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Habitat association, disturbance dynamics, and the role of spatial scale in structuring coral reef fish assemblages

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for the degree of Doctor of Philosophy
in the Department of Marine Biology
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18 Oct 1998

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Abstract

Understanding how patterns and processes at one scale are related to those at other scales is of central importance in developing ecological theory. However, in order for scaling rules to be useful to empirical ecologists, they must have a rational, measurable, and critically examinable basis. In this study I consider the role spatial scale plays in structuring coral reef fish assemblages and how habitat structure may mediate scaling rules for the assemblage.

The relationship between a population's mean and variance provide a measure of whether that population is indeed scale dependent. I counted fish and measured habitat variables in 701 transects, allocated across 12 habitat zones. Slopes of the power plots for most species lay between 1 and 2 which indicated that the variance, as a proportion of the mean, of small samples was lower than in large samples and hence scale-dependent. 28% of the variation of the data set was explained by habitat variables which indicated that a large percentage of the scale dependence could be modelled by habitat variables alone.

Peaks of variability associated with changes in scale are indicators of the scales at which organisms are spatially structured. It has been hypothesised that coincident variance peaks are indicators of common scales of organisation and thus should also correspond to the scale of maximal correlation. I tested this idea by quantifying fish-habitat associations at different scales on contiguous coral reefs. I mapped fish and habitat to a 3x3m resolution in 24 30x30m grids and then progressively aggregated adjacent squares and recalculated the correlation between fish and benthic cover, physical reef structure, and locality over 9 spatial scales ranging from 9-225m^2. Both fish and habitat variables were patchy at the smallest scale, yet maximal correlation occurred at larger scales (>54m^2). A complex suite of responses were found among fish taxa, with some species associated simply with benthic cover and locality, while others were associated with complex interactions between different types of habitat measures. The scale of maximal correlation was not indicative of the scale at which fishes responded to their environment. Maximal correlation was found when the likelihood of the occurrence of a particular fish species and the likelihood of the occurrence of preferred habitat type were symmetrised. In other words, the scale of measurable fish-habitat association was a measurement of the optimal scale at which predictability of fish given habitat type, and predictability of habitat type given fish were maximised.

Studies carried out on small patch reefs have provided the basic information from which much ecological theory of coral reef fishes has been derived. However no published studies have attempted to document what scaling effects exist in coral reef systems, and whether we can extrapolate or interpolate between studies carried out on different scales. I mapped randomly selected patch reefs, ranging in size from $0.26m^2$ to $63.5m^2$, and censused the resident fish fauna. I then partitioned variation amongst reef area, reef shape and patchiness, and benthic cover. Species responded in a variety of ways to reef parameters. Some species were strongly area-dependent, others were well predicted by reef shape and patchiness, and a considerable number of species were well predicted by the benthic cover of the reef. Further groups of species were associated with combinations of these factors. In order to measure the effect of scaling up or down, I divided the data set into small, medium, and large reefs, recalculated regression equations and measured the predictive ability of each equation. Surprisingly equations derived from the smaller reefs were better predictors of larger reefs than vice versa. As a consequence, the lessons drawn from experiments carried out on small reefs can, in the light of prior information, be cautiously, and with strong caveats, applied to large reefs. Central to these scaling rules is the incorporation of habitat as an explanatory variable.

To establish the bounds within which habitat may influence fish assemblage structure, I carried out two experiments. First, I experimentally reduced coral cover in 10x10m quadrats on contiguous reef from 55% to 47%, 43%, and 34% and monitored the assemblage over two years. Contrary to what might be expected from many correlative studies, all fish species considered were resistant, at this scale and level, to habitat disturbance. However, a large portion of variation in the fish assemblage was explainable by spatial and temporal variables. It is hypothesised that spatial-temporal structure at the landscape level may moderate local disturbance to habitat structure on contiguous reef.

The second disturbance experiment was carried out on small patch reefs. To re-evaluate the current models of reef fish assemblage organisation, I implemented a factorial combination of direct (by fish removal) and indirect disturbance (by habitat alteration) and monitored the experiment over two years. Habitat disturbance generated strong, predictable changes in the fish assemblage which explained almost half the variation in the data set. In contrast, direct disturbance generated a lesser and shorter-term effect. The results from this experiment supported a model of reef fish assemblages as deterministic (within broad bounds), yet weakly interacting systems, the determinism of which was mediated by habitat.

This study supports the initial premise that scaling rules for coral reef fish assemblages are mediated by habitat. As a consequence, habitat structure must be included into a general theory of coral reef fish ecology. An important precursor to the successful incorporation will be the parameterisation of the spatio-temporal dynamics of habitat structure, and the scales and forms of responses to habitat disturbance that fishes can be expected to make. Scale, far from being a black-box within which incongruous results are filed, can exert rational, mechanistic effects which can be incorporated both into the theoretical and empirical development of coral reef fish ecology.

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STATEMENT ON SOURCES
DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institute of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

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General Introduction

1.1 Overview

The study of reef fish ecology is a challenging and rewarding pursuit. The researcher works in an alien environment in which the familiar scales of reference no longer appear to apply. Reef fish for the most part have a bipartite life cycle in which the scales of larval dispersion appears to bear no resemblance to the scales at which the adult fish feed, mate, and otherwise carry out their existence. In addition, the researcher has a limited view of the fish community, limited by the water visibility, swimming ability, and logistical constraints. Disparities between the intuitive scale of the researcher, and the organisms they study present many problems in the study of reef fish ecology.

This thesis considers the role spatial scale plays in the ecology of coral reef fishes and aims to further the development of guidelines or 'rules' that enable studies conducted at one scale to be reconciled with those conducted at others. Coral reef fish are intimately associated with their habitat, and it is my contention that habitat structure mediates much of the scale effects that have been previously observed in coral reef fish assemblages. Furthermore, I put forward that understanding the relationships and scales at which fish are associated with different elements of their habitat will enable development of an empirical framework within which we can view scaling.

1.2 Reef fish ecology, scale, habitat, and disturbance

Despite a myriad of studies (see reviews by Ehrlich 1975, Goldman and Talbot 1976, Sale 1980b, 1991a, Doherty and Williams 1988b), a general theory of reef fish ecology has not been forthcoming. This has been, at least in part, due to a shift in emphasis from 'explainable' patterns (e.g. Smith and Tyler 1972, Sale 1974, Jones 1986, 1987 a, b, Wellington 1992) to the inherently unexplainable stochasticity that forms such a significant part of the population structure of coral reef fishes (e.g. Sale 1977, 1978, 1988, Doherty 1987, Doherty and Williams 1988 a, b). It is probably unreasonable to expect that coral reef fish assemblages are so tightly organised as to be completely predictable, and indeed it may be unreasonable that we can account for even half of the variation in population or assemblage structure. However, enough studies have shown that, at some scales and within some broad context, fishes are organised enough so that pattern emerges above the surrounding noise. A more insidious trend has been for irreconcilable results to be allocated to the catch-all black box of 'scale' (Sale 1988) and, because little is known about how exactly scale operates to generate these differences, this has become sufficient explanation to explain disparities (but see Aronson 1994). In order for scale to be an acceptable explanation for an observable phenomenon, it should have a rational mechanism, and be empirically useful - i.e. a 'science of scale' (Meentemeyer and Box 1987).

A major ecological factor in reef fish assemblages is the habitat within which they exist, and few people would doubt that reef fish are associated with reef characters at some level (Sale 1988). It has been the experience of terrestrial landscape ecologists that understanding spatial habitat structure is the key to understanding the ecology of habitat-associates (e.g. Addicott et al. 1987, Clark 1991, Bell et al. 1995, Hanski et al. 1995, Kareiva and Wennergren 1995, Collins and Barrett 1997). It is one of the contentions in this thesis that this is no less true for coral reef fish assemblages. Unfortunately, the extensive methodologies and frameworks developed by landscape ecologists are not easily applied to reef fish assemblages (pers. obs.), and generally do not provide explanatory power at the scales at which reef fish ecologists perceive and quantify their study system (pers. obs.).

The measurement of habitat and, in particular, what fishes respond to is not a trivial matter. Benthic cover, topography, depth, and locality all interact to generate a habitat that cannot be simply seen as a collection of independent factors, but as a complex suite of interacting (and often confounded) elements each conditional on the others. Despite the problems associated with quantifying habitat (Jones and Syms in press, Appendix 3), effective isolation of different habitat components is required to ascertain exactly what fishes respond to. Given the premise that habitat is central to developing scaling rules, habitat measurement must form an important part of any scaling study.

In order to ascertain the importance of habitat, it is necessary to identify the boundaries within which habitat operates to regulate fish assemblages. Coral reefs are disturbed habitats (Williams 1986, Done 1992) and so natural variation due to habitat disturbance is likely to exert an effect on fish assemblages. If habitat is indeed a key to formulating scaling rules, then the dynamics of fish assemblages in response to habitat changes must be established.

1.3 Thesis outline

This thesis is a collection of five independent investigations, presented in logical rather than chronological order, into the role of scale and habitat association, and the effects of disturbance on reef fish assemblages.

Although it has been frequently assumed that scale is important in reef fish ecology, few researchers have actually set out to test this assertion. In Chapter 2 I set the scene for the remainder of the thesis by using the spatial variance-mean relationship to establish that fish populations are indeed scale-dependent. I then consider the differing models, developed from terrestrial systems, that explain the power relationship and put forward the hypothesis that habitat structure plays a large role in generating the scale relationship. In addition, the question of - 'What defines a habitat?' is raised.

In order to measure the scale at which organisms are associated with their habitat, it is necessary to alter the scales at which measurements are made, and re-evaluate their relationship. In Chapter 3 I present associations between fish and benthic structure, physical reef-structure, and locality, at 9 scales ranging from $9m^2$ to $225m^2$. I then compare the scales of patchiness of the fish and habitat, with the scales at which associations are strongest.

Much of the current theory of how coral reef fish assemblages are organised was, and continues to be, developed from studies conducted on small patch reefs. Indeed, it was the apparent irreconcilability of studies carried out on different-sized reefs that first spawned the idea that scale was having a profound influence on the progress of fish ecology. In Chapter 4 I measure fish-habitat associations on patch reefs ranging from $0.26\text{-}63.5m^2$ in order to identify the nature of the perceived scale dependence. I then establish the context within which experiments conducted at single scales can be reconciled with the sample 'universe' of patch reefs and evaluate the ability of small, medium, and large reefs to predict assemblages on reefs of different sizes.

Having established that habitat is of importance to coral reef fishes, it follows that disturbance to habitat may be a critical process regulating fish assemblage structure. In Chapter 5 I experimentally disturb hard corals on contiguous reef, and measure the response of the fish assemblage over two years. Experiments conducted on contiguous reef in permanent quadrats require particular care with regard to spatial and temporal autocorrelation, and the analytical safeguards I employ to account for these factors in themselves yield insight into the organisation of contiguous-reef assemblages.

Having considered the effect of physical disturbance on contiguous reef, it follows that similar disturbances may be important on patch reefs. In Chapter 6 I compare the relative effects of direct disturbance (by fish removal) versus indirect disturbance (by habitat alteration) on patch-reef fish assemblages. Furthermore, I develop a model of reef fish as weakly interacting, yet deterministic (albeit variable) assemblages.

Finally, in the General Discussion I summarise the premise of this thesis that scale effects occur, and may be understood by reference to the habitat. I conclude by highlighting future directions that I believe will further centralise a theory of reef fish ecology.

Chapter Two: Habitat Heterogeneity Mediates the Scaling of a Reef Fish Assemblage

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2.1 Abstract

Scale has been invoked as a phenomenon that explains a wide range of divergent observations in different studies. However, few studies have actually addressed whether scale-dependence is in fact present and hence a possible explanation for differences in results. I considered whether damselfish populations are spatially scale-dependent and if so, what mechanism was likely to be responsible for generating scale dependence. I measured the log(variance)/log(mean) relationship for 65 species of damselfish in 701 transects around Lizard Island on the northern Great Barrier Reef, Australia. Slopes of the power plots generally fell between 1-2 and differed between species, but within a species did not differ between habitats.

Two hypotheses have been put forward to explain the variance-mean relationship. First is a hypothesis based on species-specific behavioural aggregation; the second is based on environmental heterogeneity. The results of this study shared elements of both the behavioural and habitat-heterogeneity hypotheses. However, the habitat association observed in this study, in combination with prior knowledge about reef fish ecology and behaviour, would support a hybrid model in which environmental heterogeneity mediated much of the scale-dependence of reef fish, but species-specific idiosyncracies exert a stabilizing influence at the smaller scale. These results suggest that pomacentrid populations are scale dependent, and that habitat structure is an important covariate of this scale-dependence. In order to develop scaling guidelines and establish the context for studies carried out at different scales, the scale at which fish are associated with habitat variables will need to be explicitly considered.

2.2 Introduction

The concept of 'scale' has rapidly become a cornerstone of ecological explanation (Allen and Starr 1982, O'Neill et al. 1986, Rickleffs 1987, Levin 1992, Aronson 1994, Schneider 1994). Departures of observation from prediction, conflicting results from different studies, and a wide range of other phenomena are frequently assigned to the vague catch-all term 'scale' with little consideration as to how scale actually operates, or indeed if scale-dependence is present at all (Aronson 1994). In the study of organism-habitat associations, scaling issues are fundamental to the measurement of the strength of interactions (Levin 1992). The degree of habitat association may, *a priori*, be contingent on at least three sets of scales: the scales at which the habitat is structured; the scales at which the organism perceives and responds to the habitat structure; and the scales at which the observer quantifies the interaction (Allen and Starr 1982). However, few studies have critically evaluated whether in fact their system is scale dependent, and whether differences in scale exert any influence on the system beyond simple sampling artifacts.

At a populational level, the behaviour of the variance with respect to the mean provides an insight to the scaling of and processes regulating the population structure (Taylor 1961, Hanski 1987, Perry 1988). The form of the relationship between the log of the variance and the log of the mean of populations is generally linear - indicating a power relationship of the form:

$$\text{VARIANCE} = \text{CONSTANT} * \text{MEAN}^{\text{SLOPE}}$$

This relationship has been documented across a wide array of phyla over both space and time (Taylor and Taylor 1979, Taylor and Woiwod 1982, Taylor et al. 1978, 1980, Taylor 1984). The slope of the power plots (i.e. log variance vs log mean) has been widely interpreted as a measure of aggregation (e.g. Soberón and Loevinsohn 1987), but the biological interpretation of the slope remains contentious. In a scale-independent system, the null model for the relationship is 2 (Hanski 1982, Perry and Taylor 1985), i.e. the relationship between the variance and mean is constant for all values of the mean (the slope should increase at twice the (log) rate of the mean because variances are squared entities - a squared relationship becomes multiplicative on a log scale). Because a population with a mean-variance relationship of 2 is scale-independent, dynamics derived from small samples should be simply scaleable to larger sample units. However in natural populations, the slope is generally either greater or less than 2. Taylor's original interpretation of the relationship in insects led him to hypothesise that density-dependent behavioural mechanisms regulated insect abundances (Taylor and Taylor 1979). In contrast, many others have argued that simple demographic models in combination with environmental heterogeneity can adequately explain the relationship without the requirement for such complex behavioural patterns (Hanski 1982, Downing 1986, Soberón and Loevinsohn 1987, Perry 1988).

It has been arguably agreed that power plots yield insight, but can not by themselves discriminate between behavioural versus demographic models (Soberón and Loevinsohn 1987). However the power relationship is still useful. The slope parameter describes how variability changes as a proportion of the mean, and in conjunction with a priori biological knowledge of the system can generate hypotheses about the role of scale. Non-systematic differences in the proportional variability (V_p) will result in the null model (i.e. slope=2). A slope less than 2 implies that smaller populations are proportionally less variable, and may arise if within-site variability is low - i.e. the variability between replicates is smaller than between-site variability. This may indicate habitat homogeneity within sites, or density-dependent re-assortment of organisms. A slope greater than 2 indicates a more patchy within-site distribution, and may be generated by a very patchy habitat or behavioural aggregation (Soberón and Loevinsohn 1987).

Central to interpreting the variance-mean relationship is the nature of the heterogeneity of samples (Dutilleul and Legendre 1993). If samples are collected from different habitats, then habitat variables can be used to interpret scaling relationships derived from power plots. However defining what constitutes 'habitat' may be problematic. Habitats are spatially heterogeneous over a range of scales and thus may provide problems in the estimation of their effect on organisms. In addition, an *a priori* decision must be made by a researcher about which habitat parameters an organism is responding to. The scales at which habitats are measured may have profound influences on the perception of an organism's association with that particular habitat (Syms 1995).

Coral reef fishes provide an interesting system within which to consider the importance of habitat in mediating patterns at different scales. Coral reefs are spatially heterogeneous at a range of scales (Williams 1991), with an easily-sampled fish fauna. Recent debates about the degree to which coral reef fish assemblages are organized have abounded (Sale 1977, Victor 1983, Doherty and Fowler 1994), and attempts to resolve the debates have resulted in closer attention being drawn to scaling differences between studies (e.g. Sale 1988). However, the effects of scale have been assumed rather than empirically identified as important. In the absence of systematic measurement of how assemblage parameters change with scale, the use of 'scale' as an explanatory black box is probably premature.

Measurement of habitat in coral reef systems is not a trivial matter. The central problem lies in determining which habitat parameters are relevant to the fishes ecology.

For convenience, two types of parameters have been employed. First, stratification of the reef into physiographic zones has been widely used as a measure of habitat (Russ 1984 a, b, Williams 1986, 1991). Second, habitat has been treated as a continuous variable based on benthic cover or topography (Risk 1972, McCormick 1994, Luckhurst and Luckhurst 1978 a, b). These methods have been frequently used both in isolation and in combination with each other (Green 1996). At present, it is unclear which approaches more closely parallel what fish perceive as important.

In this study, I consider whether scale is important in structuring fish populations, and if so to investigate the role habitat association has in explaining observed patterns. I approach this by comparing the slopes of power-plots across pomacentrid species and habitats, and assessing how the values of the slopes correspond with the null value of 2 - i.e. a scale independent population. The role of habitat will be addressed by considering the ability of habitat variables to explain variation within the assemblage. This investigation provides the first application of this methodology to marine organisms.

2.3 Methods

This study was carried out at Lizard Island (14° 40′, 145° 27′ E) on the northern Great Barrier Reef, Australia. Twelve habitat classes were identified and replicate sites selected for sampling. At each class*site combination, 5-10 10x3m transects were randomly sampled (the number of transects that could be placed was dependent on the area of habitat available). Within each transect all pomacentrids were counted, and benthic cover quantified from 50 regular point-intersects. Corals were classed as structural forms rather than taxonomic levels.

Analysis

Analysis of covariance (ANCOVA) was used to test the heterogeneity of slopes of the power-plots. Although, strictly speaking the log(variance) vs log(mean) regression is a model II problem (i.e. both variables are measured with statistical error (McArdle 1988)), the correlation coefficients were generally very high (>0.9) and so least squares rather than Reduced Major Axis (RMA) regressions were employed (McArdle 1988).

To quantify the reliability of the habitat classifications used in this study, I calculated a Discriminant Function Analysis (DFA) (SAS Institute 1990) on the square-root transformed benthic cover data for the classification scheme and inspected the reclassification error rates for each habitat class (i.e. the frequency at which transects would be assigned to other habitat classes).

In order to identify the independent contributions of continuous vs categorical habitat variables in explaining patterns in the fish assemblage, Partial Canonical Correspondence Analysis (Ter Braak 1988) was used to partition the assemblage variation among habitat class (coded as dummy binary variables), benthic cover (square-root-transformed continuous variables), and their interaction (see Borcard et al. 1992, Syms in press, for a full description). The structure coefficients from the ordination were then plotted to depict relationships between the three sets of variables - Fish, habitat class, and benthic cover.

2.4 Results

A total of 701 transects were sampled, and 42560 damselfish from 65 species were recorded. Only species which occurred in more than 10 sites were subsequently analysed, so 10 species were dropped from analysis and 55 species included in the ANCOVA. Twelve classes of physiographic habitat were identified *a priori* and could be broadly grouped into exposed vs sheltered, and reef top versus reef slope classes (Table 2.1). Sample effort was uneven across habitat classes and generally reflected the availability of that habitat around the island (Table 2.1). The distribution of individuals among species indicated that the pomacentrid assemblage on Lizard Island was diverse and relatively even (Fig. 2.1a) (Frontier 1985). The species-frequency distribution approximated the log-normal (Fig. 2.1b).

Scale-dependence of damselfish populations

The relationship between log(variance) and log(mean) did not differ between combinations of species and habitat (f-ratio derived from Type I sums of squares, 3-way interaction $p=0.5901$). However a significant interaction between species and habitat class (f ratio derived from Type I sums of squares, 2-way interaction $p<0.0063$), the presence of non-zero slopes and significant (covariate-adjusted) effects of habitat class and species (f ratios derived from Type III sums of squares, all $p<0.0001$) indicated species should be analysed separately.

Separate ANCOVA's conducted on each species indicated variance-mean relationships were generally not different between habitat classes. Only 2 of the 55 species analysed had statistically different slopes in different habitat classes - *Hemiglyphidodon plagiometapon* (p=0.0014), and *Premnas biaculeatus* (p=0.0006). Subsequent examination of the data indicated this heterogeneity was due to habitats in which these species were present but rare (<4 occurrences). Dropping these sites from the analysis removed the difference in slopes. All but 7 species had significant log(variance)-log(mean) relationships (*Amblyglyphidon leucogaster*, *Chrysiptera biocellata*, *Chrysiptera talboti*, *Chrysiptera taupou*, *Dischistodus melannotus*, *Pomacentrus pavo*, *Pomacentrus tripunctatus*). Examination of the Taylor plots indicated that all these species had positive variance-mean relationships, but the strength of association was reduced by a combination of low numbers and outlier points.

Because slopes for each species were not generally different in different habitats, I combined different habitat classes and calculated the combined slope for each species. Slopes were approximately normally distributed across an ecologically important range (0.51 to 2.09) (Fig 2.2). This indicated that different taxa ranged from highly overdispersed (small slope) to moderately aggregated (large slope) at the 30x10m scale.

Habitat classification

In order to identify the relative roles of habitat classification versus benthic cover as descriptors of habitat, I measured the ability of benthic cover to predict which transect belonged to which class using Discriminant Function Analysis. With the exception of 3 pairs of habitats classes, the *a priori* classification scheme was adequately predicted by DFA of the benthic cover variables. Of the exceptions, Reef Top (Exposed) habitats were misclassed as Reef Slopes (Exposed) 12.7% of the time; and Reef Top (Sheltered) habitats were misclassed as Reef Slope (Sheltered) 21.8% of the time (conversely, Reef Slope (Sheltered) habitats were misclassed as Reef Top (Sheltered) 16.9% of the time). These pairs of habitats were separable by the physical criterion of depth, and so I retained the distinction between them. Reef Slope (Lagoonal windward) habitats were misclassed as Reef Slope (Lagoonal leeward) habitats 36.7% of the time (the converse misclassification occurred 6.7% of the time). The assymetry of the misclassification indicated that the benthic cover parameters were not completely overlapping, and consequently I retained the distinction between these classes also.

Assemblage association with habitat

Species richness varied with site and habitat class (Table 2.2). Site variability subsumed most of the variation (48.7%). There was no clear association between species richness and habitat class. The lagoon slope supported the greatest diversity of damselfishes (11.7%), and lagoonal back-reef habitat the least (2.7%) (Table 2.2). Most habitats were similar in their species richness with the exceptions of rubble, cliff-edge, and lagoonal back-reefs which were considerably depauperate in the average number of species per transect.

At the family level, pomacentrid abundances were generally variable, with slightly less than a third of that variation explainable by habitat variables (habitat class and benthic cover in combination) (Fig 2.3). Benthic cover and habitat class were neither mutually exclusive nor completely overlapping in their explanatory ability. Benthic cover independently explained 8.7% variation, while habitat class independently explained 6.8%. Their interaction, however explained 12.8% of the variation. This interaction implied that habitat class and benthic cover should be used in combination, and do not provide independent measures of habitat. In other words, the relationship between fish and benthic cover data collected from samples allocated to zones cannot be unbiasedly estimated.

Two main patterns in pomacentrid assemblage structure were apparent. The contrast between cliff-edge assemblages and all other habitat types accounted for the first portion of total variation. This pattern was driven by the dominance of *Abudefduf* species, *Chrysiptera unimaculatus*, and *Pomacentrus tripunctatus* in cliff-edge habitats (Fig 2.4a). The cliff-edge habitat class was found adjacent to the granite bluffs of Lizard Island, in shallow water and was exposed to various degrees of wave action. Benthic cover was generally bare rock (Fig 2.4c). The second portion of variation was driven by depth differences. Reef tops were characterised by a suite of species (Fig 2.4a), the degree of which was more extreme in the exposed reef top habitats (Fig 2.4b). Benthic cover on the reef tops generally consisted of large hard coral forms (plating, digitate, corymbose and encrusting corals) (Fig 2.4c). In contrast, reef slopes were not characterised by many species (except for *Chrysiptera rollandi* and *Pomacentrus amboinensis*), but were characterised by the absence of both the reef-top benthic cover types (i.e. hard corals), and pomacentrids.

Table 2.1. Habitat classes and sample allocation.

Habitat class	Description/depth	Number of sites	Total number of transects
Cliff edge	Adjacent to granite bluffs; immediate subtidal	10	102
Rubble	Usually between cliff-edge and reef top; 2-3m	6	60
Lagoonal back-reef	Lagoon soft-sediment, sparse reef; <2m	3	30
Reef top (exposed)	Eastern side of island; <2m	14	79
Reef top (semi-exposed)	Southern side of island; <2m	3	15
Reef top (sheltered)	Western side of island; <2m	11	110
Reef top (lagoon)	Lagoon; <2m	4	40
Reef slope (lagoon windward)	Lagoon, east-facing; 2-6m	3	30
Reef slope (lagoon leeward)	Lagoon, west-facing; 2-6m	3	30
Reef slope (sheltered)	Western side of island; 2-8m	13	130
Reef slope (semi-exposed)	Southern side of island; 2-8m	3	15
Reef slope (exposed)	Eastern side of island; 2-12m	13	60

Table 2.2. Analysis of variance of species richness per transect.

Source	**DF**	**Type III SS**	**Mean Square**	**F Value**	**Pr > F**
Habitat Class	11	3803.116705	345.737882	8.1683	0.0001
Site (Habitat Class)	74	3077.789619	41.591752	8.7968	0.0001
Error	615	2907.758333	4.728062		

Tukey's HSD test: Variance component estimate of sites within habitat class (95% confidence interval): 48.655% (47.721 - 49.143%)

				|	reef slope (lagoon windward)	11.67
			|	|	reef top (lagoon)	10.93
		|	|	|	reef slope (semi-exposed)	10.60
	|	|	|	|	reef top (sheltered)	9.85
|	|	|	|		reef slope (sheltered)	9.61
|	|	|	|		reef top (exposed)	9.27
|	|	|			reef slope (exposed)	9.12
|	|				reef top (semi-exposed)	8.20
|					reef slope (lagoon windward)	8.03
			|		rubble	5.88
			|		cliff-edge	4.82
				|	lagoonal back-reef	2.73

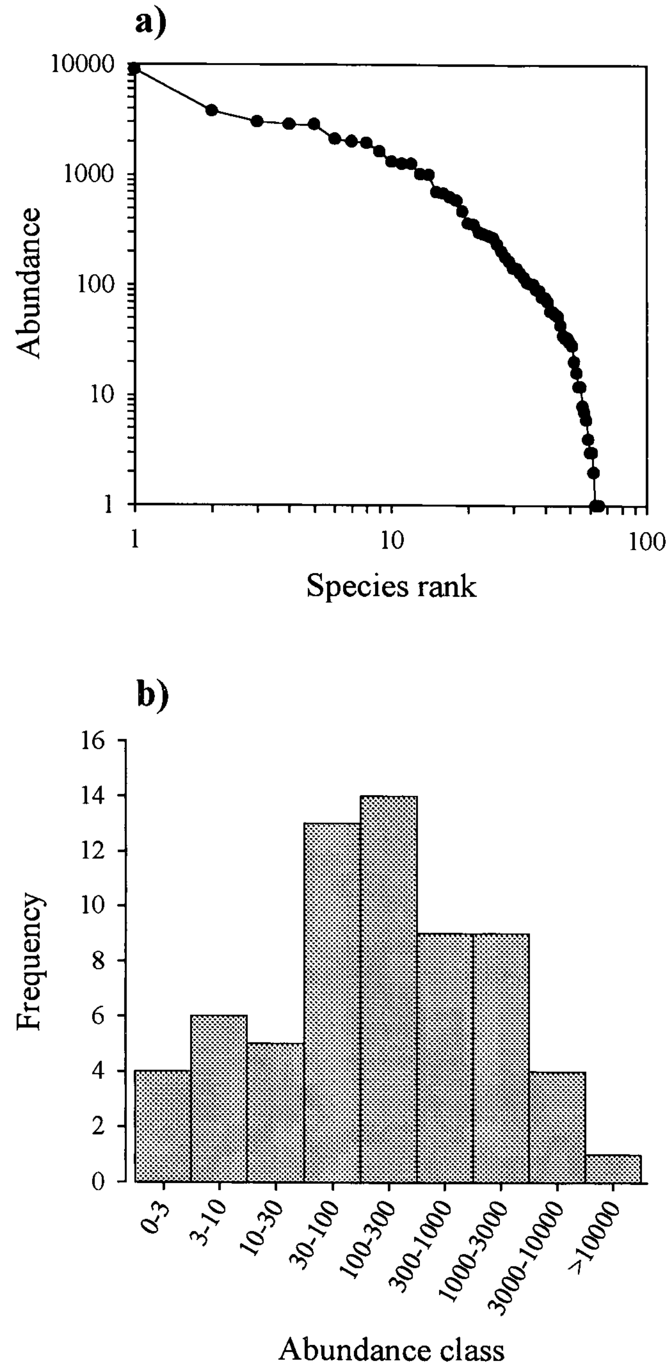

Figure 2.1. Species abundance distributions of pomacentrids. a) Rank-abundance plot, b) Frequency distribution

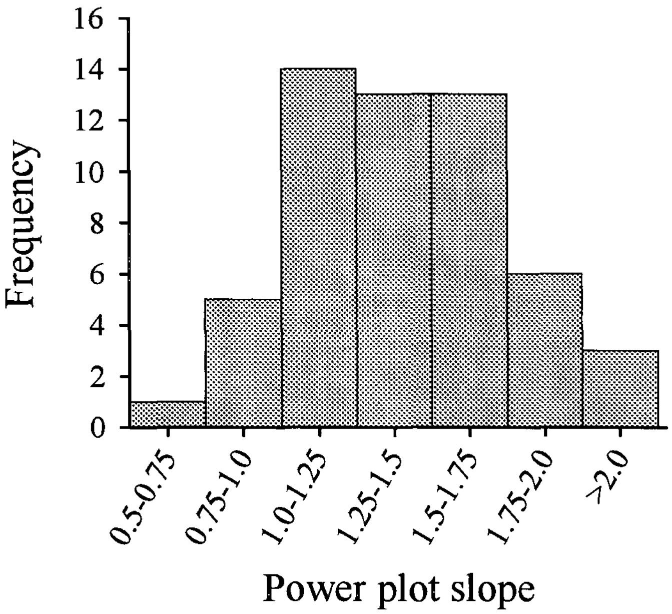

Figure 2.2. Distribution of slope parameters from power-plots of 55 pomacentrid species.

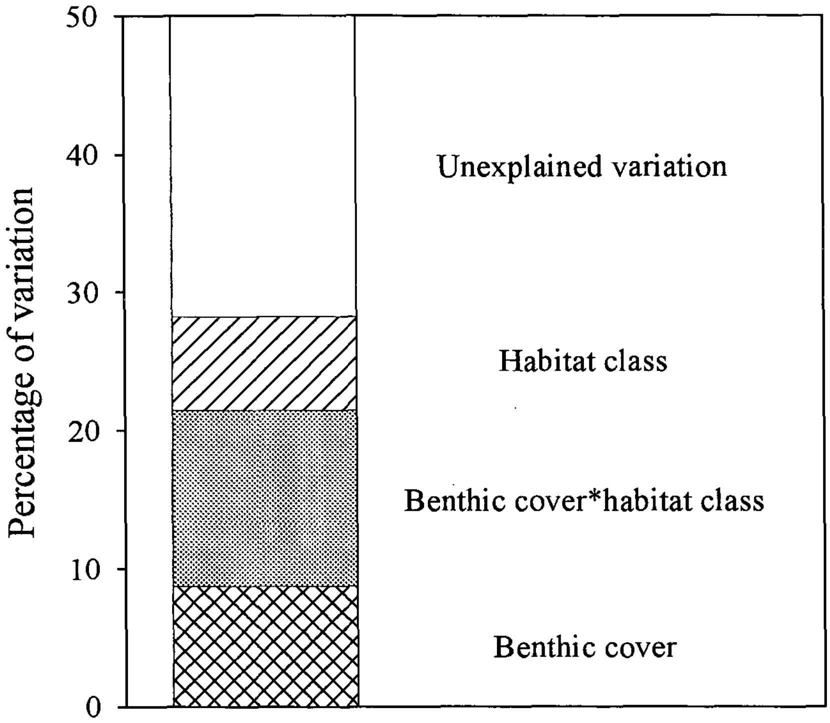

Figure 2.3. Percent variance of the pomacentrid assemblage explained by benthic cover, habitat class and their interaction. Variance components obtained from partial Canonical Correspondence Analysis.

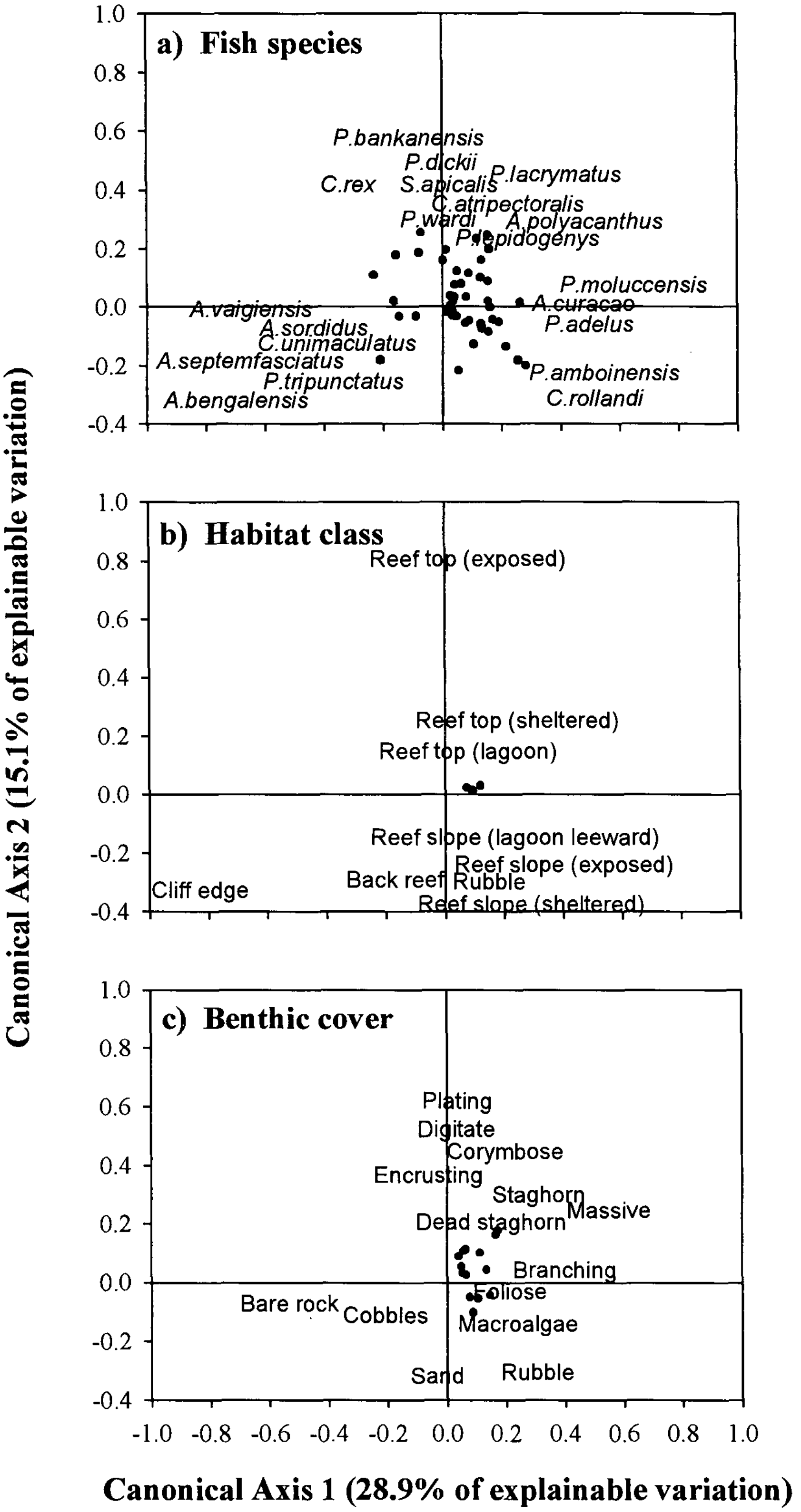

Figure 2.4. Canonical Correspondence Analysis of pomacentrids with habitat class and benthic cover. Co-ordinates are structure coefficients. Filled symbols are points with axis correlations of <0.2.

2.5 Discussion

The relationship between variability and the mean provides an estimate of the scale dependence of a population. A power-plot slope of 2 is the null model in which changes in variance are decoupled from changes in the mean abundance of an organism. In other words, population dynamics in small sample units with few organisms provide an unbiased estimate of the equivalent dynamics in large units with more individuals. Two competing models, both derived from terrestrial organisms, have been put forward to explain deviations in natural populations from this null relationship. First is a behavioural model (Taylor 1984) in which migratory and congregatory behaviours result in aggregations of organisms; second is a demographic-environmental heterogeneity model in which spatial pattern is seen as a stochastic interplay between population dynamics and environmental heterogeneity (Downing 1986). In this study I measured the variance-mean relationship within a family of coral reef fishes to establish if these populations are scale dependent. Because the power relationship does not exclusively distinguish between the models (Perry 1988), I also measured the contribution of environmental heterogeneity to explaining the patterns. These measures, in combination, yield insight into the mechanisms that may mediate scaling relationships within pomacentrids.

Power relationships within and between-species form an important way of distinguishing the behavioural from the demographic-environmental heterogeneity model (Downing 1986). In the behavioural model, spatial variance is intrinsically regulated by the species and consequently the power-relationship (β) should be constant within species regardless of habitat (Taylor et al. 1980), and β should differ between species (Taylor et al. 1980, Taylor 1984). In addition, β may assume values above 2 (e.g. 3.8 in aphids (Taylor and Woiwod 1982)). In contrast, the demographic-environmental heterogeneity model predicts that β should be constrained to lie between 1-2, and should differ within the same species in different habitats i.e. populations are extrinsically organised (Anderson et al. 1982). In reality, various model parameters can be manipulated so that β may assume a range of values and is not necessarily constrained in any model (Perry 1988). Consequently, support for either model requires a sound knowledge of the biology of the organisms.

