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**Scales and Magnitudes of Variation  
in Population Densities of  
Some Coral Reef Organisms  
*Implications for the Design of Sampling  
and Monitoring Procedures***

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## EXECUTIVE SUMMARY

McNeill (1994) pointed out that marine parks and protected areas around Australia generally have been established with little attention to monitoring their biological (resource) status, or formal assessment of the effectiveness of their management. Both tasks require structured monitoring studies tailored to test the effectiveness of protection from human use and potential environmental impacts. This report is the second in a series intended to provide empirical bases for the development of such monitoring programmes for the Great Barrier Reef Marine Park.

In this report we have concentrated on the description of variation in abundances of several coral reef organisms in the Cairns Section of the Great Barrier Reef (GBR) Marine Park. Our focus was on the implications of spatial variation for the design of sampling and monitoring programmes and the inference of spatial pattern. Patterns of interest might arise, for example, from effects of area-based management strategies or human impacts on the reef environment. The data we present indicate that spatial variation is large at most scales for most organisms. Consequently, it is unlikely that small or even moderate spatial patterns caused by management strategies, human use, or natural perturbations will be detectable reliably without considerable expense.

Our results have important implications for the design and interpretation of future studies, especially with respect to the role and scope of pilot studies. Our data do not provide the sought-after prescription of a 'best' allocation of sampling effort across different spatial scales, or a clear and unequivocal guide to the replication needed to assess either management strategies or human impacts on the GBR environment. Indeed, the analyses we present demonstrate that such messages are likely to be unavailable or flawed in ecological field studies. At best, we can provide some guidelines on the scales that are (empirically) likely to require least emphasis in future sampling programmes, and insights into the reliability of predictions of required sample sizes to detect nominated effects. Whilst there were some taxa that were conspicuously poor candidates for monitoring studies, there were no clear candidates that would provide sensitive measures of impacts, based on their sampling characteristics alone. It is clear, however, from this and a companion report that for almost all organisms we analysed (42 taxa), the common strategy of sampling only 'representative' sub-sections of reefs will result in inaccurate depictions of patterns in abundances among reefs. Sampling should be well distributed over major within-reef strata in future studies if results are to be truly relevant to whole reefs.

It is clear also that the hitherto recommended approach of doing small pilot studies to fine-tune sampling strategies for larger programmes should be reconsidered. We do not suggest that prior information is unnecessary for designing major sampling programmes. Rather, we suggest that pilot estimates should be treated more cautiously than they have been previously. We have demonstrated that predictions of 'optimum' allocations of effort, sample sizes, and statistical power are highly variable. The careful design of future field studies from pilot data will require explicit consideration of that uncertainty.

The implications of these conclusions are two fold. Firstly, the conventional approaches to sampling or funding strategies may need re-thinking, particularly where strong inferences will be made from either 'positive' or 'negative' results. It may be better in future studies to do (and fund) large 'pilot' studies to gain sound impressions of the merits of proceeding with subsequent studies, given that those subsequent studies are likely to be constrained by *reduced* funding. If the substantive pilot studies indicate that the proposed future project is weak, then funding should be refused or the approach modified. Secondly, it is likely to be inefficient to adopt a strategy for assessing management strategies in which the effects of management are compared only periodically, and where inferences of success or failure rely on the detection of spatial pattern alone. Such an approach is likely to detect only dramatic effects of management, and fail to provide insights to more subtle strengths or weaknesses of management strategies. Further attention is needed toward the development of monitoring strategies that can provide sensitive assessments of the progress (or otherwise) of management strategies for the Great Barrier Reef.

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## INTRODUCTION

Relationships between human activity and the non-human (= 'natural') environments have become increasingly important in recent decades (Hendee *et al.* 1990). In particular, human impacts on natural environments are seen as undesirable when those impacts deliberately or inadvertently drive natural phenomena beyond the limits expected in the absence of human intervention. Since natural phenomena cannot, in general, be managed directly, 'environmental management' (to reduce the deleterious effects of human activities) hinges on the regulation of human activities (Kenchington 1990). Implicit in such a strategy are the assumptions that: i) a managed activity does, or would in the absence of regulation, push the natural environment beyond its 'normal' behaviour; ii) the natural environment will take care of itself if human perturbations are minimised; and iii) the regulation of human activities successfully ameliorates their environmental impacts. Accordingly, assessing the success or failure of management strategies requires knowledge of: i) the normal status or behaviour of the natural environment; ii) the degree to which anthropogenic impacts force the environment beyond normal conditions; and iii) the effectiveness of management in reducing impacts. Sound information about the status and behaviour of the environment, both in the presence and absence of human activity, therefore, is essential for assessing the efficacy of management strategies (*e.g.*, see Alcala 1988, Russ 1984a, 1989). McNeill (1994) has emphasised, however, that little has been done toward monitoring the status of Marine Protected Areas in Australia, or toward assessing the effectiveness of their management.

### A General Monitoring Protocol for the GBR

The gazetting of the Great Barrier Reef as a multi-use marine park explicitly demanded the conservation of the biological characteristics of the Great Barrier Reef in the context of ongoing recreational use and commercial development (GBR Marine Park Act 1975, Kenchington 1990). To ensure that all provisions of the Act are met, the Great Barrier Reef Marine Park Authority (GBRMPA) must regulate human activities to minimise impacts on the (natural) GBR environment. The favoured regulatory strategy to date has been to zone the GBR for differential access and use (Kenchington 1990, GBRMPA 1983, 1985, 1987, 1988, 1992).

These responsibilities, and the concerns of users of the reef, are manifest at a variety of scales of space and time. Assessment of specific impacts and issues of reef use are typically addressed at relatively local scales (within reefs) and over short times (one to five years). Zoning of the GBR and general management strategies, however, extend to very large spatial scales (reefs, regions) and are operative over long times (5 years - decades). Adequate judgement of management strategies with respect to conservation of the GBR environment requires sound empirical knowledge of spatial and temporal patterns in the distribution and abundance of organisms on the GBR under 'normal' conditions, the variation inherent in those patterns, and of the resilience of populations to perturbation. This information is most efficiently provided by carefully planned quantitative descriptive studies over a range of spatial and temporal scales - *i.e.*, via a sound monitoring programme - combined with manipulative experimental studies.

If longer term monitoring studies and local impact assessment studies are to be designed for maximum benefit at minimum cost, reliable estimates of natural variability in abundances at a range of spatial and temporal scales are needed. Armed with knowledge of natural variability in abundances, we can predict the sensitivity of monitoring programmes and their power to detect non-natural perturbations such as anthropogenic impact and the influence of various management strategies (such as zoning plans). These predictions can, and should, be tested as opportunities arise, and revised as methodology and experience improves. It is essential that the limitations of a monitoring programme (in terms of the precision of estimates and the magnitudes of differences detectable) be clearly identified so that monitoring programmes can be designed to cater for

particular objectives, and the results of those programmes can be interpreted realistically (Andrew & Mapstone 1987, Green 1979, Keough & Mapstone 1995, Mapstone 1995, 1996).

The development of a monitoring programme is most sensibly approached in three stages, neither one of which alone provides sufficient information for the adequate definition of an optimum monitoring programme. In the first stage, the relationships between methodology and small-scale biological features should be thoroughly examined, resulting in the choice of the optimum sampling unit and method of survey for each subject species or group of organisms (Andrew & Mapstone 1987, Downing 1979, Downing & Anderson 1985, Downing & Cyr 1985, Downing *et al.* 1987, Fowler 1987, Green 1979, Kenelly & Underwood 1984, 1985, Mapstone 1988, Mapstone & Ayling 1993, Pringle 1984, Sale & Sharp 1983). It should be verified that the chosen sampling unit has adequate sampling characteristics over the range of environmental conditions (*e.g.* habitat, population density) within which it will be used (Mapstone 1988, Mapstone & Ayling 1993, Lincoln Smith 1988, 1989). These aspects of sampling a number of organisms relevant to the GBR have been examined previously (Bell *et al.* 1985, Bohnsack & Banerot 1983, Brock 1982, Fowler 1987, GBRMPA 1978, 1979, 1986, Harmelin-Vivien *et al.* 1985, Kimmel 1985, Mapstone 1988, Mapstone & Ayling, 1993, Sale & Douglas 1981, Samoily & Carlos 1992, Sanderson & Salonsky 1980, Sale & Sharp 1983).

In the second stage, the most cost-effective, least biased, and most stable sampling method is used to estimate the variation in abundances of organisms over a range of spatial and temporal scales (Caffey 1985, Doherty 1987, Eckert 1984, Keough & Mapstone 1995, Sale *et al.* 1984, Underwood 1991). Results of this stage provide the information necessary to optimise the allocation of effort to various levels in a monitoring programme such that the data obtained will provide adequate resolution and be most sensitive to changes over both time and space. The choice of scales to be considered inevitably will be arbitrary, to some extent, and/or determined by the perceived purposes of a monitoring programme, but existing knowledge of the biology of the subject organisms should also be taken into consideration (Resh 1979). In a third stage of research, the predicted performance of a suggested monitoring programme should be tested by manipulative field studies.

### Random Variances & Sampling Designs

The design of a sampling, monitoring, or experimental study typically is a trade-off between desired rigour, statistical power of hypothesis tests, or precision of estimates, and the costs of doing the research (Andrew & Mapstone 1987, Peterson 1993, Warwick 1993). Refinement of the trade-off can be considered in three main steps: i) identification of the effective experimental unit at which nominated 'treatment' or systematic effects should be replicated and the most cost-effective methods for measuring effects; ii) consideration of potential sub-sampling requirements within replicate units such that the scale of the experimental units is adequately covered with the sampling method(s) given logistic and cost constraints; and iii) estimation of the numbers of experimental units that should be sampled to detect effects that are considered important with a nominated certainty. Each of these steps depends on (usually prior) estimation of variances in measured variables (*e.g.*, abundance of organisms) and the explicit consideration of the costs of sampling (Andrew & Mapstone 1987, Bros & Cowell 1987, Cochran 1963, Cohen 1988, Green 1979, Millard & Lettenmaier 1986, Underwood 1981, Winer *et al.* 1991). Ideally, pilot studies preceding each project should provide a trial ground for sampling methods and robust estimates of the costs of sampling and variances of estimates. In most situations, however, pilot studies are either small in scope or non-existent.

The appropriate experimental unit will be case specific and a matter of definition in the context of the question being asked (Andrew & Mapstone 1987, Hurlbert 1984). The choice of sampling methods should revolve around the sampling properties and logistic considerations of alternative available methods, and will impinge directly on comparisons among studies. Hence, in many instances, similar methods will be adopted in several studies. This tendency often reflects a belief

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that standardisation of methods provides insurance against case-specific biases that impinge on comparability of results, rather than independent examinations of the properties of chosen methods (Andrew & Mapstone 1987). Visual surveys by divers are a popular method of quantifying abundances of demersal macro-biota in shallow reefs, and the sampling properties of several manifestations of visual survey methods have been examined in detail previously (see Andrew & Mapstone 1987 for review, Fowler 1987, Mapstone & Ayling 1993, Samoily & Carlos 1992, Thresher & Gunn 1986).

The necessity for sub-sampling within experimental units also will generally be case specific. Choice of sub-sampling schemes will be a product of: (i) the size of sampling units relative to experimental unit; (ii) the logistic capacity to randomly distribute sampling units over the experimental units; and (iii) prior knowledge of the scales at which variation within experimental units is likely to be non-trivial, and, therefore, should be targeted specifically in order to minimise the potential for inflated variation among replicate experimental units (Cochran 1963, Cochran & Cox 1957, Keough & Mapstone 1995, Underwood 1981). Combined with known costs of sampling, variance estimates at each sub-sampling stratum can be used to predict the allocation of available resources (effort, money) among different levels in hierarchical sampling schemes such that the overall variance is minimised for a given total expenditure (Andrew & Mapstone 1987, Cochran 1963, Snedecor & Cochran 1980, Underwood 1981).

Neither the scale-related variations in abundances of demersal reef biota nor the cost-benefit relations of sampling at different nested scales within reefs have been examined widely in tropical systems (but see Doherty 1987, 1991, Fowler 1987, Mapstone 1988). Justifiable generalisations about the scales at which biota vary most or least within coral reefs will provide clear guidance for the design of future monitoring or experimental field studies, especially where extensive dedicated pilot studies are impossible. For such generalisations to be useful, however, the uncertainty in variance estimates or in 'optimum' allocations of effort to different sub-sampling strata within experimental units must be examined. This has not been done empirically in any marine systems, with the result that point estimates of variance components or sub-sampling schemes are accepted with unknown confidence.

