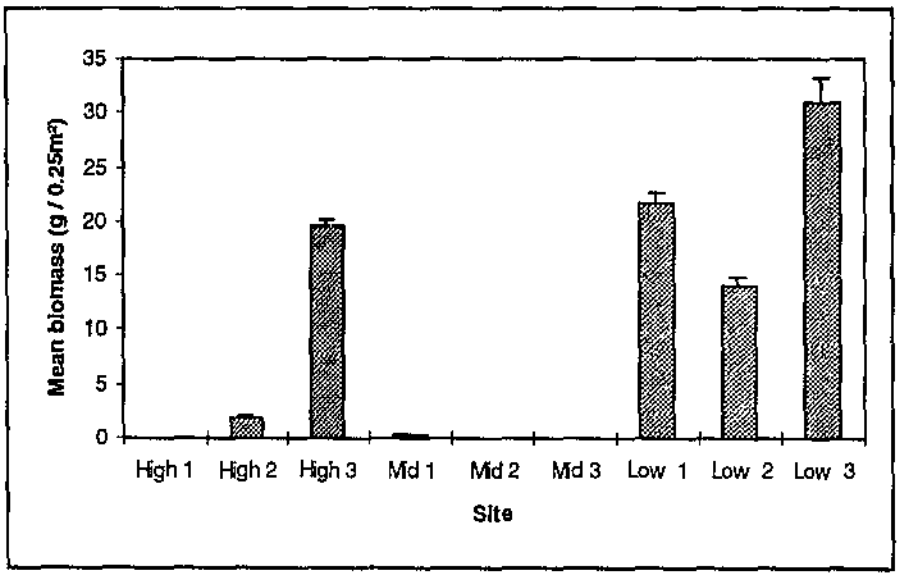


Figure 3.26. Mean biomass (+ SE, n = 10) of *Dictyomenia sonderi* recorded at three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

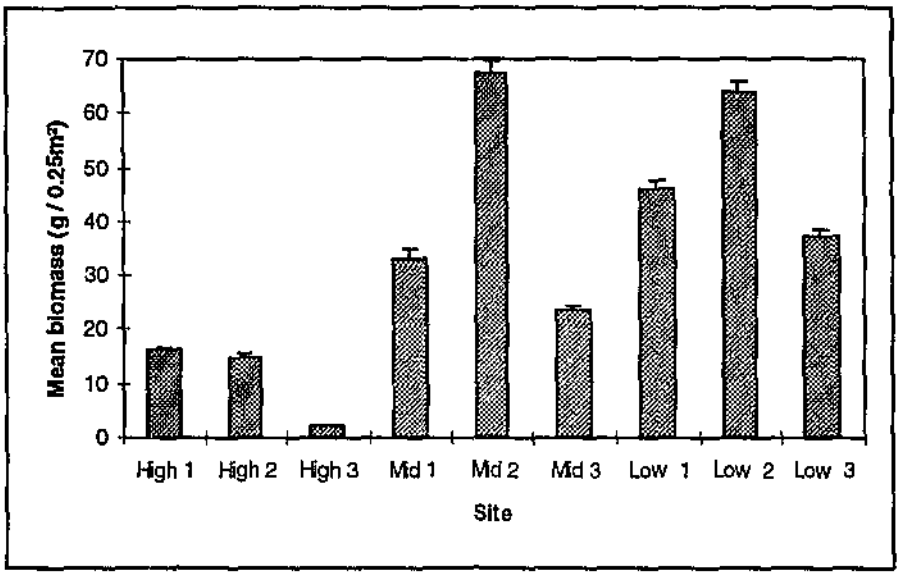


Figure 3.27. Mean biomass (+ SE, n = 10) of *Pterocladia lucida* recorded at three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

For the ordination of sites based on understorey biomass (Figure 3.22c), PCC analysis showed that three functional groups were significantly responding to the disturbance gradient (Table 3.8). The relative abundance of FG 4 and FG 6 across levels of exposure has been discussed earlier in this section, but it is interesting to note that removal of the kelp data results in increases in the correlation coefficients of these groups (Table 3.6 and 3.8). The significance of FG 5 after the exclusion of kelp biomass was also high (Table 3.8) and Figure 3.28 showed a pattern of relatively high abundances at all sites at the high level of exposure.

Table 3.8. Functional groups with a correlation coefficient > 0.8 following PCC against non-metric ordination of nine sampling sites based on understorey biomass at the functional group level, as shown in Figure 3.22c.

Functional Group	Response to Increased Disturbance	Correlation Coefficient
FG 4 (corticated terete)	– ve	0.9909
FG 5 (leathery macrophytes)	+ ve	0.9900
FG 6 (articulated calcareous)	+ ve	0.8960

KEY:

+ ve indicates overall trend of increased biomass with increased disturbance
– ve indicates overall trend of decreased biomass with increased disturbance

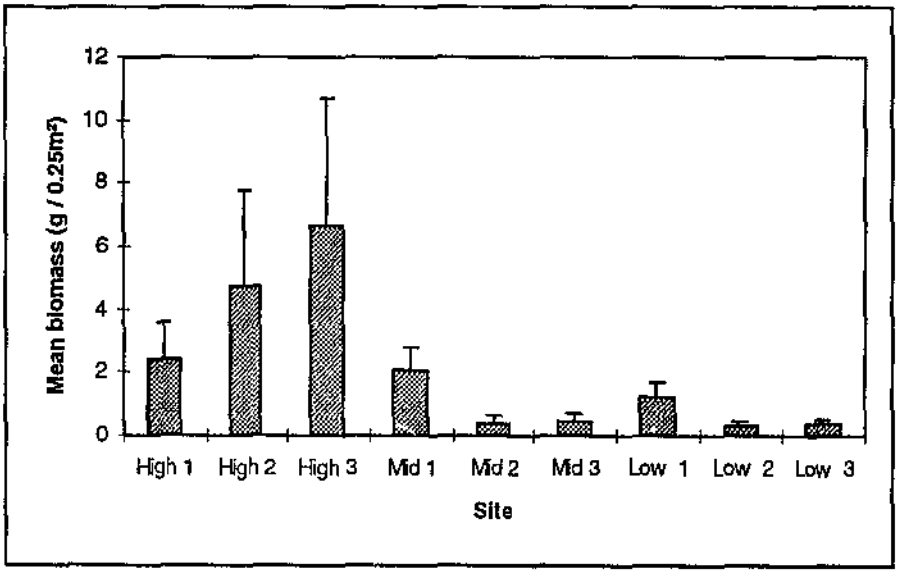


Figure 3.28. Mean biomass (+ SE, n = 10) of functional group 5 (leathery macrophytes) for understorey data only, recorded at three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

For understorey biomass at the species level, most species listed in Table 3.9 as having a significant influence on the ordination shown in Figure 3.22d were also important in driving the pattern shown for total biomass (Table 3.7). Again, the relative abundance of some of these species across levels of exposure has been discussed earlier in this section. Two other species that responded significantly to the exposure gradient are shown in Figures 3.29 and 3.30. *Plocamium preissianum* was collected only at high exposure sites (Figure 3.29), again in contrast to the general trend of FG 3.5 species, while *Euptilota articulata* was most abundant at the low exposure level and absent at high exposure sites (Figure 3.30).