In this study, β ranged from 0.51-2.09, but generally ranged from 1-2 for most species (Fig 2.2). Species differed in their values of β, and in general these values were consistent across habitats. These results are consistent with a behavioural model of spatial variability. However, two ecological characteristics of reef fish would caution against this interpretation. First, coral-reef fish are not renowned for undertaking large-scale (in the order of kilometres) movements (Jones 1991). Given that damselfish are very small and sedentary, movement is even more unlikely. Second, coral reef fish have been widely documented as associated to some degree with habitat variables (Jones and Syms 1998, Appendix III), and so habitat should play some role in their distribution. Habitat (measured as a classification variable and benthic cover) explained approximately 30% of variation in the data set, which indicated that the behavioural model at best is probably only a partial explanation of the spatial variability in damselfish.

The two models are not constrained to be mutually exclusive. Species-specific behaviour may act to moderate environmental-demographic stochasticity. Assuming species-specific habitat association such as is evident in this study (Fig 2.4), and relatively fine grained (at the scale of 100's of metres) spatial heterogeneity of habitats, species-specific β would be expected to lie within the range of 1-2 (Anderson et al. 1982, Perry 1988). These data support a model in which environmental heterogeneity contributes to the variance-mean relationship of pomacentrids, but species-specific idiosyncracies serve to moderate the stochasticity that might be expected from a conventional population model.

This finding is important when considering the scale-dependence of reef fish. As the slopes were generally less than 2, variability was therefore negatively associated with population size. In other words, small samples would be proportionally more variable than large samples. Simple extrapolation or interpolation of scales would lead to biased perceptions of the population, and ultimately the assemblage dynamics. The grain of the habitat will be an important contributor to this pattern. A $\beta<2$ implied that the high-density sites were more homogenous than would be expected under the null model i.e. species abundance from transects within a 'preferred' zone would be less variable than expected (Soberón and Loevinsohn 1987). Scaling will be, at least in part, a function of both the distribution of habitat and the strength and scales of association of fishes with that habitat.

An important barrier to developing a 'science of scale' (Meentemeyer and Box 1987) will be the measurement of habitat. Physiographic 'zones' or other classification criteria are convenient sample devices, and many studies have found that within-zone variability is far less than between-zone variability (Williams 1982, Russ 1984 a, b, Green 1986). However, determining which component of the 'zone' fish are responding to will be difficult due to the inherent confounding of benthic cover and habitat class. This difficulty is not improved by the observation that zone and benthic cover are not simply related to each other - they describe overlapping but not completely coincident patterns in data. In order for the independent components of each type of habitat measure to be identified and measured, a wide a range of habitat conditions incorporating a wide range of variability will need to be sampled.

In conclusion, this study has shown that damselfish are clearly scale dependent, and as a consequence, naive scaling by simply multiplying patterns by a scaling factor will not be productive. Scaling will require a rational, empirically and biologically relevant set of rules. Habitat structure appears to be an important covariate of scaling patterns, and may provide a means by which scaling rules can be generated. Far from scaling being an esoteric, catch-all term, the scale at which fish are associated with habitats may provide a tractable means of incorporating scale into ecological theory of coral reef fish communities.

Chapter 3: At What Scales are Reef Fish Associated with their Habitat? An Empirical Study

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3.1 Abstract

Scaling is central to establishing the context of ecological studies, and providing an estimate of the generality of studies carried out at single scales. Scales of pattern are indicated by variance increases at particular scales. It has been hypothesised that coincident scales of variance peaks may indicate the scale at which different organisms interact, however this assumption has not been critically examined. In this study I measured the association of coral reef fishes on contiguous reef with benthic cover, physical structure, and location, at nine scales ranging from 9-225m^2. Fish and habitat variables were measured to a resolution of 3x3m in 24 30x30m quadrats placed around Lizard Island, northern Great Barrier Reef, Australia. The 9m^2 squares were then progressively aggregated and associations between fish and habitat variables calculated. All fish species and habitat variables (with the exception of depth) were most variable at the finest scale. However, contrary to expectation, correlations between fish and habitat variables were generally not apparent at scales of less than 54-144m^2.

The scale at which correlations became evident varied with the type of habitat variables. Benthic cover and location associations were most evident at scales greater than 144m^2. Physical variables were generally not important on their own. In contrast, associations between fishes and combinations of habitat variables were apparent at smaller scales (>54m^2) and were generally of greater magnitude than independent effects. These results indicate that the scale at which correlations are strongest correspond to the scales at which the likelihood that both fish and habitat variables are present in the same quadrat is maximised; and not necessarily the scale at which fish are responding to their habitat.

3.2 Introduction

The association between organisms and their habitat is a fundamental parameter for ascertaining how populations and communities are organised (Bell et al. 1991). However, determining the strength and form of these associations is not a simple matter. Habitats are patchy at a range of scales (O'Neill et al. 1986, Addicott et al. 1987, Wiens 1989, Kotliar and Wiens 1990), and consequently observations of communities will be scale-dependent (Schneider 1992, 1994). In addition, habitat patchiness is the product of many covarying biotic and abiotic factors, and isolating exactly which features of the habitat an organism is associated with may prove difficult if not impossible to resolve. Habitat association is likely to be a complex product of the scales of pattern of the habitat and the scales at which organisms perceive and respond to habitat variables. Reconciling different scales of patterns, and the relationships between habitat and organism presents a challenge to ecologists (McArdle et al. 1997).

A considerable number of studies, employing a wide range of methodologies, have attempted to resolve scale-dependent patterns in populations of a wide array of organisms (Schneider 1992, Legendre and Fortin 1989, Legendre 1993). Of equal, if not greater ecological importance is to establish scale linkages between different elements of the system in question (e.g. Blanchard 1990, Pinckney and Sandulli 1990). For example, organisms may be patterned at the scale of physical processes (Schneider and Duffy 1985), with prey species (Schneider and Piatt 1986), or many other critical factors. Reconciling the scales of potentially interacting sets of variables is intuitively quite simple. Coincident scales of pattern in two sets of variables may be interpreted as correlative evidence that the variables share some scaling characteristic (Greig-Smith 1952, Schneider and Piatt 1986).

One method of describing spatial pattern relative to scale is to measure how variability changes with increases in spatial resolution (or grain). Although variability should decrease with scale (Horne and Schneider 1995), the variance of spatially structured organisms should increase as the sampling scale approaches that of the 'patch size' or spatial domain (Wiens 1989) of the organism. This approach was formalised by Greig-Smith (1952), and has received wide application (e.g. Yoshioka and Yoshioka 1989, Underwood and Chapman 1996). Coincident peaks in variance, may indicate common scales of interaction for different organisms (Schneider and Piatt 1986).

Environments are spatially heterogeneous (Addicott et al. 1987), and much attention has been paid to establishing the scales and dynamics of environmental patchiness in a wide array of systems (e.g. Duggins 1983, Dayton et al. 1984, Clark 1991, Hanski et al. 1995, Collins and Barrett 1997). The scale at which habitats are structured is of great importance to the ecology of organisms associated with those habitats (Addicott et al. 1987) and it may be predicted that strongly-associated organisms should be tightly linked to the scale of habitat structure. Consequently, we would expect maximal correlation between habitat and habitat-associates at that characteristic scale. This has strong implications for correlative and experimental studies. If the abundance of a habitat-responding (sensu Jones and Andrews 1993) organism can be viewed as a linear function of its habitat (in the sense of a linear model such as regression or analysis of variance), then the maximal explanatory power of the model should occur at the characteristic scale of their coincident variability peaks.

Coral reefs are spatially heterogeneous over a range of scales (Williams 1991). Within a reef, the primary structure is typically a physiographic zonation pattern (Done 1992) corresponding to a combination of depth and aspect. Within a zone, corals form mosaics of coral-rich patches, interspersed with rubble, bare rock and a variety of other benthic cover types (Aronson and Precht 1995). Coral reef fish are a faunal element that is intimately associated with coral reefs, although the strength and form of this association is variable. Generally, reef fish communities are distinguishable between locations of differing physical conditions (Anderson et al. 1981, Williams 1982, Russ 1984a), and across physiographic zones such as back-reefs, reef crests, and reef slopes (Bouchon-Navaro 1981, Russ 1984 a, b, Meekan et al. 1995, Green 1996). However the strength of association between coral reef fishes and finer-scale elements of the habitat (e.g. coral cover, topography) has been more widely debated. A range of correlation strengths have been recorded - ranging from very weak (Roberts and Ormond 1987, Roberts et al. 1988, Fowler 1990, Booth and Beretta 1994, Cox 1994, Green 1996); to very strong associations (e.g. Bell and Galzin 1984, Bell et al. 1985, Findley and Findley 1985, Bouchon-Navaro and Bouchon 1989, Hart et al. 1996, Jones and Kaly 1996) with fine scale habitat elements. Comparisons of these studies are difficult due to confounding effects of physiographic zone (Syms in press, Jones and Syms 1998, Appendix III, Chapter 2).

The scale at which studies are conducted has been widely acknowledged as a potential source of discrepancies between reef fish studies (Ogden and Ebersole 1981, Sale 1988). Despite this recognition, little explicit attention has been paid to the empirical effects of scale differences in reef fish studies (but see Syms 1995, Syms and Jones in press). Scales at which fish-habitat associations have been measured vary widely from less than $1m^2$ (e.g. Sano et al. 1984, Clarke 1989), to $>1000m^2$ (e.g. Alevizon et al. 1985, Bouchon-Navaro and Bouchon 1989). Further studies have even compared fish and habitat measures taken from different scales (e.g. Bouchon-Navaro and Bouchon 1989, Grigg 1994). There are two major deficiencies in single-scale approaches. First, if the scale at which the fish and the habitat variables are incommensurate, then the study will be predisposed to find little fish-habitat association. Second, different types of habitat variables are likely to exert effects at different scales. It would be expected that fine-grained responses (e.g. association with coral heads) would assume more explanatory power at smaller scale than would coarser-grained responses such as zonal associations. In order to measure the scales at which fishes are associated with different types of habitat variables it is necessary to both alter the scale at which association is measured, and remove the potential confounding between habitat types (e.g. some corals may be found only at certain depths or locations).

In this study, I alter the scale of resolution at which I measure habitat association of coral reef fishes. I consider 9 resolution scales ranging from $9m^2$ to $225m^2$. Associations between fish and three habitat types: benthic cover (e.g. hard coral growth forms, soft corals, rubble, bare rock etc.); physical structure (i.e. the depth and topography); and locality; were measured at each scale. To remove confounding of habitat types, I derived independent and interaction fractions for each combination of factors. In other words, I statistically derived the variation that could be attributed to benthic cover, physical structure, and locality - each operating in isolation, versus the variation that could be explained by one type of habitat measure conditional on another habitat type being present. Samples were taken from a wide range of localities to enable these independent and interactive effects to be isolated. The scales at which different types of habitat measures assume greater importance will suggest hypotheses about the scale at which these fish assemblages are structured.

3.3 Methods

This study was carried out at Lizard Island (14°40′S 175°27′E) on the northern Great Barrier Reef, Australia. Three 30x30m quadrats were placed on contiguous reef at each of 8 locations around the island resulting in 24 replicates (Fig. 3.1). Quadrats were established by placing a 30m baseline parallel to the shore, incorporating both reef slope and reef top habitats, to a maximum depth of 12 m, then triangulating the 30x30m quadrat from the baseline. Measuring tapes were then laid at 1.5m intervals parallel to the baseline to provide a reference for fish counts and physical measures.

Fish, benthic cover, and depth variables were recorded from each 3x3m area within of the quadrat. Four fish families were counted: Damselfishes (Pomacentridae), Wrasses (Labridae), Butterflyfishes (Chaetodontidae), and Angelfishes

(Pomacanthidae). These groups include a wide array of fish sizes and trophic groups. Continuous 1m wide video transects were recorded along each 1.5m lane and benthic cover subsequently measured from 20 random points per 3x3m square. Depth measurements were taken using a dive computer at 1.5m intervals along each transect tape. Adjacent 3x3m squares were progressively aggregated to give fish-habitat measurements at 9 different scales: 3x3m ($9m^2$); 3x6m ($18m^2$), 6x6m ($36m^2$); 6x9m ($54m^2$); 9x9m ($81m^2$); 9x12m ($108m^2$); $12x12m^2$ ($144m^2$); 12x15m ($180m^2$); and 15x15m ($225m^2$).

Fish data were square-root transformed to reduce the influence of absolute abundance. The benthic cover data were converted to proportions, and the most abundant cover categories retained for further analysis. In order to separate depth *per se* from topography, a quadratic response-surface analysis was applied to the raw depth data. The predicted values from the response-surface regression corresponded to the 'typical' depth of a point. The deviation of the observed depth from the predicted depth gave a measure of topography. This gave the ability to distinguish between depressions or high features at any given depth (e.g. a high feature in deep water was distinguishable from a depression in shallow water). In order to accomodate non-linear patterns (e.g. association with intermediate depths or topography) a set of polynomial variables was derived from both predicted depth and topography by first standardising and then calculating: $depth^2$, $topography^2$, depth*topography, $depth^2$*topography, depth*$topography^2$, and $depth^2$*$topography^2$. These parameters were standardised to zero mean and unit variance and included in the analysis resulting in 8 physical variables. Location around Lizard Island was coded as 7 dummy binary variables.

Analysis

The primary aim of the analysis was to ascertain how much of the variation in distributional patterns of fishes in the environment can be attributed to 3 sets of variables: benthic cover, location, and physical structure; and to determine at which scales these parameters are important. Multiple regression was used to directly evaluate the association between fish and these habitat variables. The approach of Whittaker (1984) was used and entails running a series of regressions to partition the residual sums of squares among interaction and simple effects, expressing these fractions as proportions of the total variation in the data set. This method is discussed by Whittaker (1984) for univariate regressions, and Borcard et al. (1992) for multivariate applications.

All species were analysed separately, rather than using a multivariate approach. There were two reasons for this. First, an important assumption of the multivariate approach (e.g. Borcard et al. 1992, Belgrano et al. 1995 a b, Syms in press) is that all species have a similar form of response to the independent variables (Ter Braak 1995). Second, the multivariate approach requires extensive quantities of data and would restrict the number of scales that could be considered due to the decrease in replication as squares were aggregated with each increase in scale.

The percentage of variation explained by the regressions was calculated for each species and each scale. To further summarise the data, I carried out a divisive clustering process based on similarity of the two largest variance portions at each split. Mean values and standard errors of the variance fractions of each cluster were then calculated and presented. Ascertaining the significance of the fractions was problematical. The large numbers of regressions calculated makes interpretation of individual statistical tests prone to Type I error, in addition the estimates derived were not independent of those from other scales. More importantly, the biological importance of a given fraction is unclear. Preliminary tests sets indicated approximately 10% of variation could be accounted for by random variables alone, consequently I treated 10% as an approximate significance level.

3.4 Results

Habitat and fish abundance variability

Although sample grids were placed so as to contain both reef slope and reef top habitats, the 'typical' zonation pattern was not a general profile (Fig. 3.1). The transition from reef top to reef slope was sharper at sites on the eastern side of the island, in contrast with the western sites in which the transition was gentler. The response-surface regressions modelled the depth profiles well (mean r-square = 0.823 ± 0.026), indicating that both long-range (depth) and short-range (topography) components could be reliably extracted from the depth data. Although the depth range was greater on eastern sites, average depths were similar regardless of the side of the island, indicating that no systematic depth bias was present (Fig. 3.2). Average topography was also consistent among sides of the island, with the exception of north-eastern sites which had a greater topographic complexity (Fig. 3.2). The variance of the physical reef structure decreased with increases in scale. Depth variability was consistently high at smaller scales but decreased sharply between 54-81m^2 (Fig. 3.3) to assume a new, relatively constant level. In contrast, topographic variability underwent a monotonic decrease, with the greatest changes occurring at the smallest scales (Fig. 3.3).

Benthic cover differed between sides of the island. Eastern sites were characterised by encrusting, branching, corymbose, and plating hard corals (Fig. 3.4). In contrast, western and lagoonal sites were typified by more gravel and sand, staghorn corals, branching soft corals, and macroalgae (Fig. 3.4). However, site clusters overlapped considerably so that cluster membership was not exclusively represented by a typical benthos. Two characteristic variability profiles were apparent among the benthic categories (Fig. 3.5) and reflected the grain of the benthic type. The gently decreasing profile was typical of evenly distributed and large patch forming categories (bare rock, sand, rubble, macroalgae, massive soft coral, plating, digitate, staghorn hard coral). In contrast, the sharper decrease of the second profile was characteristic of sparsely distributed and patchy categories (turf algae, dead corals, massive, encrusting, caespitose, corymbose, branching hard corals).

As with the habitat parameters, the proportional variance of all fish species in each family decreased sharply with increasing scale (Fig. 3.6). This pattern may represent one of two things. Either patchiness was present outside the bounds of the sampling grain (ie less than 9m^2 or greater than 225m^2) or the fishes were simply sparsely distributed.

Fish-habitat association

Pomacentrids

Within pomacentrids, eight types of habitat association were identified. Group 1 contained 18 species from 11 genera (Table 3.1) which were correlated with primarily with benthic cover variables (maximum 22% variation explained), and to a lesser extent, location around the island (maximum 12% variation explained) (Fig. 3.7a). The strength of association with each factor increased monotonically with scale and levelled at >144m^2. The species making up this group were not necessarily ecologically similar, and included shoaling planktivorous species, live-coral associated species, and sand/rock associated species (Table 3.1).

Group 2 consisted of six species from five genera, which were strongly associated with benthic cover, to some extent conditional on locality (Fig. 3.7b). As with the previous group, the strength of association with both factors increased monotonically with scale. The explanatory power of benthic cover increased rapidly to reach 21% at $54m^2$, then gently increased to plateau at $144m^2$ (30% variation explained). The benthic cover*locality interaction was far smaller (to 14%) and only became significant at larger scales. The species forming this group were not strongly ecologically similar - some were associated with sand, others with branching and staghorn corals (Table 3.1). However, all species were associated with either back-reef or lagoonal locations.

Group 3 consisted of six species in five genera which were associated with benthic cover and locality - both as independent fractions, and as interactions (Fig. 3.7c). Each portion of variation increased gradually with scale and approached approximately equal maxima (18-20% variation explained). There was no ecological similarity in the component species which included lagoonal, back-reef and exposed localities and a range of benthic cover associations (Table 3.1).

Group 4 consisted of four species in three genera which were weakly associated with benthic cover (maximum 20% variation explained), an association that increased gradually with scale (Fig. 3.7d). In addition, location, physical variables, and their interactions accounted for smaller portions of variation (maximum 12%). In isolation, these portions were barely significant but when viewed as a suite of related factors explain up to 36% of the variation. In contrast with the previous groups, the species in group 4 were ecologically similar and were found on shallow reefs in association with hard corals (Table 3.1). However at a finer level of benthic association, the species were ecologically different. *Pomacentrus chrysurus*, *Pomacentrus coelestis* and *Stegastes nigricans* were weakly associated with digitate, corymbose and massive corals respectively, while *Plectroglyphidodon dicki* was associated with a suite of plating and branching coral types.

Group 5 was composed of three species from two genera which were characterised by a strong association with benthic cover conditional on the physical structure of the reef (Fig. 3.7e). The variance portion accounted for by the interaction was evident even at the smallest scale, and increased rapidly to an initial plateau of 29% at between 54-$108m^2$, and increased again to the final plateau (37% explained) at the $144m^2$ scale. Variation attributable to benthic cover alone was lower than the interaction (19% explained), but reasonably constant above $81m^2$. A small (12%) location effect, contingent on habitat, was also evident at the largest scales. Two of the species that made up the group, *Pomacentrus bankanensis* and *Stegastes fasciolatus*, were associated with depressions in shallow reefs, and digitate corals (Table 3.1); while the other species (*Pomacentrus amboinensis*) was associated with high features in deeper, macroalgal and rubble dominated areas.

Group 6, consisting of 3 species in 2 genera, was characterised by a complex suite of associations with benthic cover, location, their interaction, and a benthic cover*physical variable interaction (Fig. 3.7f). All factors were of a similar magnitude (15-22% variation explained) and reasonably constant at scales above 81m^2. Three species that formed this group were ecologically complementary. *Chrysiptera rex* and *Pomacentrus wardi* were both shallow water dwellers, associated with hard branching and plating coral forms (Table 3.1). However, *C. rex* was generally found at more exposed localities (Washing Machine) than *P. wardi*, which was found more in back-reef and semi-exposed localities (Osprey and Palfrey). In contrast, *Chrysiptera rollandi* was generally found in deep-water at back reef and lagoonal localities and was associated with staghorn corals, macroalgae, sand, and soft corals (Table 3.1).

Group 7 contained two species which were strongly associated with benthic cover, contingent on locality (Fig. 3.7g). The benthic cover*locality interaction rose sharply to plateau above 108m^2, to maximum value of 40% variation explained. Benthic cover association alone was evident from a small scale (18% at 36m^2) and reached 27% at the largest scale. Both species in the group were found in back-reef and lagoonal habitats. *Amblyglyphidodon curacao* was associated primarily with staghorn corals, *Pomacentrus adelus* with soft and dead hard corals (Table 3.1).

Group 8 consisted of two species, *Hemiglyphidodon plagiometapon* and *Pomacentrus grammorhynchus*. At smaller scales (9-54m^2) location explained most of the variation (maximum 38% variation explained) but then dropped to 20% at the 144m^2 scale (Fig. 3.7h). At larger scales, the explainable portion of the variability was subsumed by the benthic cover*location effect which plateaued at 144m^2 to explain a maximum of 66% variation. Both species were ecologically similar; being strongly associated with staghorn corals, contingent on that habitat being in the lagoon (Table 3.1).

Labrids

Within the labrids, six habitat response classes were identified. Group 1 was composed of 13 species from 11 genera (Table 3.2) which were weakly associated with independent components of benthic cover (maximum 19% variation explained) and locality (maximum 13% variation explained). Both fractions increased in size with scale to level at 144m^2 (Fig. 3.8a). Species in this group were not ecologically similar, and included a wide range of habitat associations ranging from the typical branching coral-associated *Labrichthys unilineatus* (Randall et al. 1990), and the macroalgal-associated *Pteragogus cryptus* (Table 3.2), in addition to species that were not particularly associated with any habitat variables.

Group 2 consisted of four species from three genera which were strongly associated (maximum 30% variation explained) with benthic cover variables, plateauing at >144m^2. This association was conditional both on physical (21% variation explained) and locality (11% variation explained) interactions (Fig. 3.8b). As with the previous group, species were not ecologically similar and the group included both deep and shallow water dwellers, coral and non-coral associates, and back-reef and exposed locality dwellers (Table 3.2).

Group 3 consisted of three species from three genera which were strongly associated with benthic cover, contingent on locality (Fig. 3.8c). This interaction fraction rose sharply to reach 25% variation explained at the 108m^2 scale, then increased above 144m^2 to reach a maximum of 33% variation explained at the largest scale. A smaller independent habitat association was also evident. This fraction rose to its maximum (19% variation explained) at 144m^2, then dropped to 12% explained at larger scales. Species in the group were ecologically dissimilar (Table 3.2). *Cheilinus fasciatus* was associated with lagoonal staghorn corals, *Stethojulis strigiventer* was associated with soft corals and macroalgae in back-reef localities, and *Thalassoma lunare* was associated with branching corals at exposed localities (Table 3.2).

Group 4 was composed of three species each from different genera which were associated with an array of interaction and independent components of benthic cover and locality effects (Fig. 3.8d). Benthic cover was reasonably constant (16-18% variation explained) at scales larger than 81m^2, the locality*habitat interaction became significant above 108m^2 to reach its maximum at the largest scale (20% variation explained at 225m^2). In contrast the locality fraction only became weakly evident (13%

variation explained) above 180m². Species in the group were all coral associates, with different locality associations. *Gomphosus varius* was associated with a variety of hard coral types on exposed localities and generally not found in the lagoon, *Hemigymnus melapterus* was associated with staghorn corals in the lagoon, while *Pseudocheilinus hexataenia* was associated with branching coral forms at north-western, exposed localities (Table 3.2).

Group 5 consisted of two species, *Thalassoma hardwicke* and *Thalassoma janseni*, which were associated with a strong benthic cover*physical structure interaction (31% variation explained) which became significant at the 54m² scale (Fig. 3.8e). Benthic cover (20% explained), locality (12% exaplained) and their interaction (20% explained) accounted for further portions of variation which generally increased in strength with increasineg scale. In contrast with previous species groups, *T. hardwicke* and *T. janseni* were ecologically similar, and were found primarily on shallow, exposed, coral-rich reef tops and were least abundant in lagoonal sites (Table 3.2).

The final response was found in only one species, *Coris schroederi*, which was associated with a complex array of benthic cover, locality, and physical variables (Fig. 3.8f). Benthic cover accounted for the main portion of variability and was reasonably constant (29-33% variation explained) above 81m². Locality was only weakly significant at 54m² and appeared to be more contingent on habitat (maximum 23% variation explained). A physical variable*benthic cover interaction was present between 36m² and 144m² (13-15% variation explained), but had disappeared at the largest scales. These patterns were driven by *C. schroederi*'s association with gravel/sand, rubble, soft corals and macralgae on deeper reefal areas, and was found more at back reef and one of the exposed localities (Table 3.2).

Chaetodontids

Chaetodontids were less consistent in the strength and scales of their habitat associations. Two groups and three species-specific responses were identified. Group 1 consisted of four species which were associated with benthic cover, to some extent contingent on locality (Fig. 3.9a). Benthic cover association increased gently to reach a plateau (19% variation explained) at 144m². Locality exerted a weak (11% variation explained) interaction with benthic cover which was only evident at the largest scale. There was no similarity in either benthic cover or locality association in the group (Table 3.3).

Group 2 also consisted of four species which were similar to Group one species in the strength and form of their benthic cover association (Fig. 3.9b). However, locality assumed greater importance both as an independent fraction (maximum 17% variation explained at 225m^2), and as a weak interaction with benthic cover at the largest scale. No consistent benthic cover type was responsible for this pattern, however all species in this group were positively associated with semi-exposed localities on the southern side of Lizard Island (Table 3.3).

The final three responses were unique to individual species. *Chaetodon trifasciatus* was strongly associated with benthic cover independent of locality or physical factors (Fig 9c). This relationship was evident at small scales (18% at 36m^2), and increased to its strongest at the largest scale (40% variation explained at 225m^2). This pattern was driven by *C. trifasciatus*' association with caespitose corals (Table 3.3). *Chaetodon trifascialis* was associated with independent and interaction benthic cover fractions (Fig. 3.9d), the importance of which varied with scale. At scales of 81-108m^2 the relationship between *C. trifascialis* and benthic cover was largely contingent on physical structure of the habitat. Above 108m^2, this variation was absorbed as an independent benthic cover fraction until the largest scale. Locality effects (as an interaction with benthic cover) did not become apparent until the 144m^2 scale. These patterns were due to an association of *C. trifascialis* with plating and assorted branching corals, on shallow reefs at exposed localities (Table 3.3). *Chaetodon citrinellus* was associated primarily with benthic cover (digitate corals and bare rock) contingent on the benthic cover types being in shallow water (Table 3.3). This association was strongest at 144m^2 (24% variation explained). Smaller independent components explained further portions of variation (Fig. 3.9e).

Pomacanthids

Only three species of pomacanthid were present in sufficient numbers for analysis. *Centropyge bicolor* was not strongly asssociated with any of the habitat parameters. Benthic cover and the benthic cover*physical interaction steadily increased in importance to 18% with increasing scale (Fig. 3.10a). A benthic cover*location factor became apparent at >81m^2, rising to a level of 13% variation explained. These patterns were due to *C. bicolor*'s association with high topographic features in deeper, rubbly areas on the eastern side of Lizard Island (Table 3.4). *Centropyge vrolicki* was characterised by an association with benthic cover (branching corals, bare rock and encrusting corals), contingent on location (the eastern side of Lizard Island). The main effects of benthic cover and location peaked at 21% and 17% variation explained respectively, at 144m^2; their interaction peaked initially at 81m^2, then again at >180m^2 (Fig. 3.10b). *Pomacanthus sexfasciatus* was the only species strongly associated with benthic cover, reaching 26% variation explained at 144m^2 (Fig. 3.10c). This was due to an association with staghorn corals (Table 3.4). Physical habitat structure was important at scales of 144-180m^2. Smaller location effects increased with increasing scale, but reached only 12% variation explained.

General Patterns and Scales

Habitat variability, with the exception of depth, was greatest at the smallest scale which indicated no characteristic 'patch' size was typical within the range of scales examined. In contrast, depth variability was consistently high up to the 54m^2 scale then dropped abruptly at larger scales indicating that the 54m^2 scale corresponded to the depth structure of the habitat. Benthic cover featured prominently in explaining variation, both independently and conditional on locality and physical structure. In general however, no characteristic scale of fish-habitat association was evident. The commonest form of response was an increase in variability explained to a constant level. The scale at which the relationship plateaued varied from 54-81m^2 and 144m^2. Interactions plateaued at smaller scales than did simple effects.

Table 3.1. Correlations between pomacentrids and habitat variables. Strength of correlation denoted by font: *italic* = 0.2-0.3; normal = 0.3-0.4; **bold** >0.4. S=shallow, D=depth, M=mid-depths, H=high features, L=low features. Sign indicates direction of correlation with location.

	Physical		**Benthic Cover**	**Location**	
	Depth	**Height**		**+ve**	**-ve**
Group 1					
Abudefduf sexfasciatus			Encrusting	Washing	
Acanthochromis polyacanthus			*Plating*		
Amblyglyphidodon whitleyi			Branching, plating	*Bird Is.*	
Amphiprion akindynos			*Encrusting*		
Amphiprion melanopus			Staghorn	*Lagoon*	
Chromis atripectoralis			*Plating, corymbose*	*Washing*	
Chromis ternatensis			*Branching*		
Chromis viridis			*Corymbose*	*Crystal*	
Chromis weberi			*Branching*	*Washing*	
Chrysiptera cyanea	*S*		Digitate, *plating*	*Washing*	
Chrysiptera talboti	D		Encrusting, *turfing algae*	Crystal	
Dascyllus aruanus	*D*	*H*	Fleshy macroalgae, gravel/sand,		
Dischistodus melanotus	M		Turfing algae, massive soft corals, *sand*		
D. pseudochrysopoecilus			Rubble	*Crystal*	
Neopomacentrus azysron	*S+D*		Corymbose, plating	Washing	
Neopomacentrus cyanomos			*Encrusting algae*	Washing	
Pomacentrus brachialis	D		*Bare rock, fleshy macroalgae*		
Premnas biaculeatus			*Gravel/sand, turfing algae, staghorn*	Lagoon	
Group 2					
Amblyglyphidodon leucogaster	D		**Staghorn**, turfing algae	Lagoon	
Chrysiptera flavipinnis	*D*		**Fleshy macroalgae**, soft corals	Osprey	
Dischistodus perspicillatus			**Sand/gravel**, *sand*	Lagoon	
Neoglyphidodon melas			**Soft corals**, *dead branching corals*	Osprey	
Neoglyphidodon nigroris		H	Staghorn	*Lagoon*	
Pomacentrus moluccensis	*S+D*		**Branching**, soft corals, *staghorn*	Osprey, Palfrey	
Group 3					
Dischistodus prosopotaenia	*D*		**Gravel/sand**	Lagoon	
Dascyllus reticulatis			Fleshy macroalgae, *bare rock*	Granite,	
Plectroglyphidodon lacrymatus			Corymbose, branching, *encrusting*	Bird Is., Coconut	
Pomacentrus lepidogenys	S+D		Plating, corymbose, branching		Lagoon, Granite
Pomacentrus nagasakiensis	*D*		**Fleshy macroalgae, soft corals**	**Osprey**	
Stegastes apicalis	*S*		Branching, encrusting, plating, *digitate*, *corymbose*	*Coconut, Bird Is.*	
Group 4					
Pomacentrus chrysurus	S		*Digitate*		
Pomacentrus coelestis	*S*		*Corymbose*		
Plectroglyphidodon dicki	*S*		Plating, corymbose, digitate, branching, *encrusting*	Washing	
Stegastes nigricans	*S*		*Massive*		
Group 5					
Pomacentrus amboinesis	**D**	*H*	**Fleshy macroalgae**, gravel/sand, soft corals, *rubble*	Osprey	
Pomacentrus bankanensis	**S**	*L*	**Digitate**, *plating, encrusting, branching*		
Stegastes fasciolatus	S	*L*	**Digitate**, *encrusting, bare rock*		
Group 6					
Chrysiptera rex	S		Digitate, corymbose, plating, encrusting, *rock*	Washing	
Chrysiptera rollandi	D		Staghorn, fleshy macroalgae, soft corals, *gravel/sand*	Osprey, Lagoon	
Pomacentrus wardi	S		Corymbose, plating, *massive, soft corals*	Palfrey, *Osprey*	Lagoon
Group 7					
Amblyglyphidon curacao			**Staghorn**, *soft corals*	Lagoon, *Osprey*	
Pomacentrus adelus			Soft corals, dead corals, *staghorn*	Osprey, Lagoon	
Group 8					
Hemiglyphidodon plagiometapon			**Staghorn**	**Lagoon**	
Pomacentrus grammorhynchus			**Staghorn**	**Lagoon**	

Table 3.2. Correlations between labrids and habitat variables. Strength of correlation denoted by font: *italic* = 0.2-0.3; normal = 0.3-0.4; **bold** >0.4. S=shallow, D=depth, M=mid-depths, H=high features, L=low features. Sign indicates direction of correlation with location.

	Physical		**Benthic Cover**	**Location**	
	Depth	**Height**		**+ve**	**-ve**
Group 1					
Anampses neoguinaicus			Caespitose, *encrusting*		
Bodianus axillaris			*Corymbose, encrusting, plating*	*Washing*	
Bodianus mesothorax				*Coconut*	
Cheilinus chlorourus			Caespitose, *fleshy macroalgae*	Granite	
Cheilinus digrammus		*H*			
Choerodon fasciatus		H	Encrusting	*Washing*	
Epibulus insidiator					
Halichoeres trimaculatus			*Rubble*	Granite	
Hemigymnus fasciatus			*Branching*		
Labrichthys unilineatus			Caespitose, *corymbose*, *branching*	*Washing*	
Labroides dimidiatus	*S+D*		*Encrusting*	*Coconut*	
Pteragogus cryptus			Fleshy macroalgae, soft corals	**Osprey**	
Thalassoma amblycephalum	*S*		*Plating, bare rock*	*Crystal*	
Group 2					
Cirrhilabrus punctatus	D		**Fleshy macroalgae**	*Osprey*	
Halichoeres margaritaceous	S		**Digitate**	Washing	
Halichoeres melanurus	*S+D*		Soft corals, *massive*, *rubble*	Osprey	
Stethojulis bandanensis	S		Caespitose, digitate	*Crystal, Washing*	
Group 3					
Cheilinus fasciatus			**Staghorn**	**Lagoon**	
Stethojulis strigiventer			**Soft corals**, fleshy macroalgae	**Osprey**	
Thalassoma lunare	D		Branching, *bare rock*	Bird Is., *Coconut*	Lagoon
Group 4					
Pseudocheilinus hexataenia			Corymbose, caespitose, digitate, branching	Granite	*Lagoon*
Gomphosus varius	*S*		**Branching**, encrusting, plating, corymbose, bare rock, *digitate*	*Coconut*	*Lagoon*
Hemigymnus melapterus			Staghorn	*Bird Is., Lagoon*	
Group 5					
Thalassoma hardwicke	S	L	**Corymbose, branching, plating**, digitate, encrusting, *caespitose*	*Bird Is.*	Lagoon
Thalassoma janseni	S		**Digitate**, branching, plating, bare rock, *encrusting*	*Coconut*	*Lagoon*
Coris schroederi	D		Gravel/sand, rubble, soft corals, fleshy macroalgae	Osprey, *Coconut*	

Table 3.3. Correlations between chaetodontids and habitat variables. Strength of correlation denoted by font: *italic* = 0.2-0.3; normal = 0.3-0.4; **bold** >0.4. S=shallow, D=depth, M=mid-depths, H=high features, L=low features. Sign indicates direction of correlation with location.

	Physical		**Benthic Cover**	**Location**	
	Depth	**Height**		**+ve**	**-ve**
Group 1					
Chaetodon auriga			*Plating, staghorn*	*Palfrey*	
Chaetodon kleinii			**Caespitose**	Washing	*Lagoon*
Chaetodon melannotus					
Chaetodon vagabundus			*Massive*	*Washing*	
Group 2					
Chaetodon aureofasciatus			*Branching, caespitose*	Palfrey	
Chaetodon baronessa			Plating, corymbose, digitate	Palfrey, *Bird Is.*	
Chaetodon plebeius	S		Plating, *caespitose, corymbose, digitate, soft corals*	Palfrey	
Chaetodon rainfordi			Branching, corymbose	Palfrey	
Chaetodon trifasciatus			**Caespitose**		
Chaetodon trifascialis	S	*L*	**Plating**, corymbose, digitate, *branching, encrusting*	Washing	
Chaetodon citrinellus	S		Digitate, bare rock, *soft corals*		

Table 3.4. Correlations between pomacanthids and habitat variables. Strength of correlation denoted by font: *italic* = 0.2-0.3; normal = 0.3-0.4; **bold** >0.4. S=shallow, D=depth, M=mid-depths, H=high features, L=low features. Sign indicates direction of correlation with location.