Finally, there is increasing concern about the adequacy of replication of experimental units in ecological studies to detect effects of experimental treatments or natural phenomena that might be considered important. Several authors have recommended the consideration of statistical power when planning studies, and using power calculations to predict the amount of replication necessary to detect nominated effects (Andrew & Mapstone 1987, Bernstein & Zalinski 1983, Green 1989, Keough & Mapstone 1995, Mapstone 1995, 1996, Millard 1987, Millard & Lettenmaier 1986, Peterman 1990, Toft & Shea 1983, Underwood 1981, 1991, 1993, 1996). Again, this approach is relatively uncommon in tropical reef studies (but see Brodie *et al.* 1989, 1992, Kaly *et al.* 1993a,b, Mapstone *et al.* 1989, 1992, Mapstone 1992, Mapstone *et al.* 1994). There is potentially considerable advantage to prior derivation of estimates of the relationship between replication and detectable effects at scales that are likely to be important for future studies of, for example, management regimes or human impacts (Bence *et al.* 1996, Carney 1996, Faith *et al.* 1995, Hunphrey *et al.* 1995, Keough & Black 1996, Keough & Mapstone 1995, Osenberg *et al.* 1996, Resh *et al.* 1995, Schmitt & Osenberg 1996, Stewart-Oaten 1996, Thrush *et al.* 1996, Underwood 1993, 1996). As with cost-benefit analyses, however, the uncertainty in predictions of required replication is rarely considered.

In this study we investigated variability in the abundances of a number of reef organisms at a range of spatial scales in the interests of seeking some general empirical bases for the design of future sampling and monitoring studies. We examined estimates of variances at a hierarchy of spatial scales known to be of interest for a variety of coral reef studies, including fundamental research, management strategy evaluation, and assessments of environmental impacts. We used cost-benefit analyses to consider empirically the potential for generalisation in suggested allocations of effort to sub-sampling at different spatial scales, and the precision of those estimates given the sort of pilot data that would be available in most studies. Finally, we used our estimates of variances to

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predict the replication necessary to detect hypothetical effects on reef biota at three scales, and consider empirically the uncertainty in those predictions.

We were concerned principally with:

- *Acanthaster planci*, *Linckia laevigata*, and *Tridacna* spp.;
- Sessile benthic biota and non-living substrata, with particular emphasis on live corals;
- Fish with medium to great mobility over short periods, including *Plectropomus* spp., lutjanids, chaetodontids, and lethrinids;
- Fish with restricted home-ranges and relatively low mobility over short intervals, such as most of the pomacentrids and some labrids.

We chose to cover as many organisms as logistically possible because: 1) a general monitoring programme should take into account the status of several species; 2) the optimum sizes of sampling units proved to be the same for several organisms (Mapstone & Ayling 1993); 3) many of the organisms can be efficiently counted concurrently; and 4) much of the cost of such a study is incurred in getting to survey sites and support costs whilst in the field, and it was therefore desirable to maximise the return from such costs.

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## METHODS

### Field Methods & Data Processing<sup>1</sup>

#### Timing & Reef Selection

Fieldwork was done from the research vessel *RV Sunbird* during four cruises totalling 70 days between December 12, 1989, and April 10, 1990. We surveyed 24 reefs in the northern 2/3 of the Cairns Section of the GBR Marine Park, between latitudes 14°25'S and 16°45'S (Table 1). Twelve reefs were 'outer-shelf reefs' (OS), being located at the edge of the continental shelf, and 12 reefs were considered 'mid-shelf reefs' (MS) because they were positioned well offshore from the mainland but inshore of the continental shelf-break. The 12 reefs in each shelf position were selected with equal frequency from three latitudinal regions between Cape Flattery and Cairns. Thus, four mid-shelf and four outer-shelf reefs were sampled north of Cape Flattery, between Cooktown and Rattlesnake Point, and south of Cape Tribulation.

**Table 1:** Reefs sampled for this project. Four reefs were selected from each of 2 offshore positions in each of three regions. **Zone** = category of each reef under the 1983-90 GBRMPA zoning plan for the Cairns Section of the GBR Marine Park. **COTS History** = recent exposure to *A. planci* outbreaks: **RE** = Recent Outbreak; **NO** = No recent outbreak.

REGION	POSITION (Offshore)	REEF	LATITUDE (°:S)	ZONE (1983-90)	COTS HISTORY
Cape Flattery (Southern boundary)	Mid-shelf	<i>Lizard</i>	14:41	NPZ/2	RE
		<i>Eyrie</i>	14:43	GU	NO
		<i>Martin</i>	14:45	GU	NO
		<i>Helsdon</i>	14:57	GU	RE
	Outer-shelf	<i>Hicks</i>	14:27	GU	RE
		<i>Day</i>	14:30	GU	RE
		<i>Carter</i>	14:33	NPZ	RE
		<i>Yonge</i>	14:36	GU	RE
Cooktown (Northern Boundary)	Mid-shelf	<i>Boulder</i>	15:25	GU	NO
		<i>Egret</i>	15:29	GU	NO
		<i>Endeavour</i>	15:46	GU	RE
		<i>Pickersgill</i>	15:52	GU	RE
	Outer-shelf	<i>Ribbon #4</i>	15:26	NPZ	NO
		<i>Ribbon #3</i>	15:30	GU	NO
		<i>Ribbon #2</i>	15:33	GU	NO
		<i>Lena</i>	15:39	GU	NO
Cape Tribulation (Northern Boundary)	Mid-shelf	<i>Batt</i>	16:25	GU	NO
		<i>Hastings</i>	16:31	GU	RE
		<i>Michaelmas</i>	16:35	NPZ	NO
		<i>Arlington</i>	16:42	GU	RE
	Outer-shelf	<i>Agincourt 4</i>	15:57	GU	RE
		<i>Agincourt 3</i>	15:59	NPZ	NO
		<i>St Crispin</i>	16:06	GU	NO
		<i>Opal</i>	16:13	GU	RE

<sup>1</sup> This section is repeated in the companion report by Mapstone *et al*, 1995, which arose from the same data.

We stratified reefs by shelf position and region *a priori* because: i) Shelf Position has been invoked to explain distributions of several species of fish and corals (Done 1982, Dinesen 1983, Russ 1984b, Williams 1982, Williams & Hatcher 1983, Williams *et al.* 1986); and ii) we wished to distinguish between the hypothesised 'source' regions for COTS outbreaks (north of Cape Tribulation) and the initial 'sink' region (south of Cape Tribulation) in the propagation of COTS outbreaks southward down the GBR (Dight 1992, see companion report by Mapstone *et al.* 1995). We intended that two of each group of four reefs would have suffered recent COTS infestation and two would have been unaffected by COTS recently (Mapstone *et al.* 1989), but we were not able to find both types of reefs in all regions. In particular, COTS history and region were confounded completely on the outer shelf reefs. All outer-shelf reefs in the Cape Flattery (northern) region had suffered recent COTS outbreaks, none of the outer-shelf reefs in the Cooktown (central) region had been affected, and half of the outer-shelf reefs in the Cape Tribulation (south) region were affected (Table 1). Zoning status was standardised among reefs as far as possible after satisfying the other reef selection criteria.

### Sampling within reefs

Reefs would comprise the effective 'experimental units'<sup>2</sup> (Hurlbert 1984) or replicate instances of a management (or 'use') treatment when monitoring human activities potentially impacting on the GBR, when assessing the effectiveness of management strategies, and for many ecological studies. It was important, therefore, that we distributed sampling within reefs sufficient to make inferences about whole reefs or gross strata of them. In so doing, however, it was important also that we estimated variation at smaller scales of interest within the GBR, such as those appropriate to assessing localised impacts of human uses such as tourism.

### Habitats

The most conspicuous systematic strata within reefs were related to exposure (windward and leeward aspects) and gross habitat characteristics (reef slope, reef crest, large bommies, *etc.*) (Chave & Eckert 1974, Clarke 1977, Done 1983, Gladfelter & Gladfelter 1978, Green *et al.* 1987, Helfman 1978). Windward and leeward aspects were common to all reefs, as were reef slopes, and reef crests. Sampling reef crests, however, was logistically unfeasible on low tides and in rough weather, so we restricted sampling to substrata of more than 2m depth. Shallow (<20m depth) large bommies were restricted to back-reef (leeward) areas, and did not occur on all reefs. In order to maximise the generality of our conclusions, and facilitate straightforward comparisons among reefs, we stratified sampling within reefs only by exposure, meaning that we sampled back-reef (leeward) and front-reef (windward) habitats. This front-reef/back-reef (hereafter 'Habitat') stratification meant that we sampled only reef slopes on the front-reefs, but in the back-reef we often sampled both reef slope and bommie habitats. Only one (back-reef) location was comprised of large bommies at any reef, and that location was always towards the middle of the back-reef areas (Figure 1).

### Locations, sites, & transects

The first of the four field trips was considered a pilot survey to review field procedures and refine the within-reef sampling design for subsequent surveys. Carter, Lizard, and Eyrie Reefs (Table 1)

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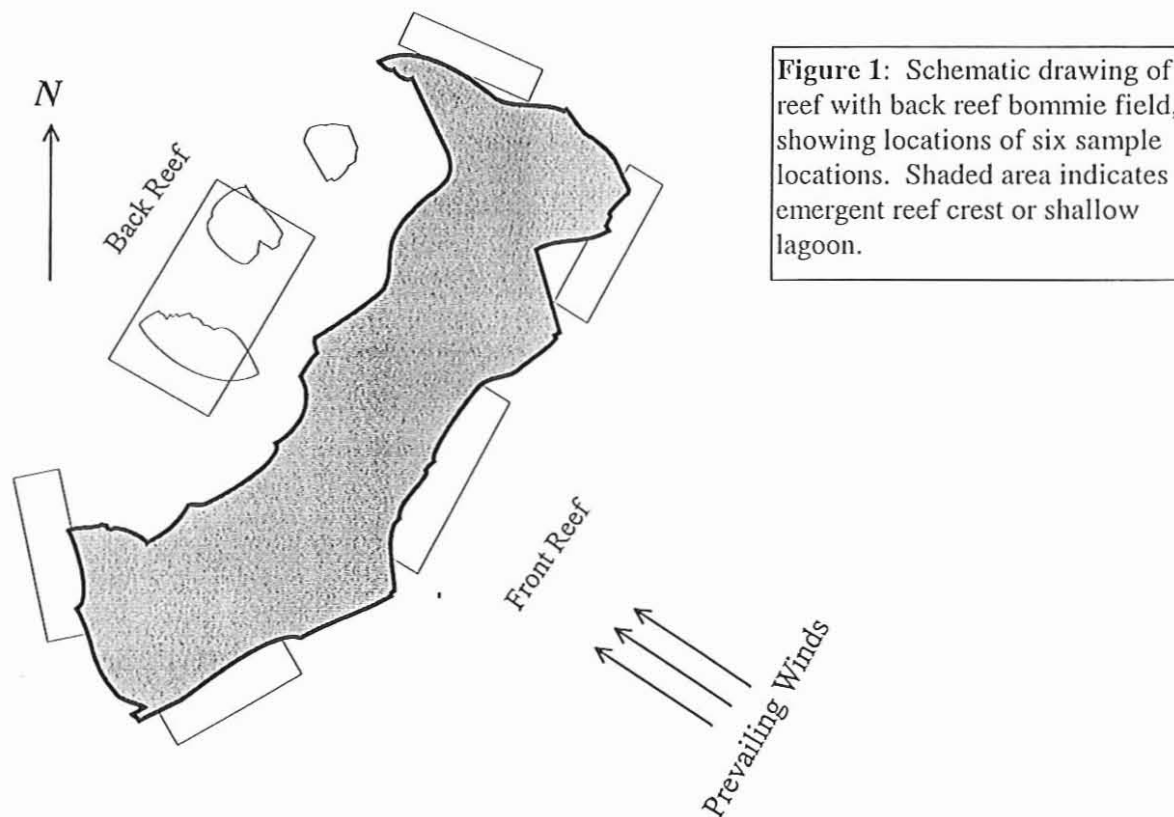
<sup>2</sup> The term 'experimental unit' is used in a general sense to indicate the largest random scale of replication of a nominated systematic effect (such as Shelf Position). In the simplest contexts, experimental units equate with sampling units (transects), but in most cases one to several levels of sub-sampling within true replicate effects will be done, and the experimental units will be the units of replication at the top of that hierarchy of sub-sampling (most often reefs in this report) (see Hurlbert 1984 for further discussion).

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were sampled in December 1989<sup>3</sup>. Each reef was sampled at three 'locations' within back-reef and front-reef habitats. The locations were selected arbitrarily such that within each habitat one location was near each end of the reef and the third was about midway along the front-reef or back-reef (Figure 1). Two haphazardly chosen sites were sampled within each location, and four transects of each type (see below) were surveyed at each site. Transects were separated by at least their length, and sites were approximately 200m apart. Thus, each location represented about 800-1000m of reef habitat, with at least 1 km between locations.