Table 3.9. Species with a correlation coefficient > 0.8 following PCC against non-metric ordination of nine sampling sites based on understorey species biomass at the species level, as shown in Figure 3.22d.

Species	FG	Response to Increased Disturbance	Correlation Coefficient
Amphiroa anceps	6	+ ve	0.8516
Chauviniella coriifolia	3.5	+ ve	0.8559
Euptilota articulata	4	– ve	0.8438
Jania sp.	6	+ ve	0.8395
Plocamium preissianum	3.5	+ ve	0.9393
Pterocladia lucida	3.5	– ve	0.8080
Rhodymenia sp.	3.5	+ ve	0.8174
Sargassum cf. *spinuligerum*	5	+ ve	0.9225
Sargassum recruits	3.5	+ ve	0.8586

KEY:

FG Functional Group
+ ve indicates overall trend of increased biomass with increased disturbance
– ve indicates overall trend of decreased biomass with increased disturbance

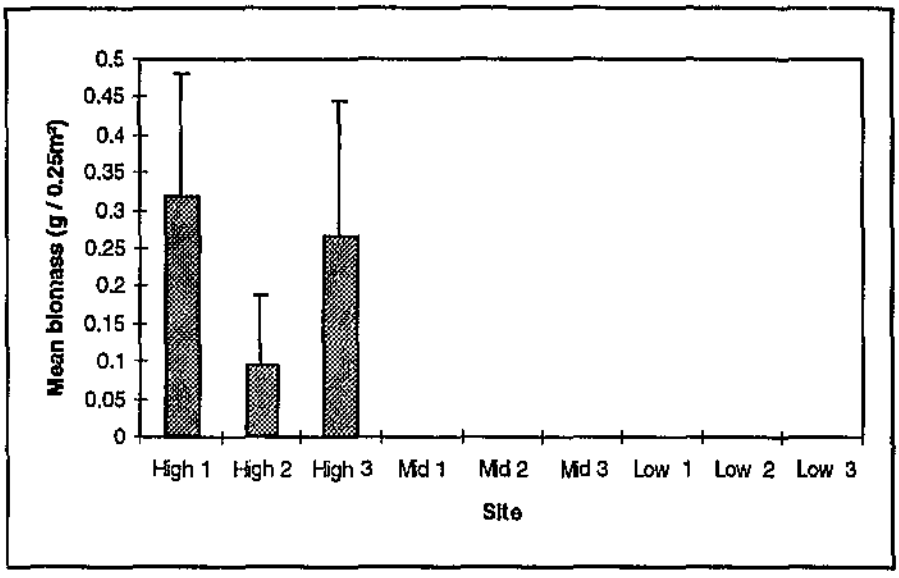


Figure 3.29. Mean biomass (+ SE, n = 10) of *Plocamium preissianum* recorded at three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

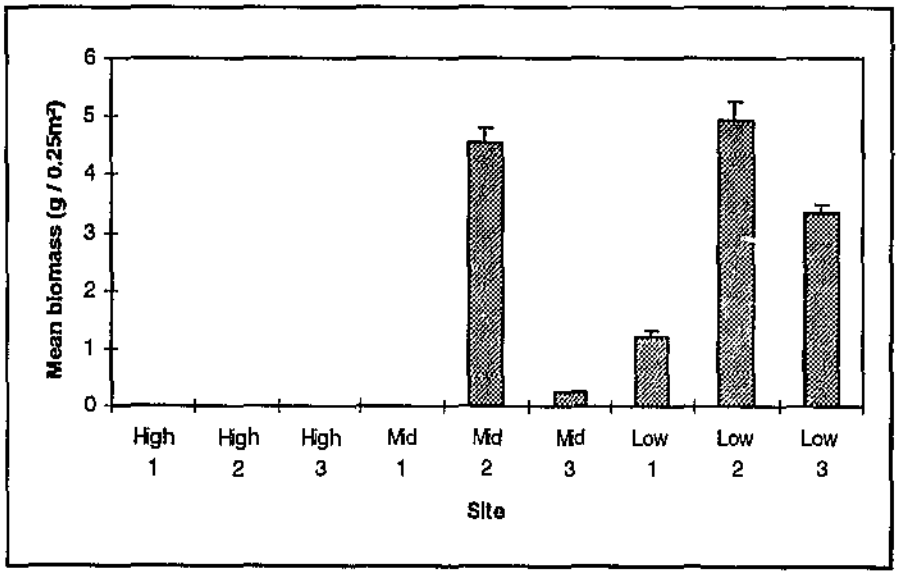


Figure 3.30. Mean biomass (+ SE, n = 10) of *Euptilota articulata* recorded at three sampling sites (1, 2, 3) within each level of exposure (High, Mid, Low).

3.6.3 Analysis of Similarities (ANOSIM)

Two-way nested ANOSIM conducted on total biomass and understorey biomass at the species level demonstrated significant differences between exposure levels and between sites within exposure levels (Table 3.10). This indicated that the chance of achieving a stronger patterns than that shown in the original species level data sets was small.

At the functional group level, there were significant differences between exposure levels and sites within exposure based on total biomass data (Table 3.10). For understorey biomass, significant differences were only apparent between sites within exposures (Table 3.10).

Overall, ANOSIM revealed that stronger patterns were evident in the assemblages when they were analysed at the species level, both between exposures and between sites within exposures.

Table 3.10. Results of two-way nested ANOSIM testing for differences between exposure levels and sites within exposures, using log(n+1) transformed biomass data. Data were associated using the Bray-Curtis association measure. The maximum number of permutations possible between exposure levels and between sites within exposures were 10 and 280 respectively.

Data set	Significance value	
	Between exposure levels	*Between sites within exposures*
Total species biomass	0.4% **	0.1% **
Total FG biomass	1.8% *	2.0% *
Understorey species biomass	0.4% **	0.0% ***
Understorey FG biomass	10.4% NS	2.2% *

KEY:

FG	Functional Group
NS	Not statistically significant
*	Statistically significant ($p < 0.05$)
**	Highly statistically significant ($p < 0.01$)
***	Very highly statistically significant ($p < 0.001$)

CHAPTER 4: DISCUSSION

The difference in the wave energy at each reef line clearly vindicated the choice of these sites as points along a gradient of physical 'disturbance' potential. Furthermore, some functional groups and species showed significant response to the gradient of disturbance, which confirms that wave energy provides a true disturbance against which the functional group model could be tested. From my observations, there were no significant differences in water depth, light levels, rugosity of the reefs and height above the surrounding substrata, and there are no nearby point sources of pollution. Therefore, I am convinced that there were no gradients of other variables, that the same habitat was sampled, and that any variations in macroalgal assemblages were more likely due to the gradient in physical disturbance than other causes.

In the sections to follow, various aspects of community structure of the habitat sampled will be discussed in reference to similar overseas and Australian communities, as well as examples of the observed responses to physical disturbance. Comparison will then be made between the sensitivity of the species and functional group approaches to detecting shifts in the community structure on limestone reefs in Marmion Lagoon.