	Physical		**Benthic Cover**	**Location**	
	Depth	**Height**		**+ve**	**-ve**
Centropyge bicolor	D	H	Rubble	Bird Is.	*Lagoon*
Centropyge vrolicki			Branching, *bare rock, encrusting*	Coconut	
Pomacanthus sexstriatus			Staghorn		

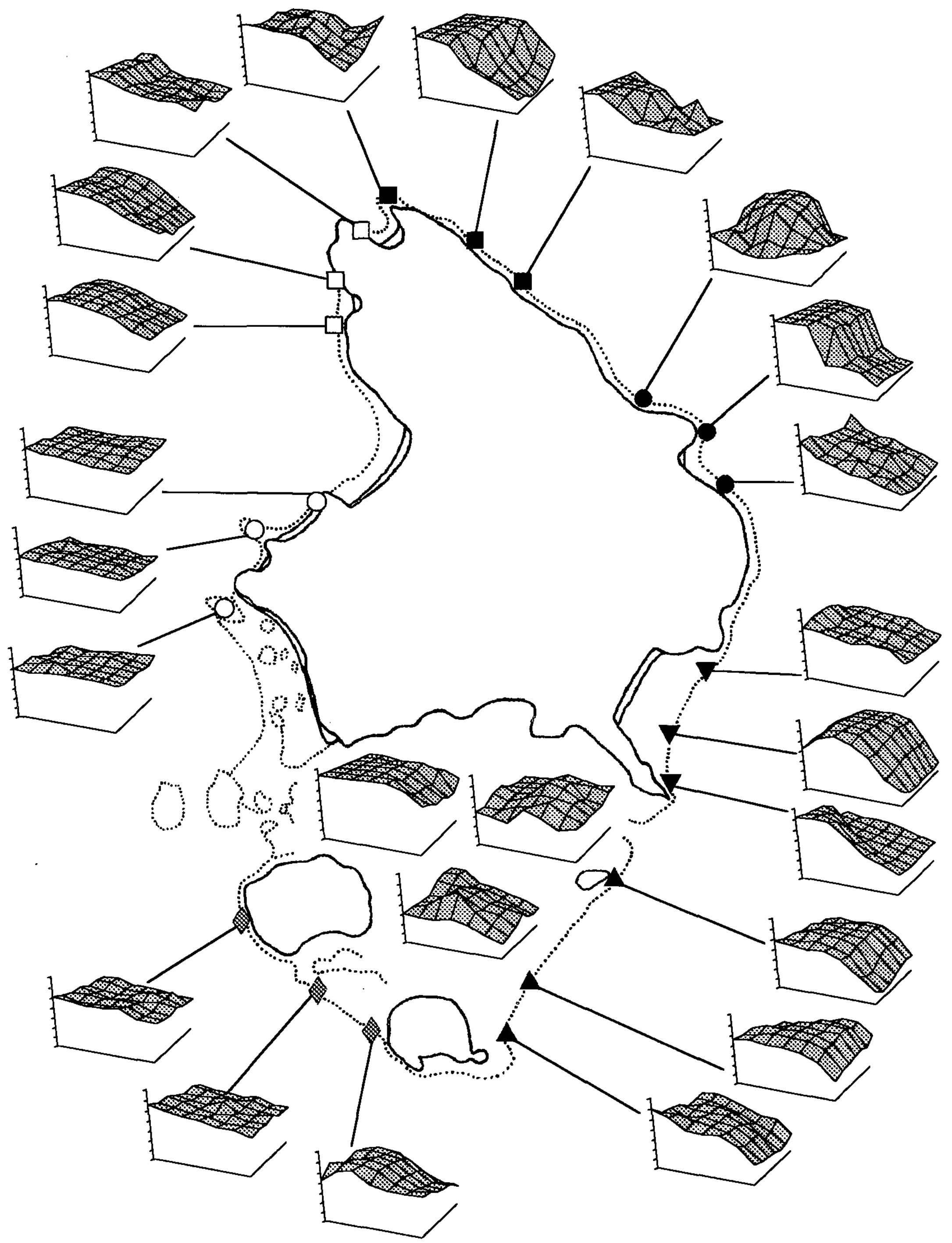

Figure 3.1. Location of sample grids around Lizard Island. All quadrats are pictured from the bottom left hand side when facing shoreward. Symbols correspond to the localities. Filled symbols are exposed localities, open symbols are sheltered localities. Grey symbols are semi-exposed. ■ Washing Machine; ● Crystal Beach; ▼ Coconut Beach; ▲ Bird Island; ◈ Palfrey Island; ❍ Osprey Island; □ Granite Bluff; ∇ Lagoon. Note Lagoon symbols obscured by the contour plots.

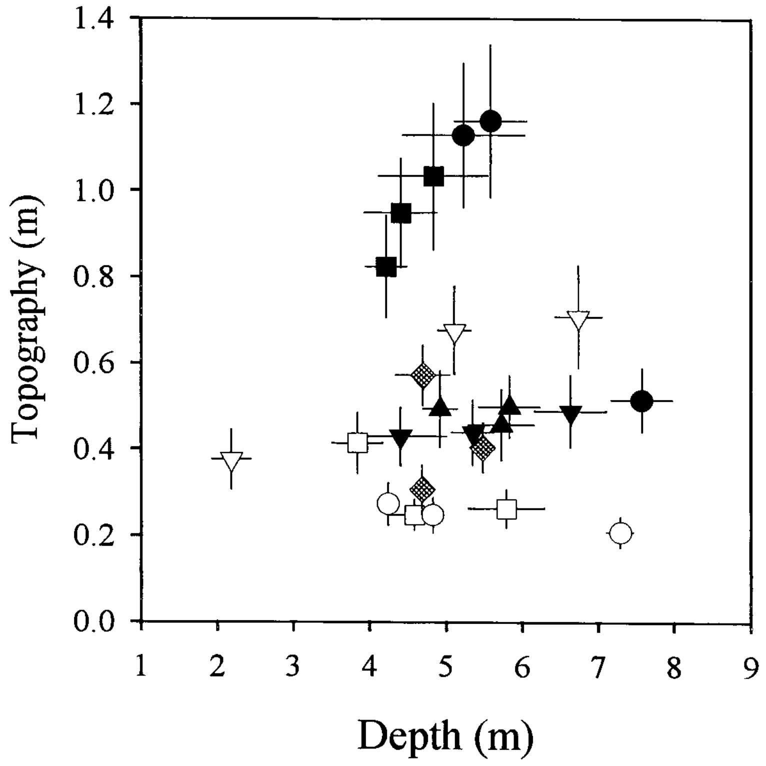

Figure 3.2. Average depth and topography for each locality. Symbols as in Figure 3.1.

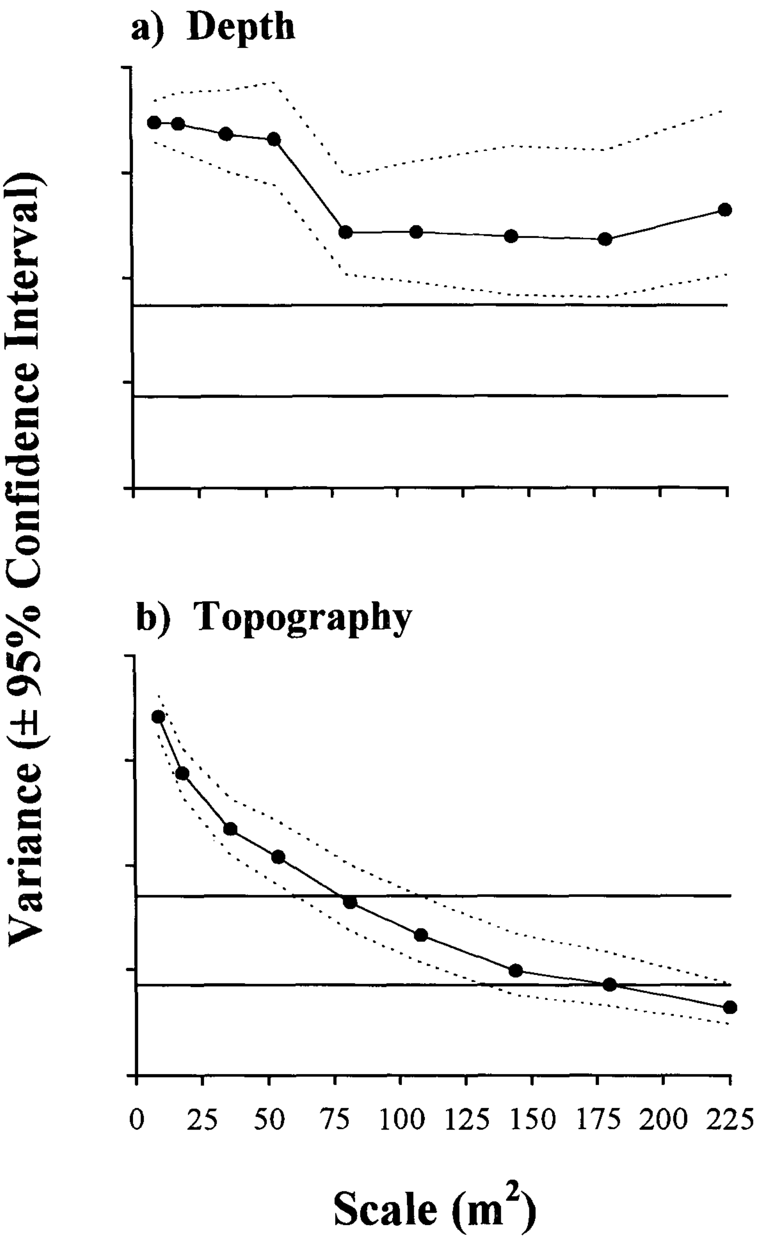

Figure 3.3. Variance of depth and topgraphy with changing scale. Horizontal lines represent the 50% and 25% reference lines.

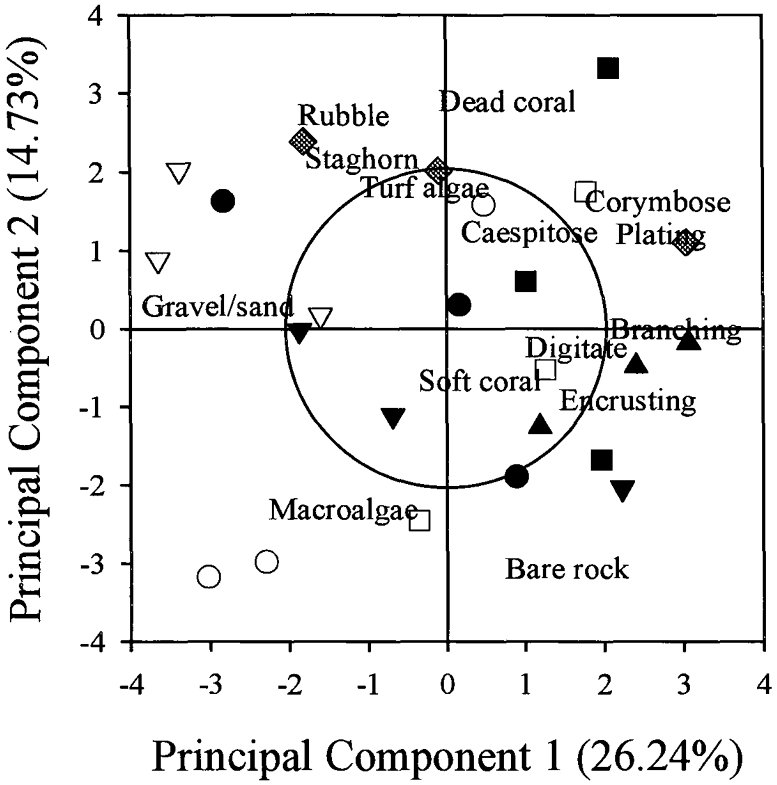

Figure 3.4. Principal components analysis biplot of benthic cover of each site. Symbols as in Figure 3.1. Benthic cover types have been rescaled for presentation, the circle represents 0.3 correlation with the axis.

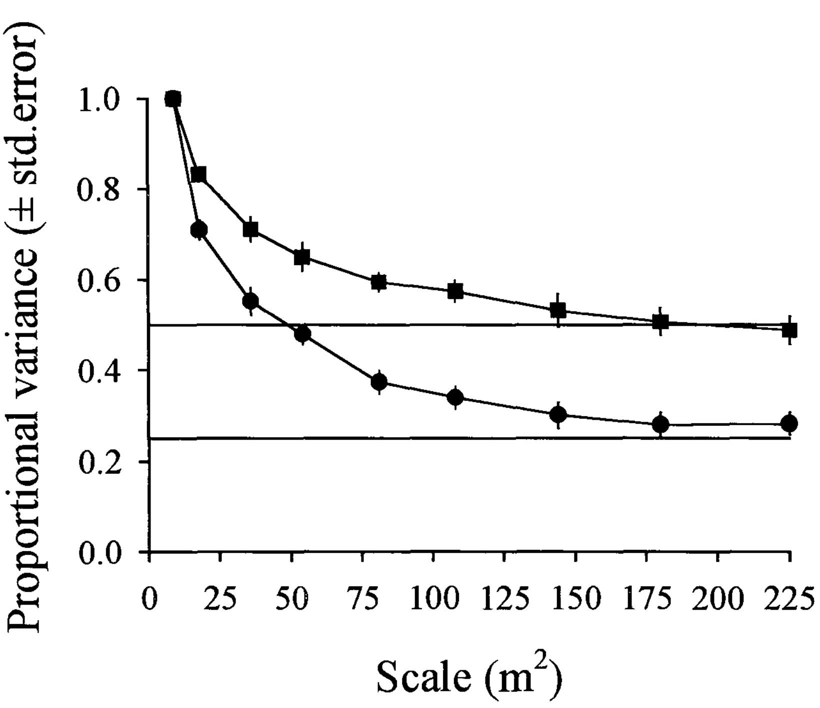

Figure 3.5. Proportional variance profiles of benthic cover (rescaled to unit maximum). ■ Evenly distributed and large patch forming (bare rock, sand, rubble, macroalgae, massive soft coral, plating, digitate, staghorn hard coral) categories; ● Sparsely distributed and patchy categories (Turf algae, dead corals, massive, encrusting, caespitose, corymbose, branching hard corals). Horizontal lines represent the 50% and 25% reference lines.

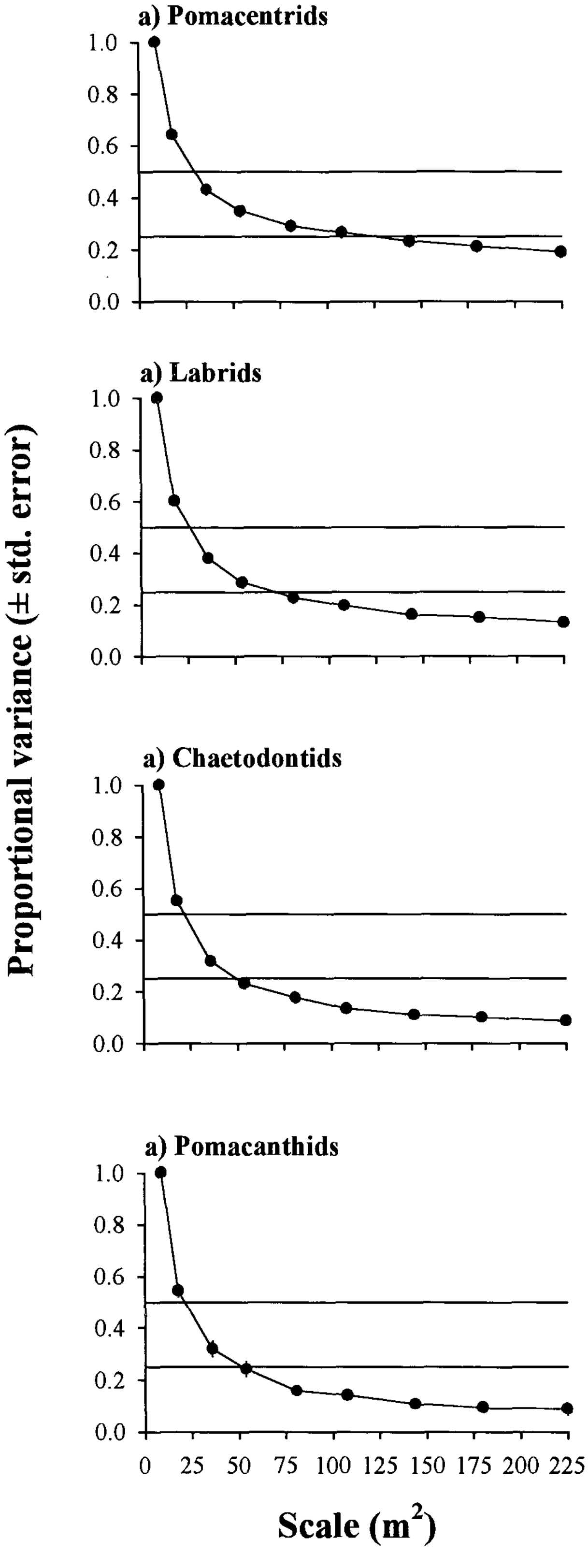

Figure 3.6. Proportional variance profiles of pomacentrids, labrids, chaetodontids, and pomacanthids. Horizontal lines represent the 50% and 25% reference lines.

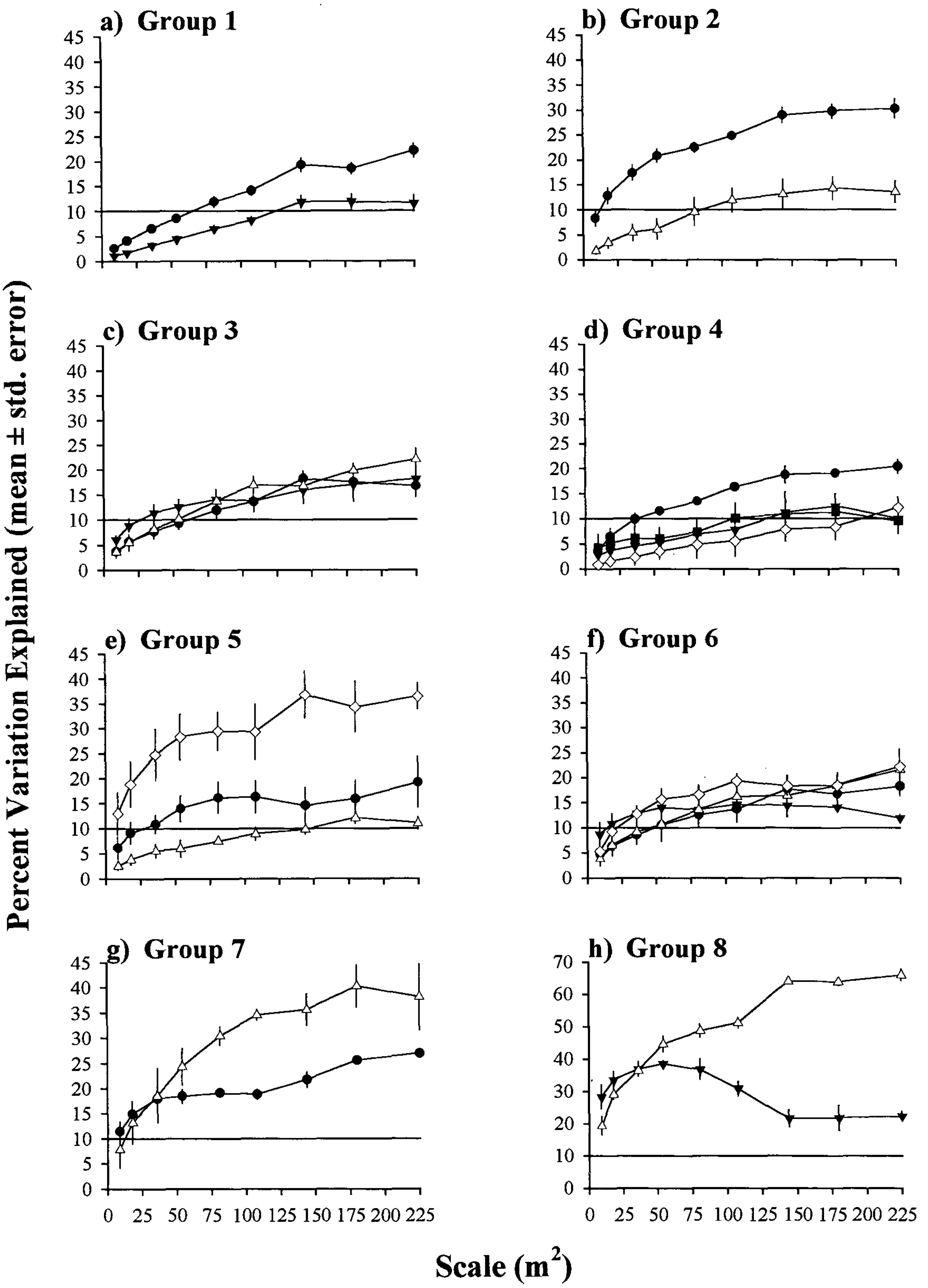

Figure 3.7. Changes in variance explained by different sets of habitat variables for pomacentrids. ● Benthic cover; ▼ Location; ■ Physical structure; Δ Benthic cover*Location interaction; ◊ Benthic cover*Physical structure interaction.

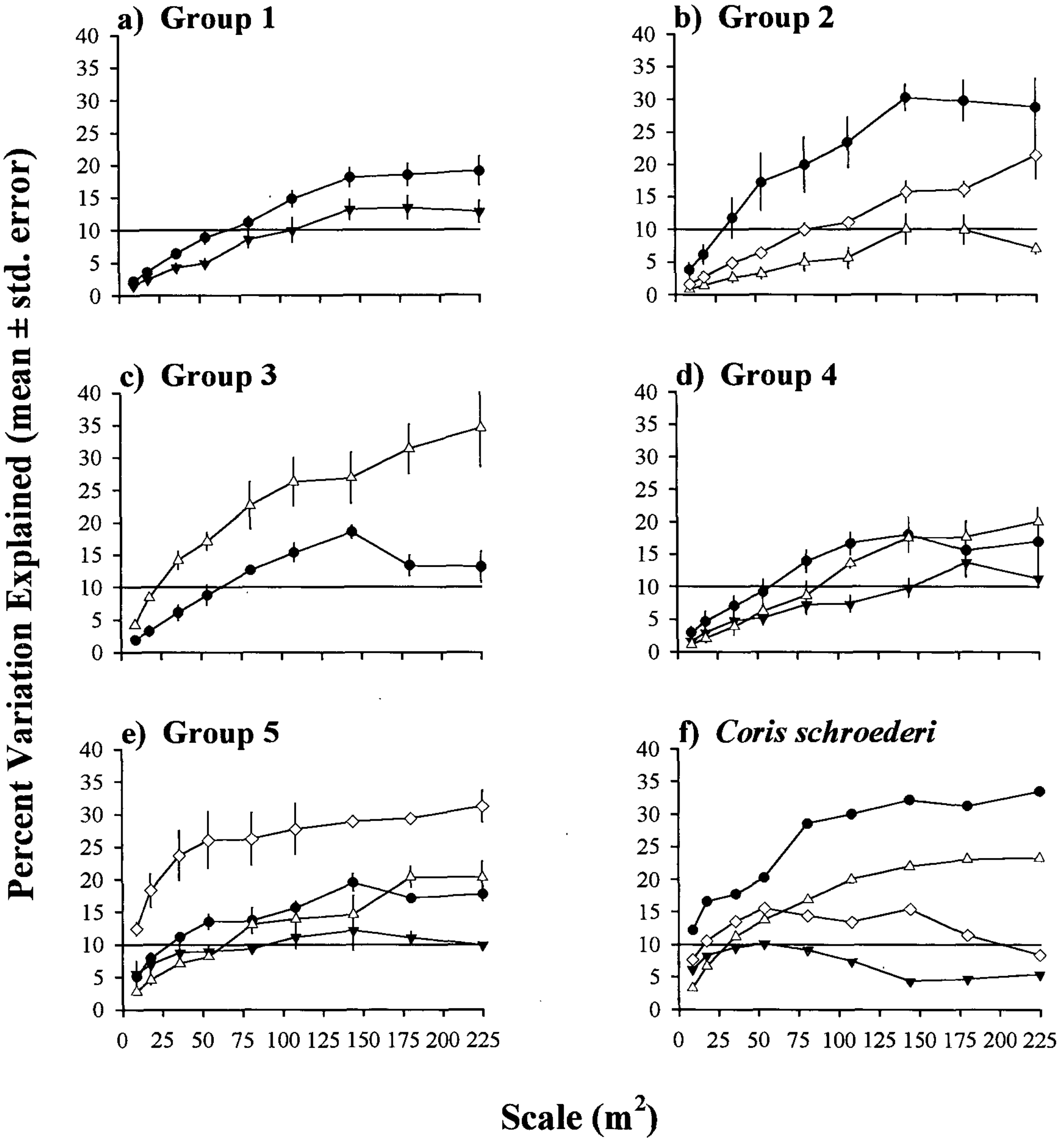

Figure 3.8. Changes in variance explained by different sets of habitat variables for labrids. Symbols as in Figure 3.7.

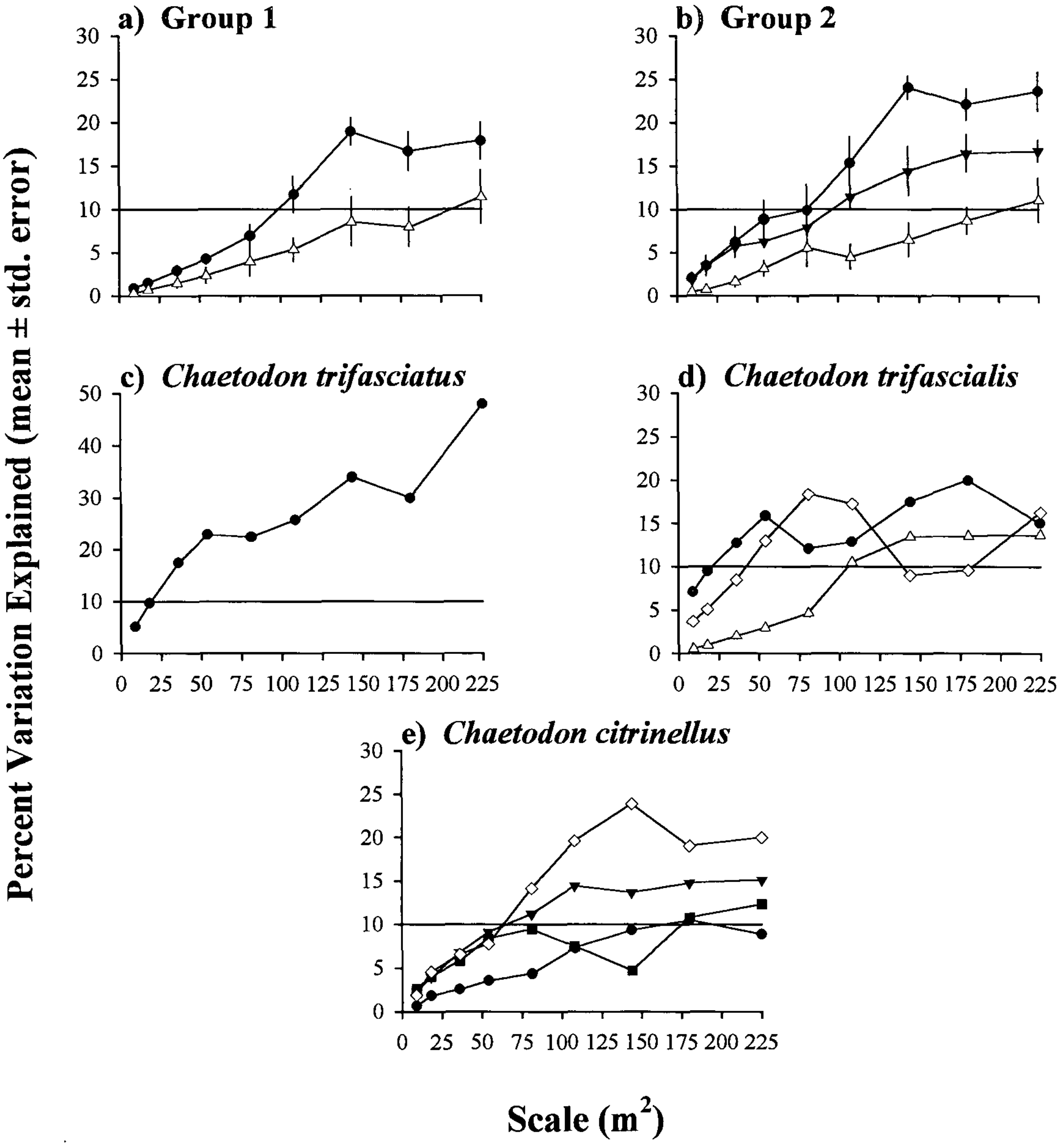

Figure 3.9. Changes in variance explained by different sets of habitat variables for chaetodontids. Symbols as in Figure 3.7.

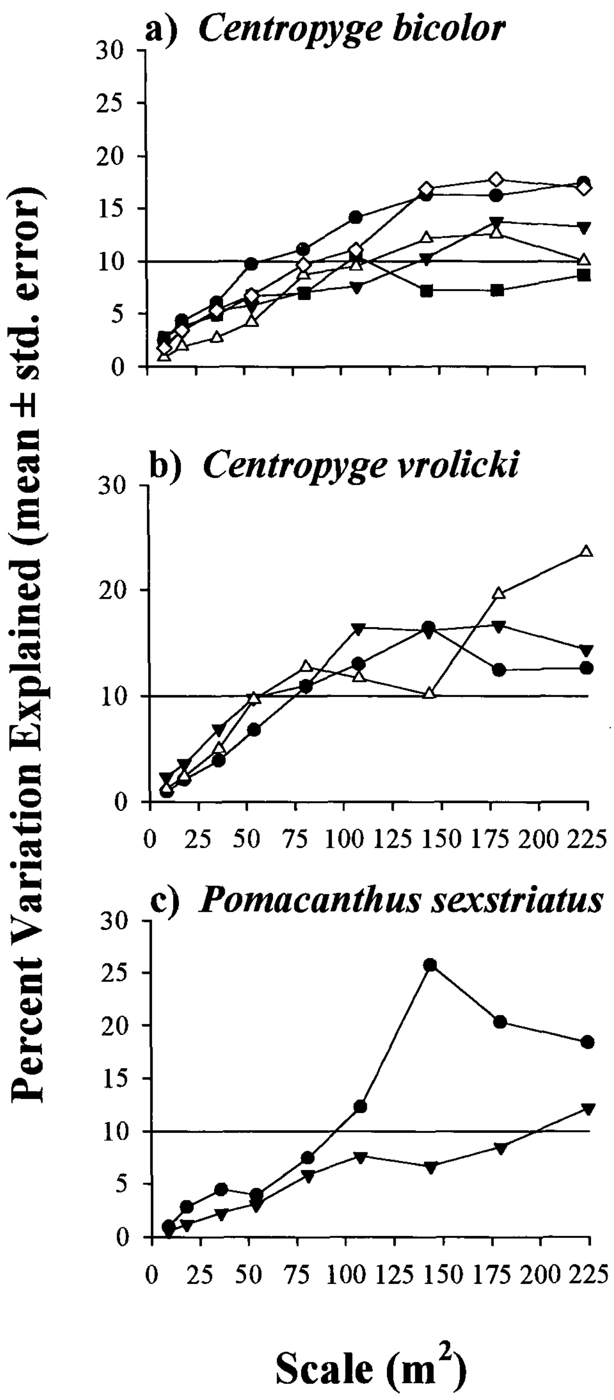

Figure 3.10. Changes in variance explained by different sets of habitat variables for pomacanthids. Symbols as in Figure 3.7.

3.5 Discussion

The distribution of an organism in space is a product of many interacting processes, each operating at particular scales. Although the scale dependence of organism/habitat associations has been frequently acknowledged (Morris 1987, Roberts and Ormond 1987, Bourget et al. 1994, Syms 1995, Flather and Sauer 1996), explicit attempts to identify the scales at which organisms are correlated with different sets of habitat variables are rare (but see Schneider and Piatt 1986, Wiens et al. 1986, Schneider 1992, Syms 1995). One way of defining these scales is to alter the grain at which the relationship between habitat and habitat-responding organisms are analysed, and recalculate the variance explained by the habitat variables. In general, variance should decrease as grain size increases (Wiens 1989). However, variance should increase at 'transition zones' or scale boundaries. Coincident peaks in variance between different sets of variables may indicate common spatial scalings or linkages. Sharp increases of explainable variation might correspond to common transition or scale domains (O'Neill et al. 1986) and accordingly with the scales of organism-habitat interactions (Greig-Smith 1979, Schneider and Piatt 1986).

In this study, variability in coral reef fish abundance, habitat variables, and their association was calculated at 9 grain scales ranging from 9-225m^2. All fish species and habitat variables (with the exception of depth) showed a typical decrease in variance with increase in scale which indicated any patches, if they existed, were smaller than the finest resolution in this study (Figs. 3.3,3.5,3.6). Depth, on the other hand, was consistently variable between 9-54m^2, and decreased sharply at greater scales (Fig. 3.5). As patchiness of both fish and habitat occurred at the smallest scale, it would be predicted that fish and habitat associations should also be greatest at the smallest scale. Contrary to this prediction, association strength generally increased with grain. Two scales were frequently important - 144m^2, and 54-81m^2. It is suggested that these are two 'characteristic' scales of the assemblages studied, however these scales were not universal across taxa. The importance of the different types of habitat variables, and the form of the relationship was dependent both on scale and the species in question.

Benthic cover emerged as a major explanatory factor for most species. In general, the strength of association increased with scale, with abrupt increases occurring either at the 54-81m^2 scale or, more commonly, at 144m^2 (e.g. Figs. 3.7a,b,3.8a,3.8b,3.9a,3.9b). When benthic cover alone was not the most important factor, the strongest explanatory factor was usually an interaction between benthic cover and either location or the physical structure of the substratum. Interactions between benthic cover and location usually exerted themselves at larger scales - reaching minor plateaus at 81-104m^2, then increasing further at larger scales (e.g. Figs. 3.7g,h, 3.8c). Benthic cover*physical structure interactions generally operated at smaller scales - often 54m^2 (e.g. Figs. 3.7e, 3.8e,f). The striking importance of benthic cover identified in this study is in contrast with many other studies (Roberts and Ormond 1987, Roberts et al. 1988, Fowler 1990, Booth and Beretta 1994, Cox 1994, Green 1996).

With the exception of the pomacentrids *P. grammorhynchus* and *H. plagiometapon*, location effects alone were not prominent in explaining variation. However, location often mediated the association of species with benthic cover and physical variables i.e. associations with these benthic cover and physical structure were contingent on locality (e.g. Figs.7g,h, 8c,f). Ecologically, this phenomenon has two interpretations - either the fish can be seen as associated with the habitat, contingent on the locality, or alternatively the fish is associated with the locality, contingent on the habitat. Establishing the primacy of one set of variables versus the other could at least be partially assessed by experimentation. An important implication of these interactions is that simple associative measures across locations may be considerably reduced in discriminatory power when locality is not taken into effect. The damselfishes that were strongly associated with location were primarily found in back reef or lagoonal sites at Lizard Island. Interestingly, 'simple' location effects featured prominently only at small scales - as scale increased, the variation was assigned to the location*benthic cover interaction.

Physical structure (depth, topography) was the least important of the habitat parameters, except when in combination with benthic cover (e.g. Figs. 3.7 e,f, 3.8 e, 3.9 d,e). Physical*benthic interactions were frequently measurable at smaller scales (generally 54m^2) than simple benthic cover alone. As with the habitat*location interaction, the primacy of importance of benthic cover vs physical habitat could be at least partially explored by experimentation. Depth has been frequently cited as a strong determinant of fish distribution patterns (Bouchon-Navaro 1981, Russ 1984 a, b, Meekan et al. 1995, Green 1996), as has topography (Luckhurst and Luckhurst 1978 a, b, Molles 1978, Carpenter et al. 1981, McCormick 1994, but see Roberts and Ormond 1987, Booth and Beretta 1994). My results would suggest that, at the scales considered in this study, depth and topography patterns, with some exceptions, are largely spurious and probably due to the association of characteristic benthic cover types with depth (e.g tabular corals are usually found in shallow water).

Similarly-scaled responses to habitat were observed for wide varieties of species, but did not necessarily imply similarity of habitat use. For example, the first pomacentrid group included typical small hard-coral associated planktivorous damselfishes such as *Chromis viridis*, *C. atripectoralis*, and *Dascyllus aruanus*, large territorial herbivorous *Dischistodus* spp., and shoaling *Neopomacentrus* spp.. Some groups however, were ecologically related; for example Group 8 of the pomacentrids contained two species that were both associated with lagoonal staghorn corals (Table 3.1), and Group 5 of the labrids was made up of two species characteristic of shallow water at exposed localities in high coral-cover areas. Interestingly, ecologically complementary species formed some groups. The fifth pomacentrid group contained two species (*P. bankanensis* and *S. fasciolatus*) which were associated with depressions in shallow water reef-tops, and digitate hard coral cover. In contrast, the third member of the group, *P. amboinensis*, was associated with high topographic features in deep water, in macroalgal-covered, rubbly habitats. Similarly, Group 6 of the pomacentrids was composed of small, site attached fishes of which one (*C. rex*) was found at exposed sites in shallow, hard-coral covered areas; the second species (*P. wardi*) was complementary in locality use i.e. *P. wardi* was found in the same benthic cover/depth combination at back-reef (cf. exposed) localities; the third species was complementary to *P. wardi* and was found in deeper areas in staghorn and soft corals in back reefs and lagoons (Table 3.1). With some exceptions, ecological similarity was not a good predictor of similarity in scales of association.

Fishes, even within the same family, responded to different habitat parameters in a wide range of ways. In this study, I quantified habitat as a set of potentially correlated but distinct groups of parameters which were treated (with the exception of locality) as continuous variables. Samples were widely distributed around Lizard Island and placed so as to incorporate as wide a range of variability as possible. In this respect, this strategy is in contrast with more conventional approaches in which the study area is subdivided into characteristic physiographic (i.e. physical structure, usually in combination with a characteristic benthic cover) ‘zones’ (e.g. Russ 1984 a, b, Williams 1982, Meekan et al. 1995, Green 1996). The distinction between classical reef tops and slopes was apparent only at a handful of sites on the eastern side of Lizard Island (Fig. 3.1), but was reflected in the relationship between depth variability and scale which indicated that samples $<54m^2$ could be regarded as occupying the same zone. Despite the perception that zonal patterns are the rule rather than the exception (Williams 1991), I found that the benthic cover*physical structure interaction was strongest only in a few groups of species (pomacentrid Groups 5 (3 species) and 6 (3 species), labrid Group 5 (2 species), *Chaetodon trifascialis*, and *Chaetodon citrinellus*). Most other groups were more strongly influenced by benthic cover and locality.

While stratification of habitat into zones is a useful sample device when precision of a mean estimate is the parameter to be optimised (e.g. McCormick and Choat 1987), this study would indicate it is ineffective as a means of isolating patterns and generating hypotheses about processes. Zones are defined by the observer, at the scale of the observer, thus introducing an implicit scale. More importantly, 'zones' become indistinguishable from the habitat variables considered. At best this would mean that associations between fish and habitat parameters across zones are tautological, at worst confounded. In addition, sites where strata are less clearly defined will get sampled less frequently. In order to obtain unconfounded information on fish-habitat associations, it is necessary to make sampling independent of *a priori* defined zones but also unbiased e.g. by depth stratification (Syms 1995), and to sample combinations of different conditions. In other words, introduce as much variability into the system so that variation can be independently partitioned into its component explanatory variables (Jones and Syms 1998, Appendix III). This objective is anathema to the principles of stratification, and reflects the different parameters (mean vs habitat association) to be quantified.

It has been hypothesised that coincident scales at which different organisms form 'patches' might correspond with interaction scales (Greig-Smith 1979, O'Neill et al. 1986, Schneider and Piatt 1986). Counter-intuitively, in this study, correlations only became apparent at large scales that were incommensurate with the univariate patterns of variance and scale. This discrepancy is of extreme importance. Variability peaks at the $9m^2$ scale signified that the smallest scale is the 'patch' size. I believe the intensity of this patchiness, however, is central to explaining why correlations were measurable only at larger scales. Despite the 'patch' size of all fish species was $9m^2$, few species occurred in real patches (with the exception of some pomacentrids, and the labrid *Cirrhilabrus punctatus*). Additionally, those species that did occur in groups did not consistently do so. Generally, the fish were sparsely distributed - occurring either singly or relatively evenly in adjacent quadrats. Similarly, habitat types were either sparsely (for some of the rarer habitat types) or evenly distributed within 9m^2 blocks. The fish species considered in this study did not form 'patches' relative to the scales considered.