Following analyses of the data from the first trip, within-reef sampling on subsequent trips was amended as follows so that each reef could be sampled within two days. Three locations were sampled in the front-reef and back-reef habitats, as before (Figure 1). This was continued to ensure adequate distribution of our sampling effort over the space about which we wished to make inferences - *ie* whole reefs and habitat strata. Five 50mx5m transects (Mapstone & Ayling 1993) were surveyed within each location, distributed over the length of the location. 'Sites' were not distinguished for organisms sampled with these transects.

Small fish and sessile benthos (Table 2, Appendix 1) were sampled along two 20mx2.5m belt transects and two line-intercept transects respectively at each of two sites within each location. The sites were separated by about 150-200m. Each reef took 1.5-2 days to sample by this design. Reefs were visited according to the opportunity to sample front-reefs on outer-shelf reefs. If the weather was calm (wind <15kts, sea <1.5m), outer-shelf reefs were sampled until weather prevented further work on the front-reef or until all outer-shelf reefs had been sampled. Although this raised the potential for confounding cross-shelf patterns with effects of weather and time of sampling, most reefs in both shelf positions were sampled in good working conditions and relatively calm weather.



**Figure 1:** Schematic drawing of reef with back reef bommie field, showing locations of six sample locations. Shaded area indicates emergent reef crest or shallow lagoon.

<sup>3</sup> Each of the 3 reefs was re-sampled on two subsequent trips in the same way as all other reefs were sampled. Tropical cyclone Ivor crossed the continental shelf off Cape Flattery between the 2<sup>nd</sup> and 3<sup>rd</sup> survey of these reefs (Van Woesik *et al.* 1991, Done *et al.* 1992). Because of the considerable habitat damage caused by the cyclone, the 3<sup>rd</sup> survey is not considered here. Thus, only the 2<sup>nd</sup> (of 3) sets of data from Carter, Eyrie, and Lizard Reefs were included in this report. The effects of Cyclone Ivor on Lizard, Eyrie, and Carter reefs will be reported elsewhere (Mapstone *et al.* in prep).



## Survey Methods

Surveys were done by five divers working from two tender vessels. The tenders were anchored at each end of a survey location, and divers completed counts whilst swimming between the boats. All data were collected using SCUBA.

### *Counts of Fish and Large Discrete Benthos*

Large, relatively mobile fishes, *Linckia laevigata*, tridacnid clams, and crown of thorns starfish (*Acanthaster planci*) were counted within 50m x 5m belt transects. Poritid corals of greater than 20cm diameter ( $\Phi$ ) were sampled within the same transects, but over a width of only 2.5m. Small, mostly site attached fishes were counted within 20m x 2.5m belt transects (Table 2, Appendix 1). Mapstone and Ayling (1993) demonstrated that transects of these sizes were most cost effective to sample and least likely to provide biased estimates of density. For safety reasons, all transects were surveyed in less than 12m of water, and 99% were between depths of 2m and 10m.

The counts were done as follows at each location. Three divers entered the water and arbitrarily chose a starting point for the first transect to be surveyed. The free ends of two 50m fibreglass tapes were attached to the substratum, 5m apart. Two divers, linked by a 5m length of cord, swam approximately parallel to the reef crest keeping the 5m cord taught between them and laying the tapes as they swam. Hence, the two divers swam along the long edges of the transect to be surveyed. The cord was buoyed at its midpoint to avoid snagging on the substratum. The third diver, and principal observer, swam abreast of the other two, counting large mobile fishes within the 5m wide belt projected ahead of the tape-layers. At the end of the 50m, the tape reels were secured to the substratum and a small weighted buoy was left to mark the end of the transect. All three divers then returned along the transect counting other organisms. The principal observer searched the substratum between the two tapes for *A. planci*, the asteroid *Linckia laevigata*, and the clams *Tridacna derasa*, and *T. gigas*. *A. planci* were counted into three size classes (<20cm diameter ( $\Phi$ ), 20-50cm  $\Phi$ , and >50cm  $\Phi$ ), whilst *T. derasa* and *T. gigas* were counted into two size classes ( $\leq$ 20cm shell length, >20cm shell length). When the principal observer reached the 20m mark on the tapes, he ceased counting the benthic invertebrates and counted small fish within 1.25m either side of the deeper tape for the remaining 20m. A 1.25m T-bar was used to measure 1.25m either side of the transect. He then returned along the same 20m completing his counts of the benthic invertebrates, over the 5m between the two tapes. This disrupted counting order was adopted to minimise the potential effects of diver activity on counts of the small fishes, which were counted only along transects 1,2,4 &5 at each location, effectively dividing the location into two sites for those species. The two tape layers returned along the 50m length of the transect, each counting massive and sub-massive poritid corals within 1.25m of the deeper tape. Each diver used a 1.25m T-bar to identify the 1.25m limit of the belt over which they counted. The poritids were classified only by family, and were counted into 4 size classes: 20<50cm  $\Phi$ , 50<100cm  $\Phi$ , 100-200cm  $\Phi$ , and >200cm  $\Phi$ . The cross-members of the T-bars were marked at 20cm, 50cm, and 100cm to assist with classification of organisms into size classes. All data were recorded directly onto pre-printed waterproof data sheets. When all counts were completed, the tapes were re-wound, and the divers returned to the small buoy left to mark the end of the transect, and then swam along the reef at least 50m further to start the next transect. The starting and ending depths of each side of each transect were recorded by the tape-layers, whilst the beginning and ending times of each count were recorded by each observer.

The above methods were the results of refinements after the pilot survey conducted on the first of the four trips. During the pilot survey, neither the clams nor *A. planci* were counted by size. Poritids were counted by size, as above, but the counts were over 2.5m either side of the deeper tape. Very large counts of poritids over that width proved too time-consuming and so the transect width was reduced to 1.25m either side of the tape for all further work. A short training exercise was done during the first day of the field work to ensure that all observers counting poritids counted in a consistent way and returned similar counts for the same set of transects.

### *Percent Coverage by Benthos and Counts of Small Corals*

Concurrent with the above counts, an independent team of two divers recorded coverage of the substratum by sessile benthos (Table 2, Appendix 1) along 20m line-intercept transects. Each diver layed a 20m fibreglass tape in 3-9m of water and approximately parallel with the reef crest. They then swam along the tapes recording sequentially the intervals of the tape overlaying each organism or substratum type. Transects were separated by at least 20m. All organisms were identified to the lowest taxonomic resolution feasible, usually species or genus. The observers recorded the starting point and length of each taxonomically distinct interval along the transect, and also indicated where non-continuous intervals arose from a single colony which was either fragmented or dead in patches. After recording the intercept data for the length of the transects, the divers returned along their respective transects counting the numbers of small corals ( $\leq 5\text{cm } \Phi$ ) within a belt 25cm either side of the tape. The corals were recorded only by family or higher taxa. Poritid corals of  $6 < 20\text{ cm } \Phi$  were also counted along these belt transects. Each observer then re-wound their tape and moved on to their next transect.

Three observers collected these data. One (AMA) was present on all trips, whilst a second (RC) surveyed transects on only the first trip. The third observer (RvW) was present on the second, third, and fourth trips. No dedicated training of observers was done, but all three were experienced in coral taxonomy and line-intercept survey methods. The first half day of the first and second trips was spent by the two observers present cross-referencing their taxonomic identifications and recording methods, and they consulted on taxonomic issues throughout the field work. Between the first and second field trips, all three observers spent a day with Dr. J. E. Veron verifying their taxonomic identifications. All data were recorded onto pre-printed waterproof data sheets.

### **Data Processing**

All raw data were stored on computer in dBase III<sup>+</sup> tables and all statistical analyses were done using SAS software running on an IBM compatible personal computer.

Data processing began on *RV Sunbird* immediately after data sheets were filled. On each day one of three general divers (tape layers) on each trip remained on *RV Sunbird* and entered data into database files on a laptop computer. This meant that ambiguities on data sheets or potential transcription problems could be identified and addressed immediately after observations were made. Data entry was completed following each field trip. Each transect was identified by an absolute number and date, reef, location, site (where applicable), and sequential position within a site or location. All observer names, transect start and end times and depths, and raw counts or interval data were entered by taxon and observer. Each taxon or substratum type was identified in databases by a 4-8 letter unique taxonomic code, which was referenced to a full taxonomic name in a master database.

All data were entered twice, by different operators. The duplicate fields for each data set were then range-checked and compared by custom written software, and any inconsistencies flagged and detailed in a third, reference, dBase file. Another programme then read the reference file, opened the two raw data files for editing, and placed cursors where inconsistencies had arisen. Operators then checked the file records against the raw data sheets to verify which of the file data were in error. The cross-check and correction cycle was repeated until both files matched exactly and all data were within logical boundaries. During data checking, all taxonomic codes were checked against the master taxonomic database. New entries were flagged to verify whether they represented taxa not seen previously or spelling errors. Finally, 100 records were selected strictly at random from the collated databases and checked manually against the corresponding raw data sheets. Despite these efforts, some errors were still found (and corrected) during data analysis.

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## Statistical Methods

### Preliminary Screening of Data

Data within each combination of Habitat, Shelf Position, and Region were examined initially by univariate descriptive statistics to identify gross patterns of distribution (presence/absence) for each taxon. Because several taxa were recorded only infrequently, we often had to pool species or genera on taxonomic grounds to get sufficient data for analyses. Taxa were pooled until at least half of the site or location means for each (pooled) group were non-zero.

Data were not transformed for analyses because:

- i. We were interested in estimating variation in abundances rather than in transformed variables;
- ii. Scale-related variations at all scales greater than among transects would be assessed *via* calculating variances among means of  $n$  or more data, and these means were expected to be (and were) approximately normally distributed (by the central limit theorem), and generally proved to be homoscedastic<sup>4</sup>;
- iii. Estimated variances among transects were averages of large numbers of values (of variance), and although many of those values were likely to be under-estimates of the mean variance because of their small sample sizes and the skewness in the count data (McArdle *et al.* 1990), the average of a large number of such estimates should be unbiased (McArdle *et al.* 1990<sup>5</sup>);
- iv. Because of the presence of numerous zero counts for most taxa, most relevant transformations would require the prior addition of a constant to all data, which may produce results as problematic as those arising from un-transformed data (McArdle *et al.* 1990).

### Estimation of Variance Components

The estimation of variance attributable to a range of hierarchical spatial scale effects was central to this project. The decomposition of total variances was by calculation and manipulation of ANOVA mean squares (MSs) (Sokal & Rohlf 1981, Winer 1971, Winer *et al.* 1991). Since we had adhered to a strictly balanced sampling design, we expected the estimation of variances from ANOVA MSs to be as unbiased and robust to moderate non-normality as alternative methods, such as Restricted Maximum Likelihood (Littell *et al.* 1991, SAS 1990, 1992)<sup>5</sup>. Further, since we were estimating variances at each scale from many independent datasets, and taking the average of those estimates as our best (point) estimate of variation, we were confident that our 'best estimates' were relatively unbiased (McArdle *et al.* 1990).

We estimated stochastic variation in abundances at four hierarchically arranged scales:

1. Among reefs kilometres-10s of kilometres apart, but within the same region and shelf position (Table 1);
2. Among locations 1000s of metres apart within each habitat on each reef (Fig. 1);
3. Among sites 100s of metres apart within each location; and
4. Among transects 10s of metres apart within each site or location.

Variation among reefs was calculated separately for each habitat at each shelf-position in each region. We adopted this strategy in order to examine whether abundances were relatively more

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<sup>4</sup> As one reviewer noted, the Central Limit Theorem would favour normality of the distribution of means, but would not necessarily ensure that they were homoscedastic. Omnibus F-tests should be robust to heteroscedasticity in balanced sampling designs (as ours were) (Underwood 1981, Winer 1971, Winer *et al.* 1991). Heteroscedasticity would have had more severe implications, however, for *a posteriori* tests and for the estimation of variance components from ANOVA models. We persisted with untransformed data because our location means were generally homoscedastic within taxa.

<sup>5</sup> Because estimation of variances from decomposition of mean squares in nested analyses involves subtraction of independently estimated mean squares, each with its own uncertainty, some variances estimates will be less than zero. These are typically set to zero (Winer *et al.* 1991), possibly resulting in bias when several such estimates are averaged. When such procedures are based on balanced ANOVA, as ours were, bias is no greater than from other methods of variance estimation (Littell *et al.* 1991, SAS 1990, 1992).

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variable at large scales if sampled in some habitats than in others, and to isolate the reef variation from the fixed effects of habitat, shelf position, and region. The risk we took in doing so was that the variance estimates from the two habitats in a given shelf position and region would be dependent because the data came from the same sets of reefs. Variances among locations were estimated independently for each habitat at each reef, variances among sites were estimated independently for each location, and variances among transects were estimated independently for each site or location (depending on the survey method). The estimation formulae for variances at each scale, and the maximum numbers of estimates available are given in Table 3.