4.1 Kelp Forest Macroalgal Communities in Marmion Lagoon

As mentioned, the level of wave-driven physical disturbance differed at each reef line sampled but a similar algal community, essentially an *Ecklonia radiata* kelp forest, was found on all reefs. Although kelp abundance differed between reef lines, its influence on understorey assemblages was shown to be the same. The amount of variability in the biomass for all community

components examined also remained the same across reef lines. These results again confirm that not only was the same habitat targeted but that this habitat occurs across a gradient of disturbance in Marmion Lagoon.

4.1.1 Community Structure: Comparison to Overseas Kelp Forests

The lower intertidal and subtidal zones of cold temperate coasts are often dominated by dense stands of kelp, which belong to the order Laminariales (Clayton, 1990; Dayton, 1994). In southern and central California, kelp forests are multilayered with each layer displaying distinct morphological adaptations (Dayton *et al.*, 1984). The upper layer is formed by floating giant kelps such as *Macrocystis pyrifera*, below this is a stipitate, erect understorey kelp canopy, a prostrate canopy, and finally a densely packed turf layer (Dayton *et al.*, 1984).

Along European Atlantic coasts, the mid sublittoral zone is dominated by *Laminaria hyperborea* (Lüning, 1990). This long-lived kelp forms a dense canopy that absorbs most of the light, thereby allowing only a scarce understorey to develop (Lüning, 1990). Cleared areas in the *L. hyperborea* kelp forest support a mixed vegetation until the canopy is re-established enough to shade out opportunistic competitors (Lüning, 1990).

The Benguela upwelling region on the southwestern coast of Africa is characterised by a large *Ecklonia* species, *E. maxima*, that attains lengths of up to 10m (Lüning, 1990). Similar to *Ecklonia* forests in Western Australia, the understorey of *E. maxima* is dominated by endemic red algae (Lüning, 1990). On the Japanese coast, *E. cava*, a small stipitate kelp similar to *E. radiata*, dominates the mid sublittoral from 3m to 25m or more (Lüning, 1990). Japanese kelp forests are similar to those in Marmion Lagoon as they support a diverse understorey (Lüning, 1990). Interspecific competition is common to both *Ecklonia* kelp communities as growth and germination of juvenile kelps is suppressed by low light levels until a gap occurs in the canopy (Kirkman, 1981; Maegawa and Kida, 1991).

From the above examples of overseas kelp forests, representative of some of the major biogeographic zones, it can be concluded that local *E. radiata* kelp communities are most similar to communities dominated by other species of *Ecklonia*. In Australia, *E. radiata* is the common forest-forming kelp, forming dense beds along temperate coastlines (Kennelly, 1995). Similarities exist between kelp forests in Marmion Lagoon and elsewhere in Australia, in terms of kelp biomass, structure of understorey assemblages and overall community richness and diversity, and will be outlined in the following section.

4.1.2 Community Structure: Comparison to Australian Kelp Forests

The algal assemblages on each of the reef lines were intensively sampled, which has provided an important inventory of species composition in local kelp forest communities. In the context of the following discussion, however it must be remembered that there was no temporal component in this study, and that community structure is rarely static (Lobban and Harrison, 1994).

E. radiata was the dominant species in terms of algal biomass and was abundant on all reef lines. Although abundance differed between reef lines the change was not significant, which agrees with Hatcher's (1989) findings for kelp distribution on offshore and inshore reefs 1-3km north of the sites used in this study. *E. radiata* biomass recorded in the present study also compares well with Kirkman's (1984) standing stock measurements, and he points out that local stands of *E. radiata* have large biomass compared to laminarians (kelps) in other parts of the world. Hillman *et al.* (1994) note the lack of biomass data available for understorey algal assemblages, and as such it is anticipated the data collected in this study will make an important contribution toward a better understanding of kelp forest community structure in local waters.

Relative abundance of the major community components was similar to that found for reef and limestone pavement in the Cape Peron, Shoalwater Bay and Warnbro Sound region (Hillman *et al.*, 1994), 50km south of Marmion Lagoon.

Paling (1991; cited in Hillman *et al.*, 1994; p. 3-5) estimated that reefs in the region were covered by approximately 80% *E. radiata*, 1% *Sargassum* spp. and 19% algal turfs. Although cover estimates were not recorded during the present study, from personal observations these figures closely approximate the community structure in Marmion Lagoon. This gives some indication as to the areal extent and continuity of kelp forest communities on limestone reefs in the Perth region.

Crustose algae (coralline and non-coralline) were another ubiquitous component of the kelp forest and, like kelp, were less abundant on inshore reefs. Hatcher (1989) reported a similar finding, with decreased cover of crustose coralline algae on onshore reef lines compared to offshore reef lines, and suggested that this was attributable to differences in exposure to swell. A positive response of crustose coralline algae to increased levels of physical disturbance, such as water motion (Littler, 1973; Dethier, 1994) and secondary effects of water motion such as sand scour (Kendrick, 1991), has been noted for other communities. While this suggests that the lower abundance of crustose algae on the inshore line of reef may have been a response to the physical disturbance gradient, the influence of a reduced kelp canopy cover cannot be dismissed as a causal factor. Kennelly (1987a, b; 1989) demonstrated that the presence of an *E. radiata* canopy maintained an understorey cover of encrusting coralline algae, and found that decreased cover of these algae after removal of kelp was due to increased light levels.

There have been few surveys of local kelp communities, which presented difficulties when attempting to compare the species richness reported in this study. Simpson and Ottaway (1987) surveyed the macroalgae in what is now the Marmion Marine Park, a large section of Perth's coastal waters (approximately 6000ha) that includes Marmion Lagoon. They recorded a total of 202 algal species, although only 44 of these were identified, mostly to genus level. However, of those positively identified, many belong to genera

identified in this study. Furthermore, as with this study, Simpson and Ottaway (1987) found the flora to be dominated (numerically) by red algae (Rhodophyta). The offshore reefs studied by the authors displayed high macroalgal species richness, and the dominant organism was *E. radiata.* Inshore understorey algae assemblages included some species found on offshore reefs, and *E. radiata* was common to all areas sampled (Simpson and Ottaway, 1987). These observations confer with results from this study.

North of Marmion Marine Park, a study of reef communities in the Quinns Rocks region (approximately 30km north of Marmion Lagoon) recorded 59 benthic macroalgae species, although reefs surveyed were low relief reefs and dissected reefs that break the surface (Walker *et al.*, 1991). Furthermore, *E. radiata* was not the dominant species on all reefs surveyed (Walker *et al.*, 1991) so only tentative comparisons can be made with this study. Of the reefs most structurally similar to those sampled in Marmion Lagoon, however, *E. radiata* was generally the visually dominant organism, with foliose red and encrusting algae common understorey components (Walker *et al.*, 1991). Twelve understorey species recorded on these reefs by Walker *et al.* (1991) were also recorded from Marmion Lagoon in this study.