Rather than considering linkages between fish and habitat variables as corresponding 'patch' sizes, correlations between two sets of variables at any given scale can be viewed as the integration of two probability functions. The first function is the likelihood that one variable will be found in a particular sample; and the second is that the other variable is found in the same sample. Independence of the two functions implies no correlation. If the intersection set exceeds that of the null hypothesis of independence, then correlation (or conditionality) can be assumed. Sparsely distributed organisms, such as the fish in this study, will have 'noisy' probability functions. In addition, the relationship between the two variables is unlikely to be symmetrical. In biological terms, the likelihood that a quadrat containing a preferred habitat contains a typically habitat-associated fish species will almost always be less than the probability that a quadrat containing the fish contains its preferred habitat (the probabilities would only approach symmetry when the habitat is saturated). The 'characteristic' scales identified in this study are likely to correspond with the scales at which the likelihood of recording a fish *and* its associated habitat becomes measurable, rather than reflecting the biological scales at which the fish are responding to their environment.

This interpretation is supported by the observation that habitat associations with 'specialised' species were measurable at smaller scales. For example, strongly 'zonal' species which occupied characteristic depth and benthic cover sites (e.g. the 'typical' reef crest dwellers *P. bankanensis*, *S. fasciolatus*, *T. hardwicke*, *T. janseni*) were measurably associated with habitat variables at scales approaching the 'zone' (54m^2). Similarly, the associations of the lagoonal/staghorn dwellers *H. plagiometapon* and *P. grammorhynchus* were very predictable even at the smallest scale. The tightness of association between these fishes and their habitat enabled the association to be measured at a much finer scale.

Ecologists working in both marine and terrestrial systems have long called for multiscale approaches in future studies, with the establishment of many scale frameworks (e.g. Forman and Godron 1981, Addicott et al. 1987, Kotliar and Wiens 1990, Levin 1992, Schneider 1994, Wu and Loucks 1995). While considerable empirical inroads have been made into scaling problems among terrestrial (e.g. Bennett 1990, Chaneton and Facelli 1991, Costanza and Maxwell 1994) and aquatic (Dayton and Tegner 1984, Dayton et al. 1992, Bourget et al. 1994, Bell et al. 1995) systems, marine reef-associated communities have received little explicit attention to manipulation of scale - either by manipulation or inclusion as an analytical covariate (however see Keough 1984, Farrell 1989, Syms and Jones in press,). Many previously published benthic-marine studies, ostensibly framed within the 'scale' problem, have synonymised 'scale' with comparisons of between and within-zone patterns - reflecting the structuring of sample allocation within physiographic strata across many sites (e.g. Roberts and Ormond 1987, Caselle and Warner 1996). This study initially aimed to identify which elements of the habitat were important to fish, and more importantly at which scale were they important? These results suggest that, while the first part of the question can be answered, the second part is less clearly addressed. When sufficient variability is incorporated into the sampling strategy, independent and interactive, biologically interpretable, variance fractions can be partitioned. The commonest scales that appeared to be important were 54-81m^2, and more commonly 144m^2. Consequently, in order to reliably measure habitat association, a 12x12m area would be sufficient. This characteristic scale, however does not (necessarily) correspond to the scale of patchiness of the habitat or fish populations. It corresponds to the scale at which enough numerical information exists so that the habitat variables are *reliably* correlated with the fish species.

Determining the scale at which sparsely distributed organisms respond to their environment is unlikely to be fully addressed by fixed-area quadrat sampling. The signal that emerges from data of this type reflects the relative overlap of two probability distributions, rather than the scale at which a single individual responds and interacts with the environment. A major problem lies in the lack of information contained in samples that do not contain the organism of interest. Alternative approaches (e.g. variable area sampling) will be required if scale is to be viewed at the level of an individual organism. However, this study has indicated that there is a minimum scale, below which we might not reliably detect associations that exist. This information in itself is useful and provides a context for interpreting experiments conducted at single scales. For example, I conducted a habitat disturbance experiment on sections of contiguous reef and found no effect. The scale on which the experiment was carried out was 10x10m and, while admittedly on the small side (cf. the optimum in this study 12x12m), the scale at which the experiment was conducted was sufficient to reasonably expect that fish responses to the disturbance should have been detected. The lack of any effect was more likely due to resistance of the assemblage to the level of disturbance imparted to the benthos rather than some mystical ‘scale’ effect. However, until alternative methodologies are developed to cope with the deficiencies of fixed area quadrats, the question of scale will still provide challenges to be overcome by ecologists.

Chapter 4: Scaling Rules and Patch Reefs: Are Large Patches Simply Collections of Small Patches?

4.1 Abstract

Studies carried out on small patch reefs have provided the basic information from which coral reef fish ecology has been derived. Conflicting conclusions drawn form patch reef studies, after causing considerable debate, were eventually attributed to the size or scale of the reefs. However no published studies have attempted to document what scaling effects exist in such systems, and whether we can extrapolate or interpolate between studies carried out on different scales.

In this study I mapped randomly selected patch reefs, ranging in size from 0.26m^2 to 63.5m^2, and censused the resident fish fauna. Multiple regression was used to partition variation amongst reef area, reef shape and patchiness, and benthic cover. Species responded in a variety ways to reef parameters. Some species were strongly area-dependent, others were well predicted by reef shape and patchiness, and a considerable number of species were well predicted by the benthic cover of the reef. Further groups of species were associated with combinations of these factors. In order to measure the effect of scaling up or down, I divided the data set into smaller, medium and larger thirds, recalculated the regression equations and measured the predictive ability of each equation. Surprisingly equations derived from the smaller reefs were better predictors of larger reefs and vice versa. It is hypothesised that this is because the effect of benthic cover and reef patchiness are parameters that are better estimated at the scale of a small patch reef. As a consequence, the lessons drawn from experiments carried out on small reefs can be cautiously, and with strong caveats, applied to large reefs, as long as the reef characters of the small reefs studied are representative of the universe to which results are to be extrapolated.

4.2 Introduction

Scaling is central to the study of ecology (Wiens 1989). Because it is not possible to measure the entire system at a single moment, ecologists rely on observations made on microcosms or samples of the system, and then must extrapolate these observations to the sample ‘universe’ of interest. In order to extrapolate, the observed samples must form an unbiased set of the larger system. Recently, the effects that the spatial scale at which studies are carried out has received attention (Dayton and Tegner 1984, Wiens et al. 1986, Meentemeyer and Box 1987, Kareiva and Anderson 1988, Levin 1992), and it is clear that simple extrapolation across scales is unlikely to be successful. However, if scale generates systematic and predictable changes in a system, it may be possible to establish sets of 'rules' that govern scaling (e.g. Ives et al. 1993, Lavorel et al. 1993, Waltho and Kolasa 1994, Kolasa et al. 1996). Identifying these rules may, at best, enable scaling up or down from studies carried out at single scales or, at worst, establish the range of scales to which studies can be generalised.

Organisms are characteristically associated with particular habitat types and so it may be hypothesised that habitat structure may provide a link between patterns at different scales (Kolasa 1989) and consequently be central to developing a set of guidelines for scaling. Habitats are structured at a range of scales, in a variety of ways (Levin and Paine 1974, Southwood 1977, Paine and Levin 1981, Bell et al. 1991). The structure of the habitat may have profound impacts on the distribution and abundance of organisms associated with the habitat type (Paine and Levin 1981, Kareiva and Anderson 1988). Two elements of pattern may be recognised as important. First is the degree of division of habitat discontinuities or patches; second is the heterogeneity or difference between patch compositions (Addicott et al. 1987). The relationship between these elements is likely to be scale dependent i.e. what may appear to be a 'patch' at one scale may in fact be a composite of subpatches. Reconciling the scales of habitat patchiness will be important to understanding the dynamics of discrete patches.

Divided patches (sensu Addicott et al. 1987) provide a convenient system within which to consider the effects of habitat patterning on organisms. Patches that are separated from each other by uninhabitable space provide easily measurable and manipulable units (Sale 1980b). Patches vary in size, shape and within-patch parameters such as sub-patch shape and composition (Pickett and White 1985), and consequently scaling patches may present problems if small patches are not an unbiased subset of large ones (and vice versa). Patch studies have usually been carried out at a tractable size (e.g. Sale and Dybdahl 1975 1978, Shulman et al. 1983, Doherty and Fowler 1990, Chapter 6), and the applicability of these types of studies have frequently been called into question (e.g. Ogden and Ebersole 1981, Ault and Johnson 1998). In order to evaluate the conclusions derived from such studies, it must be determined how small patches correspond to larger ones; in other words are large patches simply collections of smaller patches, or do scale-dependent properties emerge as patch size changes. In addition, the rules that describe scaling should have some rational basis and not simply have a 'black box' effect. This is important to establish the generality and scope of scaling rules when applied to other systems.

Marine systems, and coral reefs in particular, provide a useful system in which to consider scaling problems. Coral reefs are patchy at a wide range of scales, with tracts of heterogeneous, undivided habitat (i.e. contiguous reef), and areas of heterogeneous divided habitat or patch reefs (Sale 1980b, Williams 1991). Patch reefs, while important habitat in their own right, have been the cornerstone for mensurative and manipulative development of coral-reef fish theory (see reviews in Sale 1980b, Doherty and Williams 1988a). Small patch reefs in particular, can be easily censused and manipulated with adequate replication. It is apparent, however, that the size of the patch reefs on which research is carried out may have a profound effect on the conclusions reached (Ogden and Ebersole 1981, Sale 1988). As a consequence, it has been argued that patch reefs provide few parallels for coral reef systems as a whole, and that experimental results derived from patch reefs are not scaleable (Ault and Johnson 1998).

Coral reef fish are generally associated with some aspect of the coral reef environment (see review by Jones and Syms 1998, Appendix III). This appears no less true for patch reef assemblages (Chapter 6), despite the claims of many studies to the contrary (Sale and Douglas 1984, Sale et al. 1994, Ault and Johnson 1998) - the probable reasons for which are discussed by Jones and Syms (1998). As a consequence, it may be predicted that scaleability of patch reef fish assemblages from small to large patch reefs is likely to be, at least in part, some function of the habitat characteristics of the reefs.

Two classes of habitat parameters can be initially derived. First, the patchiness of the reef (e.g. reef shape, patch number, patch diversity and average patch shape) must be considered. Diverse reefs would be expected to hold greater numbers of species. We may also predict that edge-dwelling species would be found in greater densities on elongate (or convoluted reefs) than on circular reefs. Second, the type of habitat found on a reef is likely to exert strong effects, particularly on fishes with strong or obligate associations with characteristic habitat types. Scale (or size) of the reef is likely to be correlated with any or all of these factors (which in turn may operate independently, interactively or both). This presents a methodological problem of confounding. In order to avoid confounding, and estimate the contribution of each set of factors, it is necessary to incorporate as wide a range of the different factors as possible. This can be done by unbiasedly sampling the 'universe' of patch reefs.

In this study, I quantify fish assemblages and habitat patchiness on a range of patch reefs of different sizes and habitat types to determine scaling relationships of patch reefs. Reefs were chosen randomly with respect to patchiness and benthic cover in order to incorporate as much variability as possible and thus enable unconfounded estimates of the importance of each patch parameter. These results will be used to establish a context for studies carried out on reefs at single scales, and establish appropriate rules and limitations for scaling.

4.3 Methods

Study area

This study was carried out at Lizard Island (14° 40′ S, 145° 27′ E) on the northern Great Barrier Reef, Australia. Lizard Island is encircled for the most part by fringing coral reef and, on the leeward side, patch reef systems. A 1km area on the western (leeward) side was selected as the study area. Within this stretch of coast, large tracts of contiguous reef were bordered to the seaward side by extensive tracts of patch reefs of various sizes ($0.25m^2$ - $>100m^2$), and isolation (1m - 100m).

I randomly selected 142 patch reefs within the study area under the conditions that they were isolated sufficiently (>5m) to be recognisable as a definable patch, and that they were logistically able to be effectively censused and mapped. In practice, this restricted the maximum dimension of reefs to approximately 11m long. However, most naturally occurring reefs encountered above this size were actually fragmented collections of smaller reefs.

Census method

Visual sampling was used to count all species of fish on the patch reefs. A hierarchically organised counting regime was employed. Initially, the larger motile species (e.g. acanthurids and some labrids) were quantified at a distance to minimise diver avoidance. Upon establishing a consistent count (i.e. not recording any new individuals), I would move closer and count smaller and less mobile fish. Finally, I conducted a closer inspection of the reef to count smaller sedentary species; primarily pomacentrids and gobies; until a consistent count was achieved. These counts represent a biased subset of the resident fishes; cryptic species that lived within caverns in the reef matrix could not be sampled. This problem has been discussed elsewhere (Sale and Douglas 1981). Although completeness of faunal sampling might be important for some ecological questions, I believe the range of species sampled were sufficient for comparative purposes.

Mapping method

Transect tapes, marked at 25 cm intervals, were laid over the reef to provide a scale while video transects 75cm wide were recorded. The video images were transferred by hand from frozen frames on the video screen to gridded paper. Scaled maps were compiled to a resolution of 10cm and showed patch types (as structural categories), patch borders and composition. Although apparently less objective than screen capture methods, this procedure enabled allowances to be made for parallax distortions. Field ground-truthing of the first 4 maps indicated the method yielded a value within 10% (usually better) of the true area of a habitat patch. As I subsequently considered area on a base 10 logarithmic scale, I believe this procedure provided sufficient comparative accuracy.

Maps were digitised by scanning to a binary file, then importing into the freeware program NIH Image™. The scale was set and the image skeletonized so that each line of the map was a single pixel wide (to reduce error in area measurement). The measurement function was used to record the area, perimeter, length, width, and centre co-ordinates of each patch within each reef. These measures were combined with patch identity to form the final map data set.

Patch reef parameters

Three sets of parameters were compiled for each reef: reef area, reef patchiness, and benthic composition. Reef area was simply the total area of the reef. Reef patchiness was characterised by four parameters: reef shape

$$\text{shape} = \frac{4\pi \text{ area}}{\text{perimeter}^2}$$

(which ranged from 1 (for a circle) to approach 0 as the ratio of area/perimeter decreased); the number of non bare-rock patches; the number of patch types; and the shape of each patch on each reef. Benthic composition was the sum of the areas of similar benthic categories, divided by total reef area, which yielded a proportion of total reef area per benthic category.

Data Analysis

Preliminary treatment of patch reef parameters

Multiple regression was used to analyse the data (see below). Two important conditions were required to ensure this methodology was effective. First, all sets of variables had to be linearly related. Second, excessive collinearity (or correlation) between variables had to be removed. Logarithmic transformation (to base 10) linearized reef area, number of patches, and number of patch types. Reef and within-reef patch shape parameters did not require transformation. Within-reef patch shape was normally distributed and so I used the average patch shape as the measure of typical within-reef patch shape.

Some correlation between these four parameters was apparent, so instead of using the raw values I calculated a principal components analysis (PCA) on the covariance matrix of the data, and input the principal component scores into the regression analysis. The advantages of this approach are that orthogonality (i.e. independence) of each principal component is guaranteed by the calculation method, and the scores derived from the analysis were linear.

Benthic cover variables required a similar approach. Some categories were highly correlated with each other and, in addition, a total of 24 benthic cover categories were identified. Goodness of fit improves with every variable incorporated into multiple regression (SAS Inst. 1990), and consequently goodness of fit would have been incomparable between benthic cover and the other patch reef variables. Consequently I ran a PCA on the covariance matrix of the $x^{0.5}$ transformed data and used the PC scores as input to the multiple regression. This served three purposes. As above, independence is guaranteed mathematically, and linearity is improved. In addition, the number of variables included into the regression can be reduced because ordination axes (in correlated data) explain higher portions of variation than do the original variables.

This enabled more even comparisons of the relative importance of different sets of variables.

Regression Analyses

Univariate multiple regression was used in three ways to analyse the data. First, the variation explained by each of the three sets of patch reef parameters (reef area, reef patchiness, benthic cover) and their interactions was partitioned using the method of Whittaker (1984). This method entailed running a series of regressions:

Fish=reef area
Fish=reef patchiness
Fish=benthic composition
Fish=reef area + reef patchiness
Fish=reef area + benthic composition
Fish=reef patchiness + benthic composition
Fish=reef area + reef patchiness + benthic composition;

and partitioning the residual sums of squares among interactions and simple effects to express these fractions as proportions of the total variation in the data set. For detailed explanation and univariate examples see Whittaker (1984); for multivariate applications see Borcard et al. 1992, Belgrano et al. 1995 a, b; and Syms in press.

The univariate (i.e. species analysed in separate models) approach was used in preference to the multivariate approach. The primary reason for this was because the multivariate approach required the assumption that species had a similar form of response to the independent variables (e.g. Ter Braak and Prentice 1988, Borcard et al. 1992, Belgrano et al. 1995 a, b, Syms in press). Previous experience advised against this assumption in this system. The coefficients from a multivariate multiple regression will be the same as those derived from a series of univariate multiple regressions, so the values of the coefficients are not dependent on the approach. As this analysis was exploratory and not part of an inferential test the safeguard of the multivariate hypothesis test was not required.

The second application of multiple regression was to parameterise the importance of different independent variables and establish the biological importance and interpretability of the regression coefficients. This approach simply entailed running the saturated regression model and interpreting the significant coefficients. No model selection algorithms were employed.

The final application was to determine how measures compiled from reefs of particular sizes extrapolated or interpolated to reefs of different sizes (i.e. to what extent scale-dependence operated in the system). Reefs were ranked by area, and divided into three groups: small reefs (0.26-1m^2); medium reefs (1-4m^2), and large reefs (4-65m^2). Multiple regression equations were calculated (with and without reef area), and the deviation of the measured from the predicted values of all species were combined and plotted to indicate predictive ability. As a comparative baseline, the same procedure was conducted on a randomly selected third of the dataset.

4.4 Results

Patch reef description

A total of 142 patch reefs were sampled, ranging in size from 0.26m^2 to 63.5m^2. The smallest reef measured 0.65 x 0.40 m; the largest 13.80 x 8.10m. Maximum reef width generally increased with maximum length, however this relationship was quite variable (Fig. 4.1). Reef area was negatively correlated with reef shape i.e. the edge of larger reefs was more convoluted than in smaller reefs (Fig. 4.2), however there was considerable variability in this pattern. Both the number and type of patches were positively correlated with reef area (Fig. 4.2). Not surprisingly, larger reefs contained more patches, and a wider range of patch types. The only parameter that was uncorrelated with reef area, patch number, or number of patch types was the average patch shape which, although more variable in smaller reefs, did not systematically vary with any other parameter (Fig. 4.2).

The principal components analysis (PCA) of the reef parameters identified three independent axes which characterised the reefs in this study which, in combination, summarised 98.2% of the variation. The first axis accounted for 86.2% of the reef-parameter variation and corresponded with reefs that were elongate or convoluted and had many patches, and many different types of patches (Table 4.1). The second axis explained 7.0% of the variation and corresponded with circular reefs that had many types of patches, but few patches overall. In other words, the patch types present on these reefs were not fragmented. The third axis explained 4.6% of the variation and corresponded with circular reefs with many patches of the same type i.e. patch types were fragmented (Table 4.1). Because these axes are constrained in PCA to be uncorrelated, they were subsequently used in the regressions in place of the correlated raw measures.

Five benthic cover patterns, which explained 95.5% of the benthic cover variation, were identified by PCA. Soft coral cover dominated the first axis, which accounted for 47.6% of the variation in benthic cover (Table 4.2). The second pattern was driven by a dominance of branching corals, in combination with an absence of massive hard corals. This pattern explained 18.9% of the variation. The third pattern explained 15.1% of the variation and corresponded with reefs with high massive and branching coral cover, coupled with an absence of corymbose forms. The fourth pattern represented reefs with diverse benthic cover, including corymbose, massive and branching corals and soft corals, in combination with an absence of corals of the genus *Pocillopora*. This pattern accounted for 8.7% of the total benthic cover variation. The final pattern accounted for 5.2% variation and was driven by *Pocillopora* spp. cover, which usually occurred in combination with other hard corals and soft corals (Table 4.2). As with the reef parameters, the uncorrelated principal component axes were subsequently used in the multiple regressions in place of the raw, correlated measures.

Fish community description

The fish community was represented by 187 species in 31 families (Table 4.3). Pomacentrids were the most speciose group (32 species), followed by gobies (27 species), labrids (18 species), chaetodontids and scarids (13 species each), and apogonids (12 species). Other families were less well represented (Table 4.3). The number of reefs on which a species occurred (which was related to the species absolute abundance) was right-skewed and indicated the majority of species were rare (Fig. 4.3). For example, a total of 78 species were recorded on only 1 or 2 reefs. Only 44 species were found on >10% of all reefs in the survey. This value was my (arbitrary) cut-off for inclusion in the regression analyses, so consequently 44 species of the 187 were analysed in the regressions.

No systematic effect of reef size on the number of species occupying the reef was apparent (Fig. 4.4), with species richness linearly associated with reef area on a log-log scale (slope=0.584, r^2=0.656). The size range of reefs examined appeared to adequately sample the fish communities on patch reefs (Fig. 4.5). Reefs from 0.26m^2 to 0.5m^2 underwent a characteristic power-curve increase in species richness. Between 0.5m^2 to

$2m^2$ the relationship approximated an exponential relationship. At sizes greater than $2m^2$ the relationship levelled so that the entire curve approximated the logistic form typical of a well sampled community (He and Legendre 1996).

Fish community association with patch reef characteristics

Species richness on the patch reefs was positively correlated with reef area, with an estimated increase of 24 species per $\log_{10}$ increase in reef area (p=0.0001, Table 4.4). Soft-coral dominated reefs, however, had fewer species (4 species less per $\log_{10}$ area increase, p=0.0405) than would be predicted for their area. In contrast, branching-coral dominated reefs had proportionally more species than would be expected (7 species per $\log_{10}$ area increase, p=0.0400). Reef patchiness did not appear to strongly influence species richness, however an increase in species richness (marginally statistically non-significant) was indicated in circular reefs with large numbers of patch types (7 species per $\log_{10}$ area increase, p=0.0620).

In general, individual species abundances were not well predicted by reef characteristics (Table 4.5), with regression goodness of fits ranging from 9-34% of the total variation. Eighteen of the 44 species examined were not strongly associated with any reef features (Group 1, Table 4.5). However, a divisive clustering strategy identified eight characteristic types of association with patch reef variables.

The first group, as previously mentioned, was composed of 18 species which had no measurable association with any class of reef variable (Fig. 4.6). The second group of seven species, however, was strongly associated with benthic cover variables (23% variation), and other lesser miscellaneous factors (Fig. 4.6). Most species in this group were recognised hard coral associates. The pomacentrids *Chromis viridis*, *Dascyllus aruanus*, *Dascyllus reticulatus*, and *Pomacentrus moluccensis* were typically associated with live-coral reefs (especially those dominated by branching, corymbose, and *Pocillopora*) (Table 4.5). In addition, the gobies *Gobiodon okinawae* and *Paragobiodon echinocephalus*, which are obligate coral dwellers (Randall et al. 1990), were associated more with *Pocillopora* spp. than other branching forms. The final member of the group, *Pseudochromis fuscus*, although not recognised as a coral associate per se, was associated with branching-coral and *Pocillopora* dominated reefs (Table 4.5). Most species in the group were negatively associated with soft coral reefs.

The third group of six species were weakly associated with a reef area*reef patchiness interaction (Fig. 4.6). The variation accounted for by this interaction was small (11%), and not attributable to any single reef character (Table 4.5). No clear ecological similarity exists between members of this group, and so little can be inferred about the biological significance of the reef area*patchiness interaction.

In contrast, the fourth group of five species was associated with reef area (9% variation explained), to a large extent contingent on reef patchiness (10% variation explained) (Fig. 4.6). All species increased in abundance with increased reef area. However, no particular reef patchiness component was identified as important for any species with the exception of the acanthurid *Ctenochaetus striatus* which was associated with elongate, diversely patched reefs (Table 4.5). Three of the species in the group shared an ecological similarity - the shoal-forming pomacentrids *Neopomacentrus azysron*, *Pomacentrus brachialis*, and *Pomacentrus lepidogenys*. Both remaining members of the group (the acanthurid *C. striatus*, and the serranid *Cephalopholis cyanostigma*) were not ecologically similar but were both rare on small reefs.

The fifth group of four species was associated with independent components of reef area (9% variation explained), benthic cover (9% variation explained) and reef patchiness (7% variation explained) (Fig. 4.6). No species within this group were ecologically similar. The pomacentrid *Amblyglyphidodon curacao* was associated with large reefs and branching corals. In contrast, the pomacentrid *Pomacentrus nagasakiensis* was more abundant on small, soft coral-covered, patchy convoluted or oblong reefs (Table 4.5). The apogonid *Apogon cyanosoma* was found on large, patchy and diverse reefs, while the goby *Eviota* sp. D was found on large circular reefs with few patches and patch types (indicated by the negative values on reef patch axis 1 and benthic cover axis 5), or elongate but diversely patchy reefs (negative values on reef patch axis 3 and benthic cover axis 4).

Group 6 consisted of two species that were associated with independent fractions of reef patchiness (9% variation explained) and benthic cover (9% variation explained) fractions (Fig. 4.6). The goby *Amblygobius phalaena* was found on elongate or convoluted reefs that were diversely patchy with massive or corymbose corals (Table 4.5). *Halichoeres melanurus* was also found on elongate or convoluted reefs, but was usually associated with soft-coral and branching-coral dominated reefs.

The final two responses were found in single species only. *Pomacentrus amboinensis* was strongly associated with smaller reefs (12% variation explained) that were elongate, or convoluted reefs that were diversely patchy (7% variation explained) (Fig. 4.6). In addition, *P. amboinensis* was also found on soft coral reefs, contingent on those reefs being small (reef area*benthic cover interaction, 6% variation explained) (Table 4.5). The last response was found in the labrid, *Thalassoma lunare*, which was primarily associated with reef patchiness (Fig. 4.6), and was found on elongate or convoluted reefs with diverse patches (Table 4.5).

In summary, although the total explainable variation was not particularly great (maximum 34% of total variation explained), biologically interpretable and predictable explanatory components emerged for many species. Reef area, reef patchiness, and benthic cover operated independently, albeit in different proportions, in Groups 2, 5, 6, and *T. lunare*. In contrast, interaction effects between reef area*benthic cover or reef area*reef patchiness exerted themselves on other groups (Groups 3, 4, *P. amboinensis*) in combination with independent fractions. In both Groups 3 and 4, although the interaction component explained a measurable portion of the variation, no parameters emerged as particularly important. This was probably due to attenuation or flattening of the curve which reduced the measurable association. Parameter estimates derived from a Model I (i.e. independent variables are measured without statistical error) multiple regression for a Model II (i.e. independent variables have statistical error) problem are underestimates (McArdle 1988).

Forms of relationship with patch reef characteristics

Species that were positively associated with reef area, generally had some ‘threshold’ size, below which they were practically absent. Two such examples were *A. curacao*, and *A. cyanosoma,* which were absent on smaller reefs, but abundant and variable on large reefs (Fig. 4.7). In contrast, species that were associated with small reefs (e.g. *P. nagasakiensis*, *P. amboinensis*) did not have this threshold. They were simply more abundant (per unit area) on smaller reefs (Fig. 4.7). Of note in the plot of *P. nagasakiensis* vs reef area, is the attenuation of the line mentioned in the previous paragraph.

In contrast with reef area, relationships between fish and reef patchiness were continuous, and less well defined (Fig. 4.7). For example, both positively (*P. moluccensis*, *P. amboinensis*) and negatively (*Eviota* sp.D, *A. phalaena*) associated species were variable in their relationship with reef patchiness. This indicated that patchiness, while important, was not a strong predictor of fish abundance even for species that were associated with reef patchiness.

Species were more idiosyncratic in their association with benthic cover types. For example, the obligate coral dwellers *G. okinawae* and *D. aruanus* were associated with branching coral forms in an almost binary fashion. The presence of their associated coral types generally resulted in a sharp increase in their abundances (Fig. 4.7). Similar responses were apparent in species that were negatively associated with benthic cover types. *Chromis viridis*, for example, had an almost mutually exclusive association with soft-coral dominated reefs. *Gobiodon okinawae* had a strong negative association with reefs dominated by massive hard corals.

Scaling up and down from reefs of different sizes

In order to investigate the success of scaling up and down from reefs, separate multiple regression equations were derived from small reefs (0.26-1m^2), medium sized reefs (1-4m^2), and large reefs (4-63.5m^2) both with and without reef area included as an independent variable. The abundance of each fish was predicted from the equation, and the average difference between observed and predicted calculated. As a yardstick, predictions were also derived from a random sample of reefs.

Models derived from large reefs were largely unsuccessful in predicting the abundances of fish on smaller reefs (Fig. 4.8). Models derived from medium sized reefs were considerably better (but still quite variable) at predicting abundances on smaller reefs, and adequately predicted fish abundances on larger reefs. Surprisingly, predictions derived from the subset of smallest reefs provided the best estimate of fish abundance across the size range (Fig. 4.8) which indicated scaling up was more effective than scaling down.

Incorporating reef area into the equation introduced systematic bias into the abundance predictions regardless of whether scaling up or down (Fig, 8). When scaling up, this effect could be seen as an obvious linear increase in average deviation with increase in reef area (for example, scaling up from small and medium reefs). A similar increase in average could be seen in scaling down form either medium or large reefs. This systematic effect was not present in the baseline regression from the random subsample of reefs that included a range of reef sizes.

In summary, despite some obvious associations of fish with reefs of certain sizes, on average, explanatory equations derived from small-medium reefs provided reasonable estimates of abundance on larger reefs. In contrast, scaling down was far less successful. Incorporating reef area into such equations is not recommended, probably because any scaling 'rule' derived from a restricted range of reef sizes is likely to be poorly estimated.

Table 4.1. Correlation of reef parameters with principal components.

	Correlation with Principal Component		
	1	**2**	**3**
Reef Shape	-0.32	0.76	0.55
# of patches	0.84	-0.04	0.54
# of patch types	0.44	0.64	-0.63
Patch Shape	0.00	-0.11	-0.04

Table 4.2. Correlation of benthic cover with principal components.

	Correlation with Principal Component				
	1	**2**	**3**	**4**	**5**
Soft Corals	0.93	0.09	0.11	0.23	0.25
Branching	-0.26	0.82	0.30	0.30	0.25
Massive	-0.21	-0.55	0.60	0.46	0.26
Corymbose	-0.13	-0.09	-0.73	0.60	0.27
***Pocillopora* spp.**	-0.09	-0.07	-0.08	-0.52	0.84

Table 4.3. Number of species in each family.

> 10 Species		**3-10 Species**		**1-2 Species**	
Pomacentridae	32	Blenniidae	7	Monocanthidae	2
Gobiidae	27	Pseudochromidae	7	Mullidae	2
Labridae	18	Serranidae	6	Nemipteridae	2
Chaetodontidae	13	Acanthuridae	5	Scorpaenidae	2
Scaridae	13	Caesionidae	4	Siganidae	2
Apogonidae	12	Lutjanidae	4	Tetraodontidae	2
		Balistidae	3	Cirrhitidae	1
		Holocentridae	3	Haemulidae	1
		Lethrinidae	3	Microdesmidae	1
		Pinguipedidae	3	Ostraciidae	1
		Pomacanthidae	3	Plesiopidae	1
		Synodontidae	3	Syngnathidae	1
		Tripterygiidae	3		

Table 4.4. Multiple regression of species richness with patch reef parameters.

Variable	**DF**	**Parameter**	**Std Error**	**P**
INTERCEPT	1	8.06	0.77	0.0001
AREA	1	24.88	2.51	0.0001
REEF 1	1	1.64	2.19	0.4536
REEF 2	1	7.44	3.95	0.0620
REEF 3	1	6.65	5.45	0.2250
HABITAT 1	1	-4.69	2.27	0.0405
HABITAT 2	1	7.25	3.50	0.0400
HABITAT 3	1	0.53	3.87	0.8918
HABITAT 4	1	-0.98	5.30	0.8529
HABITAT 5	1	1.13	7.26	0.8763

Table 4.5. Multiple regression parameters of species with reef parameters. Strength of significance denoted by font: *italic* = 0.05-0.01; normal = 0.01-0.001; **bold** <0.001

Species	**Family**	**Reef Area**	**Benthic Cover**					**Reef Patchiness**		
			1	**2**	**3**	**4**	**5**	**1**	**2**	**3**
Group 1										
Bryaninops sp.	Gobiidae									
Eviota bifasciata	Gobiidae									
Eviota spp.	Gobiidae									
Fusigobius neophytus	Gobiidae	0.39								
Gobiodon citrinus	Gobiidae								0.37	
Istigobius decoratus	Gobiidae		0.38							
Cheilinus chlorourus	Labridae									
Coris schroederi	Labridae									
Labroides dimidiatus	Labridae									
Neopomacentrus cyanomos	Pomacentridae	0.44								
Premnas biaculeatus	Pomacentridae							0.16		
Cephalopholis boenak	Serranidae									
Pseudochromidae flammicauda	Serranidae									
Pomacanthus sexstriatus	Pomacanthidae	0.09								
Cheatodon auriga	Chaetodontidae									
Cheilodipterus quinquelineatus	Apogonidae	0.41							0.74	
Helcogramma sp.	Tripterygiidae	0.11								
Ecsenius australianus	Blennidae	*0.27*								
Group 2										
Chromis viridis	Pomacentridae		**-1.28**	**1.82**						
Dascyllus aruanus	Pomacentridae		**-1.13**	**2.11**		*1.52*	1.44			
Dascyllus reticulatis	Pomacentridae		**-0.86**	*0.88*	**-1.22**		*2.19*			
Pomacentrus moluccensis	Pomacentridae			**2.46**	-1.46		**4.89**		1.62	
Gobiodon okinawae	Gobiidae		*-0.49*	**0.86**	**-1.24**	**1.75**	**1.78**			
Paragobiodon echinocephalus	Gobiidae		-0.30			*-1.07*	0.89			
Pseudochromis fuscus	Pseudochromidae	-0.34		**0.95**			0.94	0.29		
Group 3										
Chrysiptera rollandi	Pomacentridae	*0.34*								
Neoglyphidodon melas	Pomacentridae									
Pomacentrus wardi	Pomacentridae									
Pseudocheilinus hexataenia	Labridae									
Ctenogobius pomastictus	Gobiidae									
Escenius bicolor	Blenniidae	0.10			0.13				-0.16	
Group 4										
Neopomacentrus azysron	Pomacentridae	**1.13**								
Pomacentrus brachialis	Pomacentridae	**0.26**								
Pomacentrus lepidogenys	Pomacentridae	**0.47**								
Ctenochaetus striatus	Acanthuridae	**0.26**								-0.28
Cephalopholis cyanostigmus	Serranidae	*0.18*								
Gourp 5										
Ambglyphidodon curacao	Pomacentridae	**0.39**		*0.48*						
Pomacentrus nagasakiensis	Pomacentridae	*-1.38*	*1.17*					0.73		
Apogon cyanosoma	Apogonidae	**0.77**						-0.39	0.73	
Eviota sp. D	Gobiidae	**0.48**				-0.63	**-1.27**	**-0.36**		-0.66
Group 6										
Amblygobius phalaena	Gobiidae			-0.43	-0.51					-0.68
Halichoeres melanurus	Labridae		*0.66*	0.71				0.52		-1.04
Group 7										
Pomacentrus amboinensis	Pomacentridae	**-1.63**		0.88				*0.89*		
Group 8										
Thalassoma lunare	Labridae	-0.51						*0.52*		

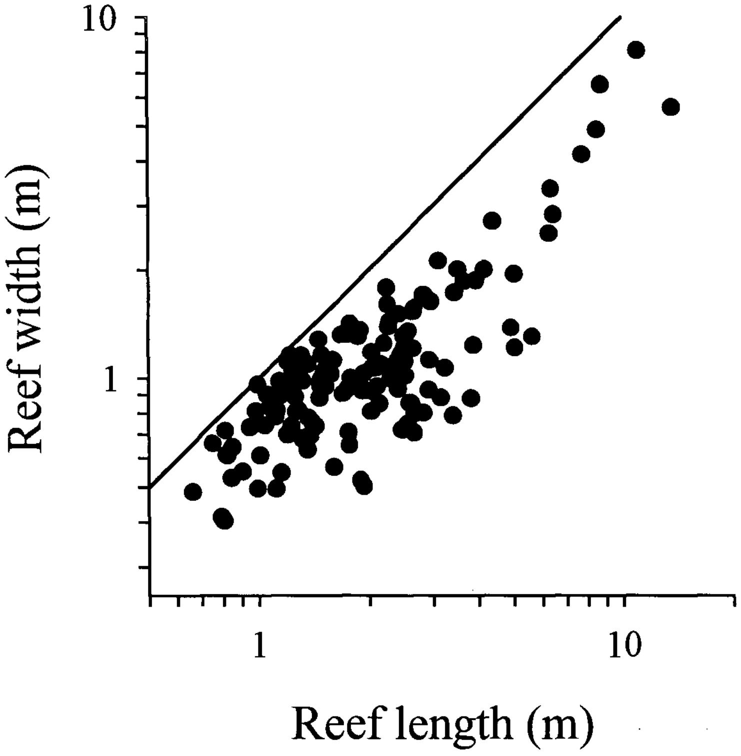

Figure 4.1. Maximum length and width of patch reefs examined. Diagonal line corresponds to a slope of 1.