**Table 3:** Estimation formulae and maximum potential sample sizes for estimates of variance at the scales of reefs, locations, sites, and transects. All estimates were derived from manipulations of ANOVA Means Squares (MS). The ANOVA models from which estimates were derived are also given.

Scale of Variation	ANOVA Model	Estimate of Variance	Number of Estimates
reef	$y_{ijk} = \mu + \bar{r}_{i...} + \bar{l}_{j(i)...} + \bar{s}_{k(ij)} + \epsilon_{ijk}$	$(MS_{reef} - MS_{locn}) / nml$	12
location	$y_{jk} = \mu + \bar{l}_{j..} + \bar{s}_{k(j)} + \epsilon_{jk}$	$(MS_{locn} - MS_{site}) / nm$	48
site	$y_{k} = \mu + \bar{s}_{k.} + \epsilon_{k}$	$(MS_{site} - MS_{res}) / n$	144
transect	N/A	$\frac{\sum (y_i - \bar{y})^2}{n-1}$	144 / 288

$y_{ijk} = i^{\text{th}}$  (of  $n$ ) observations at site  $k$  (of  $m$ ) within location  $j$  (of  $l$ ) in each habitat on reef  $i$ .

Variance among transects was calculated for the replicate transects at each site (or location) provided that the (pooled) group being considered was observed on at least 20% of the transects sampled in the reef and habitat where the site or location occurred. We adopted this selection criterion to reduce the bias introduced by including estimates of zero variance from situations in which a taxon apparently did not occur. The cut-off of 20% was arbitrary. Similarly, we only accepted estimates of inter-site and inter-location variance from habitats and reefs where the subject taxon was recorded in at least one site or location. Variation among reefs for each habitat type was estimated only if at least one of the four reefs sampled in a region and shelf position had non-zero means.

### Systematic Patterns in Variation

In addition to comparing variation among different scales, we wished to examine the degree to which variation at each scale varied predictably with shelf position, habitat, or region. It was expected that the abundances of at least some organisms would vary substantially with shelf position, habitat, or regions, however (See companion report - Mapstone *et al.* 1995). It was also expected that variances would vary with abundance (Sokal & Rohlf 1981). We used Coefficients of Variation (CV), therefore, as a measure of variation for these comparisons because it was standardised for the effects of abundance on variance estimates. We sought to standardise variation before comparing across (potential) systematic effects by calculating the CV from the estimated variances and mean abundances at each scale. Hence:

$$\begin{aligned}
 CV_{reefs} &= CV_r = S_{reefs} / \bar{x}_{reefs} && \text{(within each Shelf Position, Region, \& Habitat)} \\
 CV_{locn} &= CV_l = S_{locs} / \bar{x}_{loc} && \text{(within each reef \& Habitat)} \\
 CV_{sites} &= CV_s = S_{sites} / \bar{x}_{sites} && \text{(within each location)} \\
 CV_{transects} &= CV_t = S_{tran} / \bar{x}_{tran} && \text{(within each site or location)}
 \end{aligned}$$

where

- $s_{scale}$  = the standard deviation of the data (for transects) or the means (for higher scales) at the scale indicated by *text*, and  
 $\bar{x}_{scale}$  = the mean of the data from which the corresponding standard deviation was calculated.

Independent estimates of CV were calculated for each variance estimate described above (see *Estimation of Variance Components*). The CVs were then compared among scales graphically and compared among habitats, shelf positions, and regions by analyses of variance, with CVs as data. For  $CV_b$ ,  $CV_s$ , and  $CV_t$ , CVs were averaged within each habitat at each reef and those mean CVs used as data in the following model:

$$y_{ijk} = \mu_{...} + H_{i..} + R_{.j.} + S_{..k} + HR_{ij.} + HS_{i.k} + RS_{.jk} + HRS_{ijk} + \epsilon_{ijk}$$

where

- $y_{ijk}$  = the  $r^{\text{th}}$  observation in Habitat  $i$  in Region  $j$  at Shelf Position  $k$ ,  
 $\mu$  = population mean of  $CV_{scale}$ , and  
 $\epsilon_{ijk}$  is a normally distributed random error associated with observation  $y_{ijk}$ .

For  $CV_r$ , there was only one estimate from each combination of Habitat, Shelf Position, and Region and the resultant general ANOVA model was<sup>6</sup>:

$$y_{ijk} = \mu_{...} + H_{i..} + R_{.j.} + S_{..k} + HR_{ij.} + HS_{i.k} + RS_{.jk} + \epsilon_{ijk}$$

The degrees of freedom, Mean Square (MS) estimates and F-ratio denominators for these models are given in Table 4.

In both models, and throughout the report, Habitat (front-reef, back-reef), Shelf Position (mid-shelf, outer-shelf), and Region (Cape Flattery, Cooktown, Cape Tribulation) are considered fixed effects. Because of the criteria for including data in these analyses (see above), not all combinations of Habitat, Shelf Position, and Region were included in the analyses for all taxa. This meant that for some taxa the above analyses were restricted to some subset of the complete data set, whilst for others the models were changed. The reduced models used for analyses of  $CV_b$ ,  $CV_s$ , and  $CV_t$ , and the relevant taxa, were:

- As above but based on data from only two regions instead of all three, for *Amblyglyphidodon curacao*;
- $y_{ijk} = \mu_{...} + H_{i..} + R_{.j.} + HR_{ij.k} + \epsilon_{ijk}$   
using data from only mid shelf reefs, for the fishes *C. aureofasciatus*, *L. carponotatus*, *C. rollandi*, Recruit *C. rollandi*, *P. moluccensis*, Recruit *P. moluccensis*, *T. lunare*;
- $y_{ijk} = \mu_{...} + R_{.j.} + \epsilon_{ijk}$   
using data from back reef habitats of outer shelf reefs only, for the fishes *L. carponotatus*, *C. rollandi*, Recruit *C. rollandi*, *P. moluccensis*, Recruit *P. moluccensis*, *T. lunare*.

Restricted analyses of  $CV_r$  were as above for *A. curacao* and *C. aureofasciatus*, except that it was not possible to estimate the highest level interaction in each case. For *L. carponotatus*, *C. rollandi*, Recruit *C. rollandi*, *P. moluccensis*, Recruit *P. moluccensis*, and *T. lunare*,  $CV_r$  was analysed by the following model:

$$y_{ijk} = \mu_{...} + H \cdot S_{i.} + R_{.j} + \epsilon_{ijk}$$

where H-S is a composite effect of Habitat and Shelf Position incorporating three levels: back reef on mid-shelf reefs, front reef on mid-shelf reefs, and back-reef on outer shelf reefs.

<sup>6</sup> It was necessary to assume here that the three way interaction was trivial.

**Table 4:** Structure of ANOVA to test for effects of Habitat, Region, and Shelf Position on scale specific Coefficients of Variation. The degrees of freedom and MS Estimates for analyses of  $CV_l$ ,  $CV_s$ , &  $CV_r$  are shown separately from those for  $CV_r$ . Note that no test of the H\*R\*S interaction was possible for  $CV_r$ , and it was assumed for tests of all other terms that this interaction was trivial ( $\delta_{HRS}^2 \approx 0$ ).

Source of Variation	df		MS Estimates*		F-ratio Denominator
	$CV_{l,s,t}$	$CV_r$	$CV_{l,s,t}$	$CV_r$	
Habitat	1	1	$\sigma_\epsilon^2 + 24\delta_H^2$	$\sigma_\epsilon^2 + 6\delta_H^2$	$MS_{res}$
Region	2	2	$\sigma_\epsilon^2 + 16\delta_R^2$	$\sigma_\epsilon^2 + 4\delta_R^2$	$MS_{res}$
Shelf Pos <sup>n</sup>	1	1	$\sigma_\epsilon^2 + 16\delta_C^2$	$\sigma_\epsilon^2 + 4\delta_C^2$	$MS_{res}$
H*R	2	2	$\sigma_\epsilon^2 + 8\delta_{HR}^2$	$\sigma_\epsilon^2 + 2\delta_{HR}^2$	$MS_{res}$
H*S	1	1	$\sigma_\epsilon^2 + 12\delta_{HC}^2$	$\sigma_\epsilon^2 + 3\delta_{HC}^2$	$MS_{res}$
R*S	2	2	$\sigma_\epsilon^2 + 8\delta_{RC}^2$	$\sigma_\epsilon^2 + 2\delta_{RC}^2$	$MS_{res}$
H*R*S	2	-	$\sigma_\epsilon^2 + 4\delta_{HRC}^2$	-	$MS_{res}$
residual	36	2	$\sigma_\epsilon^2$	$\sigma_\epsilon^2$	-

\*:  $\delta^2$  is used to indicate variations attributable to fixed effects, as opposed to random variances ( $\sigma^2$ )

### Hypothesis Testing

The above analyses (Table 4) involved inferential hypothesis testing, specifically the use of univariate Analyses of Variance (ANOVA). We did so because: i) The tools commonly used for the design of sampling or experimental programmes (and with which this work was mainly concerned) are generally based, implicitly or explicitly, in an hypothesis testing paradigm; and ii) This work was intended to provide insights to sampling strategies for use by other researchers, probably working on a subset of the species we examined. In such cases, it seemed more likely that information about specific taxonomic groups would be more useful than multivariate information that would be specific to the assemblages of taxa we sampled.

We followed the hypothesis testing procedures suggested by Mapstone (1992, 1995, 1996) and adopted non-conventional criteria for the rejection or non-rejection of null-hypotheses.

Mapstone's procedure involves the following steps:

- i. Choose the smallest alternative hypothesis ( $H_a$ ) considered noteworthy or important. Assuming the null hypothesis ( $H_0$ ) is, in general, one of 'no effect', this means nominating the smallest size of an effect (ES) that would be considered non-trivial, if it existed. Details of the ES we chose for each test are discussed later.
- ii. Weight the relative importance of: a) failing to detect an effect of (on average) that size or greater when it existed; and b) erroneously inferring that such an effect did exist when it did not. That is, weight the relative importance of committing a Type II error ( $\beta$ ) or Type I error ( $\alpha$ ). In all our hypothesis tests, we had no clear basis for weighting differently the consequences of Type I and Type II errors. For example, failing to infer a cross-shelf pattern in coefficients of variation of organisms might suggest that sampling characteristics established for one shelf position would be well suited to another. Alternatively, inferring significant cross shelf patterns in variation would suggest stratifying sampling intensity to better account for systematic changes in variability. Erroneous advice of either type could result in poor or inefficient sampling designs, and we made no judgements about which would be more dangerous. Accordingly, we weighted Type I and Type II errors equally for all analyses.
- iii. Express the above relative weighting of [concerns about] Type II/Type I errors as  $k$  ( $k=1$  here).
- iv. Given the nominated ES, estimate the likelihood of Type II error ( $\beta$ ) if  $H_0$  was not rejected against a critical significance value of  $\alpha_c$ . The value of  $\alpha_c$  set initially is arbitrary.

- v. Iteratively adjust  $\alpha_c$  and recalculate  $\beta$  at the revised level of  $\alpha_c$  until  $\beta = \alpha_c/k$ .
- vi. Compare the value of  $\alpha$  for the observed data ( $\alpha_o$ ) with the value of  $\alpha_c$  that satisfied the above relation ( $\beta = \alpha_c/k$ ). If  $\alpha_o \leq \alpha_c$ , reject  $H_o$ , otherwise do not reject  $H_o$ .

When  $k=1$ , this procedure amounts to a decision based on estimating whether the observed data were more likely to have arisen from two or more populations with the same mean ( $ES=0$ ) or from two or more populations with means different by, on average,  $ES$  or greater.

### *A posteriori Separation of Effects*

The nature of effects were interpreted only from the highest order ANOVA interaction in which they were involved and which was statistically significant. Thus, if an  $A*B$  interaction was significant, then neither of the main effects of  $A$  or  $B$  alone were considered.

In the absence of their involvement in significant interactions, significant main effects were resolved, where more than two means were involved, by the Ryan-Elliot-Gabriel-Welsch multiple range procedure (SAS 1992, 'Ryan's Test' in Day & Quinn 1989). If interaction terms were significant, they were separated into orthogonal one-way ANOVAs and where significant effects of one factor were indicated at a given level of the other factor(s), those effects were then resolved by Ryan's Tests. In all *a posteriori* procedures, the significance criterion used for tests was that applied to the initial omnibus F-tests, as derived by Mapstone's (1995, 1996) procedure (above).

### Estimation of Sample Sizes

The data were next analysed as pilot data for planning future sampling schemes over large areas of the GBR. Two procedures were considered:

- a) Cost-benefit procedures were done to indicate the best relative distribution of effort across random nested levels of sub-sampling in order to minimise total random variation within effective experimental units; and
- b) analyses of statistical power were done to predict the numbers of replicate experimental units that should be sampled to detect nominated patterns in higher order fixed effects.