Reef macrophyte communities in the nearshore Dawesville environment, 75km south of Perth, appear to have higher species richness and diversity compared to the reefs in Marmion Lagoon (Montgomery and Walker, 1996). Over the three year period that Dawesville reefs were surveyed (1994-96), a total of 120 species of macroalgae were identified, compared to 82 species collected over five weeks in this study. A higher level of disturbance (wave energy and sedimentation), and the longer study period, may account for this (Montgomery and Walker, 1996). A poorly-developed fringe of limestone reefs in the area, unlike areas further north, means that a sheltered lagoon environment does not exist (Walker, 1994). *E. radiata* stands occurred as localised patches that were not widespread in the Dawesville area, and the

most frequently occurring species was *Dictymenia sonderi* (Montgomery and Walker, 1996). The most frequently occurring species other than *E. radiata* in the present study was *Pterocladia lucida*. This indicates that forces structuring the Dawesville reef communities are not the same as for Marmion Lagoon reefs, resulting in different community structure and a shift in dominance.

A comparable study from eastern Australia was conducted by Kennelly (1987b) on an *E. radiata* community in Fairlight Bay, Port Jackson, Sydney, 4m below low-tide level on sandstone reefs (Kennelly, 1983). A total of 36 macroalgae species were recorded over the 14 month duration of the study (Kennelly, 1987b), which is considerably lower than the total species richness of kelp assemblages in Marmion Lagoon. Another notable disparity was that Kennelly (1987b) found species richness to be lowest in patches occupied by turfing algae and greatest in kelp-dominated areas. On Marmion Lagoon reefs, high species richness on the offshore reef line was attributable to diverse turfing assemblages in patches, but in general areas of high kelp biomass supported a depauperate understorey in terms of species richness (pers. obs.). According to Paine (1974), this suggests that Marmion Lagoon kelp forests represent a climax community with characteristically low diversity attributed to the presence of a competitively dominant species.

Spatial patchiness appears to be an inherent feature of *E. radiata* kelp forests, and has been reported by several authors (e.g., Kennelly, 1987a; Hatcher, 1989; Kennelly and Underwood, 1992) at several spatial scales. A similar pattern was observed for the kelp communities in Marmion Lagoon. The high level of spatial patchiness was observed for the kelp forest assemblage as a whole, and this level of variability was consistent along the disturbance gradient.

4.2 Kelps and Physical Disturbance

Kelps characteristically occupy moderate to high energy environments (Duggins *et al.*, 1990). Kirkman (1981) suggests that *E. radiata* is well adapted to grow in areas subjected to continual swell and frequent wave action, and the observed (biomass) dominance of kelp, particularly on the offshore and midshore reef lines in Marmion Lagoon, provides substantiation of this suggestion. Increased tolerance to wave stress (disturbance) may be associated with a reduced competitive ability in less stressful environments (Dayton *et al.*, 1984), which may explain the reduced dominance, in terms of biomass, of *E. radiata* on the inshore reef line. Conversely, physiological nutrient requirements may be restricting the abundance of *E. radiata*. In areas of relatively low turbulence, the transport of nutrients across the (velocity) boundary layer is limited by the rate of diffusion (Pasciak and Gavis, 1974; Wheeler and Neushul, 1981; cited in Lobban and Harrison, 1994, p. 176). The effect of such diffusion-limited transport rates may be more pronounced for thick, multicellular algae, such as kelp, that have a lower surface-area to volume ratio (Lobban and Harrison, 1994).

Patches are often created in *E. radiata* forests following the removal of kelp plants after storm events and big waves (Kennelly, 1987a, b, c). From personal observations, such patches occur on the limestone reefs in Marmion Lagoon and are occupied by relatively dense stands of turfing and foliose algae. *Ecklonia radiata* maintains its dominance, however, by gradually re-invading the patches and re-establishing a canopy (Dayton, 1994). Under Dayton *et al.'s* (1984) model of community stability, local kelp communities can be said to be resilient, that is, the patch is returned to its original composition following a perturbation sufficient to allow colonisation by different species. Patch dynamics have been investigated in eastern Australian kelp forest assemblages (Kennelly, 1987a, b, c; 1989; Kennelly and Underwood, 1993), with the conclusion that structure and dynamics occurring within those forests were

reasonably similar, but unfortunately no comparative studies have been conducted in local waters.

Disturbance is an important structuring process in kelp communities elsewhere in the world. The sea palm *Postelsia palmaeformis* characterises shore environments of high wave energy, and its local persistence has been shown to be reliant on wave-driven disturbance to the mussel *Mytilus californianus*, the competitive dominant (Paine, 1979; Blanchette, 1996); the kelp is not found in areas of minimal wave action (Paine, 1979; 1988). *Laminaria hyperborea*, a canopy forming kelp in the northeastern Atlantic, was found to have higher biomass at a more wave-exposed site in Norway, and it was suggested that there may be an optimal range of wave exposure favouring its growth (Sjøtun *et al.*, 1993). In Californian multilayered kelp communities, Dayton *et al.* (1984) found that the understorey kelp species, *Pterygophora californica*, *Eisenia aborea*, *Laminaria setchellii* and *L. farlowii*, are more tolerant of physical disturbance than the giant kelp *Macrocystis pyrifera*. A well-developed surface canopy of *Macrocystis* has been demonstrated to inhibit the photosynthesis and growth of the understorey kelp *Pterygophora* (Watanabe *et al.*, 1992). Disturbance in the form of wave exposure is indirectly implicated to the degree of development and persistence of the understorey kelps, since storms are the primary mechanism for removing the surface canopy, thus increasing benthic light levels (Watanabe *et al.*, 1992).

4.3 Definition of Functional Groups

Before proceeding with a comparison of functional group and species level approaches to detecting community shifts, it is important to highlight problems encountered with the definition of functional groups. If functional groups are to be of use in the analysis of ecological components, they must represent clear functional units with predictive value (Walter and Ikonen,

1989). Although Littler and Littler (1984) pointed out that the algal functional group model was intended to represent points along a continuum rather than discrete groups, this study has shown that significant functional information may be lost in the adoption of the functional group model currently in use.

A large proportion of species identified (14 out of 82; refer to Table 2.3) did not clearly fit any of the algal functional groups outlined in the most recent model proposed by Steneck and Dethier (1994). Two of the difficulties that arose when assigning functional groups to species were attributable to the life history stage collected (i.e. *Tylotus obtusatus* and *Callophycus oppositifolius*), a problem in definition that was anticipated by Littler and Littler (1984), while one species (*Metamastophora flabellata*) does not strictly conform to the description of the group which it was assigned to. The remaining eleven species, however, have morphological, anatomical and physiological characteristics distinct from those currently incorporated into the functional group model.

Notable examples of such distinct forms were the coenocytic algae collected, which included *Caulerpa* spp. and *Codium* cf. *harveyi*. Coenocytes are multinucleate without transverse cell walls (Phillips, 1990) or cortication (Womersley, 1984); in *Caulerpa* a single coenocytic siphon forms the thallus while *Codium* are pseudoparenchymatous and composed of branched interweaving siphons (Phillips, 1990). Coenocytes are therefore unlike any of the functional forms described by Steneck and Dethier (1994) and probably warrant a separate group, particularly since they are widespread not only in temperate and tropical Australia (Phillips, 1990) but overseas as well (Round, 1981; Lüning, 1990).

Hollow, tubular algae also presented a problem when assigning functional groups. These species (*Gloiosaccion brownii*, *Champia viridis* and *Webervanbossea splachnoides*) have no internal differentiation into an outer cortex and inner

medulla and hence lack structural complexity, but were placed in the functional group with such characteristics based on similar overall morphology. A more appropriate group for such species would be the saccate cushion-like form group originally proposed by Littler (1980) but omitted from later functional group models.