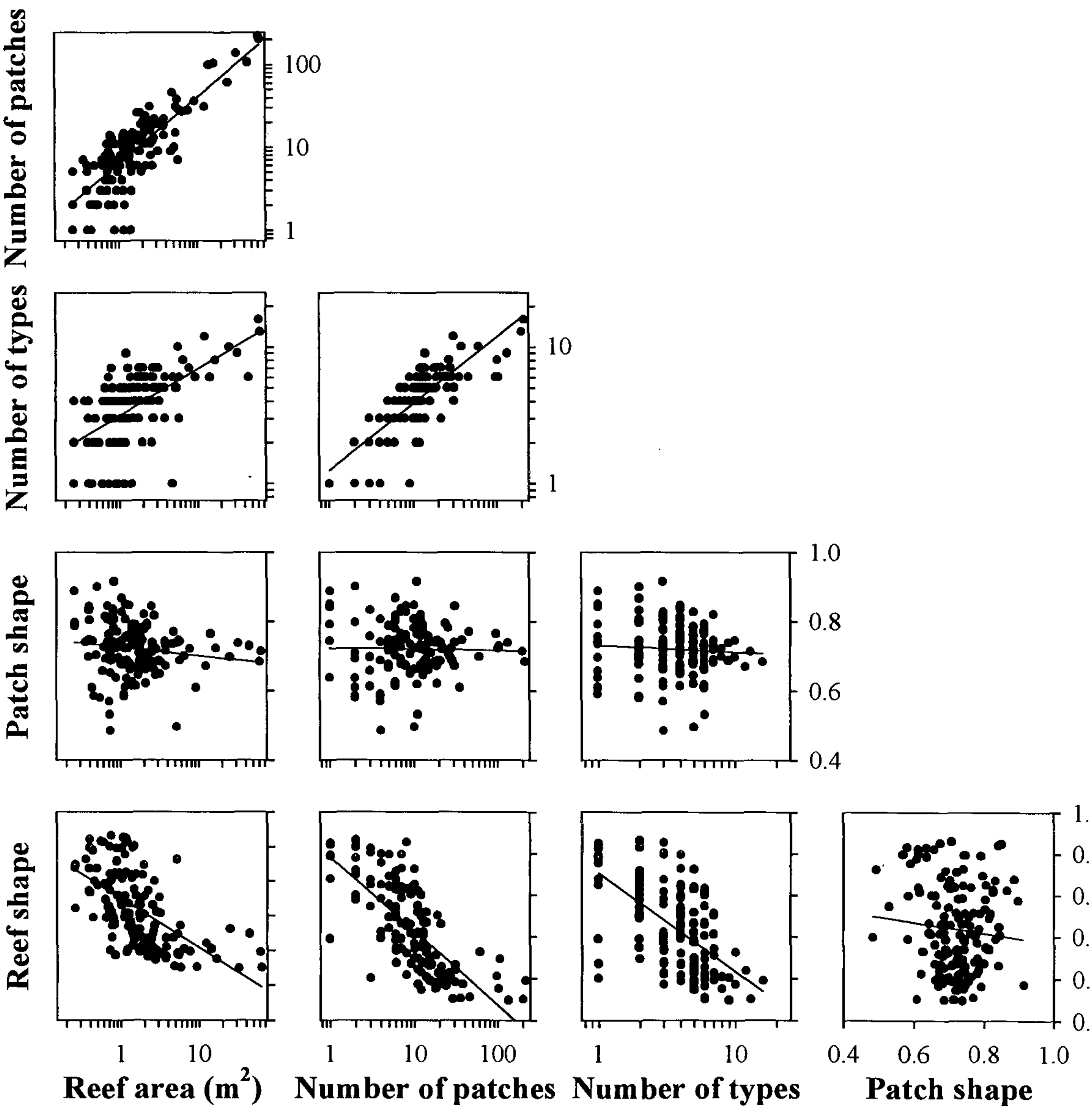

Figure 4.2. Correlations between reef patchiness parameters. Lines are ordinary least squares regressions.

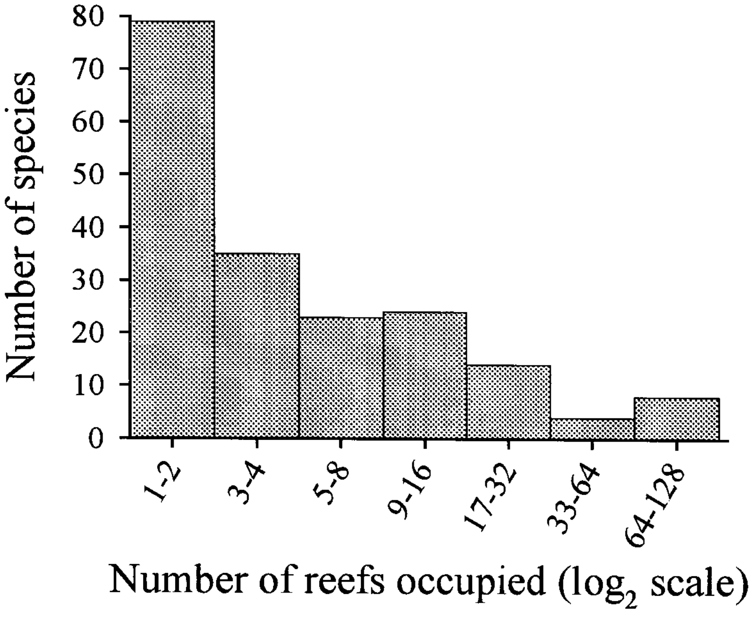

Figure 4.3. Number of reefs occupied by different species.

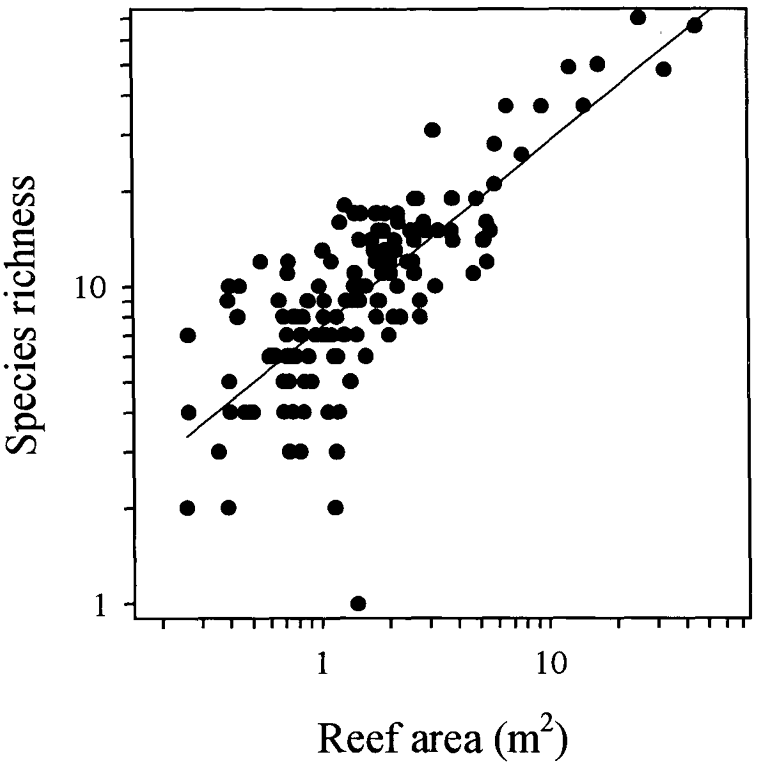

Figure 4.4. Relationship between species richness and patch reef area; slope=0.584, r^2=0.656.

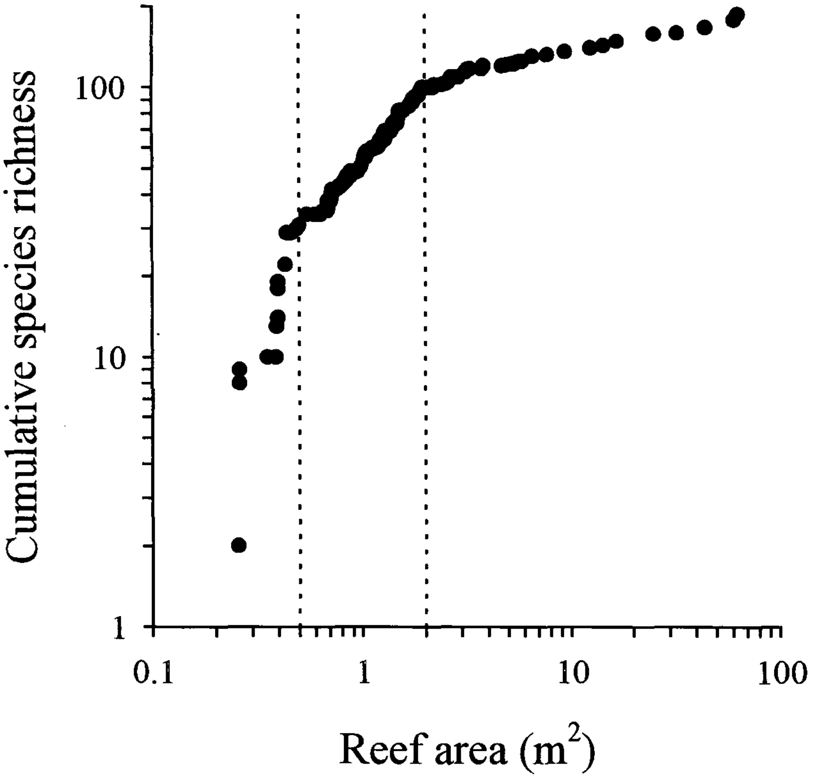

Figure 4.5. Cumulative species richness vs ranked reef area. The dotted line at 0.5m^2 indicates the transition from a power relationship to an exponential relationship. The dotted line at 2m^2 indicates the transition to a logistic relationship.

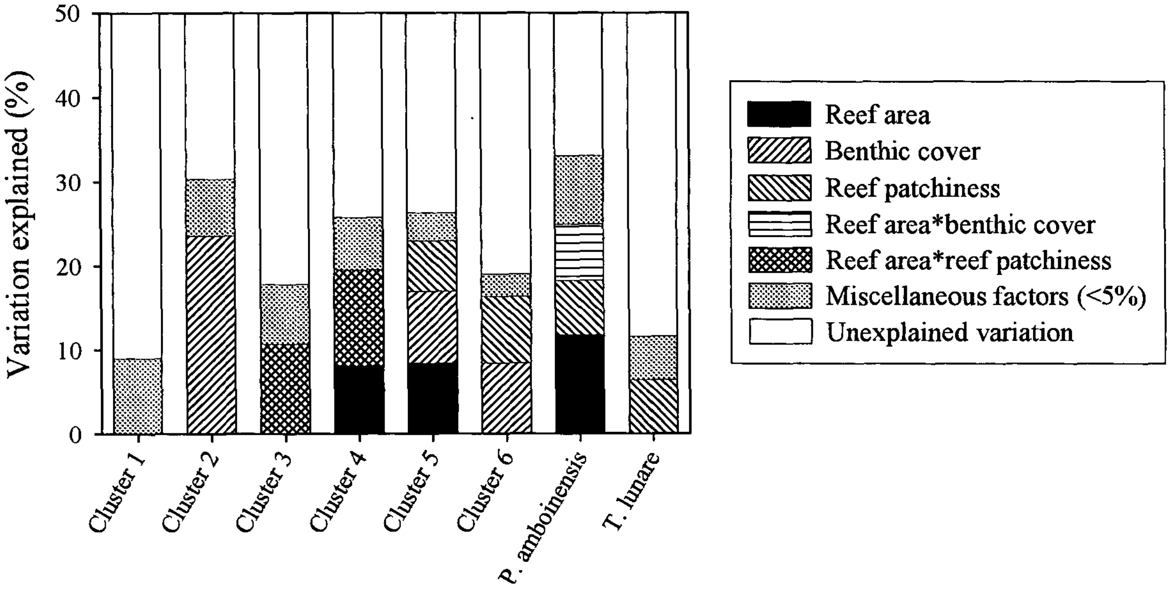

Figure 4.6. Percent variance explained by reef area, benthic cover, reef patchiness, and their interaction effects. Miscellaneous factors are those which explain <5% of the total variation. Variance components derived from multiple regression.

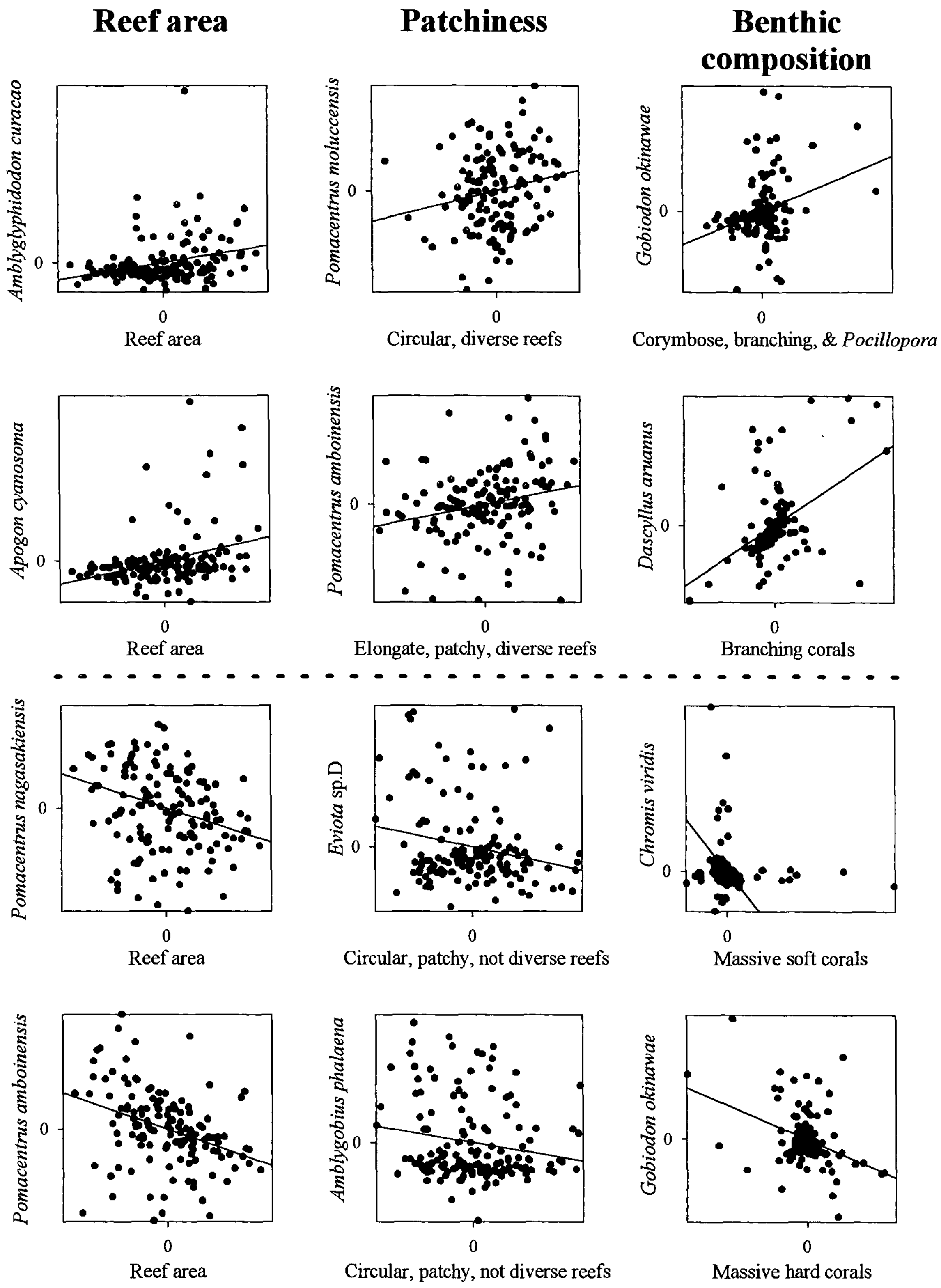

Figure 4.7. Partial regression plots of selected fish-habitat relationships. The ordinate axis is the residual of the fish species on the saturated multiple regression model minus the independent variable. The abscissa is the residual of the independent variable on the same model. Slopes are derived from the saturated multiple regression model.

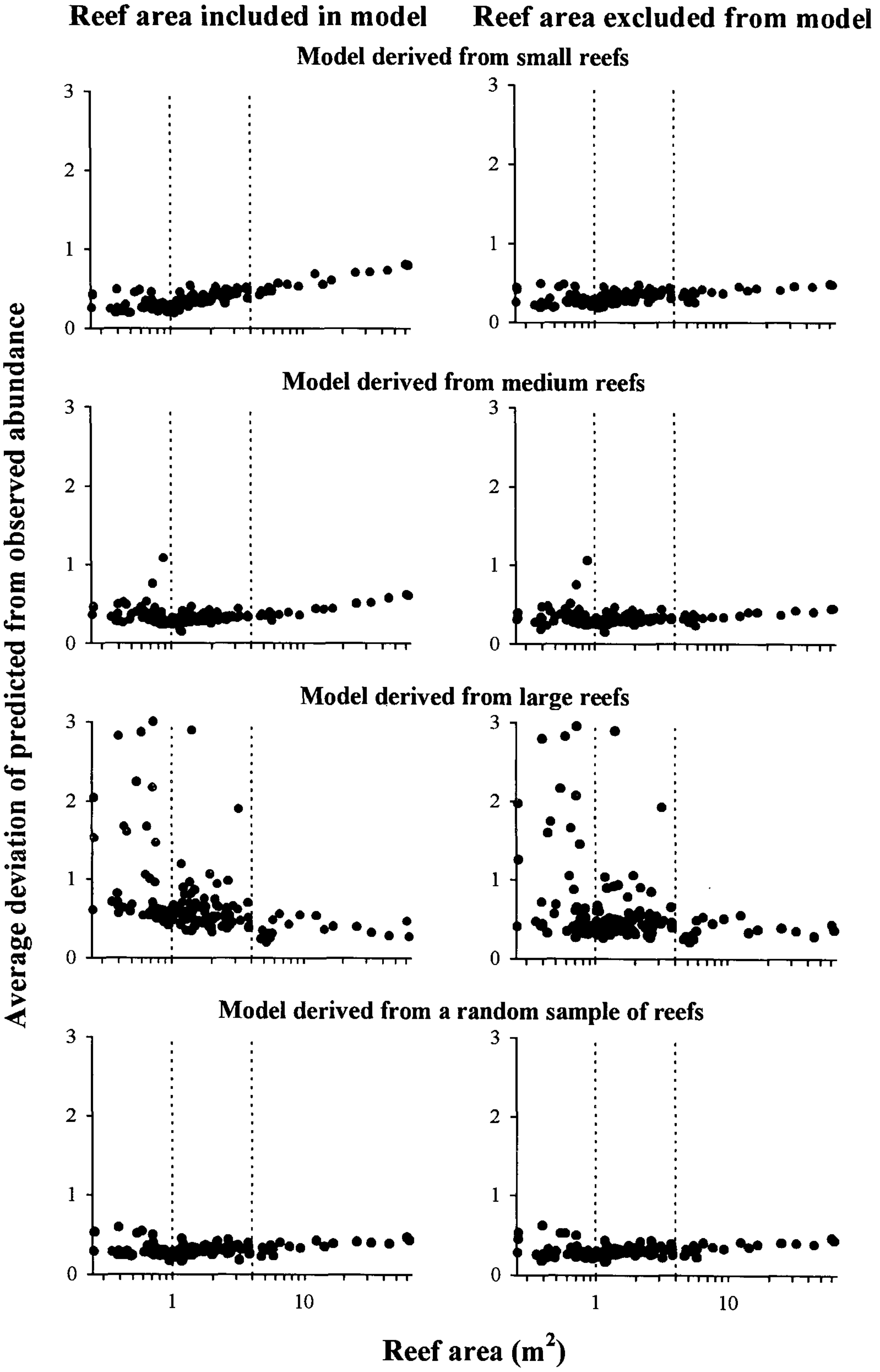

Figure 4.8. Predictive ability of small, medium, large, and a random subsample of reefs. Each point on the graph is the average deviation of observed from predicted abundance per reef. Graphs on the left have the full model fitted, graphs on the left have reef area excluded from the model. The dotted lines indicate the classification of the reefs as small, medium, and large.

4.5 Discussion

Determining the scale dependence of patterns is central to establishing the context for studies carried out at single scales (Levin 1992). In this study, I measured the relationship of fish assemblages with benthic cover and reef patchiness on a range of patch reefs spanning two orders of magnitude (0.26-63.5 m^2). The fish assemblages found on these reefs contained many rare species, and of those species that were sufficiently abundant for analysis, slightly less than half were strongly associated with any patch reef characteristics. However, of the species for which associations could be measured, a diverse set of responses to habitat and scale could be identified. These results enabled an assessment of the scale-dependence of individual species. On average, extrapolating from small reefs to large reefs was subject to less error than interpolating from large reefs.

One criticism of naive scaling (i.e. simply multiplying small-scale studies to extrapolate to larger scales) is that 'emergent' properties may appear at larger scales (Meentemeyer and Box 1987, Levin 1992). In this study, two sources of emergent effects were evident. First, passive sampling artifacts increased the number of rare species that were recorded on large reefs. An important consequence of this is that measures derived from fish assemblages on small reefs would not contain any information on these species with which to extrapolate to large-reef fish communities. The second emergent property was caused by the association of some fish species with reefs of a certain size. Species that were associated with larger reefs (e.g. *A. curacao*, *A. cyanosoma*, Fig. 4.7) generally had some 'threshold' size below which they would be absent from a reef. However species that were associated with smaller reefs (e.g. *P. amboinensis*, *P. nagasakiensis*, Fig. 4.7) generally had a monotonic relationship with reef size. The implications for scaling up and down are different for the two response types. As small reefs contain no information on the large-reef species (the first response), no scale extrapolation is possible for those species. Scaling up would lead to a strong underestimate of their abundance and, conversely, scaling down would lead to an overestimate of their abundance. In contrast, predicting the species abundance of the small-reef dwelling species (the second response) might be possible if scale was taken into account in the equation.

Reef patchiness was important to most species, either as an independent factor (Groups 5, 6, *P. amboinensis*, and *T. lunare*) or in combination with either reef area

(Groups 3, 4) or benthic cover (*P. amboinensis*). Two types of patchiness generated these patterns. *Pomacentrus nagasakiensis*, *P. amboinensis*, *H. melanurus*, and *T. lunare* were positively associated with elongate or convoluted reefs with many patches and patch types, but *A. cyanosoma* and *Eviota* sp. D were negatively associated with these types of reefs. In contrast, most patch-responding species were negatively associated with circular reefs with many patches of the same type. This suggests that species that respond to reef patchiness may have been responding to patch interfaces or edges rather than any particular patch shape or structure. Although fish associations with patchiness parameters were generally monotonic (e.g. Fig. 4.7), the form of the relationship was scale dependent for some species (e.g. Groups 3 and 4, Fig. 4.6).

Benthic cover featured as an important explanatory variable in many groups (Fig. 4.6). Interestingly, Group 2 was primarily associated with benthic cover only and so, across the range of scales examined, was scale independent. Benthic cover was also important for Groups 5 and 6, and operated in a scale-dependent fashion in *P. amboinensis* - which was associated with smaller reefs. Species that were associated with particular benthic covers were rather idiosyncratic in their association. This has important implications for scaling. A 'pure' habitat associate is essentially scale-independent (within the range examined) and consequently information derived from small reefs could be simply multiplied to the large reef (e.g. Group 2). However, if small reefs do not (or can not by virtue of their size) contain a certain benthos that a species is associated with, then no extrapolation can be made for that species. The reverse will also be true. This is a problem in the representativeness of the small sample unit relative to the universe of patch reefs (see Syms and Jones (in press) for discussion in an experimental context).

Despite the obvious problems with scaling up, for the species that were sufficiently abundant for analysis scaling up provided better predictions of fish abundance than did scaling down. In addition, better predictions were obtained by removing any estimate of scale effects from the equation. This indicated that benthic cover and reef patchiness were sufficiently predictive of fish abundance i.e. a considerable amount of habitat determinism was independent of scale. The asymmetry of the relationship is of interest and requires explanation. Small reefs appeared to provide a more precise estimate of the association of fishes with characteristic patch types in contrast with estimates derived from large reefs. This might be because the size of small reefs approximates the average patch size on larger reefs. Estimates of fish-habitat association derived from small reefs are closer to the scale at which the fish perceive their habitat. In contrast, the same estimates derived from larger reefs are likely to be averaged over a wider number of patches, possibly with the additional effect of noise from the other patch-types present on the reef. This study supports the view that, within several constraints, some aspects of the patch reef fish community on large reefs can be seen as the summation of smaller patches (Sale 1988).

It is now possible to evaluate the role that experiments carried out at single scales play in the development of reef fish ecology. Scale emergent properties will appear for some community measures. Species richness will increase with area, and thus measures based on numbers of species will be scale dependent, but also mediated by reef patchiness and benthic cover. In addition, some species will be idiosyncratic in the sizes of reefs they occupy, and in the absence of prior information, will not be well modelled by small reefs. Despite prior published assertions (Sale and Douglas 1984, Ault and Johnson 1998), habitat variables such as reef patchiness and benthic cover mediate much of the association of fish with patch reefs. Tests of hypotheses based on associations of fish with habitat are heuristically scaleable for those species (e.g. Chapter 6).

This study has evaluated the scaling relationships of patch reefs and found that, within bounds and with extreme caution, studies carried out on small reefs can be set into a context of the universe of patch reefs, and heuristically provide an adequate model of habitat-mediated processes. Understanding the dynamics of habitat association is central to scaling patch reefs experiments. Importantly, scaling can be expressed as a biologically interpretable function and not the ‘black box’ it is so frequently assigned to.

Chapter 5: Disturbance and the Structure of Coral Reef Fish Communities on the Reef Slope[†]

5.1 Abstract

Three levels of physical disturbance were applied to corals in permanent 10x10m quadrats along a section of fringing reef at Lizard Island on the Great Barrier Reef to investigate the response of fish assemblages. Tabular and corymbose corals were overturned and left in situ, reducing total hard coral cover from ~55% to ~47%, ~43%, and ~34%. Despite pre-existing associations with benthic cover, all fish groups examined (pomacentrids, labrids, chaetodontids, and acanthurids) were resistant to benthic disturbances at the level and scale at which they were applied. Partial Mantel's tests, in combination with partial Canonical Correspondence Analysis enabled spatial and temporal variation to be factored out from experimental effects. Most of the variation in the fish community could be assigned to spatio-temporal variables, indicating that spatial structure over the reef landscape may moderate localised disturbance effects. This study indicates that coral reef fish assemblages may be more resistant to disturbance than many correlative studies would suggest, and highlights a need for further information on levels and scales of natural habitat disturbance in order to apply a structured approach to the experimental investigation of the importance of habitat in structuring coral-reef fish assemblages.

5.2 Introduction

Stands of coral share many characteristics with other sessile communities such as terrestrial forests (Connell 1978) and macroalgal beds (e.g. Dayton et al. 1984) in that they form a structural 'veneer' (Done 1992) on the substratum. As with forests and macroalgae, corals are susceptible to disturbance. Storms and cyclones (Done 1992; Letourneur et al. 1993), runoff (Van Woesik et al. 1995), and bioerosion (Hutchings 1986) can alter both the overall coral cover and the structural forms of corals present on

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a reef. It may be hypothesised that the disturbance regime of the coral reef may exert a considerable effect on other species living on the reef.

The strength of association between organisms and their habitat can provide an indication of the level of habitat change required to exert a response in habitat 'responding' (sensu Jones and Andrew 1993) organisms. An array of studies have documented positive relationships between fish abundance and diversity and coral cover (e.g. Bell and Galzin 1984, Bell et al. 1985, Findley and Findley 1985, Bouchon-Navaro and Bouchon 1989, Hart et al. 1996). In contrast, an equally abundant array of studies have found little evidence of strong coral/fish association (Roberts and Ormond 1987, Roberts et al. 1988, Fowler 1990, Booth and Beretta 1994, Cox 1994, Green 1996). Despite this wide correlative literature on coral reef fish and habitat associations, no general patterns have emerged and consequently little can be adduced about the level of habitat disturbance that could be reasonably expected to induce changes in fish assemblages (Jones and Syms,1998).

Non-manipulative studies of fish community responses to coral disturbance (i.e. natural 'experiments') have provided equivocal estimates of the importance of coral cover in structuring fish assemblages. Kaufman (1983), Pfeffer and Tribble (1985), and Sano et al. (1987) reported varying responses of a range of fishes from different trophic categories to natural catastrophic habitat disturbance. In contrast, Wellington and Victor (1985) and Williams (1986) found little effect of similar forms of disturbance. Manipulative studies of disturbance are rare in the tropics. Coral removal and topographic reduction induced predictable community changes on small (2-3 m^2) patch reefs on the Great Barrier Reef (Syms and Jones in prep.) and demonstrated that conventional disturbance theory can be applied to reef fishes. In contrast with tropical studies, macroalgal disturbances have been widely and successfully applied to explore temperate reef fish communities on contiguous reef (Choat and Ayling 1987; Bodkin 1988; Jones 1988; Carr 1989 1991; DeMartini and Roberts 1990; Holbrook et al. 1990; Syms and Jones, in revision). The wide variety of responses to such disturbances in temperate systems may indicate a profitable direction for coral reef studies.

Unlike terrestrial and benthic marine ecology, most coral-reef fish community theory has been developed from research conducted on small (0.25-10 m^2), relatively isolated habitat patches (e.g. Sale and Douglas 1984; Victor 1986; Doherty and Fowler 1994). Although parallels have been drawn between patch reef models and island biogeography theory (Doherty and Williams 1988), the processes responsible for biogeographic immigration/extinction patterns may not be directly translatable for reefal marine organisms which, for the most part, have large-scale larval dispersal capabilities relative to adult motility. While patch reefs are important habitats in the coral-reef landscape, most reefal area consists of relatively contiguous (compared to the motility range of many fishes) hard substratum (Williams 1991). Despite this, research on contiguous reef has not featured prominently in coral reef fish community studies.

Experiments conducted on reef slopes which consist of large expanses of contiguous reef present certain difficulties. While migration of fish between 'isolated' patch reefs may be deemed to be relatively low (Sale and Dybdahl 1975,1978; but see Robertson 1988) - this is not the case on contiguous reef and defining the 'resident' fauna becomes problematic. Perhaps a more insidious problem is the degree of spatial structure inherent in a continuous reef mosaic. Spatial patterns such as wave-exposure gradients may combine with within-area temporal autocorrelation to influence the inferential base of such experiments (Dutilleul 1993), as well as obscuring experimental results.

In this study I investigated the response of coral reef fish assemblages to 3 levels of physical disturbance to corals within permanent quadrats on a continuous fringing reef on the Great Barrier Reef. The intensity of disturbance was designed to simulate moderate natural wave disturbance rather than catastrophic cyclonic destruction. I incorporated spatial and temporal variables in the analysis to explicitly take into account spatio-temporal autocorrelation due to pre-existing physical gradients and temporal populational changes.

5.3 Methods

This study was carried out over 24 months (January 1993 - January 1995) at Lizard Island (14° 40′ S, 145° 27′ E) on the northern Great Barrier Reef, Australia. Twelve 10x10 m permanent quadrats were established along a 400m stretch of fringing reef on the south-west side of Palfrey Island, an islet to the south of Lizard Island (Fig. 5.1). The reef was obliquely exposed to the prevailing south-east winds. Quadrats were located on sloping reef spurs, from a depth of 1.5 m on the island side to 5 m on the seaward side of the quadrat. All quadrats were separated by groove systems, but movement of fish between quadrats could not be discounted. Initial benthic cover was quantified as 500 regularly-spaced point intercepts from video-tape of 1 m wide lanes of the entire quadrat, with corals classified into structural groups.

Visual sampling was used to count fish within the quadrats. Four families of fish were counted, representing a wide range of sizes and trophic affiliations: damselfishes (Family: Pomacentridae), wrasses (Family: Labridae), butterflyfishes (Family: Chaetodontidae), and surgeonfishes (Family: Acanthuridae). Prior to sampling, the quadrat was delineated with a transect tape around the perimeter. I then moved away from the area for five minutes to reduce diver-associated disturbance to the fish fauna. A hierarchically organised counting regime was employed. Initially, the larger motile species (e.g. acanthurids and some labrids) were quantified at a distance to minimise diver avoidance. Upon establishing a consistent count (i.e. not recording any new individuals), I would move closer and count smaller and less mobile fish. Finally, I conducted a close search of the quadrat to count the smaller, more sedentary species - primarily pomacentrids. These counts represent a 'snapshot' in time of the resident fish assemblage, and are undoubtedly susceptible to edge effects from fish moving into and out of the quadrat and other sampling biases. However, assuming biases are consistent across sampling units the data provide valid comparisons between quadrats.

As the quadrats lay along a section of reef in line with the prevailing wind, I felt that this exposure gradient may induce spatial confounding. Consequently I used a randomised block design to ensure that replicates of each treatment were dispersed along the gradient (Dutilleul 1993). This design does not remove spatial structure, it merely ensures the treatments are distributed randomly with respect to the gradient thus avoiding confounding. This problem will be discussed below.

All quadrats were censused 3 times over 3 months prior to manipulation. After manipulation, the experiment was sampled at 12 time intervals over the following 21 months. I applied 3 levels of physical disturbance to corals within the treatment quadrats. The disturbance consisted of overturning tabular and corymbose corals, leaving them in place, and was applied at 25%, 50% and 75% of the numbers of these coral types within the quadrats. These structural forms were chosen because they tend to be vulnerable to lower levels of wave disturbance (Done 1992). The levels corresponded to *a priori* reductions in total coral cover of approximately 7.25%, 14.5%, and 22%. Control quadrats were not physically disturbed. A natural analog of this type of disturbance would be minor storm damage.

Analysis

Pre-existing patterns

Spatially organised samples present some methodological problems. The fish assemblage within any quadrat can be seen as a summation of independent components of spatial pattern, benthic cover, and their interaction. In order to measure the independent portion of each component, it is necessary to partial out the others. Pre-existing associations between fish, benthic cover, and position of the quadrat along the reef were assessed using the partial Mantel approach of Smouse et al. (1986) in which multivariate distance matrices are regressed on a covariate matrix, and the resultant residual matrices from the regressions submitted to the standard Mantel's test. Both fish assemblages and benthic cover were converted to the Manhattan distance for compositional data:

$$d_{ij} = 0.5\sum_k \left| p_{ik} - p_{jk} \right|$$

where p_{ik} and p_{jk} are the proportions of the *k*th species in samples *i* and *j* respectively. Spatial position was converted to a distance matrix by calculating the difference between the ranked position of the quadrat. All analyses were programmed in the Statistical Analysis System's (SAS) Interactive Matrix Language (IML) (SAS 1990). 1000 randomisations of the row and column labels of one of the triangular residual matrices provided the statistical test of the null hypothesis of no association between elements of the matrices.

In addition to the partial tests, associations between benthic cover and spatial position of the quadrat were investigated using simple Mantel tests. Benthic cover and fish were tested against treatment to ascertain whether *a priori* differences between treatments (i.e. confounding) existed. Treatment was coded as a binary distance matrix and, as with the partial analyses, 1000 randomisations ascertained statistical significance.

Temporal patterns

Differences in the temporal trajectory of the fish community between treatments (i.e. the treatment*time interaction) provided the logical and statistical test of treatment effects in this experimental design. However repeated samples of quadrats located within contiguous tracts of reef provide many analytical difficulties. Temporal autocorrelation may both confound and obscure the response of organisms to experimental manipulation. Repeated measures of spatially structured quadrats will exacerbate spatial dependence of observations. In order to separate the effects of spatial and temporal structure from those of the experimental manipulation, I used the multivariate approach of Borcard et al. (1992) to partition overall variation between space, time, experimental treatment, and the interactions between these factors.

Canonical ordinations are generalisations of multiple regression that describe relationships between two sets of variables e.g. biotic/abiotic variables. Canonical Correspondence Analysis (CCA) maximises the amount of variation in one data set that can be explained by unimodal relationships with another set (Ter Braak 1995). Partial forms of these analyses enable variation in a data set to be partitioned between subsets of variables (demonstrated by Whittaker 1984 in the univariate case). As organisms often respond in a unimodal fashion to environmental gradients, I used CCA to analyse this experiment. The analysis was programmed in the Statistical Analysis System (SAS) Interactive Matrix Language (IML) using the formula in Ter Braak (1995). The eigenanalysis solution was used instead of Ter Braak's iterative approach. Consequently the algorithm is based on the singular value decomposition of the matrix $S_{11}^{-0.5} S_{12} S_{22}^{-0.5}$, where S_{11} is a diagonal matrix containing the species totals of a sample*species table, S_{12} denotes the between-set sums of squares matrix, and S_{22} is the within-set sums of squares and cross-products matrix of the independent variables, weighted by the row totals of a sample*species table ($\mathbf{Z'NZ}$, where $\mathbf{Z}$ is the independent variable matrix, and $\mathbf{N}$ is the diagonal matrix of row totals). The partial forms of the analysis were calculated by replacing the values in the independent variable matrix ($\mathbf{Z}$) with the residuals from the fitted values of a multivariate multiple regression of the independent variables on the covariates.

Three sets of independent variables were included in the analysis. Experimental treatments were coded as dummy binary variables. Space was coded as the standardised rank of the quadrats along the gradient (i.e. from 1-12). To incorporate non-linear spatial structures, I included 2nd, 3rd, and 4th order polynomials of the standardisation, which were themselves standardised. All spatial measures were standardised to unit variance and 0 mean. Consequently, space was represented as 4 variables - x, x^2, x^3, x^4. Time was coded as the standardised number of months following initial sampling -

allowing uneven sampling intervals to be incorporated into the analysis. As with space, I included 2nd, 3rd, and 4th order standardised polynomials (i.e. t, t^2, t^3, t^4) to represent more complex temporal patterns such as annual changes.

The total variation in the data set can be derived from the sum of eigenvalues of a Correspondence Analysis (CA) of the dependent variables and then partitioned between each of these sets of independent variables by calculating the sums of eigenvalues from partial CCA. Particular combinations of partialled variables correspond to different fractions of the explainable variation (see Borcard et al. (1992) for a fuller description). A summary of the calculations used is provided in Table 5.1. Statistical significance of the fractions was derived from a permutation test in which the rows of the dependent variable matrix were randomised with respect to the independent variables, and the sum of eigenvalues re-calculated. 100 permutations provided a test to the 0.01 level.

5.4 Results

Pre-existing patterns and effectiveness of manipulation

Pomacentrids were the most speciose group (39 species in 14 genera) followed closely by labrids (37 species in 16 genera). Chaetodontids were represented by a moderate number of species (18 species in 2 genera) as were the acanthurids (11 species in 4 genera). I excluded rare species prior to the analysis - 'rare' being defined as less than 6 occurrences over the whole data set, or occurrence in less than 3 quadrats. Consequently pomacentrids were represented in the final analysis by 24 species, labrids by 21 species, chaetodontids by 18 species and acanthurids by 5 species.

Benthic cover was related to the position of the quadrat along the reef indicating a spatial habitat gradient was present (Table 5.2). Principal components analysis of the correlation matrix indicated the north western quadrats were characterised by greater cover of arborescent, tabular and corymbose corals (Fig. 5.2). Quadrats at the south-eastern end had less hard coral cover and a greater amount of bare rock. Quadrats in the middle were characterised by various degrees of encrusting and sheeting hard corals, columnar forms, and branching forms (Fig 2.). All fish families counted were associated with benthic cover after the spatial gradient had been factored out (Table 5.2). Labrids and pomacentrids were also associated with a spatial pattern unrelated to benthic cover i.e. spatial compositional changes - independent of benthic cover - were evident along the reef. However no pre-existing associations were evident between the treatments and either fish groups or benthic cover, which indicated blocking the quadrats was sufficient to avoid confounding.

On average quadrats had a total hard coral cover of 55% (Fig. 5.3). Experimental disturbance was applied only to tabular and corymbose corals which comprised 29% of total cover. The 3 levels of manipulation (25%, 50% and 75% of tabular and corymbose corals) corresponded to reductions of 8.3±8.4 %, 12.4±7.0 %, and 20.9±2.3 % total cover (Fig. 5.3). Disturbed corals generally did not survive over time, either abrading against the rock and sliding down the slope or fragmenting. Regrowth was limited to a few fragments from some colonies.