Estimates of required sample sizes were calculated at three spatial scales in order to provide insights to the sampling requirements for different management issues:

- i. Whole reefs, to indicate replication needed to detect nominated effects of zoning plans or other effects instrumental over whole reefs;
- ii. Reefs sampled only within specific habitat strata, as appropriate for assessing habitat-specific effects such as cyclonic effects, 'split-reef' zoning, and effects of some fishing activities;
- iii. Locations, as the scale nearest to that likely to be appropriate for estimating the effects of localised tourism such as pontoon-based reef visits.

### *Cost-Benefit Procedures*

Cost benefit procedures are well documented (Andrew & Mapstone 1987, Cochran 1963, Cochran & Cox 1957, Snedecor & Cochran 1980, Underwood 1981, Winer 1971, Winer *et al.* 1991). The general expression for the expected optimum number of sampling units ( $\hat{v}$ ) at the lower of two levels [ $U, V(U)$ ] in a nested sampling structure is:

$$\hat{v} = \sqrt{\frac{c_u s_v^2}{c_v s_u^2}}$$

where

$c_u, c_v$  = the specific costs of sampling a single unit of level  $U$  and  $V$  respectively, and  $s_u^2, s_v^2$  = the variance among units of levels  $U$  and  $V$  respectively.

Not commonly discussed, however, is the uncertainty associated with estimated optimum sample sizes (but see Cochran 1963, Cochran & Cox 1957). Because both numerator and denominator in the variance ratios employed for cost-benefit procedures are themselves estimated, each with uncertainty, the variance ratio will have considerable error in most cases, though the implications of this uncertainty on the suggested sampling strategies are rarely considered. In many cases, the measured costs will also be slightly variable, based on logistic considerations, further increasing the uncertainty of the predicted sample sizes. In order to obtain empirical estimates of uncertainty about the predicted optimum sample sizes, therefore, we calculated optimum sampling strategies within each habitat stratum at each reef sampled in each region and shelf position.

Hence, we used our estimates of variances among transects (averaged over sites or locations), sites (averaged over locations), and locations, and the average measured times taken to survey each of these scale units (=cost) within each habitat at each reef to estimate the numbers of transects, sites, and locations that would minimise within reef variation for a given (arbitrary) allowable cost. Cost limits were set at one sampling day per reef (where entire reefs were to be sampled) or Habitat (where sampling was restricted to only one habitat type). These estimates derived from the following formulae:

$$n_s = \sqrt{\frac{c_t s_t^2}{c_s s_t^2}}$$

$$n_l = \sqrt{\frac{c_l s_l^2}{c_s s_l^2}}$$

$$l_r = \frac{C_r}{c_t + \hat{m} c_s + \hat{m} \hat{m} c_l}$$

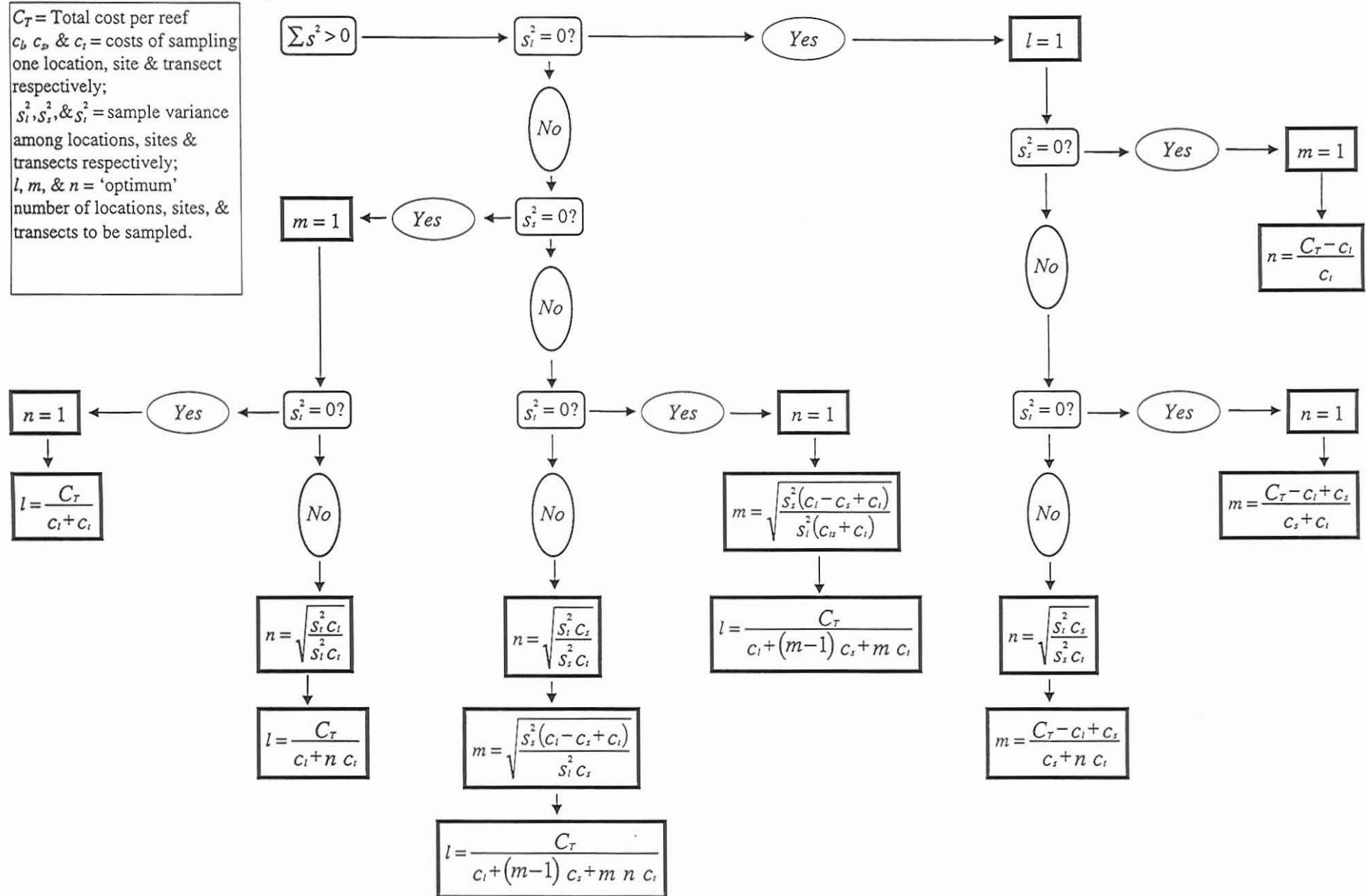
where:

- $c_t, c_s, c_l$  = the average exclusive costs of sampling one transect, site, and location respectively;
- $s_t^2, s_s^2$  = the estimated average variance among transects and sites in each Habitat at each reef respectively;
- $s_l^2$  = the estimated variance among locations in each Habitat at each reef;
- $n_s$  = the predicted optimum number of transects to sample per site or location;
- $\hat{m}$  = the predicted optimum number of sites to sample per location;
- $l_r$  = the number of locations to sample per reef (or Habitat), given total available budget per reef (or Habitat) of  $C_r$ .

Note, however, that we assumed that the costs of sampling were constant within each habitat at each reef (though possibly variable among reefs and habitats), and we averaged the variances among transects, and sites over the three locations in each habitat at each reef. Consequently, we have almost certainly under-estimated the true variation in predicted optimum sample sizes.

Where the (average) variance at a given scale was estimated to be zero, we inferred that it was not necessary to replicate sampling at that scale. We then apportioned the measured costs of sampling at that scale to the next remaining scales to be sampled. Calculations of sample sizes at the surviving scales were then adjusted accordingly. The schema for these adjustments is given in Figure 2.

Figure 2: Flow diagram of steps in cost-benefit calculations for allocation of effort within reefs.



### Sample Sizes to Detect Specific Effects

The numbers of experimental units to be sampled were estimated as a function of the desired statistical power to detect nominated effects of higher level factors, such as zoning status. This approach assumed that data would be analysed within a paradigm of Hypothesis testing, and we (arbitrarily) based our calculations on F-tests. In order to do so we first had to:

- i. Nominate the effect size (ES) consistent with an alternative hypothesis ( $H_a$ ) of interest in terms of both the magnitude and arrangement of means being examined (Bernstein & Zalinski 1983, Cohen 1988, Winer *et al.* 1991), or the variation among populations relative to that within populations (Cohen 1988, Fleiss 1969, Tiku 1967, 1972, Winer *et al.* 1991);
- ii. Specify a desired critical Type I error rate ( $\alpha_c$ ) against which to test the null hypothesis ( $H_0$ );
- iii. Specify the desired statistical power to detect the nominated  $H_a$  (if it existed), given the significance criterion  $\alpha_0 < \alpha_c$  (where  $\alpha_0$  is the probability of the data arising from  $H_0$ ).
- iv. Have estimates of the error variance(s) against which  $H_0$  would be tested.

We were then able to estimate the required numbers of samples necessary to realise the desired statistical power (or its complement, Type II error,  $\beta$ ) (Andrew & Mapstone 1987, Cohen 1988, Mapstone 1995, 1996, Peterman 1990, Winer *et al.* 1991) by varying sample size and deriving  $F'$  to satisfy the relations:

$$P(F_{u,v,0} > F') < \alpha_c \quad P(F_{u,v,\lambda} < F') < \beta$$

where

$\alpha_c$  = critical Type I error rate for the test of  $H_0$ ;

$\beta$  = the desired Type II error rate if  $H_0$  was not rejected;

$P(F_{u,v,0} > F')$  = the proportion of F-ratios from an F-distribution with numerator and denominator degrees of freedom  $u$  and  $v$  and non-centrality parameter of zero that would be greater than  $F'$ ;

$P(F_{u,v,\lambda} < F')$  = the proportion of F-ratios from an F-distribution with numerator and denominator degrees of freedom  $u$  and  $v$  and non-centrality parameter of  $\lambda$  ( $\lambda > 0$ ) that would be less than  $F'$ .

The non-centrality parameter,  $\lambda$  (Lambda), is the representation of the hypothesis under which the distribution of F is derived ( $H_0$ ,  $\lambda=0$ ;  $H_a$ ,  $\lambda>0$ ). Lambda can be parameterised in various ways, but all are based on the ratio of two measures of variation. In general, (for fixed effects)<sup>7</sup> the numerator is calculated from the Effect Size expected under  $H_a$ , and is specified exactly as that variation among means which would result if the alternative hypothesis were (exactly) true. The denominator, however, is error variance (within populations) and is invariably estimated from data - and therefore has uncertainty associated with it. Since each F-distribution depends on the exact value of  $\lambda$ , variation in the error variance (which means uncertainty in  $\lambda$ ) will mean uncertainty in the choice of F-distribution appropriate for the alternative hypothesis from which the above relation is satisfied<sup>7</sup>. The value of  $v$  necessary to satisfy the relations will depend on which (alternative) F-distribution is used, and, therefore, sample sizes estimated from power analyses will vary with variations in  $\lambda$ . Thus, in the most common manifestation, sample sizes predicted from analyses of statistical power will be inexact (Keough & Mapstone 1995, Mapstone 1995, 1996).

Exact predictions of sample size can be derived only if either: a) the denominator (error) variance for the F-ratio, and hence also for the non-centrality parameter, is known and known to be absolutely stable under future sampling regimes (which is unlikely); or b) the non-centrality parameter is specified exactly - *ie* the *ratio* is stipulated rather than only the numerator (ES). The latter means that the effect size likely to be detectable with nominated power and predicted sample

<sup>7</sup> Note that the use of non-central F-distributions is appropriate only for calculating power to detect fixed effects (Winer 1971, Winer *et al.* 1991). When considering random effects, the distribution of F under  $H_a$  is a variant of the central F-distribution and does not involve non-central distributions. All our calculations were for detecting fixed effects, and we accordingly always estimated power from non-central distributions.

size will be known *a priori* only as a multiple of the (realised) error variance (Cohen 1988). That is, differences among means will increase or decrease in direct proportion to the estimate of the numerator of  $\lambda$ , and can be depicted as a specific set of differences only *a posteriori*, and then only for the data set in hand. Effectively, this means that uncertainty in the result has been moved from the estimated sample size to the linear measure of the effect size(s) detectable.

In considering the properties of statistical power for future studies, then, we did three things.