It is interesting to note that Littler himself appears to have had difficulties in assigning functional groups to species, further demonstrating the need for better definition of groups. A comparison of Littler's (1980) study with later work by Littler and Arnold (1982), both conducted on the Pacific Coast of southwestern North America, revealed that five species (*Pterocladia capillacea, Endocladia muricata, Gelidium pusillum, G. purpurascens* and *G. robustum*) placed in the 'delicately-branched' group in the former study were placed in the 'coarsely branched' group in the latter study. Similarly, *Pelvetia fastigiata* and the kelp, *Egregia menziesii*, were originally included in the 'coarsely-branched' group but were later classified by Littler and Arnold (1982) into the 'thick leathery' group. While some of these inconsistencies may in fact be due to the particular life-history stage or part of the thallus under examination, no explanation was given for the new assignment of species to functional groups (Littler and Arnold, 1982).

If biogeographic comparisons are to be made on the basis of functional form models, a revision of the definition of functional groups is required so that the model is less generalised and there is less ambiguity when classifying certain species. Functional forms that presently don't fit the model should also be incorporated as new groups, or a consensus reached as to their classification within the current model. Alternatively, functional group models could be developed specific to the context in which they are to be applied (e.g. for southern hemisphere temperate waters) so that they account for regionally endemic or abundant forms.

4.4 Detecting Shifts in Community Structure: Species Level vs. Functional Group Level Approaches

Comparison of species level and functional group level results to be discussed in the following sections are based on the functional group model as it is currently proposed by Steneck and Dethier (1994), notwithstanding the comments made in the previous section.

4.4.1 Responses at the Level of Individual Species and Functional Groups

It is worth opening the discussion on how individual species and functional groups responded to the exposure gradient by looking at the assemblages occurring at the mid level of exposure. When examined at the univariate level, algal assemblages on the midshore reef line did not show a systematic response to the exposure gradient. Total biomass and kelp biomass (and, consequently FG 5 biomass) was generally higher on the midshore reef line, and was accompanied by lower understorey biomass. Crustose algae (FG 7) biomass was higher compared to reef lines with comparatively less kelp, supporting the theory that crustose algae cover is associated with the low light conditions below the canopy, as discussed earlier. Accordingly, domination by kelp resulted in reduced richness and diversity of the understorey assemblage.

Several hypotheses as to what conditions allow kelp to dominate on the midshore reef line can be forwarded. Firstly, environmental conditions on the midshore reef line may be generally more favourable for settlement of kelp propagules. Alternatively, episodic storm events that create gaps in the kelp canopy allowing other species to invade may not impact as severely as they do on the offshore and inshore reefs, due to some degree of buffering afforded by the relatively close proximity to the offshore reef line. It may also be a complex interaction of these two factors, or others, that is responsible for the observed trends.

Despite the seemingly inconsistent trends of kelp and understorey components, many individual species responded in a systematic way to the exposure gradient. Articulated calcareous species such as *Amphiroa anceps* and *Haliptilon roseum* were more prevalent at high levels of disturbance, presumably because they are theoretically adapted to withstand such conditions. Conversely, many foliose species, such as *Dictymenia sonderi* and *Pterocladia lucida*, which morphologically appear less able to withstand the higher levels of disturbance, flourished under the less stressful conditions on the inshore reef.

Similarly, in some cases, individual functional groups showed predictable and systematic responses to the exposure gradient. The articulated calcareous (FG 6) and leathery macrophyte (FG 5) groups, which due to their structural complexity have a relatively high degree of resistance to physical damage, were more abundant at higher levels of disturbance while lower abundance on the inshore reef line may have been due to competition for primary space by faster-growing, less complex forms.

The systematic response displayed by these groups prompts the notion that it may be possible to monitor physical disturbance using indicator functional groups, as opposed to indicator species. The results from this study, however, suggest that responses are not predictable for all functional groups due to the amount of variability in physiological responses encompassed in one functional group. As an example, the thin, sheet-like foliose forms (FG 3) which includes the sea lettuce, *Ulva* sp., would not be expected to withstand high levels of physical disturbance given its delicate structure. In this study, however, this group was in fact most abundant on the offshore reef line. Similarly, *Plocamium preissianum* and *Dictymenia sonderi* are examples of two species that belong to the same functional group yet responded in an opposite manner to the disturbance gradient; *Plocamium* responded positively to higher levels of disturbance while *Dictymenia* responded negatively. It may be argued

that this simply reflects a reduced kelp canopy on the inshore reef, and *Dictymenia* is physiologically capable of responding to an associated increase in light levels. However, the important point to be made is that the amount of variation in physiological response is so great within some functional groups that it reduces the predictability of the group as a whole. Dethier (1994) actually investigated the amount of variation within one functional group, crustose algae, and concluded that crusts varied widely in their responses to both disturbance and productivity potential. Indicator functional groups, if they are to be used, should therefore be selected with caution, based on a sound knowledge of the predicted response of the group as a whole given the range of physiological responses within the group. This requires that the function of all the species in each group is known and not simply assumed (Underwood and Petraitis, 1993).

4.4.2 Diversity Measures

Underlying trends at the species level in the diversity measures used were reflected at the functional group level. Differences between levels of exposure were, however, much more pronounced at the species level. At the level of functional groups, differences in diversity between reef lines were greatly reduced with the result that reef lines appeared to have similar levels of assemblage diversity. Although it must be remembered that using the functional group model adopted for this study there can only be a maximum functional group richness of seven groups, this only serves to highlight the effect of summarising information on community structure into a fairly small number of functional groups.

The use of diversity measures can also be misleading at the functional group level because significant changes in community structure may occur without any reduction in functional group diversity. For example, the loss of certain species from an area as a result of disturbance would not be accompanied by a reduction in functional group richness as long as at least one other species of

the same functional form persisted. Monitoring of community change at the species level would obviously be more sensitive to detecting such changes.

Monitoring for community change in term of shifts in dominance may be appropriate at the functional group level in certain circumstances. If one particular functional form is expected to respond more significantly to a disturbance gradient than other forms, this shift would be detected using a diversity measure that accounts for the degree of dominance by one group. If dominance of an algal assemblage is of interest, a functional group approach could be more appropriate than a species level approach in some situations. A particular disturbance may, for example, result in the proliferation of numerous opportunistic 'nuisance' species of the same functional form, all equally dominant. Examined at the species level, the assemblage would appear relatively diverse due to the lack of domination by one species. Of more interest to managers, however, would be the fact that the assemblage had become dominated by an opportunistic growth form, which would be more evident at the functional group level.

4.4.3 Patterns of Assemblage Change

The existence of a physical disturbance gradient effected a turnover of species and functional groups between reef lines. This turnover was, however, more evident when assemblages were examined at the species level. This pattern of assemblage change across the disturbance gradient was also reflected in the degree of similarity of assemblage composition between reefs lines. The greater sensitivity of the species level approach in detecting these assemblage shifts suggests that while individual species are responding to the disturbance gradient, at the functional group level there is simply replacement of species within a functional group.

Species richness and diversity of assemblages on the offshore and inshore reef lines were more similar to each other than they were to midshore assemblages.