Temporal patterns following manipulation

No interaction effects between treatment and time were apparent, indicating that none of the families of fish responded to the level of disturbance imposed on the reef (Fig. 5.4.). Overall explainable variation ranged from 24.4 % for chaetodontids to 65.6% for acanthurids (Fig. 5.4). Indeed the only interaction present was between treatment and space for chaetodontids only. Although statistically significant ($p<0.01$), the variation explained by this interaction was small (1.3%).

Spatial and temporal variables, for the most part, accounted for most of the explainable variation (Table 5.3). Despite factoring out space and time, and the absence of confounding, the main effect of experimental treatment did explain small but significant amounts of variation ranging from 3.3% (chaetodontids), 7.5% (labrids), 13.8% (pomacentrids), to 14.0% (acanthurids). As there were no spurious 'treatment' effects prior to manipulation (Table 5.2), this variation is likely to represent repeated-measures autocorrelation that could not be factored out using the spatial and temporal variables.

No individual species responded to the treatment. Particular fishes could be classed *a priori* into species that are positively associated with the coral forms manipulated, and those that are likely to be negatively associated with those forms. None of the 'typical' coral associated species (Randall et al. 1990): the pomacentrid, *Pomacentrus moluccensis*; the chaetodontids *Chaetodon aureofasciatus*, *C. baronessa*, *C. trifasciatus*, *C. plebeius*, *C. trifascialis*; the labrids *Pseudocheilinus hexataenia*, *Labrichthys unilineatus*; showed any temporal response to the treatment (Fig. 5.5). Similarly, no negatively-associated species (i.e. species typically associated with bare rock, rubble or algae): the pomacentrids *Stegastes apicalis, Plectroglyphidodon lacrymatus, Pomacentrus wardi, P. bankanensis, Chrysiptera rex*; the acanthurids *Ctenochaetus striatus, Acanthurus nigrofuscus*; or the labrid *Halichoeres melanurus*; responded to the treatment (Fig. 5.6).

Table 5.1. Decomposition of variation to different fractions. Total variation is derived from an unconstrained Correspondence Analysis on the dependent variables. The source of variation is derived from a Canonical Correspondence Analysis of the dependent variables with the appropriate independent variables, after partialling the relevant independent variables. Fractions explained by interactions have the simple effects removed by subtraction.

Source	**'With' Variables**	**'Partialled' Co-variables**	**Subtract**
Trt	Trt	Time Space	
Time	Time	Trt Space	
Space	Space	Trt Time	
Trt*Time	Trt Time	Space	- Trt - Time
Trt*Space	Trt Space	Time	- Trt - Space
Time*Space	Time Space	Trt	- Time - Space
Trt*Time*Space	Trt Time Space		- Trt - Time - Space
Total			

Table 5.2. Pre-existing associations between fish, benthic cover, and assignment of quadrats to treatments. Mantel and partial Mantel tests were used to test association of fish and benthic cover with both position of quadrat and arbitrary assignment to treatments. 1000 randomisations were used to test significance.

Variables	**With**	**Partialled**	**Proportion of randomisations > observed**	
Benthos	Space		0.010	**
Pomacentrids	Space	Benthos	0.043	**
Chaetodontids	Space	Benthos	0.140	
Labrids	Space	Benthos	0.028	**
Acanthurids	Space	Benthos	0.152	
Pomacentrids	Benthos	Space	<0.001	**
Chaetodontids	Benthos	Space	<0.001	**
Labrids	Benthos	Space	<0.001	**
Acanthurids	Benthos	Space	<0.001	**
Benthos	Treatment	Space	0.173	
Pomacentrids	Treatment		0.933	
Chaetodontids	Treatment		0.898	
Labrids	Treatment		0.471	
Acanthurids	Treatment		0.928	

Table 5.3. Importance of factors relative to total variation explained by Canonical Correspondence Analysis.

Family	**Total Variation Explained**	**Order of Importance of Factors**
Pomacentrids	60.96%	Time>Space>Treatment
Acanthurids	65.64%	Space>Treatment>Time
Labrids	42.13%	Space>Time>Treatment
Chaetodontids	24.40%	Space>Time>Treatment

Figure 5.1. Location of study site at Lizard Island (14°40′8′′S, 145°27′34′′E), northern Great Barrier Reef. Arrows indicate direction of prevailing south-east wind, numbers indicate order of quadrats along the fringing reef of Palfrey Island.

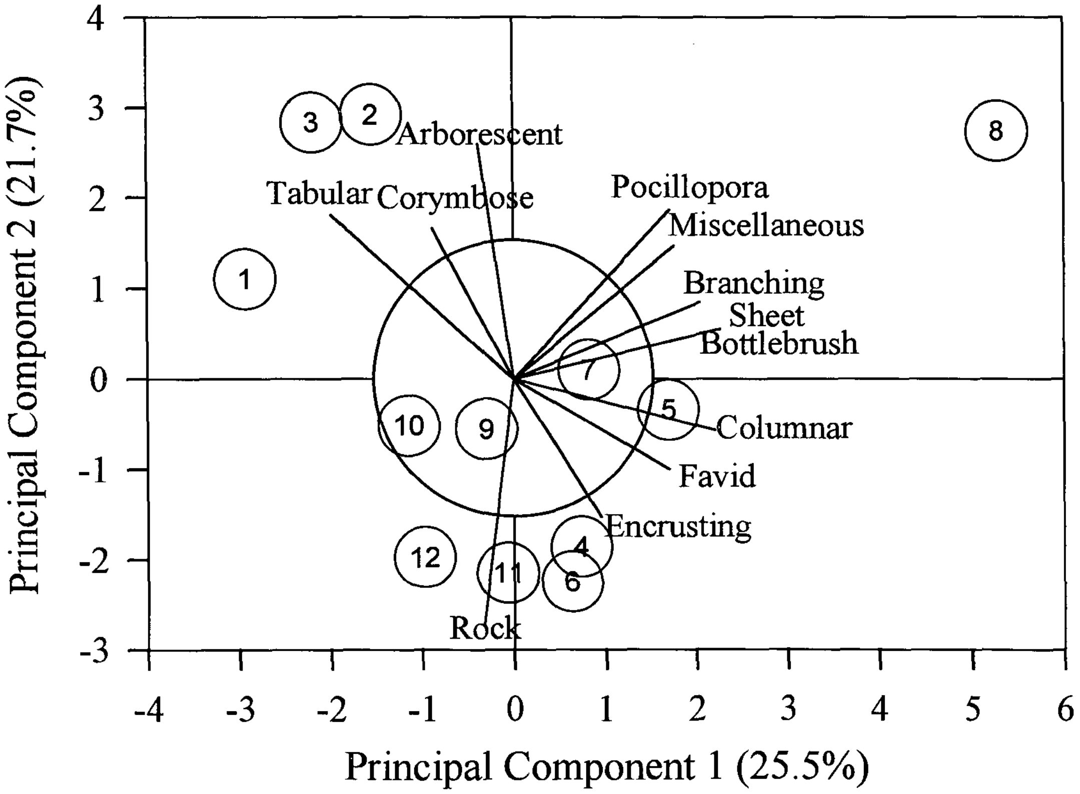

Figure 5.2. Principal components analysis of the correlation matrix of benthic cover in quadrats prior to manipulation. Numbers correspond to quadrats, vectors are the eigenvectors of the benthic cover categories (interpretable as a correlation coefficient). The circle centred on the origin corresponds to an eigenvector of 0.3.

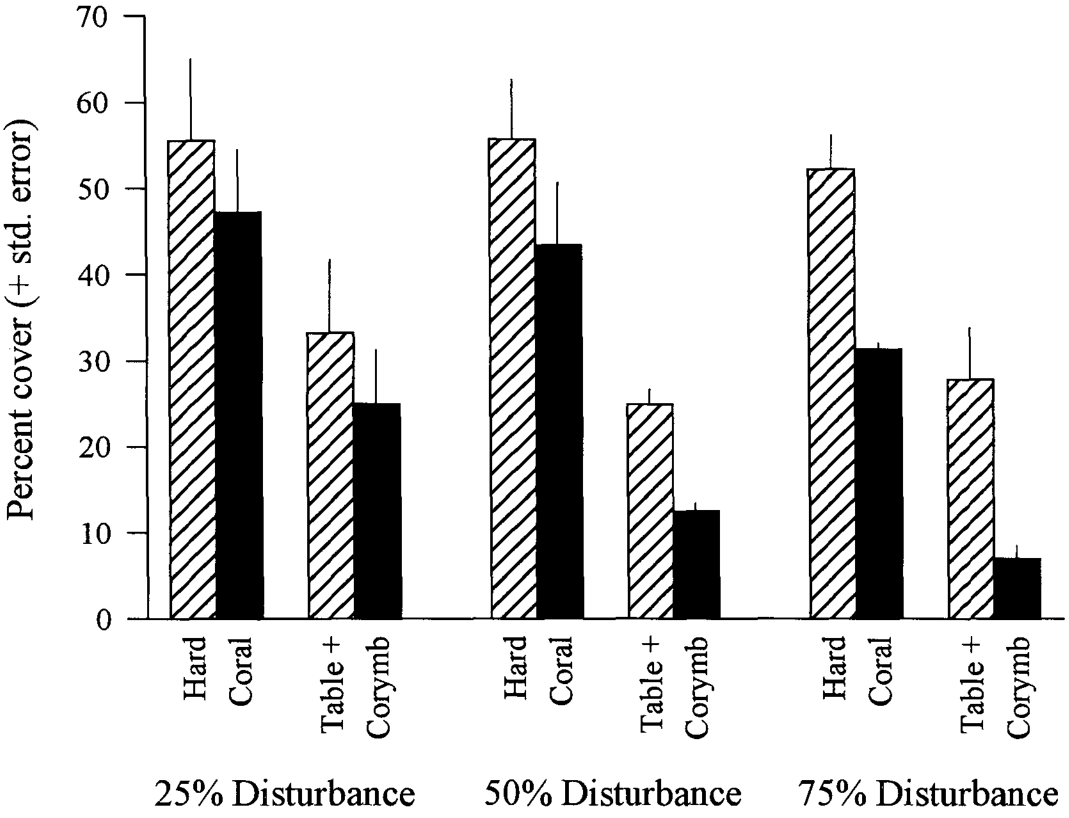

Figure 5.3. Coral reductions in experimental quadrats expressed as proportions of total hard coral cover and table/corymbose forms only. Cross-hatched bars = before manipulation, solid bars = after manipulation.

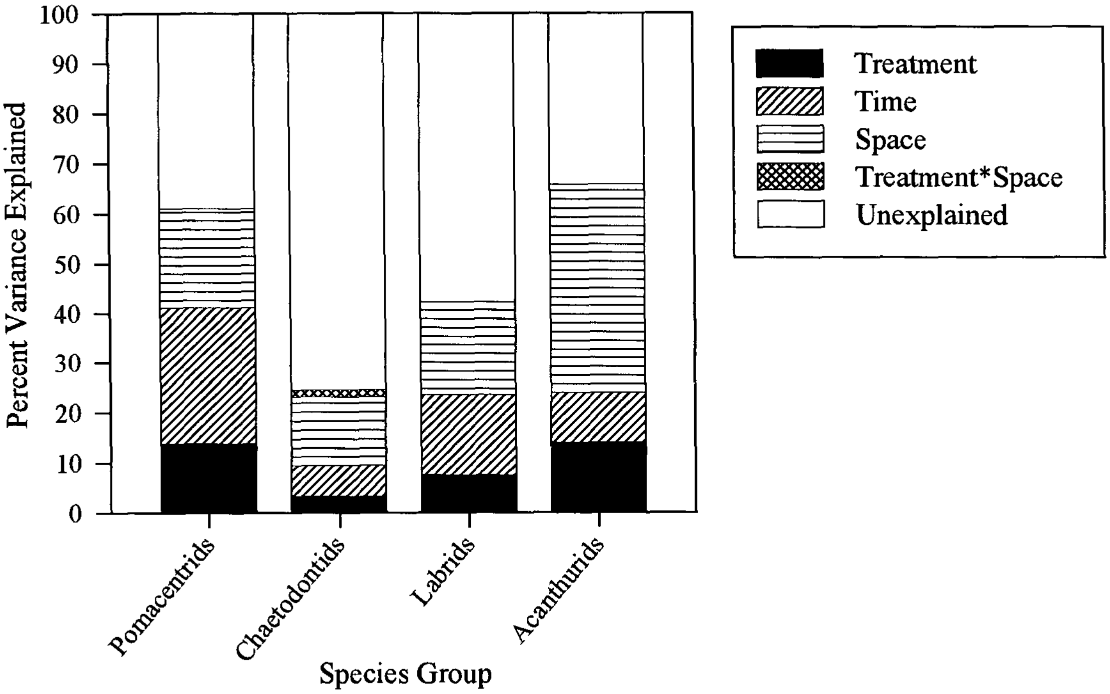

Figure 5.4. Percent variance explained by treatment, temporal, spatial, and interaction effects for 4 fish families. Variance components obtained from partial Canonical Correspondence Analysis.

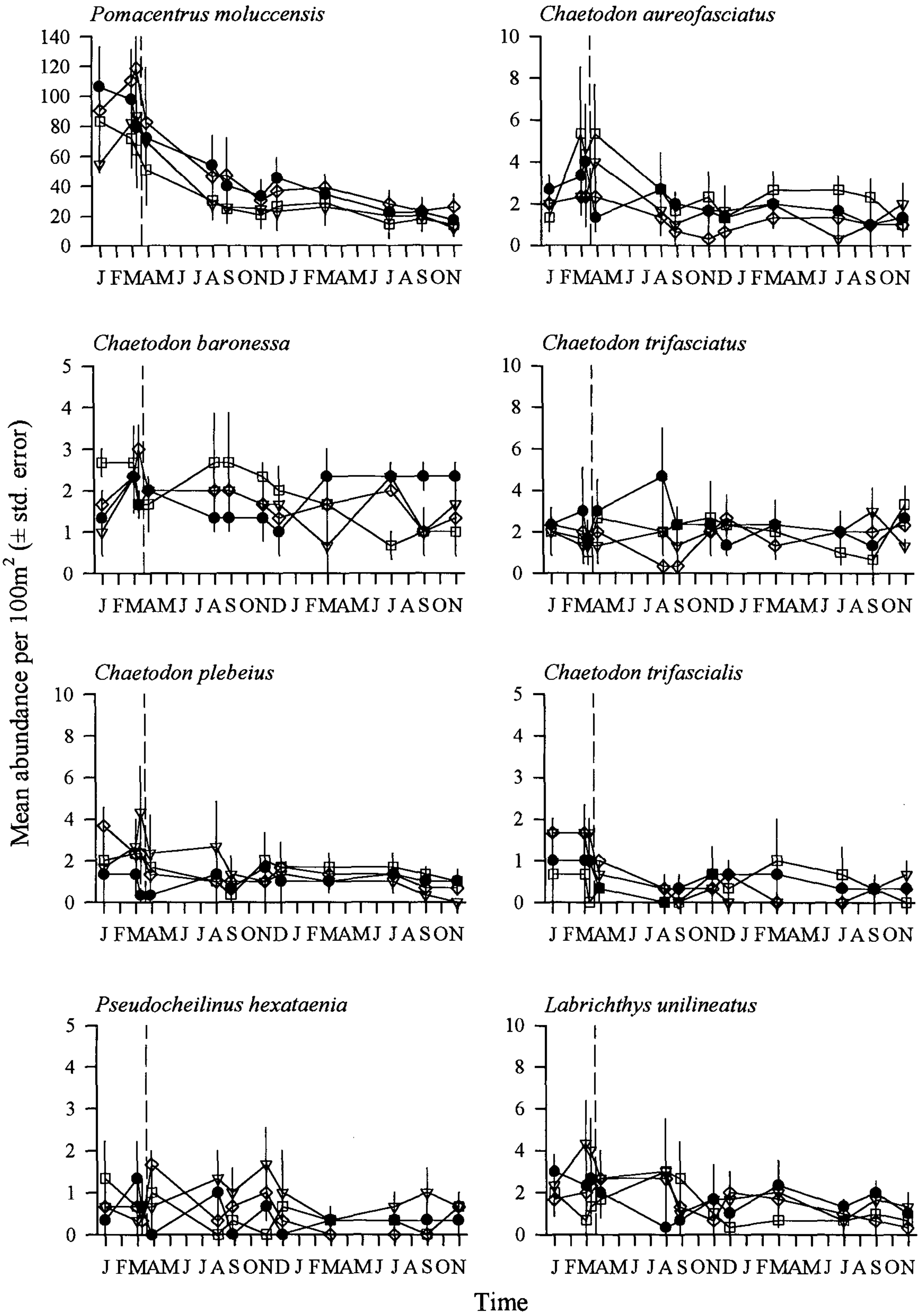

Figure 5.5. Abundances of a selection of positively coral-associated fish species through time. Dashed vertical line represents time of disturbance. ● control; ∇ 25% disturbance; ◊ 50% disturbance; □ 75% disturbance.

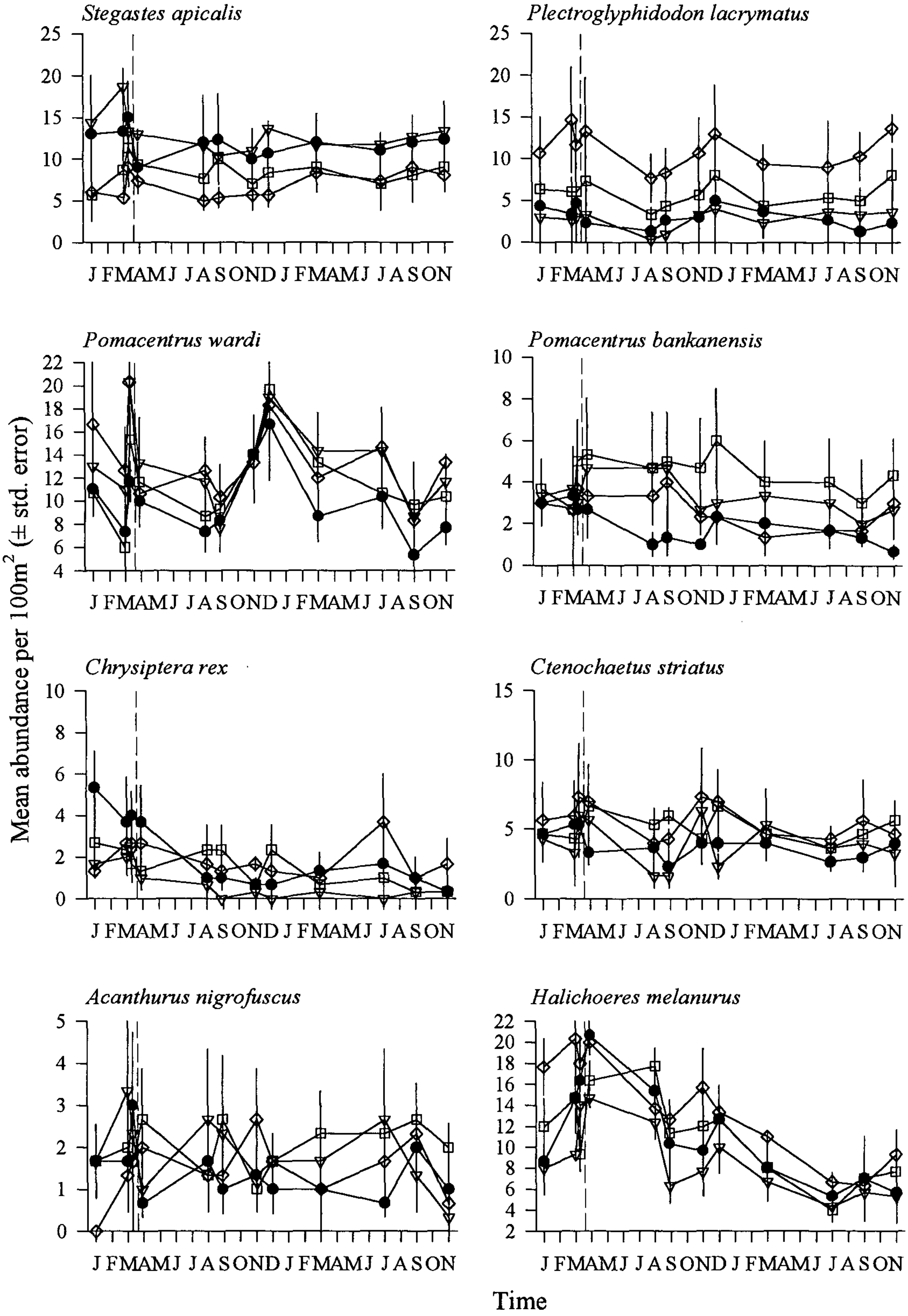

Figure 5.6. Abundances of a selection of negatively coral-associated fish species through time. Dashed vertical line represents time of disturbance. ● control; ∇ 25% disturbance; ◇ 50% disturbance; □ 75% disturbance.

5.5 Discussion

Although correlative studies and natural 'experiment' studies may hint at the importance of habitat variables in structuring communities, unequivocal estimates of habitat importance is perhaps best explored by experimentation. In this study I disturbed hard coral communities in 100m^2 areas of contiguous reef to ascertain whether changes in coral cover would result in corresponding changes in reef fish communities. Pre-existing spatial and habitat gradients were factored out by blocking quadrats in space and explicitly incorporating space and time into the analysis. No effect of disturbance at this scale could be detected despite total reductions of 8%, 12% and 21% from an initial level of 55% coral cover. Of the explainable variation, most was accounted for by spatial and temporal variables indicating natural spatio-temporal changes were responsible for most of the pattern in the data set. The main factor of 'treatment', independent of time, explained significant but small amounts of variation which indicated the partialling method used did not completely remove spatio-temporal effects.

The strength of correlations between fish and habitat variables has frequently been cited as evidence for the importance of habitat in structuring communities e.g. Bell and Galzin 1984, Bell et al. 1985, Findley and Findley 1985, Roberts and Ormond 1987, Roberts et al. 1988, Bouchon-Navaro and Bouchon 1989, Fowler 1990, Booth and Beretta 1994, Green 1996, Hart et al. 1996). Many studies are difficult to compare due to the varying number of habitat types crossed during sampling, and the numerical range of benthic cover. Inter-zonal differences may confound patterns due to easily measured habitat variables, such as benthic cover, being correlated with less tangible and unmeasured features such as aspect, topography, or spatial proximity to currents, exposure etc.. In addition, the range of values considered may predispose studies to either finding or not finding fish-habitat associations (Jones and Syms, 1998). Gradients may only appear when community parameters are measured over a large range of coral cover. Notwithstanding this comparative difficulty, few researchers agree on the level of differences in benthic cover required to induce a change in fish community structure. Obligate corallivorous chaetodontids may respond to as little as 10% difference in coral cover (Bell and Galzin 1984), but this relationship may depend on specific composition of the corals (Cox 1994). In contrast, Jones and Syms (in prep.) found in a correlative study that 30-40% difference in coral cover was required to obtain a 10% difference in fish community structure.

In this study I found within reef-zone patterns of fish-benthos association in labrids, acanthurids, chaetodontids, and pomacentrids. An important aspect of all the measurable relationships is that the benthos itself was spatially patterned. Simple correlations between fish and space would have confounded the spatial and benthic components of this pattern. Partial Mantel tests indicated labrid and pomacentrid distributions were patterned along the exposure gradient by some process not mediated by benthic cover (e.g. wave action). An important implication is that spatial organisation may exert an effect on fish assemblages at the landscape scale.

The absence of any treatment*time interactions indicated that the fish families studied were resistent to reductions in coral cover from 55% to 34% when applied in 100m^2 patches. Behavioural responses to disturbance have received little attention. Cox (1994) reported that Hawaiian chaetodontids expanded their home range in response to reduction in coral levels. Chaetodontids, labrids, and acanthurids are also potentially mobile over a greater range than the quadrat sizes in this experiment (Sutton 1985; Robertson and Gaines 1986; Roberts and Ormond 1987; Driscoll and Driscoll 1988), and so it is not unreasonable to hypothesise that these groups may simply move away from or into disturbed areas at will. Pomacentrids, however, are generally more site attached and would be expected to be very sensitive to benthic changes. It would appear that the disturbance applied during this experiment was simply not enough to induce a change in community structure in any of the families studied at this scale of observation.

Little is known about natural levels, forms, and scales of disturbance in coral reef systems (Done 1992). Many previous studies have focused on either extreme of the disturbance range - from minor, localised and often sub-lethal damage caused by divers fins and anchors (e.g. Shinn 1989) to catastrophic and infrequent cyclonic disturbances that may exfoliate tracts of reef 10s to 100s of metres in extent to 20m depth (e.g. Van Woesik et. al. 1991). The spatio-temporal dynamics of disturbance in the day-to-day functioning of the reef mosaic at the scales of reef-fish motility has received very little attention (however see Aronson and Precht 1995). Similarly, the form such disturbances would take can only be hypothesised at present. It has been put forward that coral size and structure will affect susceptibility to physical disturbance (Denny et al. 1985; Done 1992). This was the premise in this experiment, in which only the most susceptible coral forms in the quadrats, tabular and corymbose, were disturbed. While this form of disturbance is likely to occur naturally, it is unknown whether the level at which I applied the disturbance is appropriate.

The scale at which an experiment is applied will fundamentally affect the results. An inappropriately scaled experiment will severely limit the conclusions that can be drawn (Wiens et al. 1986, Syms and Jones, in revision), and the generality of those conclusions. Habitat manipulations in temperate systems have induced fish responses at a range of scales from 4m^2 (Holbrook and Schmitt 1984) to in excess of 500 m^2 (Bodkin 1988; Carr 1994). A large number of studies operating at scales intermediate to these extremes (e.g. Carr 1989 1991; Levin 1993; Syms and Jones, in revision) and commensurate with this experiment, have also generated fish community responses to habitat alteration. If the form and level of manipulation applied in this experiment do correspond to natural disturbances, it may be surmised that temperate kelp and coral-reef assemblages are responding at rather different scales to each other. A multi-scale experimental approach (e.g. Syms and Jones in revision) would be productive in this respect.

The total variation in a fish community is the product of a variety of environmental and biological influences. Physical variables may overlay or interact with abiotic parameters which may in turn interact with populational or behavioural idiosyncracies of the organisms in question. Pattern common to different types of variables but independent of their relationship (e.g. a common spatial structure) will tend to cause overestimation of the strength of their 'true' relationship (Legendre and Troussellier 1988).. Conversely, different spatial responses may obscure relationships between sets of variables. In recognition of this problem, Borcard et al. (1992) put forward a method of applying the constrained ordination approach of Ter Braak (1986) to partial out effects of potentially confounding variables. This approach has received further attention (e.g. Belgrano et al. 1995a,b) and the utility of the method is increasing in correlative studies. In this study I applied the method in an experimental context and have found it to increase the depth of insights into the results. Reef-fishes within the study area appear to be associated with habitat variables, which were in turn spatially organised. Labrids and pomacentrids were spatially patterned - independent of habitat - and possibly related to wave exposure. Pre-existing temporal and spatial patterns may have 'damped out' the effect of experimental manipulation. The method did not successfully assign all spatio-temporal pattern to the appropriate factor. Variation explained by simple treatment effects corresponded to repeated-measures variation that could not be factored out. I believe this was due to low replication combined with the fortuitous presence of less common resident species. Future applications of the method should be aware of these problems. An additional caution is that the method will not remove confounding. Interspersion of treatments such as in a blocked design will still be required to enable the method to factor spatial from treatment effects.

This study indicates that coral reef fish are resistent to disturbances at the scale of 10x10m and a level of 21% reduction of hard corals - when that reduction consists of overturning tabular and corymbose corals and leaving them in situ. This experiment has also highlighted several important issues in reef ecology and in particular problems associated with measuring the importance of physical disturbance in structuring assemblages. Experiments conducted on contiguous reef will require that consideration be given to problems of spatial and temporal autocorrelation. Repeated measures of permanent quadrats will tend to magnify these differences because of the disparity between within-quadrat and between-quadrat variance structures. While methodological precautions may be taken to safeguard against or quantify spatio-temporal patterns, these methods do not guarantee complete removal of such effects. The scale, level, and form of disturbance should also receive close attention. Correlative data may obscure relationships due to confounding and measurement at different scales to experimental manipulation. A clear need exists for some measure of the patch sizes that organisms and communities are likely to respond to prior to experimental manipulation. Given that there are likely to be logistical and ethical problems with conducting physical disturbances, a more structured approach based on hypotheses derived from appropriately scaled correlative data, and with due consideration given to spatio-temporal autocorrelations will maximise the benefits from applying future experiments.

Chapter 6: The Structure of Coral Reef Fish Communities: Direct versus Indirect Effects of Disturbance

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6.1. Abstract

Coral reef fishes occupy habitats that are subject to frequent natural disturbances. However, the relative effects of perturbations that directly impact on fish communities versus indirect effects caused by habitat modification have not been compared. Here I test a series of models predicting their direct and indirect responses to these disturbances, with different outcomes predicted depending upon whether fish communities are: (a) stable and habitat-determined, (b) stable and determined by strong biological interactions among the fishes, or (c) unstable, nonequilibrial systems. The models were tested experimentally at Lizard Island (Great Barrier Reef, Australia) by subjecting a series of natural patch reefs to a factorial combination of direct disturbance (by removing fish from reefs) and indirect disturbance (2 levels of mechanical damage to the patch reefs), with the response of the resident fish communities monitored over a two-year period.

The results of these manipulations indicated that fish assemblages on patch reefs exhibit a degree of stability, with their structure determined to a large extent by habitat characteristics. Unmanipulated assemblages persisted through time and, although total abundance varied, the relative composition of the fish communities remained the same. Directly disturbed communities (in the absence of reef damage) were highly resilient, with fish clearances and control reefs becoming indistinguishable after only a few months, through immigration and juvenile recruitment. Indirect disturbance by physical habitat damage generated predictable and persistent changes to the fish assemblages, with disturbance explaining almost half (46.6%) of the variation in the fish community data set. Patch reefs with the resident fish community left intact, but subject to different levels of physical disturbance, diverged in structure over time. Reefs with different direct disturbance histories converged in structure with those subject to the same level of habitat disturbance. These effects resulted from species-specific patterns of decline in live coral-associated species and increases in rubble-associated species, with an overall decline in species richness. Declines in the abundance of coral-associates on damaged reefs were abrupt, with no recovery observed. Increases in the abundance of

rubble associates were more ephemeral, with high levels of recruitment and immigration to begin with, followed by a high rate of loss.

These results support a model of patch reef fish assemblages as deterministic systems that are constrained within broad limits by the structure of the habitat, but vary greatly within these limits through stochastic recruitment and migration. Although biological interactions may limit the abundance of individual species, interactions among species offer no resilience to the effects of changing habitat characteristics.

6.2. Introduction

Disturbance plays a central role in the perturbation and dynamics of a wide variety of ecological communities (Dayton and Hessler 1972, Sousa 1984, Krummell et al. 1987, Paine and Levin 1981, Karlson and Hurd 1993). Ultimately, disturbance operates directly by removing individuals from a community and, when extreme, can reduce diversity and alter community structure by eliminating species (Petraitis et al. 1989, Pickett et al. 1989). In contrast, moderate levels of disturbance may promote diversity "indirectly", by reducing the abundance of competitively dominant species and allowing inferior competitors to persist (Connell 1978, Petraitis et al. 1989). Recently, there has been increasing attention given to indirect effects in ecology, particularly those involving competitive and trophic interactions (Strauss 1991, Wootten 1994, Menge 1995, 1997). However, in the context of disturbance, there has been one form of indirect effect that the theory has largely ignored. When the disturbance acts to remove organisms (e.g. trees, macroalgae, corals) which essentially represent habitat to other suites of organisms (e.g. insects, amphipods, fishes), then a whole range of indirect effects may follow (Jones and Andrew 1993, Syms and Jones in press). The relative importance of direct and indirect disturbances, in systems where the disturbance may act directly on the focal community or indirectly on their habitat, have received little attention.

In developing testable predictions about the relative effects of direct and indirect (hereafter via habitat-modification) disturbance on communities, two factors are critically important. Firstly, there is the degree of stability of the community for which the predictions are well-known (Dayton et al. 1984). Stable systems should persist in the absence of disturbance and exhibit some tendency to return to their original condition following a perturbation (= resilience). Secondly, if stable, the community structure could be determined by either the structure of the habitat itself or be the result of strong interactions among the members of the community (that may be unrelated to habitat structure). If a community is stable and strongly associated with habitat type, then following a direct disturbance, the community should eventually reassemble to the same structure as undisturbed communities (Fig. 6.1a). If on the other hand the community is independent of habitat structure, but member species are strongly interacting, "multiple stable states" may arise, depending upon the patterns of colonization and the interactions among individual species (Sutherland 1974, 1990, Connell and Slatyer 1977) (Fig. 6.1b). If intrinsically unstable, both disturbed and undisturbed communities will deviate from their original structure over time and no persistence or resilience will be observed (Sale 1980) .

The predicted responses to indirect disturbances are somewhat different. If stable and habitat-determined, a disturbance by habitat alteration will result in the community diverging from its initial or undisturbed condition and it will adopt an alternative state determined by the new habitat structure (Fig. 6.1c). If the community structure is independent of habitat characteristics the communities will persist in the same state, regardless of whether habitat is altered (Fig. 6.1d). Again, if there are no attributes of stability, no divergence or persistence will be observed, as the structure of the community will vary unpredictably over time.

As these predictions represent hypothetical extremes, and communities are likely to be subject to direct and indirect disturbances at the same time, the relative importance of these processes can only be tested when both types of disturbances are applied to the same community. The predictions are as follows: If the community is to some extent stable and habitat-determined, the communities on disturbed habitats will diverge from undisturbed habitats over time. However, the important point here is that directly disturbed communities will converge with communities that have a similar habitat structure (Fig. 6.1e). If the community is to some extent stable and independent of habitat structure, then there will be no deviation in community structure of indirectly disturbed communities, and importantly, no tendency for directly disturbed communities to converge on those with like habitats (Fig. 6.1f). Thus, the relative importance of direct and indirect disturbance will be evident from the degree of divergence among fish communities on different habitats and the degree of convergence among communities on the same habitats.

Coral reef fish communities are an appropriate system to examine the consequences of different types of disturbance. They are subject to frequent, often catastrophic disturbances such as cyclones and crown-of-thorns starfish damage, that may impact on the fishes and/or the coral reef habitat (Connell 1978, Bouchon-Navaro et al. 1985, Harmelin-Vivien and Laboute 1986, Dollar and Tribble 1993, Hughes 1994). However, disturbance processes have been ignored in coral reef fish community theory and predictions about the role of disturbance in structuring these assemblages have yet to be tested (Jones and Syms 1998). Instead, theory has been centered on the predictability of reef fish assemblages and the roles of competition and recruitment. The preconception of these communities as tightly organized, predictable units (e.g. Smith and Tyler 1972, Gladfelter and Gladfelter 1978, Smith 1978) was superseded by the view that coral reef fish assemblages are nonequilibrial in nature. An initial formulation of this idea held that the community was composed of competitors of equal ability vying for space on the reef and replenished at random from the plankton (the 'lottery' hypothesis, Sale 1977). With the realization that space is not necessarily limiting, the lottery hypothesis was itself superseded by a model emphasizing recruitment variability in the absence of competitive processes that limit the overall size of the community (the 'recruitment limitation' hypothesis, Victor 1983, Doherty 1983). The recruitment-limitation hypothesis remains the current paradigm, although there is increasing evidence that both recruitment and postrecruitment processes are important (Jones 1990, 1991, Forrester 1995, Hixon and Carr 1997, Caley et al. 1996, Ault and Johnson 1998). Regardless of which model is correct, the implications of these different ideas, for predicting responses to disturbance, have not been evaluated.

Disturbance experiments, in which perturbations were applied directly to the reef fish community, have been carried out ostensibly to measure the degree of determinism in their structure (e.g. Sale and Dybdahl 1975, 1978, Sale 1980). Natural analogs of direct disturbance, however, have been rarely recorded. Hypothermic conditions caused fish kills at Big Pine Key, Florida (Bohnsack 1983), and catastrophic storms altered fish numbers in Hawaii (Walsh 1983) and on the Great Barrier Reef (Lassig 1983). The importance of these events in structuring fish assemblages has not been critically examined. Indirect disturbances by habitat alteration have received little attention in coral reef fish communities, despite their potential importance and frequent natural occurrences (Jones and Syms 1998). Much of this disinterest might be attributed to the weakness of correlative evidence of habitat association at scales that habitat can be manipulated (e.g. Sale et al. 1994, Ault and Johnson 1998). In contrast with tropical systems, experimental habitat disturbances have been widely and successfully applied to temperate reef fish assemblages (Choat and Ayling 1987, Bodkin 1988, Jones 1988a, 1992, DeMartini and Roberts 1990, Holbrook et al. 1990, Carr 1989, 1991, Syms and Jones, in press). These studies have generally have demonstrated that indirect disturbance is an important process. The effects of both direct and indirect disturbances on coral reef fish assemblages needs to be examined.

Despite the absence of any tests of how coral reef fish should respond to disturbance, it is possible predict the likely outcomes of direct and indirect disturbances, conditional on habitat determinism, interaction strength, and recruitment limitation. Empirical studies have been divided about whether fish are strongly (e.g. Bell and Galzin 1984, Bell et al. 1985, Findley and Findley 1985, Bouchon-Navaro and Bouchon 1989, Hart et al. 1996) or weakly (e.g. Roberts and Ormond 1987, Roberts et al. 1988, Fowler 1990, Booth and Beretta 1994, Cox 1994, Green 1996) associated with habitat variables. Unfortunately many of these studies are difficult to compare and evaluate, due to confounding and the different ranges of habitat conditions considered (Jones and Syms 1998). For example, Ault and Johnson (1998) have shown a strong association of fish assemblages and habitat variables on large patches of contiguous reef and only weak associations on small patch reef habitats. Generally, if fish communities are sampled along a wide range of habitat types, the assemblage becomes more predictable. A high degree of habitat determinism would lead to the patterns of convergence and divergence predicted in Figure 1a,c,e.

Tropical fish communities do not appear to be organized by strong biological interactions, with no examples of facilitation known to affect community succession. Competition may have sub-lethal effects (Doherty 1982, 1983, Victor 1986, Jones 1987a,b, Forrester 1990) and influence small-scale patterns of distribution (Ebersole 1985, Robertson and Gaines 1986, Clarke 1989, Robertson 1996), but may not lead to the elimination of species (Jones 1991). Predation has certainly been implicated as an important process in determining patterns of abundance (Doherty and Sale 1986, Caley 1993, Hixon and Beets 1993, Hixon and Carr 1997). However, there are few examples where predation has been attributed responsibility for priority effects in reef recolonization, which might lead to alternative community states (but see Shulman et al. 1983).