1. We predicted required sample sizes based on error terms of  $MS_{\text{reef}}$  and  $MS_{\text{Hr(SR)}}$  estimated from the data from each Shelf Position x Region combination. We then used these multiple values to estimate empirically the variation in such predicted sample sizes likely in field sampling of GBR organisms. In this procedure, we used both the Mean Squares from our data, and those expected if sampling had been optimised within reefs and Habitats. For example, assuming the average predicted optimum numbers of locations, sites, and transects to be sampled within a reef in a given Region and Shelf Position were  $\hat{l}$ ,  $\hat{s}$ , and  $\hat{t}$  respectively, the expected  $MS_{\text{reefs}}$  would be  $MS_e = \sigma_e^2 + \hat{l}\sigma_l^2 + \hat{s}\hat{t}\sigma_s^2 + \hat{l}\hat{s}\hat{t}\sigma_t^2$ . In both cases, we stipulated the ES as two means separated by 50% of existing grand mean population density within the respective Shelf Position and Region.
2. We calculated the (exact) number of reefs that would have to be sampled to detect effects stipulated as a fixed value for  $\lambda$ . The parameterisation of  $\lambda$  we used was that employed in the SAS software,  $\lambda = n' SS_{\text{effect}} / MS_{\text{within}}$ , where  $n'$  is the total number of data from which each mean of the *effect* is estimated and  $MS_{\text{within}}$  is the denominator of the relevant F-ratio (see also Tiku 1967, 1972). The alternative hypothesis here was that  $\lambda = n'$ , that is  $SS_{\text{effect}} = \sigma_{\text{within effect}}^2$ .
3. We calculated, on the basis of the data from the four reefs in each region at each Shelf Position, the ES expected to be detectable having sampled only 4 reefs.

In the first case, weight is given to the magnitude *per se* of differences among means, and imprecision or variation in estimates of the within population variance will result in uncertainty in either the expected Type II error rates (if sample size is fixed) or predicted sample sizes required to detect the ES (if Type II error rates are fixed). In the second, emphasis is on the amount of variation among population means relative to the variation within populations (see also Cohen 1988), but the actual value of the ES is not emphasised because it will vary with variation in the size of within-population heterogeneity (variance). Here, Type II error rates or predicted sample sizes will be invariable, but for tests of effects of uncertain (linear) size.

We also considered the likely sampling requirements for monitoring the effects of local effects of human activities such as tourism. To do so, we considered an hypothetical example of monitoring the difference (*post hoc*) between one location subject to impact and a number of control (= non-impact) locations. Such a case would parallel the monitoring of pontoon installations on the GBR. We considered the locations to represent the effective experimental units and allowed for five replicate transects (= sub-samples) at each location. We assumed that the data in such cases would be analysed as unbalanced (one impact and  $n$  control locations) one-way ANOVA with sub-sampling of each location. The error variances for contrasts between the 'impact' and 'control' conditions were  $MS_{\text{locations}}$  estimated from our data for front reefs and back reefs at each of the 24 reefs we sampled. This provided 48 estimates of: i) predicted sample sizes to detect 50% difference between control and impact conditions; and ii) ESs detectable if only 4 control locations were sampled. As with the analyses of reef-scale replication, critical Type I error and potential Type II error were set at 0.10 ( $\alpha_c = \beta_o = 0.1$ ). Keough and Mapstone (1995) have described the calculations of power for such analyses. Note, however, that the designs we considered did not conform to BACI designs since we had no estimates of space-time interactions for location variances. Thus, we were considering the characteristics of 'one-off' comparisons, for example after a pontoon had been installed without baseline monitoring, or where the effect of an unexpected local event (such as an oil spill or vessel grounding) was being estimated.



### Effects of Incomplete Sampling within Reefs

We also examined some location effects within reefs in order to consider the implications of sampling only selected parts of reef perimeters in previous or subsequent monitoring (*e.g.*, Ayling 1983a,b, Ayling & Ayling 1984a,b,c, 1985, 1986a,b; AIMS 1992, Sale *et al.* 1984, Doherty 1987). We compared mean abundances among Regions and Shelf Positions for each of the locations within each habitat. For these analyses we treated the locations as fixed effects that potentially characterised reefs in different ways because of consistent environmental effects of, for example, being at the northern or southern extremities of reefs. We used means from the same relative locations on the four reefs at each shelf position in each region as replicates for the analyses in order to test whether the same sets of reefs were characterised in the same way by data from different locations. Interactions between locations and Regions and/or Shelf Position would indicate that sampling only single locations might misrepresent the larger scale effects on abundances over whole reefs, although the severity of misrepresentation (if any) would depend on the specific form of pattern(s) underlying the interactions.

The analytical model for the analyses within each habitat type was:

$$y_{ijk_r} = \mu_{...} + L_{i..} + R_{.j.} + S_{..k} + LR_{ij.} + LS_{i.k} + RS_{.jk} + LRS_{ijk} + \varepsilon_{ijk_r}$$

where

$\mu_{...}$  is the population grand mean abundance over all factors;

$y_{ijk_r}$  is the  $r^{\text{th}}$  mean of data taken from the relative Location  $i$  on several reefs in Region  $j$  and Shelf Position  $k$ ; and

$\varepsilon_{ijk_r}$  is a random normal error associated with each location mean.

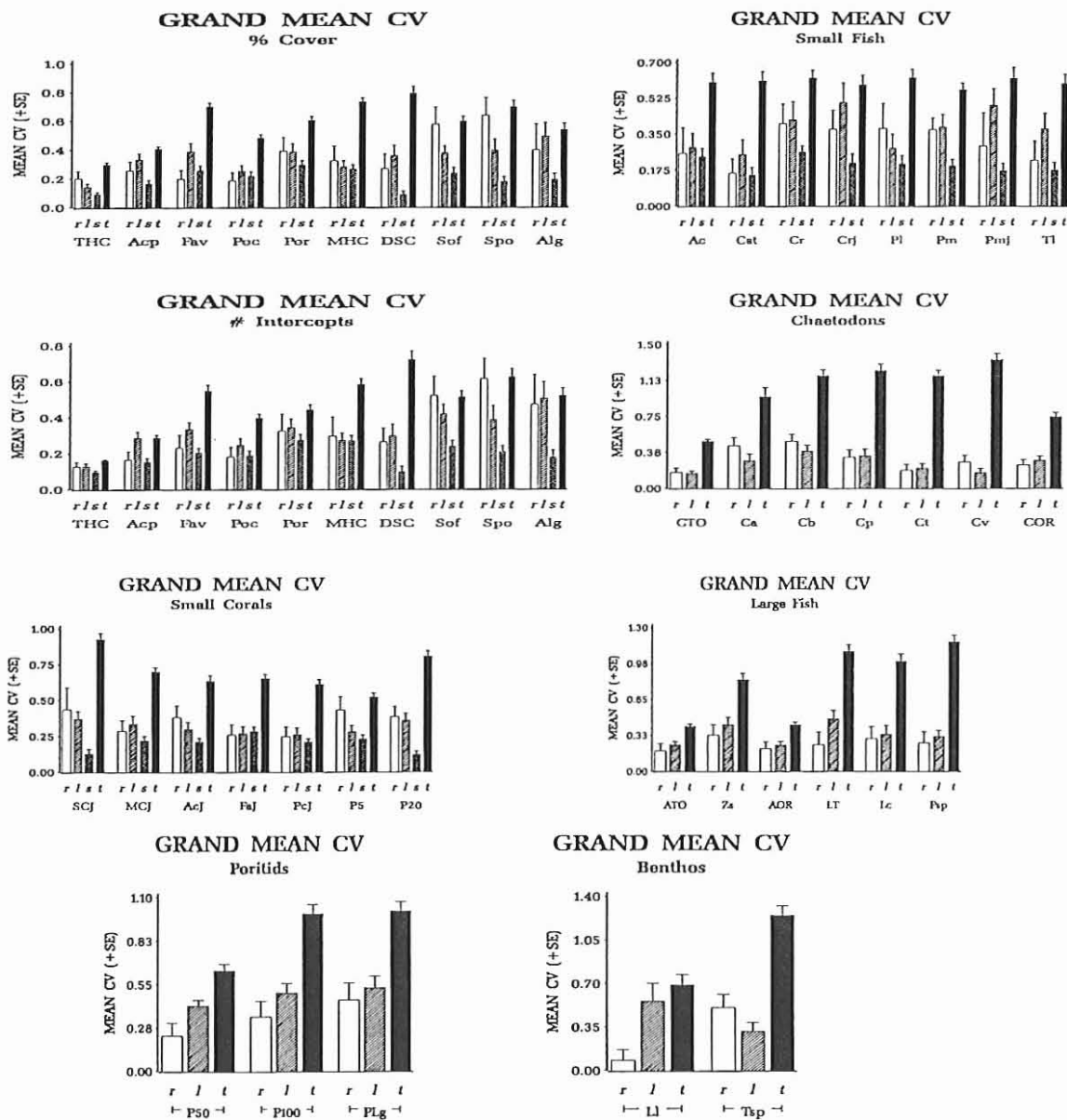
Since all main effects and their interactions were considered fixed, all terms were tested against the residual Mean Square.

## RESULTS

### Scale Related Components of Variation

Variations in abundance estimates showed consistent scale-related patterns. For both fishes and benthic organisms Coefficients of Variation (CV) among transects within sites or locations ( $CV_t$ ) were considerably greater than those among reefs ( $CV_r$ ), locations ( $CV_l$ ), or sites ( $CV_s$ ) (Fig. 3).  $CV_t$  were typically at least 0.5, and often closer to 1.0 or greater. Neither  $CV_r$ , nor  $CV_l$ , nor  $CV_s$  usually exceeded 0.4-0.5. Standardised variation among reefs and locations were most often of approximately equal magnitude for both fishes (19 cases out of 21 taxa) and benthos (25 of 32 variables). Variation among sites within locations was uniformly the scale of smallest variation (Fig. 3).

**Figure 3:** Overall mean Coefficients of Variation at each scale sampled for each taxon analysed. Abbreviations: SE - Standard Error; *r*, *l*, *s*, & *t* indicate variations among reefs, locations, sites, and transects respectively; Taxonomic abbreviations - see Table 2.



### Spatial patterns in Coefficients of Variation

Spatial analyses of coefficients of variation indicated relatively few significant changes in average levels of variation across habitats, shelf position, and regions at most scales (Table 5, Appendix 2). When significant effects did occur, they were most often at reef-scale variation - *ie*,  $CV_r$  differed systematically more often than  $CV_l$  (locations),  $CV_s$  (sites), or  $CV_t$  (transects) (Table 5). Indeed, not one taxon showed significant variation in  $CV_l$  (Table 5, Appendix 2), and of those taxa sampled at different sites within locations, only one (Juvenile pocilloporids) showed any significant patterns in  $CV_s$  (Table 5, Fig. 4). In this case, the interaction between Habitat and Region significantly affected  $CV_s$ , but no consistent patterns were evident.

**Table 5:** Summary results of ANOVA testing for the effects of Habitat, Shelf Position, and Region on Coefficients of Variation at each scale sampled. Results are included only where at least one term in the ANOVA proved statistically significant by scalable decision criteria (Mapstone 1995, 1996). Analyses for some taxa were restricted because those taxa of fish were absent or extremely uncommon in some strata (see previous section). The analyses for fish are indicated at the bottom of Table 5B. Detailed results of all analyses are provided in Appendix 2. \* :  $\alpha_o < \alpha_c = \beta$ ; - :  $\alpha_o > \alpha_c = \beta$ ; n/a : term not testable.

#### A: Line transects and small corals

VARIABLE	TAXON	HAB	REGn	SHELF	HR	HS	SR	HSR
$CV_{reef}$ % Cover	Pocilloporidae	*	-	-	-	-	-	n/a
	Poritidae	-	-	-	-	-	-	n/a
	Total Hard Coral	-	-	-	-	-	*	n/a
	Soft Corals	*	-	*	*	*	*	n/a
	Sponges	*	*	*	*	*	*	n/a
Intercepts	Poritidae	-	*	-	*	-	-	n/a
	Total Hard Coral	-	-	-	*	*	*	n/a
	Dead Standing Coral	-	-	-	-	*	-	n/a
	Soft Corals	*	-	*	*	*	*	n/a
	Sponges	-	*	-	*	-	*	n/a
All Algae	-	-	-	-	*	-	n/a	
$CV_{site}$	Small Pocilloporids	-	-	-	*	-	-	-
$CV_{transect}$ % Cover	Pocilloporidae	*	-	-	-	-	-	-
	Dead Standing Coral	*	-	*	-	-	-	-
	Sponges	*	-	-	-	-	-	-
Intercepts	Dead Standing Coral	*	-	*	-	-	-	-
Small Corals	Small Soft Corals	*	-	-	-	-	-	-

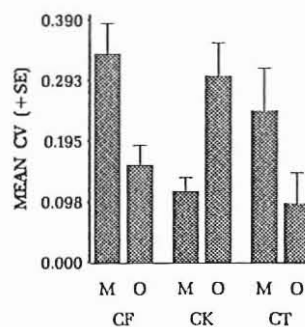
**B: Fishes & Sessile Benthos counted in 50m x 5m Transects**