Again, examination of assemblage patterns at the species level revealed this more clearly, even when the effects of the dominance of kelp were removed from analyses. The adoption of a functional group approach to looking for shifts in the assemblage as a whole meant that a similar loss of information occurred to that noted when assessing assemblage diversity.

4.5 Management Implications

Any attempt to detect changes in community structure need to be conducted at the scale at which management decisions are made. In this study, conducted at a local scale (tens of km^2), I have demonstrated that the species level approach is more sensitive to detecting community shifts than the functional group approach. It can be assumed from this that at a bioregional scale, the species level approach would still be more capable of detecting changes. Despite species being highly variable in distribution and abundance, a functional group approach proved to be the worse option for the temperate reef communities studied. The functional group approach did not perform as well as the species approach, which was attributable to the amount of variability encompassed in each functional group. This raises questions as to how robust the functional group model actually is.

In light of these observations, it must be pointed out, however, that both approaches failed to reveal a strong change in community structure along the gradient of wave disturbance. Explanation for this may be that the communities have, over time, become so well adapted to the environmental conditions that, as a whole, they have evolved survival strategies that enable them to withstand the level of physical disturbance at each reef line. Alternatively, it may be that even though there was a three-fold increase in the amount of wave energy at the offshore reef, this range of disturbance may in

ecological terms fall within the tolerance limits of the reef communities. That is, the ecological threshold of disturbance for this kelp forest community may not have been reached.

4.6 Conclusions

The fundamental problem encountered when attempting to monitor for changes in community structure was that a species response is not always a functional group response. Assumptions cannot be made that all species will respond the same as the functional group as a whole, due to the variability of species responses in a single functional group. Small scale shifts in community structure were separated out by the species and not by the functional groups, as functional groups tended to summarise and generalise the community information beyond the point of detectable change. Use of individual functional groups showed more promise, but a better understanding of the physiological responses incorporated into each group is required. Only when this variability has been accounted for can a decision be made as to which functional group is most appropriate as an indicator, that is, which is most likely to respond in a measurable way to the particular disturbance in question.

The use of functional groups as a measure of diversity is not recommended, based on the results of this study. A significant loss of information, resulting from the summation of information on community structure at the functional group level, was noticed. An exception to this, however, may be the use of a functional group approach to detecting shifts in the dominant algal form. This would again, however, require a good understanding of responses of individual species.

The comparative lack of sensitivity of the functional group approach to detecting changes resulting from wave-driven physical disturbance in local kelp forest communities does not mean that such an approach would be inapplicable to other disturbance types. Chemical disturbance, for example, may affect different physiological functions of algae than physical disturbance does, and produce a more predictable and discernible trend at the functional group level. What can be concluded, however, is that Steneck and Dethier's (1994) claim to the generality of the functional group model does not hold true for the type of disturbance and macroalgal communities examined in this study. Even if it were argued that this study was limited by the fact that sampling was only conducted in one season, and that trends in functional groups may be more discernible in one or more other seasons, this actually only substantiates the conclusion that the model is not generalisable to all situations. A better definition of the functional group model is required before we can continue to test the applicability of this approach for other disturbance types and other communities.

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Appendix 1: Macroalgal biomass data from Marmion Lagoon, Western Australia.

Raw biomass data for each species collected during macroalgal sampling conducted April-May, 1996, from high relief reefs in Marmion Lagoon, is contained on the computer disk at the rear of this thesis. The following explanatory notes pertain to the computer file on disk:

File name: Rawdata.txt

File format: Excel spreadsheet, in text format (IBM and Apple Macintosh compatible).

Column heading descriptions:

"Exposure"	refers to level of exposure to wave-driven physical disturbance, represented by each of three reef lines in Marmion Lagoon. High = offshore reef line, Mid = midshore reef line, Low = inshore reef line. Refer to Figure 2.1 in main text for reef line locations.
"Site"	refers to site number (1, 2, or 3) located within each reef line (exposure level). Refer to Figure 2.1 in main text for site locations.
"Rep"	replicate samples 1 - 10, using 0.25m^2 quadrat
"Species"	name of each species collected in each replicate sample
"FG"	functional group number assigned to each species. Refer to Table 1.1 in main text for description of functional groups.
"AFDW"	ash-free dry weight recorded for each species.

NB: Explanatory notes have also been included in spreadsheet.

Appendix 2: Species list of benthic macroalgae collected from Marmion Lagoon, Western Australia, during sampling conducted April-May 1996. The functional group (FG) number assigned to each species is shown, based on the functional group model employed by Steneck & Dethier, 1994. Species belonging to FG 7 (crustose algae) were not identified and hence are not listed here.

RHODOPHYTA	
GIGARTINALES	
Callophycus dorsiferus	3.5
Callophycus oppositifolius	5
Callophyllis rangiferina	3.5
Carpothamnion gunnianum	4
Craspedocarpus blepharicarpus	3.5
Cryptonemia undulata	3.5
Erythroclonium sonderi	4
Gelinaria ulvoidea	3.5
Gigartina disticha	5
Hennedya crispa	3.5
Kallymenia sp.	3.5
Mychodea australis	3.5
Plocamium mertensii	3.5
Plocamium preissianum	3.5
Red sp. 1	3.5
Rhodopeltis borealis	6
Stenocladia sp.	3.5
Thamnophyllis lacerata	3.5
Tylotus obtusatus	3.5
CORALLINALES	
Amphiroa anceps	6
Haliptilon roseum	6
Jania sp.	6
Metagoniolithon radiatum	6
Metamastophora flabellata	6
GELIDIALES	
Pterocladia capillacea	3.5
Pterocladia lucida	3.5
RHODYMENIALES	
Champia viridis	4
Erythrymenia minuta	3.5
Gloiocladia halymenioides	3.5
Gloiosaccion brownii	4
Red sp. 2	3.5
Rhodymenia sonderi	3.5
Rhodymenia sp.	3.5
Sebdenia flabellata	3.5
Webervanbossea splachnoides	4
GRACILARIALES	
Curdiea obesa	5
Gracilaria preissiana	3.5

RHODOPHYTA cont.

CERAMIALES

Acrosorium minus	3
Apoglossum sp.	3
Chauviniella coriifolia	3.5
Chondria sp.	4
Dictymenia sonderi	3.5
Dictymenia tridens	3.5
Euptilocladia spongiosa	4
Euptilota articulata	4
Griffithsia monilis	2
Haloplegma preissii	2
Haraldiophyllum erosa	3
Heterodoxia denticulata	3.5
Heterosiphonia sp.	4
Heterostroma nereidiis	3.5
Jeannerettia pedicellata	3.5
Laurencia clavata	4
Laurencia elata	4
Laurencia sp. 1	4
Laurencia sp. 2	4
Laurencia sp. 3	4
Lenormandia spectabilis	3.5
Nitophyllum sp.	3.5

PHAEOPHYTA

SPACELARIALES

Cladostephus spongiosus	4

DICTYOTALES

Dictyota sp.	3
Lobophora variegata	3
Zonaria turneriana	3

LAMINARIALES

Ecklonia radiata	5

FUCALES

Sargassum cf. *fallax*	5
Sargassum cf. *spinuligerum*	5
Sargassum cf. *tristichum*	5
Sargassum recruits	3.5
Sargassum small plants	5
Sargassum sp. 1	5
Sargassum sp. 2	5
Sargassum sp. Subg. Arthrophycus	5
Sargassum sp. Subg. Phyllotrichia	5
Sargassum spinuligerum	5
Scytothalia dorycarpa	5

CHLOROPHYTA

ULVALES	
Ulva sp.	3
CLADOPHORALES	
Apjohnia laetivirens	2
CODIALES	
Codium cf. *harveyi*	4
CAULERPALES	
Caulerpa brownii	4
Caulerpa cactoides	4
Caulerpa distichophylla	3.5

Appendix 3: Correlation coefficients for all species/functional groups resulting from Principal Axis Correlation (PCC) performed in PATN analysis package against 2-dimensional ordination plots using log(n+1) transformed biomass data. Ordination co-ordinates for nine sampling sites shown first. FG = functional group.