The over-riding source of variability in coral reef fish communities in small patches of habitat lies in the recruitment dynamics (Doherty and Williams 1988, Doherty 1991, Doherty and Fowler 1994) and species-specific patterns of movement (Lewis 1997, Ault and Johnson 1998). Replenishment of local sub-populations is a large-scale dynamic that theoretically should be independent of any direct disturbance. Increasingly, the evidence suggests that the structure and dynamics of communities on patch reefs are not constrained by habitat structure or biological interactions (Sale et al. 1984, Ault and Johnson 1998). Therefore, it would be predicted that recruitment variability alone (and stochastic movement) will over-ride any local effects of direct or indirect disturbances.

In this study I experimentally test predictions concerning the effects of direct and indirect disturbance on the structure of fish assemblages occupying small coral patch reefs at Lizard Island (Great Barrier Reef, Australia). In particular, I set out to detect any apparent stability in response to these disturbances, and if so, determine if this is related to the structure of the habitat (changes primarily mediated by indirect disturbance – Fig. 6.1a,c,e) or strong interactions among the fishes themselves (identical responses in disturbed and undisturbed habitats – Fig. 6.1b,d,f). The experiment was necessarily carried out on a small scale. I administered a factorial combination of direct disturbance (by removing fish from reefs), with 2 levels of indirect disturbance (level 1: the breaking-up of all hard corals on the patch reef; level 2: the breaking-up of hard corals coupled with reducing the physical structure of the reef). The response of the community to these disturbances enabled the assemblages to be characterized on the basis of their persistence (tendency to remain constant in the absence of disturbance) and resilience (tendency to return to the pre-disturbance community structure following a perturbation) (Dayton et al. 1984). In addition, the role of habitat was measured by divergence (the degree to which initially similar communities develop differences over time) and convergence (the degree to which initially different communities develop the same structure over time).

6.3. Methods

This study was carried out over 24 months (July 1993-June 1995) at Lizard Island (14° 40′ S, 145° 28′ E) on the northern Great Barrier Reef, Australia. A 200 x 300m field of patch reefs ranging in size from 0.25m^2 to > 100m^2 at 5-7 m depth on the western side of the island was chosen as the study area. A subset of 48 patch reefs of similar size and coral composition, interspersed among numerous other reefs, was selected as experimental units. Reefs were between 2-3 meters long, 0.75-1 m wide, and generally less than 1 m high. The spacing between reefs was variable, but experimental reefs were on average about 10m from other patch reefs. The proximity of reefs in this system was such that movement of more mobile fish species between reefs was likely, so they cannot be considered as true isolates (cf. Sale 1991).

Experimental design

Two forms of disturbance were applied to the reefs in a factorial design, with 8 replicates per treatment (Fig. 6.2). Direct disturbance was carried out by removing fish from half of the reefs using the anaesthetic Quinaldine (dissolved in alcohol and seawater) and hand-nets. Because the fish occasionally fell into crevices in the reef matrix during anaesthetizing, I visited the reef the following day and removed any fish still present. Based on the baseline fish counts immediately before manipulation, the clearance was effective. Indirect disturbance was applied at two levels (Fig. 6.2). The first level entailed the breaking up of most of the branching corals with a hammer; and the second level was achieved by both breaking up the hard corals and reducing the height and complexity of the reef matrix itself. All rubble resulting from the manipulation was left in place. Control reefs for the indirect disturbance were not altered.

Fish were visually censused at 10 intervals - three before manipulation and seven afterwards over a two-year period. Each sample interval was a compilation of between two and three repeated censuses, approximately following the procedure of Sale and Douglas (1981). Although visual censuses sample a subset of fish (Sale and Douglas 1981), they provide an unbiased comparison across reefs. During each census, recently settled recruits were distinguished from the resident population for each species.

The reefs were measured and coral cover quantified at 3 time intervals - before manipulation, 3 months after, and 12 months after manipulation. Reef height was measured as the maximum height above the sand substratum. Coral cover was measured from a 30cm wide videotape-transect running over the top and around the side of the reef. 20 regularly spaced frames were selected from the videotape, and the benthic cover under 5 random point intersects were recorded to give a total of 100 point intersects per reef. Coral growth forms were recorded, as the video did not allow resolution to species level.

Analysis

Pre-disturbance ordinations of benthic cover and fish assemblages using Principal Components Analysis indicated there were no pre-existing compositional or spatial patterns in either the fish assemblages or coral cover which could confound results (Dutilleul 1993). However as a precaution against spatial confounding, the reefs were grouped a priori into three spatial blocks and 8 replicates from within these blocks were assigned randomly to each treatment.

To assess pre-existing relationships between fish assemblages and benthic cover I used Mantel's test (Mantel 1968). The fish data were root-root ($x^{0.25}$) transformed and converted to a similarity matrix using the Manhattan or Czekanowski proportional similarity index (Schoener 1968). Benthic cover data were square-root transformed ($x^{0.5}$) and converted to a similarity matrix using the same index. A plot of fish vs. benthic similarities did not reveal any non-linearity's that would affect the Mantel's test. 1000 randomization's provided the statistical test to the 0.001 level.

The experimental design contained 3 fixed factors - direct disturbance, indirect disturbance and time and consequently the appropriate tests of treatment effects were the 2 and 3-way interactions i.e. the trajectory of each manipulated factor over time; and not the simple effects. As the data were repeated measures over time, I also included reef as a blocking factor to accommodate within-reef temporal structure. This split-plot approach (SAS Inst. 1991) is an approximate test but provides a useful statistical guide. The model can be specified as (excluding mean and error term):

VARIABLE1--VARIABLEN = DIRECT + INDIRECT + DIRECT*INDIRECT +
REEF(DIRECT*INDIRECT) + TIME + DIRECT*TIME + INDIRECT*TIME +
DIRECT*INDIRECT*TIME

where DIRECT, INDIRECT, and DIRECT*INDIRECT are tested over the blocking factor REEF(DIRECT*INDIRECT), and all other terms tested over the error.

I could not carry out a full Multivariate Analysis of Variance (MANOVA) of the fish data due to there not being enough degrees of freedom (i.e. there were too many fish species relative to the number of reefs and levels of each factor). Consequently I ran a Principal Components Analysis on the covariance matrix of the ($x^{0.25}$) transformed fish data and analyzed the first 20 Principal Components (which summarized 77.8% of all the variation in the data set) with MANOVA using Pillai's trace as the test statistic.

After MANOVA, I developed a graphical presentation using Canonical Discriminant Analysis (CDA) of the $x^{0.25}$ transformed fish data using the 3-way classification of DIRECT*INDIRECT*TIME as the hypothesis matrix.

Recruitment data were analyzed by combining recruit numbers across each census, transforming by $x^{0.25}$, and analyzing the 2-way factorial MANOVA of DIRECT crossed with INDIRECT disturbance. Canonical Discriminant Analysis (CDA) of the $x^{0.25}$ transformed data using the 2-way classification of DIRECT*INDIRECT provided the graphical data presentation.

6.4. Results

Pre-manipulation patterns and disturbance effectiveness

No pre-manipulation patterns of either benthic cover or fish community structure were apparent from initial ordinations. In addition, there was no association between fish community structure and coral cover on each reef (Mantel's statistic p=0.080). Consequently there was little likelihood of spatial or habitat confounding. The numbers of fish removed from directly disturbed reefs were comparable to baseline abundances, which indicated the direct disturbance was effective. In the first month after manipulation, hard coral cover had been reduced on indirectly disturbed reefs from 20-30% to less than 10% (Fig. 6.3). The hard corals that remained were generally encrusting favids – most branching coral forms had been destroyed. Indirect disturbance level 2 also caused a 15% decrease in soft coral cover, which persisted for most of the experiment. None of the indirectly disturbed reefs regained their baseline coral compositions over the course of the experiment. During the experiment control reefs and level 1 disturbances remained the same height, while level 2 disturbance reduced the reef height by 5-7 cm (Fig. 6.4).

Temporal patterns in community structure

Both direct and indirect disturbances exerted effects (DIRECT*TIME p=0.0133; INDIRECT*TIME p=0.0001; Table 6.1), which were additive (DIRECT*INDIRECT*TIME p=0.2028). Two major trends were evident in the experiment and the disturbance treatments were clearly involved in explaining them both. Species composition accounted for the first portion of variation (Canonical Discriminant 1=37.4%). Compositional changes were driven by contrasting proportions of the pomacentrids

Pomacentrus moluccensis, *Dascyllus reticulatus*, *D. aruanus*; *Amblyglyphidodon curacao*, *P. nagasakiensis*, gobies of the genera *Gobiodon* and *Paragobiodon*, and the wrasse *Halichoeres melanurus*; versus *Parapercis* species, the pomacentrids *Dischistodus perspicillatus*, *Pomacentrus coelestis*, *Chrysiptera rollandi*, *C. flavipinnis*, the wrasse *Halichoeres trimaculatus*, and the goby *Amblygobius phalaena* (Table 6.2). Overall abundance accounted for the next portion of the explainable variation (Canonical Discriminant 2=9.2%). For ease of interpretation, total abundance instead of canonical values was plotted.

One month following manipulation, the composition of directly disturbed reefs was distinct from control reefs (Fig. 6.5a), although no differences in total adult abundance were apparent (Fig. 6.5b). This indicated that reefs were quickly recolonised, but not by the same species. However, the compositional difference did not persist and assemblage structure on directly disturbed reefs was indistinguishable from that on controls after 3 months. That is, the patch reef communities were resilient to direct disturbance. The overall community structure on undisturbed or control reefs exhibited little change over the two-year period (relative to the effects of the direct disturbance – Fig. 6.5a), but a long-term change in total abundance was evident (Fig. 6.5b).

Both levels of indirect disturbance induced changes in fish assemblage structure. When indirect disturbance only was applied, the more extreme levels of manipulation generated greater departures from control assemblage composition (Fig. 6.5c). Clearly, habitat-disturbance was responsible for the greatest change in community structure observed in any of the treatments. This was due to a loss of the coral-associated species, and a corresponding influx of small rubble-dwelling carnivores (e.g. *Istigobius* species, *Parapercis* species, *Amblygobius phalaena*), and the pomacentrids *Chrysiptera flavipinnis*, and *Pomacentrus coelestis* (Table 6.2). There was no evidence of recovery toward control values over the course of the experiment, with relatively little change once the new community structure had developed. Three months after manipulation, overall adult abundances of both indirect disturbance levels were, on average, 15-20 individuals per reef lower than undisturbed reefs (Fig. 6.5d). There was no tendency for a return to the control community over time, but common temporal patterns in total numbers were observed.

Direct disturbance in combination with indirect disturbance removed any differences in assemblage structure between the two levels of indirect disturbance (Fig. 6.5e). However, overall the pattern of divergence on reefs of different structure was similar to the situation with residents present (Fig. 6.5c). That is, reefs subject to the same level of indirect disturbance converged in structure over time. Again, there were no indications of recovery, although there was a gradual change in community structure over time. Overall abundance was consistently lower in disturbed reefs relative to their controls in subsequent months (Fig. 6.5f). No interaction effects were apparent, indicating that the two disturbance forms had simple additive effects.

Recruitment

Recruitment differed between indirectly disturbed reefs (Table 6.3, INDIRECT p=0.0005). Undisturbed treatments had proportionally more *D. aruanus*, *P. moluccensis*, *D. reticulatus*, and *A. curacao* (Fig. 6.6). In contrast, reefs that were indirectly disturbed received proportionally more *D. perspicillatus*. In terms of absolute abundance, these differences were relatively small (Fig. 6.7). The greatest absolute change was an exchange in numerical dominance from *P. nagasakiensis* to *P. amboinensis* with increasing levels of indirect disturbance (Fig. 6.7). Although not statistically significant (Table 6.3. DIRECT p=0.6345), a direct disturbance effect was indicated by the CDA (Fig. 6.6). Reefs that were directly disturbed only received proportionally lower numbers of *D. aruanus*, *P. moluccensis*, and *D. reticulatus* than their corresponding undisturbed controls.

Species-specific responses

Several forms of species-specific response were identified. Strongly coral-associated species (e.g. *P. moluccensis, D. reticulatus*) exhibited dramatic declines in numbers on indirectly disturbed reefs, with no evidence of recovery in numbers (Fig. 6.8a-d, Table 6.4). These species also did not fully recover from direct disturbance. They tended to recruit through settlement in very low numbers, although once established, juveniles tended to persist throughout the year (Table 6.4).

Species that were more normally associated with dead coral surfaces (e.g. *P. amboinensis, P. nagasakiensis*) recovered from direct disturbances rapidly, through settlement and movement (Fig. 6.9a-d, Table 6.4). The abundance of these species peaked immediately after the disturbances were carried out in all treatments. After which they exhibited moderate declines in abundance on mechanically damaged reefs relative to controls, but their numbers did not fall as low as live coral associated species.

Interestingly, the abundance of *P. nagasakiensis* on undamaged reefs increased to greater than control levels following the direct disturbance, although this was followed by a substantial decline (Fig. 6.9d).

Species associated with broken coral and rubble substrata (e.g. *Parapercis* spp., *D. perspicillatus*) initially increased on damaged reefs, but the numbers of adults did not always persist (Fig. 6.10a-d, Table 6.4). The increase was initially greatest on reefs subject to direct disturbance. Two different categories of response by these fishes could be identified. Firstly, a number of mobile carnivorous rubble-dwelling species (*Parapercis* spp., *I. decoratus*, *A. phalaena*) moved onto disturbed reefs as adults rather than settlers. A rapid increase on damaged reefs was followed by a gradual decline towards the end of the experiment. Secondly, several damselfishes recruited specifically to disturbed reefs (*D. perspicillatus*, *P. coelestis*, *C. flavipinnis*, *C. rollandi*). They recruited in relatively high numbers on damaged reefs, particularly where the residents were removed, but juveniles did not persist through the year. Survivorship, assuming a direct relationship between persistence and survivorship, appeared lower in the rubble-associated than the coral-associated species.

Species richness

The combination of species-specific patterns of loss and colonization of reefs resulted in a significant overall decline in species richness on reefs subject to the two levels of indirect disturbance (Fig. 6.11). There was also a gradual decline in species richness on undamaged reefs, but the decline was more substantial on damaged reefs. The same pattern was evident on reefs with the resident community left undisturbed (Fig. 6.11a) and reefs subject to the direct disturbance (Fig. 6.11b), although in the latter there was a greater distinction between the two levels of indirect disturbance.

Table 6.1. Multivariate analysis of variance of the first 20 principal components of the covariance matrix of the $x^{0.25}$ transformed data using a split-plot approximation model to incorporate repeated measures.

Source	Pillai's Trace	Numerator df	Denominator df	p
DIRECT	0.4475	20	24	0.5210 ns
INDIRECT	1.3042	40	50	0.0023 **
DIRECT*INDIRECT	0.9292	40	50	0.3894 ns
REEF(DIRECT* INDIRECT)	6.6827	860	7720	0.0001 ***
TIME	2.5367	180	3375	0.0001 ***
TIME*DIRECT	0.5653	180	3375	0.0133 *
TIME*INDIRECT	1.5300	360	6912	0.0001 ***
TIME*DIRECT* INDIRECT	0.9444	360	6912	0.2028 ns

Table 6.2. Structure coefficients of species in the Canonical Discriminant Analysis of temporal changes in adults. Coefficients are interpretable as simple correlation coefficients with the canonical axis. Only species with coefficients greater than ±0.18 are included.

Species	**Correlation with CD 1**
Pomacentrus moluccensis	0.911
Dascyllus reticulatus	0.522
Dascyllus aruanus	0.487
Gobiodon okinawae	0.384
Paragobiodon echinocephalus	0.347
Halichoeres melanurus	0.335
Amblyglyphidodon curacao	0.328
Pomacentrus nagasakiensis	0.239
Pseudochromis fuscus	0.202
Gobiodon spp.	0.188
Pomacentrus amboinensis	0.187
Chrysiptera flavipinnis	-0.185
Chrysiptera rollandi	-0.198
Amblygobius phalaena	-0.267
Pomacentrus coelestis	-0.273
Halichoeres trimaculatus	-0.337
Dischistodus perspicillatus	-0.375
Parapercis spp.	-0.440

Table 6.3. Multivariate analysis of variance of total recruits per reef ($x^{0.25}$ transformed).

Source	Pillai's Trace	Numerator df	Denominator df	p	
DIRECT	0.3473	17	27	0.6345	ns
INDIRECT	1.2440	34	56	0.0005	***
DIRECT*INDIRECT	0.7641	34	56	0.4667	ns

Table 6.4. Characteristic features of species responses to different disturbances derived from raw data. ⬇, reduction in abundance; ⬇⬇ strong reduction in abundance; ⇧, increase in abundance; ⇧⇧, strong increase in abundance; **0**, no change. Juvenile settlement ratio is the ratio of recruits to adults at any one census interval.

Species	**Direct disturbance**	**Indirect disturbance (Level 1)**	**Indirect disturbance (Level 2)**	**Juvenile Settlement Ratio Settlers:Adults**	**Juvenile Persistence**
P. moluccensis *D. aruanus* *D. reticulatus*	⬇	⬇⬇	⬇⬇	Low	Continuous
A. curacao	**0**	⬇	⬇⬇	High	Continuous
H. melanurus	⬇	⬇	⬇	Low	Continuous
P. amboinensis *P. fuscus*	**0**	⬇	⬇	Low	Continuous
P. nagasakiensis	**0**	**0**	⬇	Mod	Continuous
C. rollandi *Parapercis* spp. *H. trimaculatus*	**0**	⇧	⇧	Mod	Low (4 months)
C. flavipinnis *P. coelestis*	**0**	⇧	⇧⇧	High	Low (4 months)
D. perspicillatus	**0**	⇧⇧	⇧⇧	High	Moderate (9 months on disturbed reefs)

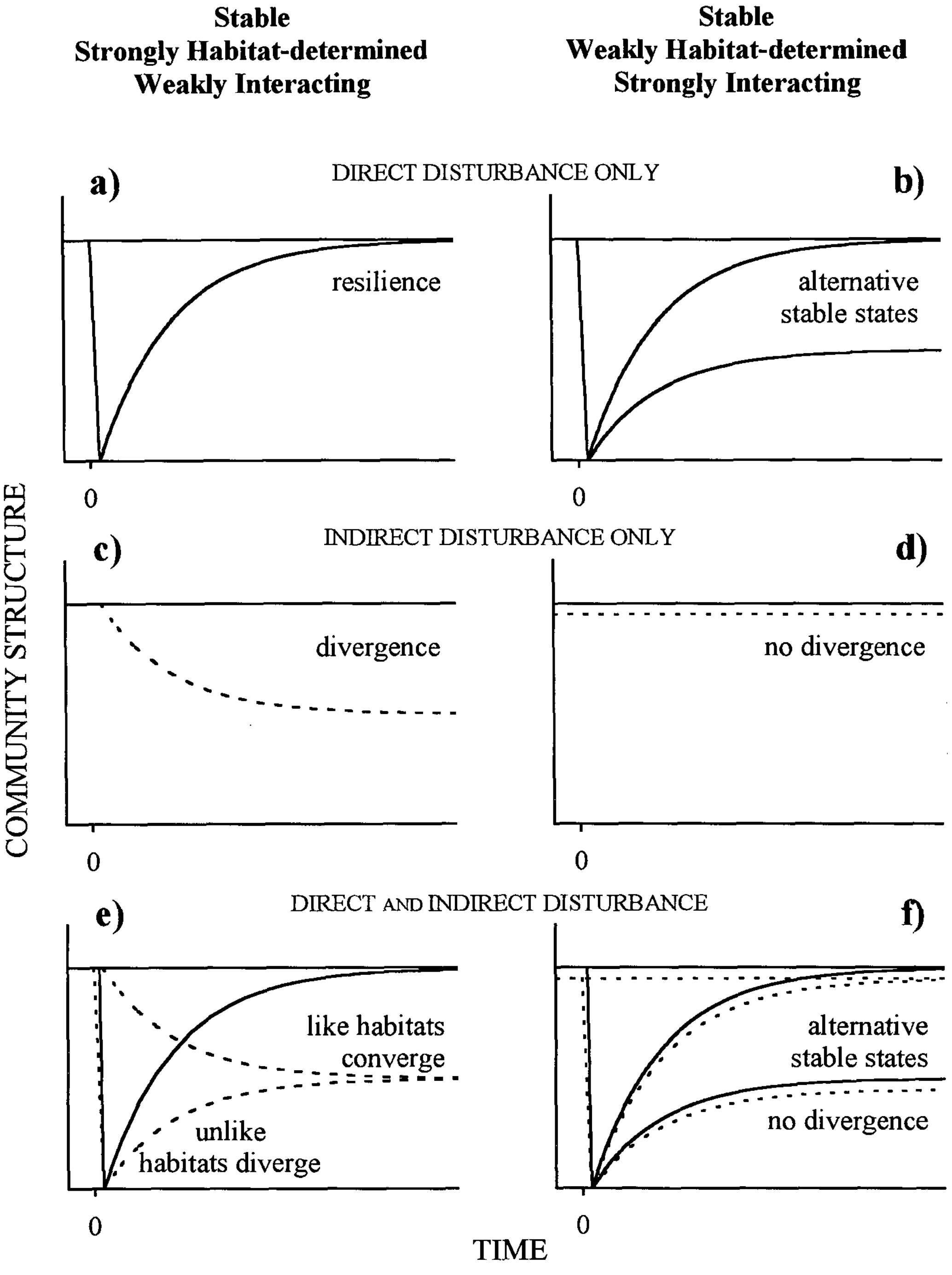

Figure 6.1. Models predicting the responses of stable communities to direct, indirect and a combination of direct and indirect disturbances incurred at time 0. Direct disturbances are perturbations acting to remove focal organisms, and indirect disturbances refer to the destruction of the habitat. Different outcomes are predicted depending upon whether the community structure is strongly habitat-determined (assuming interactions among species are unimportant) and weakly habitat-determined (assuming strong interactions are responsible for stability). The term resilience refers to the tendency for disturbed communities to recover to their previous undisturbed condition (horizontal line). Divergence refers to the tendency for initially identical communities to adopt a new stable structure over time. Convergence refers to the tendency for different communities to adopt the same structure over time.

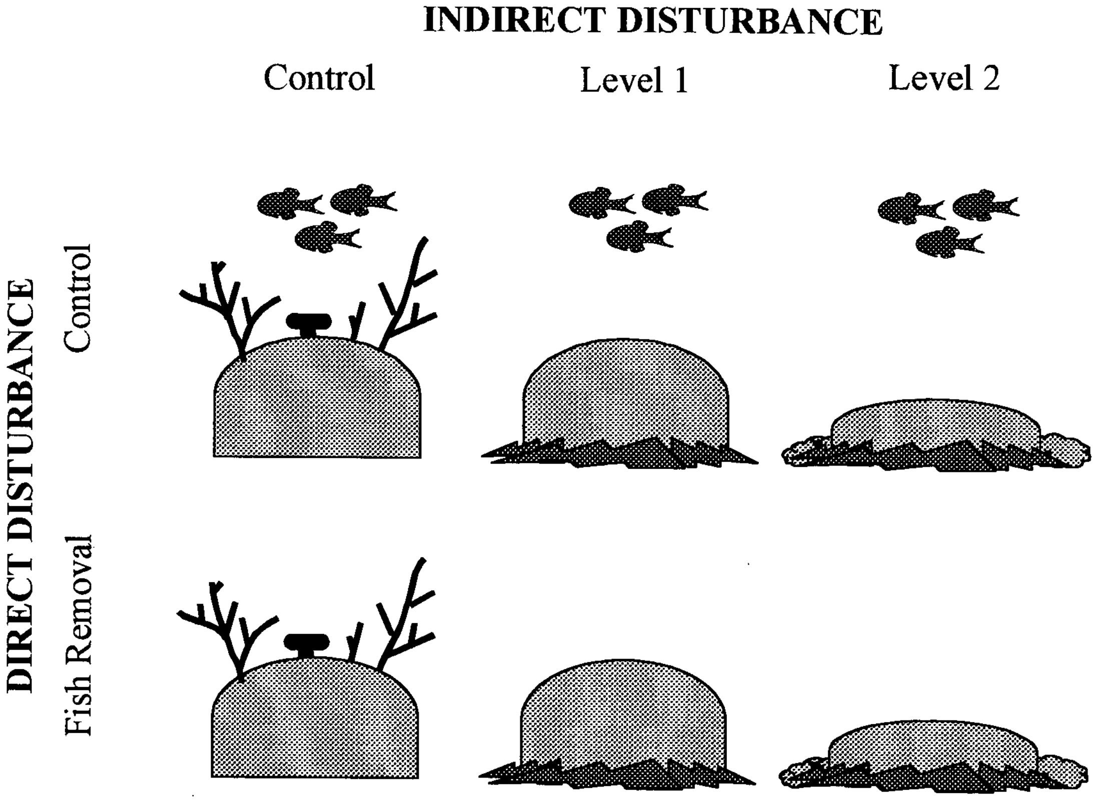

Figure 6.2. Schematic representation of the experimental design

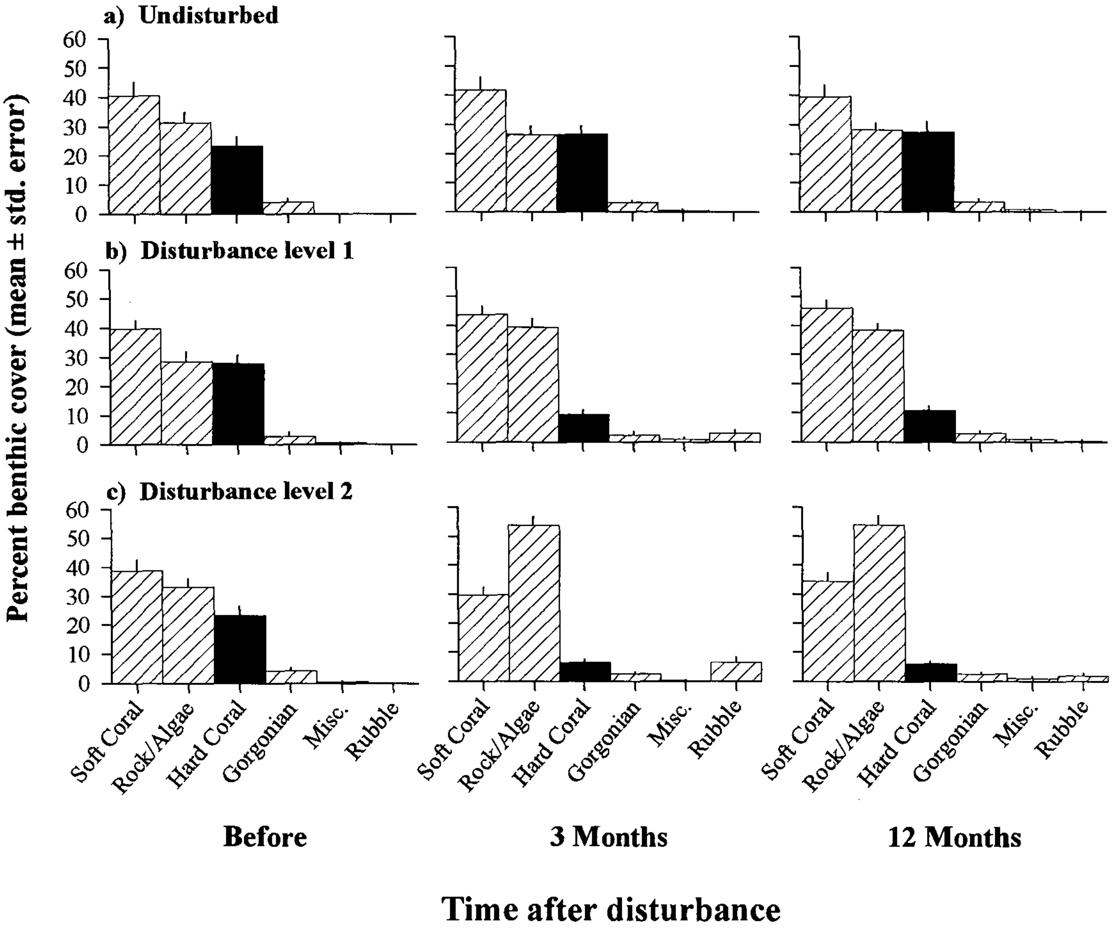

Figure 6.3. The benthic cover of the major substratum categories on experimental patch reefs, before, 3 months after and 12 months after the habitat damage was carried out. Hard coral cover is highlighted in black.

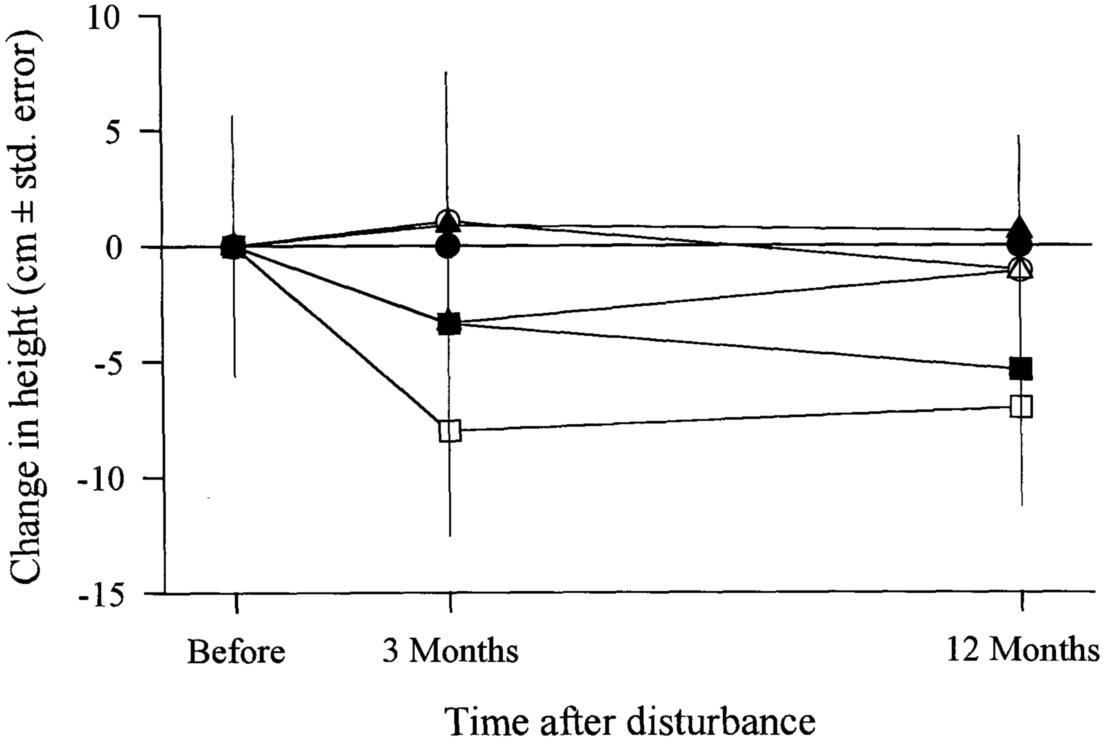

Figure 6.4. The mean change in the height of experimental patch reefs, before, 3 months after and 12 months after the damage to the habitat was carried out. O Control reefs; ● Directly disturbed only; Δ Level 1 indirect disturbance; ▲ Level 1 indirect disturbance + direct disturbance; □ Level 2 indirect disturbance; ■ Level 2 indirect disturbance + direct disturbance.

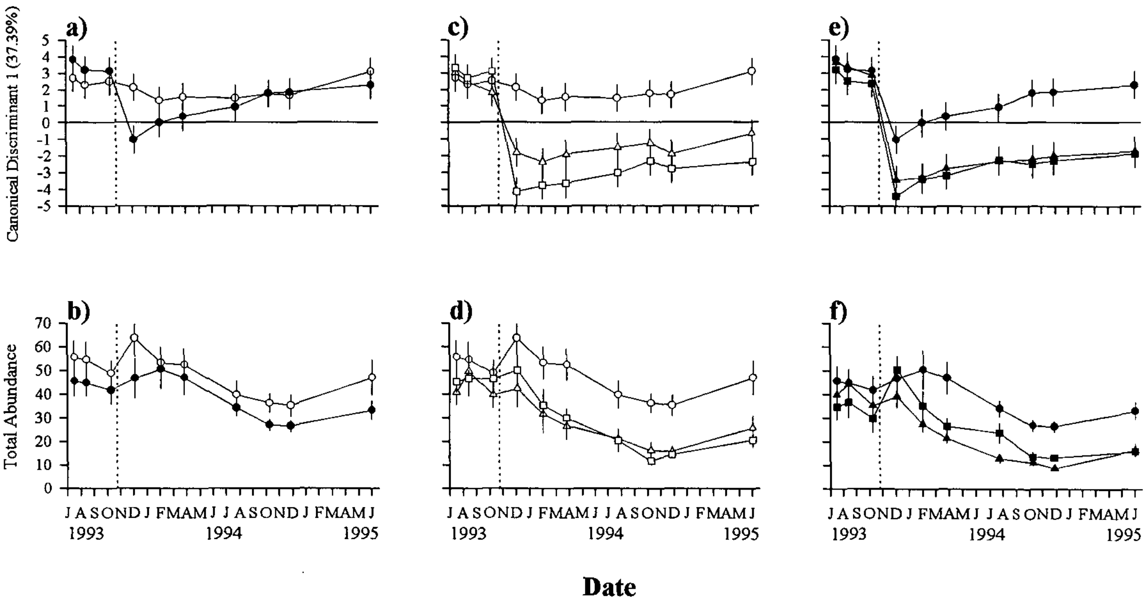

Figure 6.5. Temporal changes in composition (Canonical Discriminant 1) and abundance across the experiment. Symbols as in Fig. 6.4. Dashed line indicates time of disturbance.

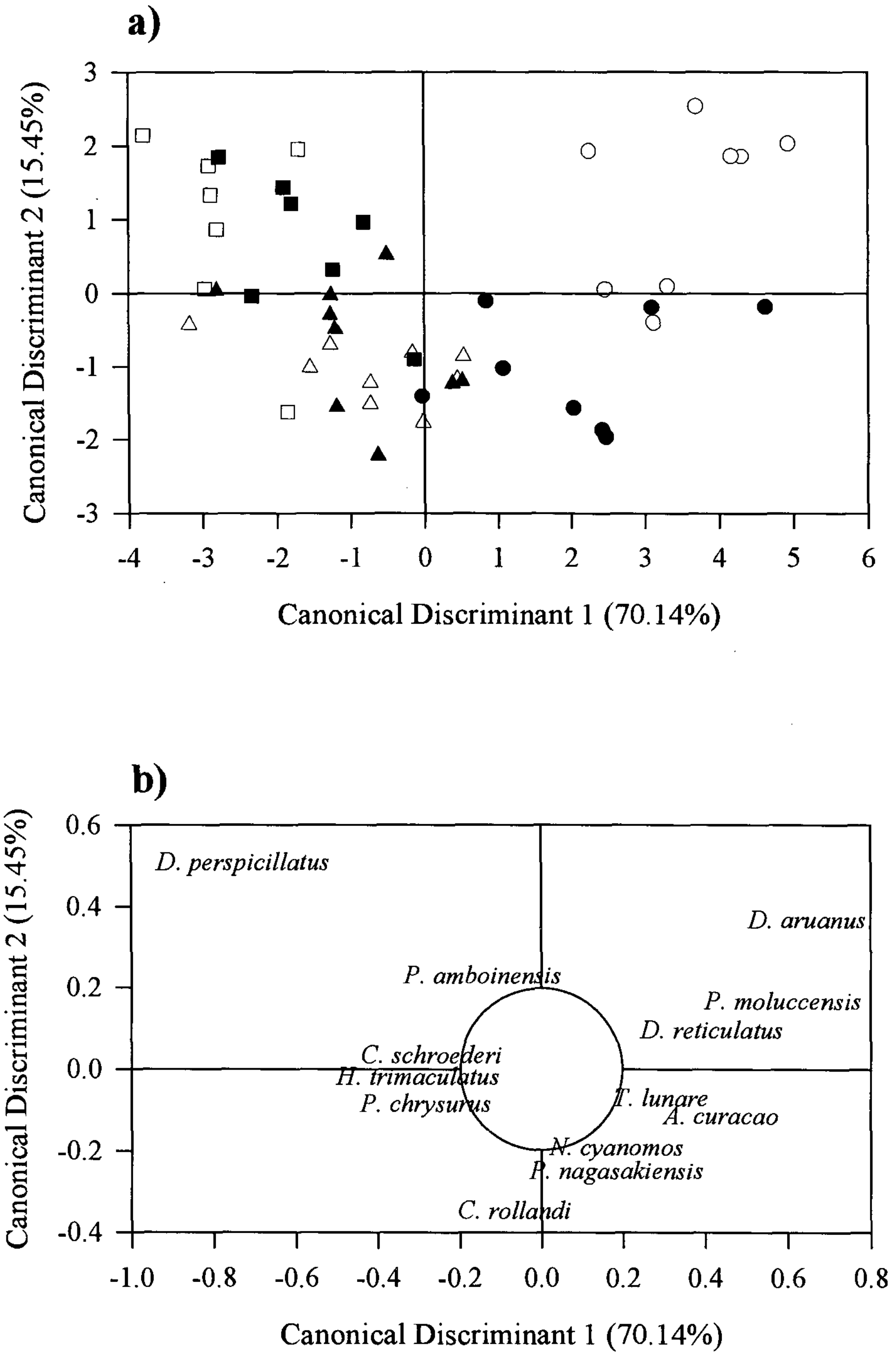

Figure 6.6. Canonical Discriminant Analysis of recruit abundance pooled across the experiment. a) Positions of reefs in ordination space (symbols as in Fig. 6.4.); b) Structure coefficients (correlations with ordination axes) of species contributing to the ordination pattern. The circle represents the 0.2 correlation cutoff point.