VARIABLE	TAXON	HAB	REG <sup>n</sup>	SHELF	HR	HS	SR	SRH	H-S	H-SR
<i>CV<sub>reef</sub></i> Large Fish	All Lutjanids <sup>1</sup>	-	-	*	-	-	-	n/a	n/a	
	Total Acanthurids <sup>1</sup>	-	-	-	-	*	-	n/a	n/a	
	<i>Z. scopas</i> <sup>1</sup>	-	-	-	-	*	-	n/a	n/a	
	Other Acanthurids <sup>1</sup>	-	*	-	-	-	-	n/a	n/a	
	All Chaetodonts <sup>1</sup>	*	*	*	*	-	*	n/a	n/a	
	<i>C. aureofasciatus</i> <sup>4</sup>	*	*	n/a	n/a	n/a	n/a	n/a	n/a	
	<i>C. baronessa</i> <sup>1</sup>	*	*	*	*	*	*	n/a	n/a	
	<i>C. trifasciatus</i> <sup>1</sup>	-	*	*	*	-	*	n/a	n/a	
Small Fish	<i>P. lacrymatus</i> <sup>1</sup>	-	-	-	*	-	-	n/a	n/a	
	Recruit <i>P.m.</i> <sup>3</sup>	n/a	*	n/a	n/a	n/a	n/a	n/a	-	
	<i>T. lunare</i> <sup>3</sup>	n/a	-	n/a	n/a	n/a	n/a	n/a	*	
Benthos	<i>Tridacna</i> spp. <sup>1</sup>	-	*	*	*	*	-	n/a	n/a	
	Poritids 21-50cm <sup>1</sup>	-	-	-	-	-	*	n/a	n/a	
	Poritids >100cm <sup>1</sup>	-	*	-	-	-	*	n/a	n/a	
<i>CV<sub>transect</sub></i> Large Fish	All Chaetodonts <sup>1</sup>	-	*	-	-	-	-	-	n/a	n/a
	<i>L. carponotatus</i> <sup>3</sup>	*	-	n/a	-	n/a	n/a	n/a	n/a	-
Small Fish	<i>A. curacao</i> <sup>2</sup>	*	-	-	-	-	-	-	n/a	n/a
	<i>P. moluccensis</i> <sup>5</sup>	n/a	*	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	Recruit <i>C.r.</i> <sup>4</sup>	*	-	n/a	*	n/a	n/a	n/a	n/a	n/a
Benthos	Poritids 21-50cm <sup>1</sup>	*	*	-	-	-	*	-	n/a	n/a

ANOVA Models: <sup>1</sup> Full HxSxR; <sup>2</sup> HxSx2 Regions; <sup>3</sup> All of MS reefs + OS back-reefs; <sup>4</sup> HxR, MS only; <sup>5</sup> R, OS back-reefs only.

**Figure 4:** Region specific effects of Habitat on CV<sub>s</sub> for juvenile pocilloporids. Abbreviations: SE - Standard Error; BR - Back-reef; FR - Front-reef; CF - Cape Flattery; CK - Cooktown; CT - Cape Tribulation; M - Mid-shelf; O - Outer-shelf.

**Small Pocilloporids**



Significant systematic effects on CV<sub>r</sub> were few also, and all but one were simple main effects, usually of Habitat. Counts of *L. carponotatus*, 21-50cm poritids, and juvenile soft corals were all about 30% more variable in front-reef habitats than in back-reef habitats (Fig. 5), whilst counts of *A. curacao*, percent coverage by pocilloporids and sponges, and coverage and numbers of fragments of dead coral were 30-50% more variable in back-reef habitats than in front-reef habitats (Fig. 5). These effects were strong relative to within-effects variation ( $\alpha_c = \beta < 0.01$ , Appendix 2).

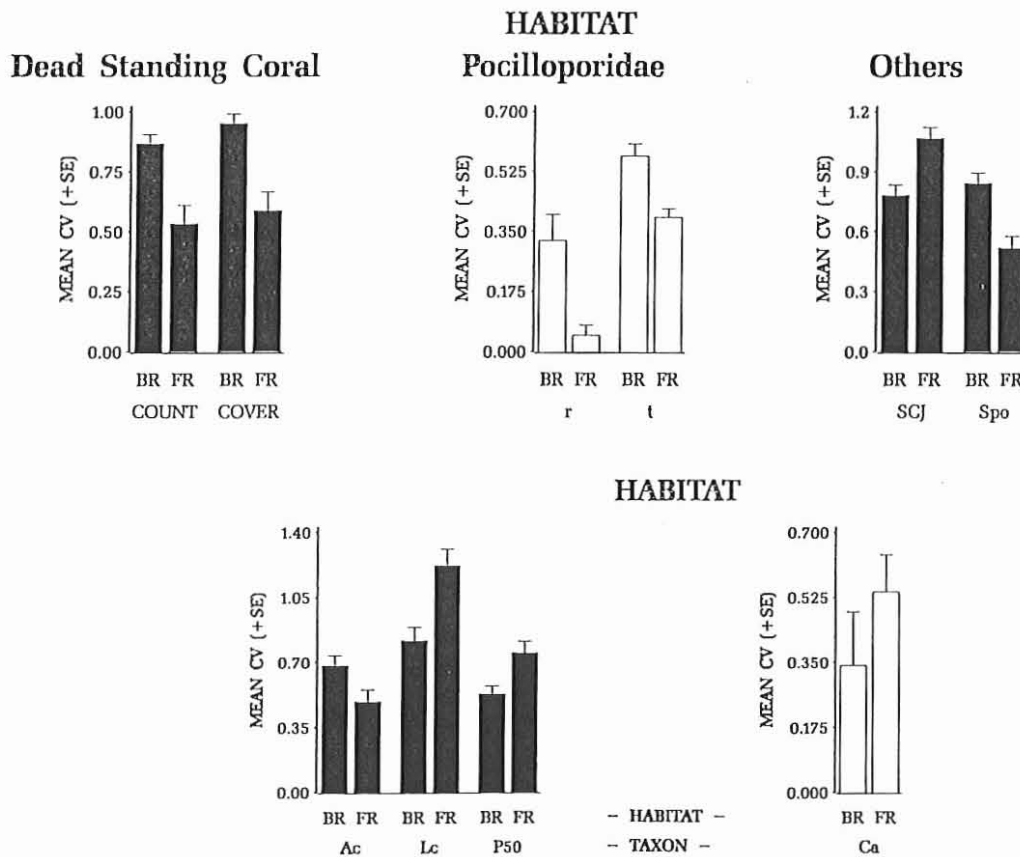
Main effects of Shelf Position on CV<sub>r</sub> were also present for dead standing corals (MS>OS; Fig. 5), and Region effects were significant for total chaetodons (Cooktown>Cape Tribulation>Cape Flattery) and *P. moluccensis* (Cape Tribulation > Cooktown ≈ Cape Flattery) (Fig. 5).

Unlike effects on CV<sub>r</sub>, straightforward main effects on CV<sub>t</sub> were relatively few, with most effects on CV<sub>t</sub> involving the interaction of two factors (Table 5, Appendix 2). Main effects of Habitat on CV<sub>t</sub> were clear, however, for *C. aureofasciatus* (FR>BR), and percent coverage by pocilloporid corals (BR>FR) (Fig. 5).

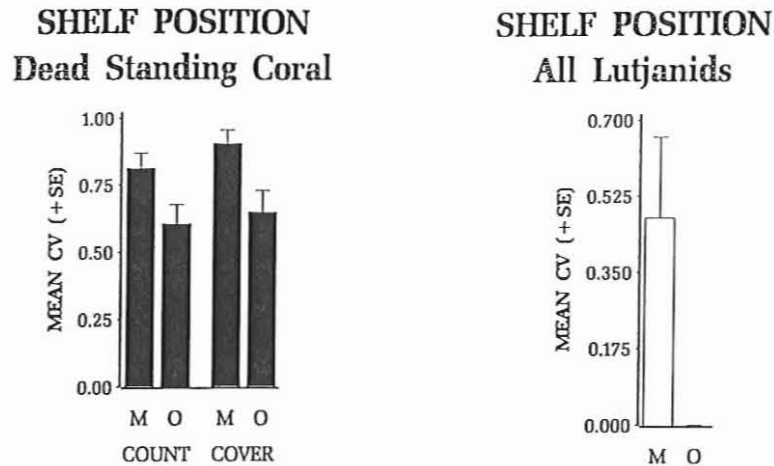
It is important to recognise, however, that the ‘significance’ criteria for these effects (on CV<sub>t</sub>) were relatively liberal (0.14-0.2, Appendix 2), mainly because of the low degrees of freedom of the F-tests (df=1,2 at best). Nevertheless, the probability of the observed effects arising from a null model of no effect were generally low compared to the significance criterion ( $\alpha_o < 0.1$  in most cases).

**Figure 5:** Statistically significant main effects of Habitat (A), Shelf Position (B), and Region (C) on CV<sub>r</sub> (shaded bars) and CV<sub>t</sub> (open bars). Abbreviations: SE - Standard Error; BR - Back-reef; FR - Front-reef; CF - Cape Flattery; CK - Cooktown; CT - Cape Tribulation; M - Mid-shelf; O - Outer-shelf; r - CV<sub>r</sub>; t - CV<sub>t</sub>; Taxonomic abbreviations - see Table 2.

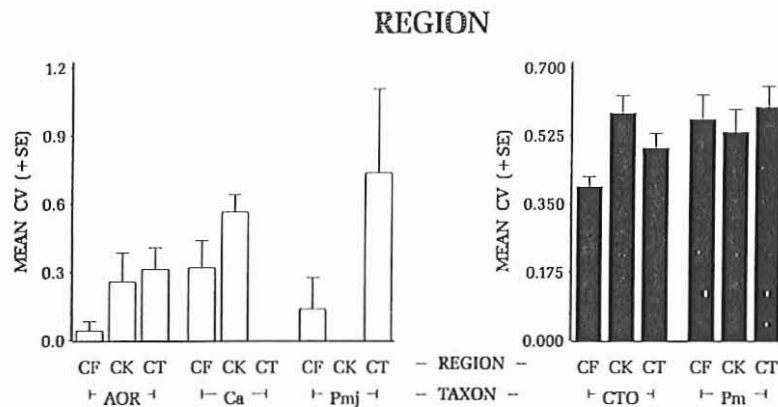
**A: Habitat Main Effects**



### B: Main Effects of Shelf Position



### C: Region Main Effects



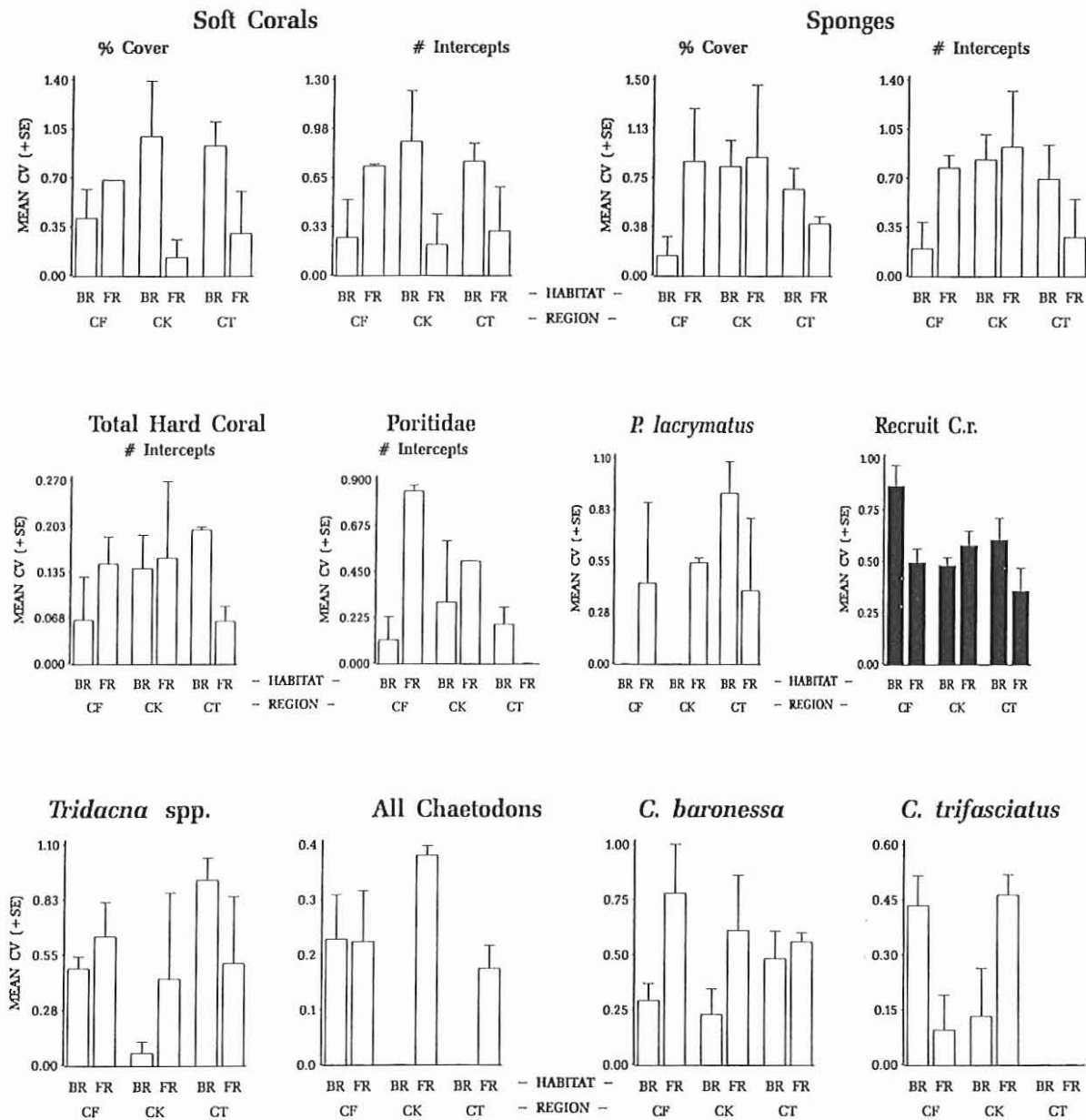
Habitat and Region interacted to effect CV<sub>i</sub> for juvenile *C. rollandi* ( $\alpha_c = \beta < 0.033$ ), but differences among regions were not consistent across both habitats and nor were Habitat effects consistent among regions (Fig. 6). The interaction between Shelf Position and Region significantly affected CV<sub>i</sub> for 21-50cm poritids ( $\alpha_c = \beta = 0.002$ ), but again the effects of neither factor were consistent across the levels of the other (Fig. 7).