PCC correlation coefficients for functional groups, using total biomass data.

Label	Vector 1	Vector 2	Correlation
High 1	-0.8048	-0.1054	
High 2	-0.1416	-1.2287	
High 3	0.4429	-1.2028	
Mid 1	-0.8842	0.8797	
Mid 2	0.3910	-0.0907	
Mid 3	-1.0247	0.1142	
Low 1	0.9347	0.4012	
Low 2	0.5864	0.6243	
Low 3	0.5004	0.6082	
FG 2	0.2571	-0.9664	0.7993
FG 3	-0.1373	-0.9905	0.4431
FG 3.5	0.9597	0.2812	0.9403
FG 4	0.9420	-0.3356	0.9208
FG 5	-0.8767	-0.4811	0.8464
FG 6	-0.0787	-0.9969	0.9787
FG 7	-0.9008	-0.4342	0.6623

PCC correlation coefficients for species, using total biomass data.

Label	Vector 1	Vector 2	Correlation
High 1	-0.5252	-0.8096	
High 2	0.0916	-1.1895	
High 3	1.4416	-0.7855	
Mid 1	-0.9721	0.2565	
Mid 2	-0.3411	0.7136	
Mid 3	-0.7618	-0.0194	
Low 1	0.6529	0.5921	
Low 2	0.0342	0.4801	
Low 3	0.3799	0.7617	
Acrosorium minus	0.7228	0.6911	0.4731
Amphiroa anceps	0.3427	-0.9394	0.9421
Apjohnia laetivirens	-0.5729	-0.8196	0.5174
Apoglossum sp.	-0.9877	0.1562	0.4853
Callophycus dorsiferus	0.4034	-0.9150	0.8234
Callophycus oppositifolius	-0.9872	-0.1597	0.3826
Callophyllis rangiferina	0.8201	0.5722	0.0655
Carpothamnion gunnianum	0.7046	0.7096	0.5229
Caulerpa brownii	-0.5729	-0.8196	0.5174
Caulerpa cactoides	0.7228	0.6911	0.4731
Caulerpa distichophylla	-0.0575	-0.9983	0.6009
Champia viridis	-0.0575	-0.9983	0.6009
Chauviniella coriifolia	0.9661	0.2583	0.9630
Chondria sp.	0.4959	0.8684	0.5363
Cladostephus spongiosus	0.9079	-0.4192	0.7765
Codium cf. harveyi	0.7228	0.6911	0.4731
Craspedocarpus blepharicarpus	0.9746	-0.2241	0.7358
Cryptonemia undulata	0.9288	0.3705	0.6677
Curdiea obesa	-0.8464	0.5325	0.6146

Dicteymenia sonderi	0.9235	0.3836	0.8988
Dictymenia tridens	-0.9872	-0.1597	0.3826
Dictyota sp.	0.9079	-0.4192	0.7765
Ecklonia radiata	-0.7301	-0.6833	0.7616
encrusting algae	-0.8336	-0.5524	0.4637
Erythroclonium sonderi	-0.3327	0.9430	0.3800
Erythrymenia minuta	0.5022	-0.8648	0.8692
Euptilocladia spongiosa	0.4991	0.8666	0.4539
Euptilota articulata	0.2257	0.9742	0.8020
Gelidium ulvoidea	0.6186	0.7857	0.6913
Gigartina disticha	0.8423	-0.5389	0.5088
Gloiocladia halymenioides	0.9269	-0.3752	0.7949
Gloiosaccion brownii	0.8876	-0.4607	0.7985
Gracilaria preissiana	0.5982	0.8014	0.6737
Griffithsia monilis	0.4140	-0.9103	0.4231
Haliptilon roseum	0.7336	-0.6795	0.8964
Haloplegma preissii	0.3660	-0.9306	0.4367
Haraldiophyllum erosa	-0.3327	0.9430	0.3800
Hennedya crispa	-0.8982	0.4396	0.4694
Heterodoxia denticulata	0.4128	0.9108	0.7552
Heterosiphonia sp.	0.7228	0.6911	0.4731
Heterostroma nereidiis	0.1947	0.9809	0.2472
Jania sp.	-0.3126	-0.9499	0.7985
Jeannerettia pedicellata	0.9240	0.3825	0.8583
Kallymenia sp.	0.7228	0.6911	0.4731
Laurencia clavata	-0.4235	-0.9059	0.4895
Laurencia elata	0.7180	-0.6960	0.8534
Laurencia sp. 1	-0.0575	-0.9983	0.6009
Laurencia sp. 2	-0.0575	-0.9983	0.6009
Laurencia sp. 3	-0.0575	-0.9983	0.6009
Lenormandia spectabilis	0.9079	-0.4192	0.7765
Lobophora variegata	0.8857	-0.4643	0.8061
Metagoniolithon radiatum	0.8566	-0.5160	0.8276
Metamastophora flabellata	-0.3327	0.9430	0.3800
Mycodea australis	0.6511	0.7590	0.6628
Nitophyllum sp.	0.4991	0.8666	0.4539
Plocamium mertensii	-0.4144	-0.9101	0.4721
Plocamium preissianum	0.2560	-0.9667	0.8584
Pterocladia capillacea	-0.7019	0.7123	0.4379
Pterocladia lucida	-0.4686	0.8834	0.8782
Red sp. 1	-0.9872	-0.1597	0.3826
Red sp. 2	-0.9835	0.1806	0.5026
Rhodopeltis borealis	0.8167	-0.5770	0.8578
Rhodymenia sonderi	-0.1320	0.9913	0.8113
Rhodymenia sp. 1	-0.3431	-0.9393	0.7761
Sargassum cf. fallax	0.4640	-0.8858	0.4078
S. cf. spinuligerum	0.5667	-0.8239	0.9459
S. cf. tristichum	-0.9889	0.1489	0.5317
Sargassum recruits	-0.1141	-0.9935	0.8353
Sargassum small plants	0.9710	0.2390	0.5769
Sargassum sp. 1	-0.2452	-0.9695	0.4545
Sargassum sp. 2	0.6162	-0.7876	0.7211
S. sp. subg. Arthrophycus	0.9988	0.0485	0.7825
S. sp. subg. Phyllotrichia	0.5304	-0.8478	0.8290
S. spinuligerum	-0.5729	-0.8196	0.5174
Scytothalia dorycarpa	-0.1626	-0.9867	0.6142
Sebdenia flabellata	0.4991	0.8666	0.4539
Stenocladia sp.	-0.3327	0.9430	0.3800
Thamnophyllis lacerata	0.4991	0.8666	0.4539
Tylotus obtusatus	0.6616	-0.7498	0.2665
Ulva sp.	-0.2010	-0.9796	0.6444
Webervanbossea splachnoides	-0.9872	-0.1597	0.3826
Zonaria turneriana	0.3453	-0.9385	0.6437

PCC correlation coefficients for functional groups, using understorey biomass data.