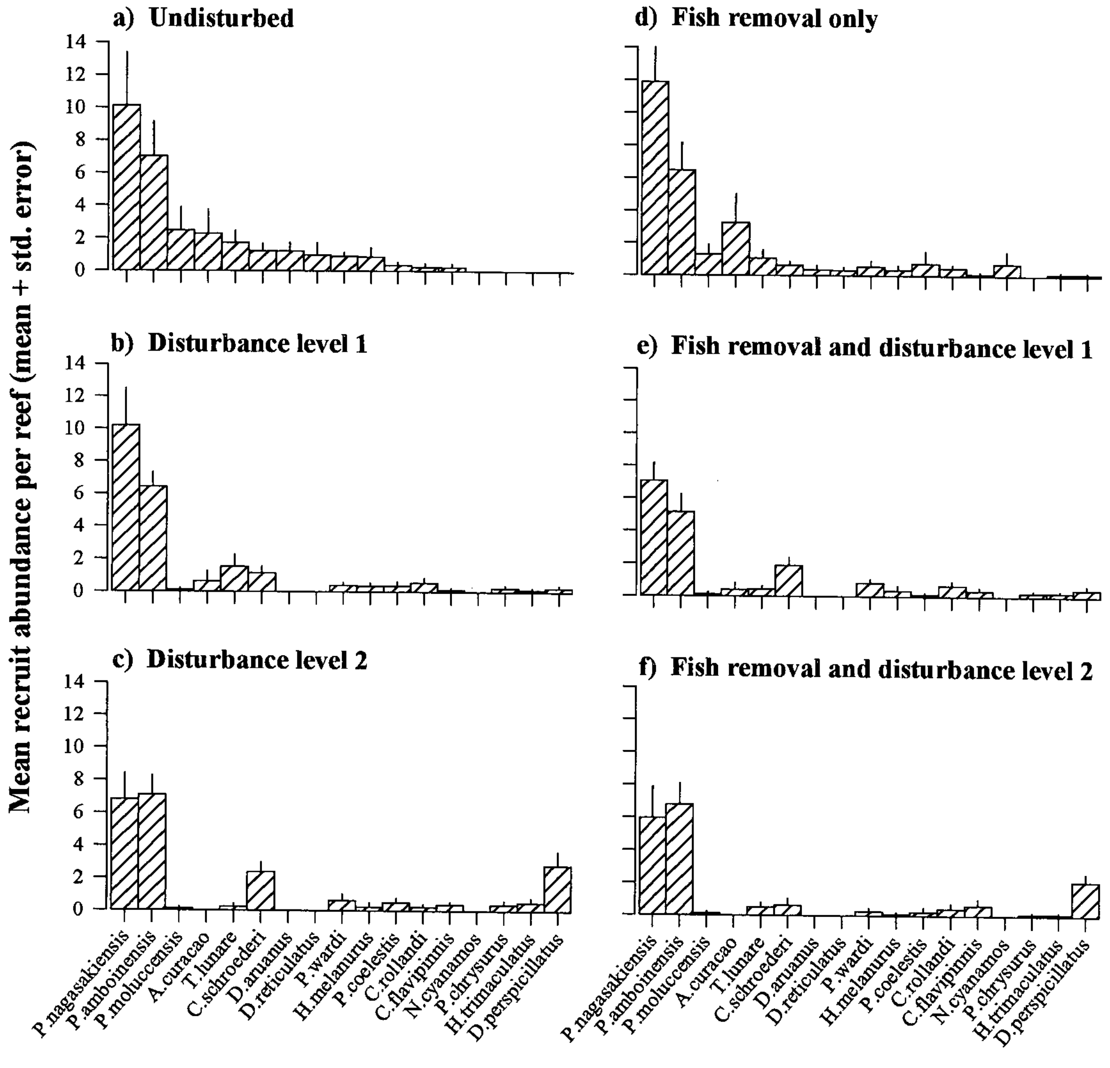

Figure 6.7. Mean recruit abundance pooled across the duration of the experiment.

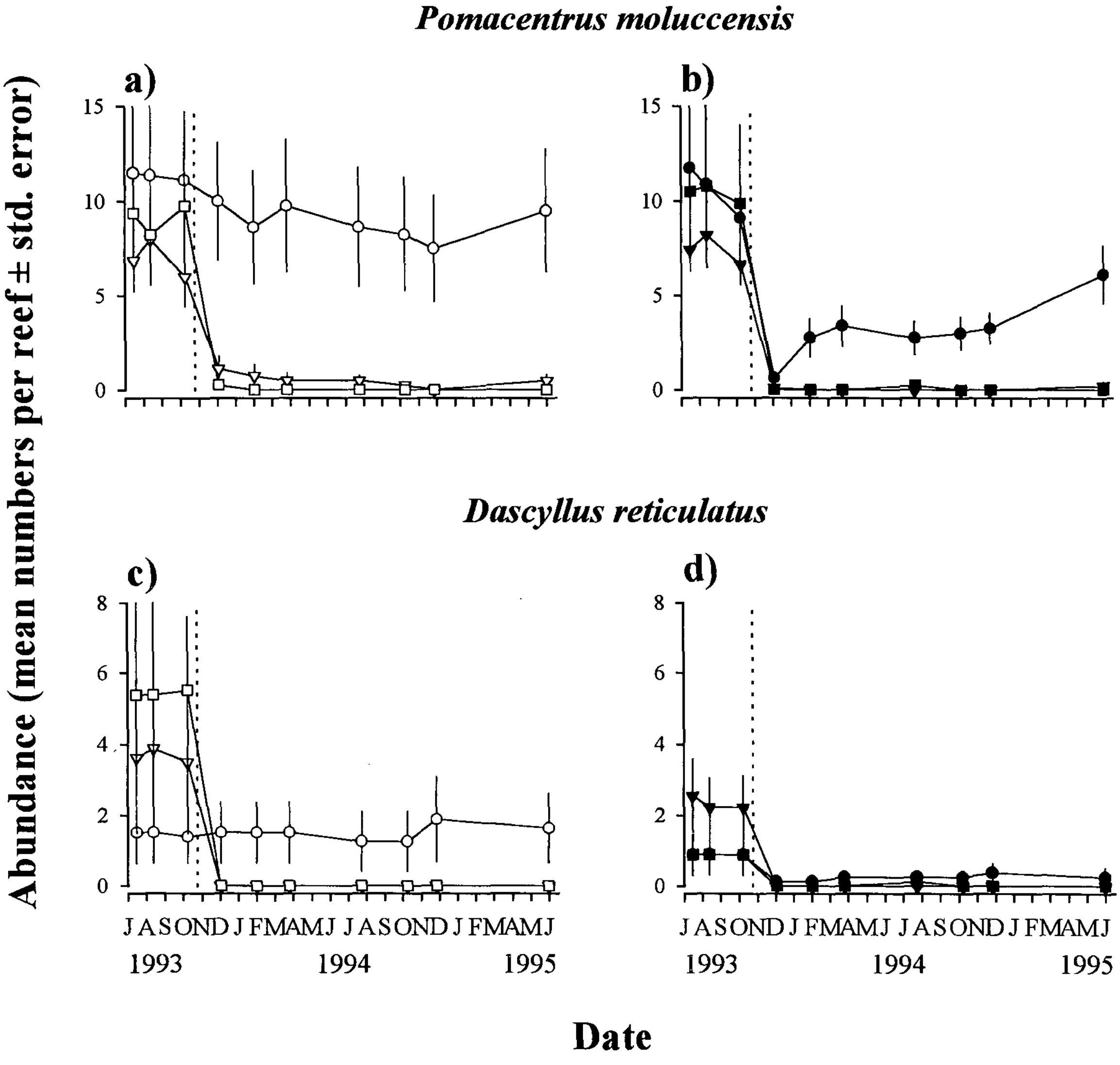

Figure 6.8. Patterns of change in the abundance of two abundant live coral associated species, *Pomacentrus moluccensis* and *Dascyllus reticulatus*, in response to direct and indirect disturbance. Symbols as in Fig. 6.4. Dashed line indicates time of disturbance.

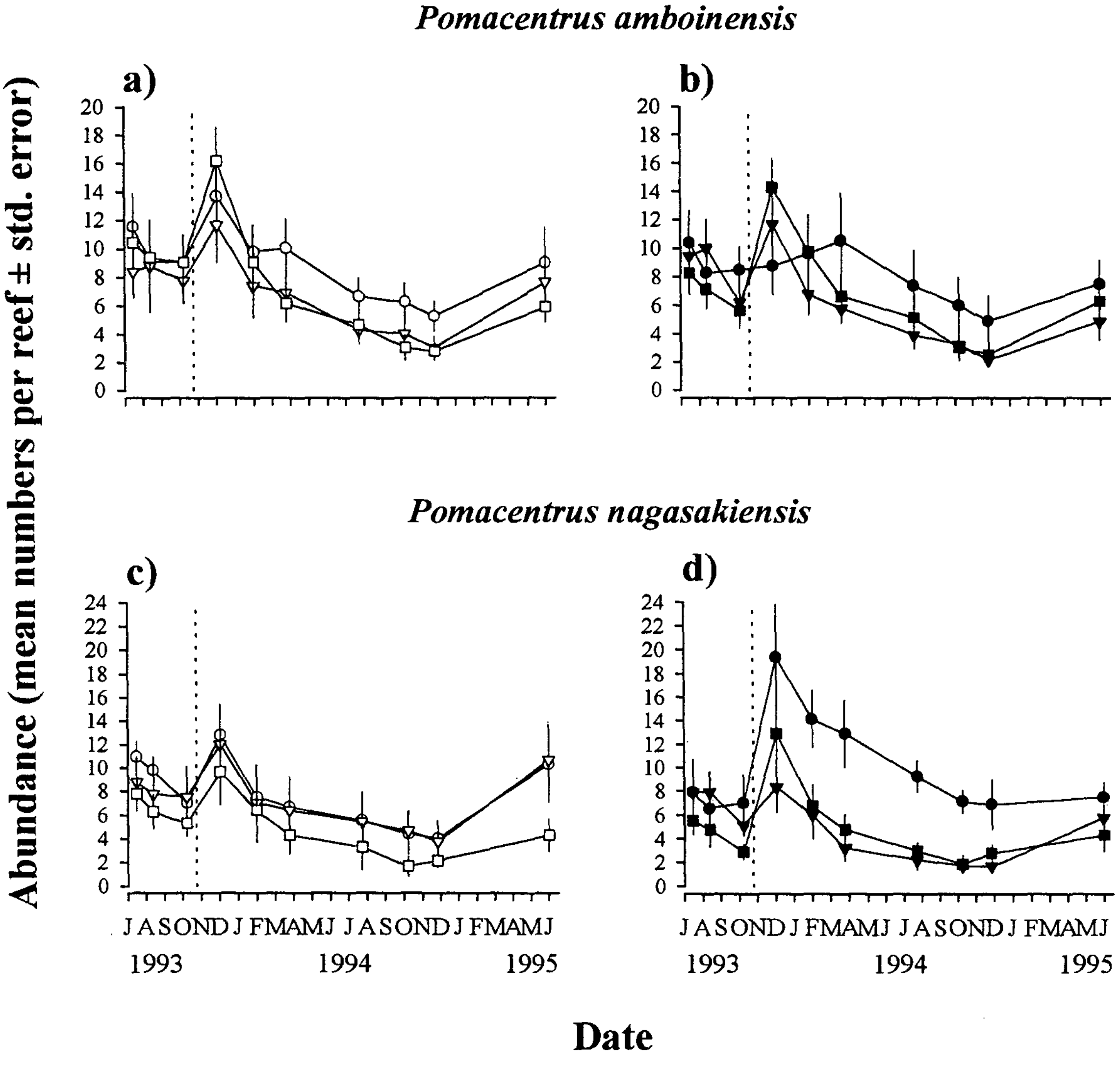

Figure 6.9. Patterns of change in the abundance of two abundant species associated with dead coral substrata (*Pomacentrus amboinensis* and *P. nagasakiensis*), in response to direct and indirect disturbance. Symbols as in Fig. 6.4. Dashed line indicates time of disturbance.

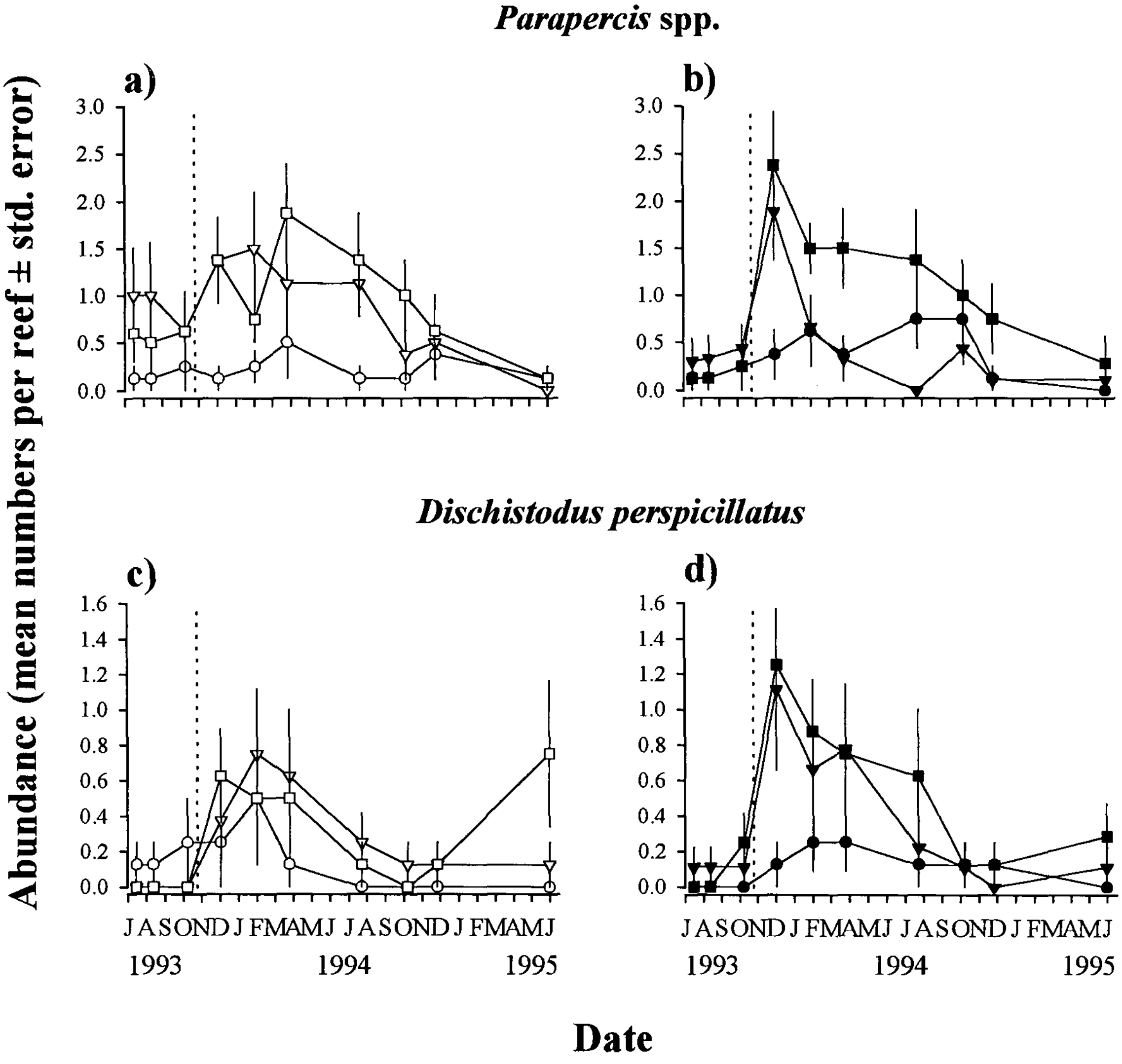

Figure 6.10. Patterns of change in the abundance of two abundant rubble-associated species (*Parapercis spp.* and *Dischistodus perspicillatus*), in response to direct and indirect disturbance. Symbols as in Fig. 6.4. Dashed line indicates time of disturbance.

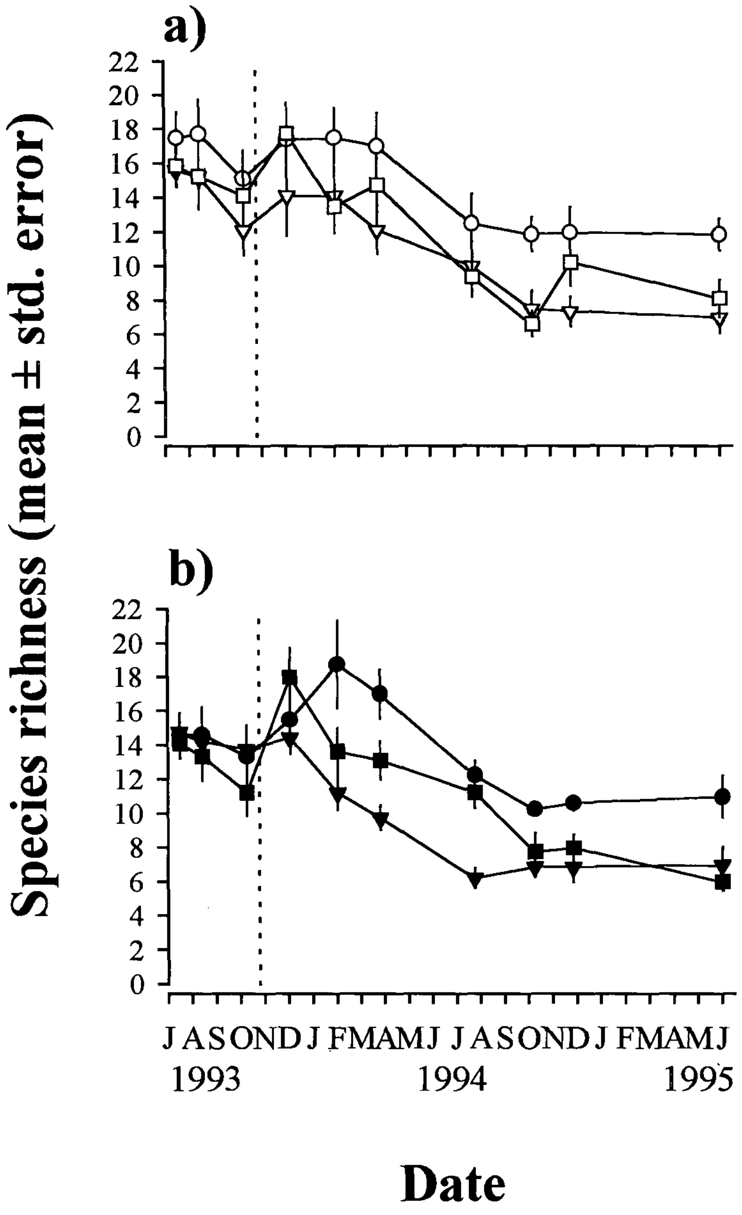

Figure 6.11. Patterns of change in mean species richness in response to direct and indirect disturbance. Symbols as in Fig. 6.4. Dashed line indicates time of disturbance.

6.5. Discussion

Patterns of community response to disturbance have assumed a central place in ecological theory (Connell 1978, Sousa 1984, Petraitis et al. 1989). However, to date this theory has not addressed the relative importance of direct disturbances that cause perturbations in the focal community and indirect effects induced when other key organisms in the habitat are disturbed. Disturbance appears to be an especially important process in the dynamics of benthic marine communities, such as coral reefs (Connell 1978, Huston 1979, 1985, Jackson 1991, Karlson and Hurd 1993). It has not, however, been prominent in the development of theory addressing the processes that structure coral reef fish communities (see Sale 1991a). The current perception of reef fish communities is that they are nonequilibrial assemblages, their structure the result of stochastic recruitment processes, rather than being determined by the availability of resources or biological interactions (Doherty 1991, Sale 1991b, Doherty and Fowler 1994). However, recent evidence suggests that habitat structure can to a large extent determine the structure of fish assemblages (Ault and Johnson 1998, Jones and Syms 1998) and biological interactions can be strong enough to stabilize the constituent populations (Caley et al. 1996, Robertson 1996, Hixon and Carr 1997). These alternatives have important implications for how these communities will respond to disturbance.

Here I developed conventional disturbance theory to put forward a series of models to predict responses to direct and indirect disturbance, with outcomes dependent upon whether communities are stable and habitat-determined, stable and determined by biological interactions among fishes (habitat-independent), or nonequilibrial assemblages. The key predictions are that if habitat structure determines the structure of assemblages, communities will be resilient to direct disturbance (Dayton et al. 1984), habitats subject to different regimes of disturbance will diverge over time, and disturbed fish assemblages on the same habitat will converge. Applying direct and indirect disturbances to coral patch reef fish communities at Lizard Island tested these predictions.

Responses to direct and indirect disturbance

In contrast to the widely held view that coral reef fish communities on patch reefs are disorganized, unpredictable systems (Sale 1980, Sale and Steel 1989, Sale et al. 1994, Ault and Johnson 1998), this study demonstrated that patch reef assemblages do have a high degree of structural determinism. The unmanipulated assemblages on these reefs were persistent through time and, despite abundance fluctuations during the study, the relative composition of the fish communities remained the same. Direct disturbance alone did not generate any appreciable differences between experimental and control reefs, which indicated that an ongoing mechanism and not temporal autocorrelation due to fish longevity was responsible for maintaining the community in a particular state. Two non-mutually exclusive types of process might be responsible for the maintenance of these patterns – external interactions between the fishes and their habitat or interactions within the fish community. The relative community response to direct vs. indirect disturbance enabled these alternative explanations of stability to be distinguished.

Indirect disturbance by physical habitat destruction generated predictable (in the sense that replicates assumed similar temporal trajectories) and persistent changes to the fish community. Patch reefs with the resident community left intact but subject to different intensities of disturbance diverged in structure over time. Those with the fish assemblage initially removed converged in structure with those subject to the same level of habitat disturbance. This suggests that fish-habitat interactions, rather than fish-fish interactions, primarily determined the community response. However, in the absence of direct disturbance, the community response to the lower level of indirect disturbance was slightly moderated by the resident fish assemblage. The changes observed included both declines in live coral associated (and some dead coral associated) species and increases in rubble-associated species, with a slight overall decline in species richness.

Demographic mechanisms determining community structure

The observed responses to direct disturbance took one of two forms. First, immigration to disturbed reefs was largely responsible for negating direct disturbance effects. Although reefs were at least 10 m apart, they were not effectively isolated. The first wave of immigration did not completely remove treatment effects however. Although total fish abundance on treatment reefs was the same as controls, compositional differences remained until after the recruitment season. Second, settlement from the plankton provided individuals of species (typically coral associates (Randall et al. 1990)) that appeared more reluctant to move between reefs (e.g. *P.*

moluccensis, *Dascyllus* spp., *Gobiodon* spp.). A weak (statistically non-significant) effect of resident fauna on recruit numbers was indicated for coral-associates (previously noted by Sweatman (1985) for *D. aruanus*), but had no effect on the resulting adult abundance of these species. The absence of strong positive or negative priority effects indicated that strong interactions among the resident fauna (e.g. predation, competition) were not important in maintaining the community structure (cf. Shulman et al. 1983).

A suite of species-specific responses to the alteration of habitat structure explained the community-wide pattern. An influx of mobile rubble-dwelling carnivorous fish such as *Parapercis* species and large gobies (*Istigobius* species, *Amblygobius phalaena*), coupled with either emigration or mortality of the coral-associates (*P. moluccensis*, *Dascyllus* spp., *Gobiodon* spp.) was largely responsible for the initial change. In addition, marked changes in recruitment were noted. Increasing levels of indirect disturbance resulted in a corresponding change in numerical dominance from *Pomacentrus nagasakiensis* to *P. amboinensis* and numerically lesser but consistent reductions of typical coral-dwelling species (e.g. *Dascyllus* species, *Pomacentrus moluccensis*), and increases of typical rubble-dwelling species (e.g. *Dischistodus perspicillatus*, *Chrysiptera flavissimus*, *Pomacentrus coelestis*, *Halichoeres trimaculatus*). Habitat choice at settlement appeared to have been largely responsible for these patterns and would have been operating at reasonably small scales (a few square meters).

A revised model of the processes structuring coral reef fish communities

The results from this study support a model of patch-reef fish assemblages as deterministic, yet weakly interacting communities. Direct and indirect disturbances acted independently of each other (as indicated by a lack of interaction between combinations of direct and indirect disturbance) to yield a relatively predictable assemblage. A large component of this predictability appeared due to habitat-mediated processes, which appear to constrain the community and most of the constituent populations within broad limits. The underlying mechanisms explaining this determinism may include patterns of habitat selection at settlement (Sale et al. 1984, Ohman et al. 1998) or through subsequent migration (Booth and Beretta 1994, Lewis 1997). Biological interactions mediated by habitat structure or resource requirements

(Shulman 1985, Jones 1988b, Hixon and Beets 1993, Forrester 1995, Hixon and Carr 1997, Beukers and Jones 1997) may also provide an element of stability to community structure.

This conclusion, on face value, appears counter to the ruling coral reef fish paradigm of reef fish assemblages as recruitment-limited, highly unpredictable assemblages. Reconciling this study with this paradigm is contingent on the validity of two types of evidence that are used to characterize these communities - the degree of habitat association, and the degree of stability.

The lack of strong association between patch reef fish assemblages and habitat variables has been cited as evidence that habitat is not important in structuring fish assemblages (e.g. Sale and Douglas 1984, Sale et al. 1994, Ault and Johnson 1998). Measurement of habitat association is contingent on scale (Syms 1995), and while most fish ecologists acknowledge larger scale physiographic or zonal differences in fish assemblages (e.g. Williams 1991), the role of finer-scale (operating at spatial scales of a few meters) habitat characters has been more widely debated (Gladfelter and Gladfelter 1978, Ogden and Ebersole 1981, Roberts and Ormond 1987). The strength of organism-habitat association is also contingent on the range of the habitat variables over which the association is measured (Jones and Syms 1998). In an experiment in which replicates are chosen so as to be similar to each other, it is probably unreasonable to expect strong patterns within the (pre-manipulated) sample units because habitat variability has been actively reduced. Indeed in this study, no pre-existing habitat association was apparent. The habitat determinism only became apparent after an experimentally induced habitat gradient was generated.

Central to the concept of stability is the degree to which a system is predictable over time. Initial stochastic models of coral reef fish communities (Sale 1977, Victor 1983) took as their initial observation the fact that a large portion of the variability of fish communities was unexplainable. Notwithstanding the analytical problems of measuring community concordance through time (Rahel et al. 1984, Rahel 1990, Ebeling et al. 1990), it appears in the majority of studies that predictions of species composition and abundance over time are vague. This study does not disagree with this view. Across the experiment, less than half (46.6%) of the total variation in adult community structure (from CDA) was associated with the experimental manipulation. Two elements of variation could be identified - a compositional element explaining 37.4% and an abundance element explaining 9.2%. The remaining 53.4% was not explainable.

Recruit abundance fared better; a total of 85.6% of the variation was explainable, again associated with the experimental manipulation. Yet despite the fact a large portion of the variability was unexplained (in agreement with other studies), it appears than, within a suitable context (e.g. an experimental manipulation or a habitat gradient), there still existed a sizeable predictable element of fish community structure.

The importance of scale

Stability is a relative, scale dependent concept (Rahel 1990). Scale is a problem inherent in studies conducted on habitat patches and unfortunately in coral reef systems (and marine reef systems in general, but see Syms and Jones in press) little work has been done to identify the effects experimental scale may have. Clearly, it is inadvisable to extrapolate these results to different coral reef habitats, such as the large tracts of contiguous reef (Ault and Johnson 1998, Syms in press). However, in areal terms patch reef are a significant component of coral reef systems, particularly in back reef areas. Despite the absence of a specific test of the effects of scale of disturbance, it might still be possible to speculate about the generality of these results with respect to the larger sample universe of patch reefs. The results of this experiment may be scaleable, conditional on three factors. First, the habitat types on the experimental reefs should form an unbiased subset of the universe of reefs to which extrapolation is made (i.e. habitat types, proportions etc. should not be very different). This caveat is important because habitat determinism mediates the fish assemblage predictability. Second, differences in fish assemblage composition should not be great. It appeared from this study that the fish community on the experimental reefs was not strongly interacting. However, the addition of higher trophic groups (e.g. large predatory serranids) may change this. In addition, species-specific behaviour and habitat association may generate relatively unpredictable scale effects (Syms and Jones in press). Third, the replenishment scales of the sample universe must be commensurate. Due consideration must be given to these factors and naive scaling (e.g. assuming large patches are simply the summation of smaller patches) is not advisable in the absence of other information.

Conclusions

This study has presented an alternative view of coral reef fish assemblages as deterministic, weakly interacting, but to some extent predictable systems. This view appears to counter the ruling paradigm, but on closer examination may be seen as a shift in focus from the unpredictable to the predictable portion of variability. Habitat mediated a significant portion of the community structure, indicating that the constituent populations were being constrained within broad limits by the their habitat requirements. When habitats diverge in structure as a result of different regimes of disturbance, so to will fish community structure. When fish communities are directly perturbed, communities associated with similar habitats will converge in structure over time. Certainly, stochastic variation in recruitment and migration may be responsible for the considerable variability in community structure that occurs within the limits set by the habitat. However, while unexplainable variation is important, in an inherently variable system it is the explainable portion that provides the soundest platform from which to develop a theory of reef fish ecology.

General Discussion

Despite frequent assertions that scale lies at the heart of developing general ecological theory, few studies have attempted to empirically derive rules to govern scaling of patterns and processes from one scale to another (Addicott et al. 1987, Meentemeyer and Box 1987, Morris 1987, Kotliar and Wiens 1990, Levin 1992, Horne and Schneider 1995). The development of ecological theory of coral reef fish communities has followed a similar path, with little attempt to use scale beyond a convenient label for unexplainable variation.

The current ecological paradigms for coral reef fish focus on the undeniably high stochasticity of the population structure of these fishes (e.g. Sale 1977, 1978, 1988, Doherty 1987, Doherty and Williams 1988 a,b), of which the main part may be attributed to recruitment variation (Victor 1983). However, there are two primary shortcomings of this pre-occupation with stochastic variation. First, variation *per se* can only be partitioned and attributed to a random and hence unexplainable factor. Unless this variation covaries with an environmental or biological parameter, then it serves only to establish the precision with which the state of a population or system can be predicted. Second, the explainable portion of variation tends to be ignored or dismissed as less than the stochastic element and hence in some way less important.

High variation is a fact of life in coral reef fish assemblages, and predictability of exact numbers of fishes at a given place and time is probably unrealistic. However, at some scales and contexts, fish abundance and assemblage structure covary with biologically important parameters, and pattern emerges from stochasticity. In order for pattern to emerge, however, rational biological covarying patterns or processes must be identified and the bounds of their roles established.

In this thesis I put forward the premise that habitat structure mediates the scaling of coral reef fishes, and that understanding habitat structure and dynamics will occupy a central role in developing scaling guidelines in this system. In order to support this premise, two things needed to be established. First, it had to be ascertained that fish are indeed scale dependent, and that scale was not simply assumed to be important. Second, I had to establish that habitat provided a means by which rational scaling rules could be developed. I undertook five independent yet complementary approaches to determine the parameters within which this premise would hold.

Are reef fish scale dependent?

Prior to any investigation into the scale-dependence of fish assemblages, it was first necessary to establish that there was a pattern to explain. Fish populations and assemblages were indeed scale-dependent. Three lines of evidence supported this assertion. First, the power relationships between variance and mean of pomacentrid abundance were consistently less than the null value provided by demographic theory (Chapter 2). Pomacentrid populations had negative mean-related stochasticity i.e. the variance of a small sample was lower than would be expected for a large sample, thus implying some 'stabilizing' influence at smaller scales. The perceived variability of naively extrapolated (i.e. scaling by multiplication of the parameter of interest by some scaling factor) populations would be highly underestimated and conversely, variability from interpolated studies would be highly overestimated.

The second piece of evidence for scale-dependence came from altering the grain at which variability was measured by progressive aggregation of adjacent quadrats from $9m^2$-$225m^2$. Variance of all fish species counted was maximal at the smallest scale, and decreased as a decay function with increasing scale (Chapter 3), indicating that fish were 'patchy' at $<9m^2$. The strength of this patchiness was variable; fish may have either been present in true patches or shoals (e.g. some pomacentrids of the *Chromis* or *Neopomacentrus* genus and the labrid *Cirrhilabrus punctatus*); or they may simply have been sparsely distributed over the quadrat and hence either present or absent (e.g. many labrids, chaetodontids, and pomacanthids).

The final piece of evidence for scale dependence, both at the species and assemblage level, came from patch reef assemblages (Chapter 4). Many species were associated with reef size, some exclusively so. Species associated with large reefs generally had some sort of 'threshold' size, below which they would not be found on a reef. In contrast, species associated with small reefs were negatively but generally monotonically related with reef size. Species richness was identified as an inherently scale-dependent parameter and increased in an approximately logistic fashion with reef size. The rarity of the majority of species (143 of 187 species were present on <10% of the 142 reefs) precluded any estimate of their habitat or reef size association, and so it is not clear what their importance is to scaling. However, assemblage-level studies that rely on species richness-sensitive measures (e.g. Simple matching metric, Canberra metric, Jaccards coefficient) are likely also to be sensitive to scale.

Can habitat structure be used to scale studies of reef fish?

Habitat was important in explaining the structure of fish assemblages on both contiguous and patch-reef systems, and fish-habitat associations covaried with scale. Almost one-third of the negative-mean related stochasticity in pomacentrid populations might have been accounted for by habitat variables (Chapter 2). On contiguous reef, the comparative explanatory ability of different habitat parameters changed with scale, and was taxa-specific (Chapter 3). In general, most species on contiguous reef were associated with benthic cover, either as an independent factor or in combination with other locality or physical conditions. Contrary to the predicted pattern, the scale of maximal association was incommensurate with the scale of the spatial pattern. Scales of association represented the optimal scale at which the likelihood that a certain type of fish *and* the likelihood that the habitat with which it was associated was maximised. On contiguous reef, habitat-association (measured as variance explained) was more a function of relative predictability rather than the scale at which fishes interacted with their habitat. As a criterion for evaluating association, variance explained may not be the optimal measure.

Patch reef assemblages were more variable, and less strongly associated with habitat variables than were contiguous reef fishes (Chapter 4). Benthic cover and patchiness were important for a range of species to a maximum of one third of the total variation. However, regression parameters derived from this one third gave sufficient predictive value (for species in sufficient abundance for parameter estimation) to be useful. The success of this predictive ability was contingent on the reef size from which parameters were estimated. Equations derived from small reefs could be extrapolated to larger reefs, but the reverse was not true. I hypothesised that this was because the size of small patch reefs corresponded to the typical habitat patch size on larger reefs, and thus provided a better parameter estimate. In effect, rules derived from small reefs could be applied to estimate the abundance of many numerically dominant species on large patch reefs. Central to the success of this extrapolation however, is the precision with which the fish-habitat covariation can be estimated.

The correlative patterns (Chapters 2, 3, 4) indicated that habitat was a reasonably consistent, if somewhat variable, covariate of scaling patterns. It remained to experimentally identify the strength of the fish-habitat relationship. On the contiguous reef, fishes were resistant to habitat disturbance by coral removal (maximum reduction from 55-34% at 10x10m scale), over a two year period (Chapter 5). This result supported the conclusion from the correlative chapters that fish-habitat association is noisy. Of interest in this study was the explanatory power of the landscape-level spatio-temporal structure which accounted for between 25-68% of the total variation dependent on taxa. The covariation of this fraction with space and time occurred within definable bounds and, far from simply being 'noise', indicated a coherence of dynamics at scales of many hundreds of square metres. This variation was estimable, covaried with other ecological parameters, and hence was able to be modelled.

In contrast with contiguous reef, patch reef assemblages responded very strongly to habitat disturbance involving a reduction from 25-5% total coral cover (Chapter 6). The disturbance response was predictable, in the sense that fish assemblages on disturbed reefs converged to similar composition and abundance. This effect was independent of, and far greater than, direct disturbance by fish removal. Despite similar absolute changes in coral cover in both the contiguous and patch reef experiments (maximum 21% reduction approximately), as a proportion of initial coral cover the patch reef disturbance was the larger disturbance (see Appendix III for a discussion of this).

Scaling coral reef fish studies - a perspective

Habitat is clearly important, and the systematic covariation of fish with habitat provides a means of scaling ecological studies on coral reef fishes. In contrast with scaling frameworks that aim to describe the relationship between scale and noise (e.g. hierarchy theory; see Kotliar and Wiens 1990, Lavorel et al. 1993, Waltho and Kolasa 1994), I believe scaling is best achieved by modelling the relationships between biologically relevant parameters. It is wise however to establish the context and some cautions in this view of scaling, and highlight some future research directions.

Coral reef fish assemblages are highly variable, and goodness-of-fit based on variances is almost always likely to appear low (in the order of one to two-thirds total variation). In fact, an extremely high goodness of fit should probably be viewed with caution as it indicates excessive redundancy (and hence non-independence) of the explanatory variables (e.g. Ault and Johnson 1998). Of greater importance to scaling questions is the strength of covariance between different sets of variables, rather than the total variation explained. In addition, variance is probably not the best parameter of which to measure goodness of fit. Fish are distributed as counts and not continuous variables so the parametric variance is only an approximate estimate of the 'noise' about the mean value. In addition, fish counts can only assume positive values in transects (in my experience), and so the left hand side of their abundance distribution will be truncated. A more productive set of parameters would probably be based on likelihood distributions (probabilities, like fish, only assume positive values) and I suspect would provide a more intuitive summary of fish-habitat distributions (Syms in prep).

If covariation, rather than total goodness of fit, provides the key to effective scaling of fish with habitat (whether measured as a covariance, correlation, or conditional probability), then its parameters and bounds must be estimated precisely. Two key considerations must be taken into account when estimating covariance parameters. First, the commensurability of variables measured at different scales must be taken into account. In order to measure the covariation of a variable, that variable must not be constrained or restricted to certain other conditions. For example, the association of fish with a coral type that occurs only in one physiographic habitat 'zone' would not be independently estimable because of the confounding of coral with zone. An example of the consequence of this can be found in Bell and Galzin (1984) in which a reported difference in fish composition was attributed to <5% difference in coral cover - however coral cover was indistinguishable from zone (see Jones and Syms in press). Similarly, the fish must have some likelihood of existing on a certain habitat type. The existence of 'thresholds' (e.g. Chapter 4) provides problems in covariance estimation, but may not be so much of a problem within a likelihood framework.

The second consideration in the estimation of covariance is the problem associated with lack of information in small quadrat sizes. Empty quadrats contain no information with which to calculate a parameter. This problem may be solved by increasing the size of the sample unit, but then one is confronted with a change in sample scale that may not correspond to the scale of interest. This effect was most apparent in Chapter 3 of this study, in which the optimal scale of fish-habitat association was a function of the scale at which covariation in both fish and habitat variables was reliably estimated. Many of the fish species on contiguous reef were sparsely distributed, and consequently at small scales many samples would have had zero values and hence not contributed any information to the estimation of covariance. I foresee that the resolution of this problem will be critical to establish minimum scales of association. At present, two avenues appear promising: Modelling fish and habitat as conditional likelihoods (Syms in prep); and using variable-area quadrats to standardise the information content of samples (Syms in prep).

Tempering any extrapolation (scaling or otherwise), is the prior biological and ecological knowledge of the researcher. This thesis has argued that naive scaling will not be productive; similarly scaling by modelling covariation should not be done blindly. At present, much of the scaling guidelines are species-specific. Ecological or taxonomic similarity does not necessarily imply scaling similarity. As a consequence, I feel confident about putting my experimental results into a scaling context, but would be wary of doing the same for an experiment conducted in the Caribbean - a system in which I have no prior empirical experience. Extrapolation (and indeed interpolation) is always likely to throw up some mathematically unpredicted phenomenon which, in retrospect, appears logical given what is known about the system. An intuitive example would be the association of some predatory serranids which had a patch reef 'threshold' size (Chapter 4). One would expect that unforeseen interactions with prey species may exert unpredicted (yet systematic and biologically interpretable) deviations from small scale studies. However scaling is done, at present no quick-fix solutions exist. But there are clear, rational ways in which we can account for, model, and even predict the effects of scale. It is my belief that only when we incorporate scale as a mechanistic process will a useful general ecological theory of coral reef fishes emerge.

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Community Assembly of Fish on Small Patch Reefs: Direct vs Indirect Disturbance[†]

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