Label	Vector 1	Vector 2	Correlation
High 1	-0.8283	0.1379	
High 2	-0.7995	-0.9559	
High 3	-0.6252	-1.0912	
Mid 1	-0.8338	0.8752	
Mid 2	0.9114	-0.0450	
Mid 3	0.0913	0.9298	
Low 1	0.1860	-0.2475	
Low 2	1.0400	0.1726	
Low 3	0.8580	0.2241	
FG 2	-0.0175	-0.9998	0.7255
FG 3	-0.8653	-0.5013	0.7373
FG 3.5	0.8568	-0.5156	0.7608
FG 4	0.6160	-0.7878	0.9909
FG 5	-0.8371	-0.5471	0.9900
FG 6	-0.4822	-0.8760	0.8960
FG 7	-0.4483	0.8939	0.3051

PCC correlation coefficients for species, using understorey biomass data.

Label	Vector 1	Vector 2	Correlation
High 1	0.6050	0.7754	
High 2	0.5838	0.8224	
High 3	-0.9374	1.2318	
Low 1	-0.5564	-0.3093	
Low 2	-0.5298	-0.3340	
Low 3	-0.5607	-0.3298	
Mid 1	0.9563	-0.7681	
Mid 2	-0.5341	-0.3578	
Mid 3	0.9733	-0.7307	
Acrosorium minus	-0.8122	-0.5834	0.3503
Amphiroa anceps	0.2874	0.9578	0.8516
Apjohnia laetivirens	0.6284	0.7779	0.5523
Apoglossum sp.	0.7834	-0.6216	0.5574
Callophycus dorsiferus	0.2224	0.9749	0.7328
Callophycus oppositifolius	0.8205	-0.5717	0.5543
Callophyllis rangiferina	-0.9235	0.3836	0.3279
Carpothamnion gunnianum	-0.8112	-0.5848	0.3913
Caulerpa brownii	0.6284	0.7779	0.5523
Caulerpa cactoides	-0.8122	-0.5834	0.3503
Caulerpa distichophylla	0.6050	0.7962	0.5658
Champia viridis	0.6050	0.7962	0.5658
Chauviniella coriifolia	-0.9757	0.2190	0.8559
Chondria sp.	-0.8003	-0.5995	0.5016
Cladostephus spongiosus	-0.5200	0.8542	0.7120
Codium cf. harveyi	-0.8122	-0.5834	0.3503
Craspedocarpus blepharicarpus	-0.7454	0.6667	0.7469
Cryptonemia undulata	-0.9967	0.0808	0.6632
Curdiea obesa	0.4514	-0.8923	0.6893
Dicteymenia sonderi	-1.0000	-0.0009	0.7577
Dictymenia tridens	0.8205	-0.5717	0.5543
Dictyota sp.	-0.5200	0.8542	0.7120
encrusting algae	0.9894	0.1453	0.4007
Erythroclonium sonderi	-0.7774	-0.6291	0.3568

Erythrymenia minuta	0.1164	0.9932	0.7699
Euptilocladia spongiosa	-0.8021	-0.5972	0.3589
Euptilota articulata	-0.7638	-0.6455	0.8438
Gelidium ulvoidea	-0.8070	-0.5905	0.5361
Gigartina disticha	-0.3226	0.9465	0.4213
Gloiocladia halymenioides	-0.5578	0.8300	0.7182
Gloiosaccion brownii	-0.4736	0.8807	0.7282
Gracilaria preissiana	-0.8062	-0.5917	0.5254
Griffithsia monilis	0.4597	0.8881	0.3572
Haliptilon roseum	-0.1907	0.9816	0.7981
Haloplegma preissii	-0.0873	0.9962	0.4861
Haraldiophyllum erosa	-0.7774	-0.6291	0.3568
Hennedya crispa	0.2485	-0.9686	0.4168
Heterodoxia denticulata	-0.7679	-0.6406	0.7730
Heterosiphonia sp.	-0.8122	-0.5834	0.3503
Heterostroma nereidis	-0.7892	-0.6141	0.3467
Jania sp.	0.6143	0.7891	0.8395
Jeannerettia pedicellata	-0.9984	0.0562	0.7970
Kallymenia sp.	-0.8122	-0.5834	0.3503
Laurencia clavata	0.5579	0.8299	0.5490
Laurencia elata	-0.0711	0.9975	0.6977
Laurencia sp. 1	0.6050	0.7962	0.5658
Laurencia sp. 2	0.6050	0.7962	0.5658
Laurencia sp. 3	0.6050	0.7962	0.5658
Lenormandia spectabilis	-0.5200	0.8542	0.7120
Lobophora variegata	-0.4281	0.9037	0.6840
Metagoniolithon radiatum	-0.4082	0.9129	0.7495
Metamastophora flabellata	-0.7774	-0.6291	0.3568
Mycodea australis	-0.8085	-0.5884	0.5084
Nitophyllum sp.	-0.8021	-0.5972	0.3589
Plocamium mertensii	0.5170	0.8560	0.4552
Plocamium preissianum	0.2072	0.9783	0.9393
Pterocladia capillacea	-0.3580	-0.9337	0.2927
Pterocladia lucida	-0.1840	-0.9829	0.8080
Red sp. 1	0.8205	-0.5717	0.5543
Red sp. 2	0.7618	-0.6478	0.5561
Rhodopeltis borealis	-0.3315	0.9435	0.7712
Rhodymenia sonderi	-0.5086	-0.8610	0.7298
Rhodymenia sp. 1	0.6101	0.7923	0.8174
Sargassum cf. fallax	0.0804	0.9968	0.5232
S. cf. spinuligerum	-0.0079	1.0000	0.9225
S. cf. tristichum	0.7471	-0.6647	0.4677
Sargassum recruits	0.5213	0.8534	0.8586
Sargassum small plants	-0.9001	0.4358	0.6606
Sargassum sp. 1	0.5763	0.8172	0.5445
Sargassum sp. 2	-0.1095	0.9940	0.7894
S. sp. subg. Arthrophycus	-0.8953	0.4454	0.6035
S. sp. subg. Phyllotrichia	0.0390	0.9992	0.7550
S. spinuligerum	0.6284	0.7779	0.5523
Scytothalia dorycarpa	0.7086	0.7056	0.5786
Sebdenia flabellata	-0.8021	-0.5972	0.3589
Stenocladia sp.	-0.7774	-0.6291	0.3568
Thamnophyllis lacerata	-0.8021	-0.5972	0.3589
Tylotus obtusatus	0.1698	0.9855	0.1948
Ulva sp.	0.5582	0.8297	0.6884
Webervanbossea splachnoides	0.8205	-0.5717	0.5543
Zonaria turneriana	0.0921	0.9957	0.7601