Similarly, for CV<sub>r</sub> significant interactions between Habitat and Region (Fig. 6) and Shelf Position and Region (Fig. 7) occurred, but patterns were generally not consistent among taxa nor even for one of the factors across all levels of the other for even one taxon. Perhaps the only generalisation to be made would be that results from the Cape Flattery region were far more consistent than those from the other regions. CV<sub>r</sub> in the Cape Flattery Region was generally greater on front-reefs than in back-reef habitats (Fig. 6), and greater on outer-shelf reefs than on mid-shelf reefs (Fig. 7). Although large Habitat or Shelf Position effects were present in the other regions, clearly they were not consistent among taxa.

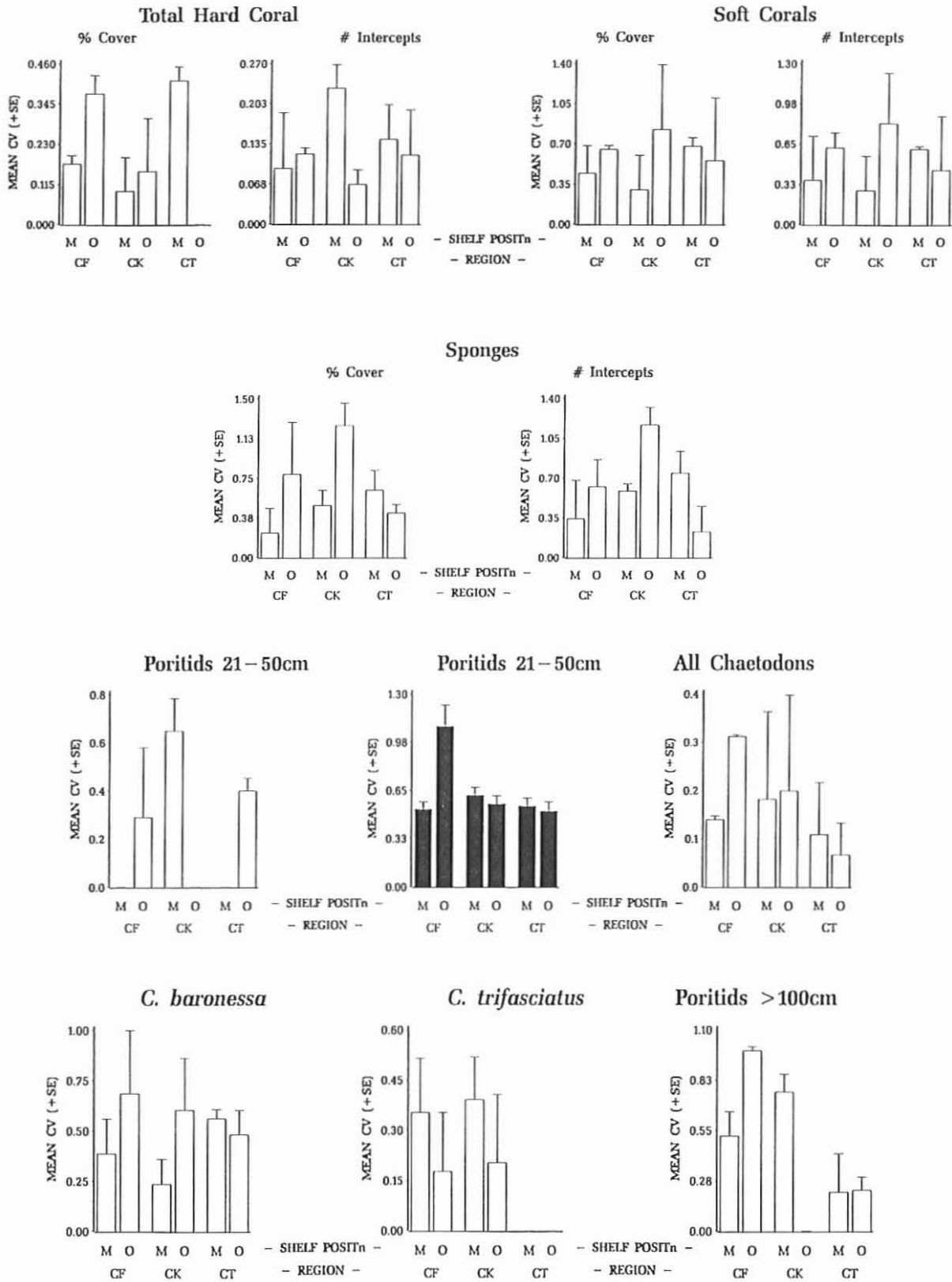
Standardised variation in hard coral coverage was significantly greater on outer-shelf reefs in the Cape Flattery and Cape Tribulation regions, but not in the Cooktown region, whilst precisely the opposite pattern was true when abundances of hard coral were measured by numbers of intercepts (Fig. 7). For soft corals and sponges (by either measure), and juvenile pocilloporids, abundances were more variable on outer-shelf reefs than on mid-shelf reefs off Cooktown, but the same effect was not present in the other regions, being either reversed (juvenile pocilloporids and sponges) or non-existent (soft corals) (Fig. 7). Further, for no group were effects of shelf position consistent

across regions (Fig. 7), and regional patterns in the effects of Shelf Position on standardised variation were not the same for any two groups (Fig. 7). Effects of Region on variation were equally variable with habitat, and Habitat effects were not consistent across regions for any group (Fig. 6).

**Figure 6:** Interactions of Habitat and Region effects on standardised variations in estimates of abundances. Unshaded bars represent  $CV_r$ , and shaded bars represent  $CV_t$ .  
**Abbreviations:** SE - Standard Error; BR - Back-reef; FR - Front-reef; CF - Cape Flattery; CK - Cooktown; CT - Cape Tribulation.

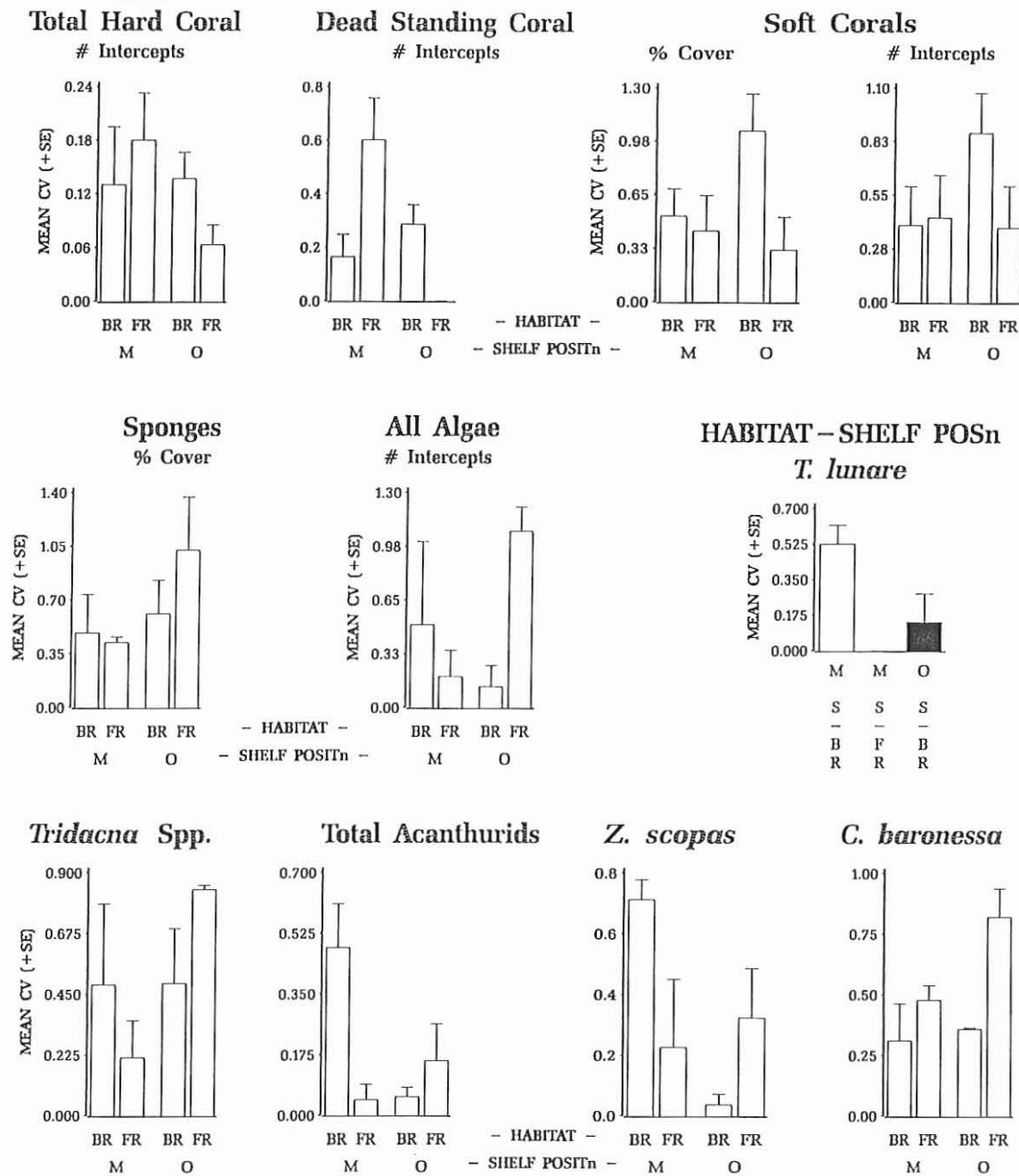


**Figure 7:** Interactions of Shelf Position and Region that affected standardised variations in estimates of abundances. Unshaded bars represent  $CV_r$ , and shaded bars represent  $CV_t$ . Abbreviations: SE - Standard Error; CF - Cape Flattery; CK - Cooktown; CT - Cape Tribulation; M - Mid-shelf; O - Outer-shelf.





**Figure 8:** Interactions between Shelf Position and Habitat effects on standardised variations in estimates of abundances. Only effects on CV, were significant for any group.  
**Abbreviations:** SE - Standard Error; BR - Back-reef; FR - Front-reef; M - Mid-shelf; O - Outer-shelf.



Interactions between Habitat and Shelf Position affected standardised reef-scale variation in abundances of 5 groups of sessile benthos and 4 fishes (Table 5). Again, however, there was little generality to be found in the genesis of the significant interactions. For intercept data for total hard corals and dead standing corals, and both cover and intercept data for soft corals, variation among outer-shelf reefs was greater in back-reef habitats than in front-reef habitats, whereas on mid-shelf reefs either variation was relatively similar across habitats (hard corals & soft corals) or greater in the front-reef habitats (dead corals) (Fig. 8). Variations in abundances of sponges were not statistically significant in either habitat, whilst variation in algal abundance (by intercepts) was greater on front-reefs only on outer-shelf reefs (Fig. 8). Similarly, there was no conspicuous consistency in the effects of shelf position on variation. For total hard corals and dead standing

corals, variation was small on the fronts of outer-shelf reefs relative to that on mid-shelf reefs (though the reverse was true for algae and sponges), but in back-reef habitats variation was comparable in both shelf positions (Fig. 8). For soft corals variation was greater on back-reefs of outer-shelf reefs than mid-shelf reefs, but variation on fronts of reefs was relatively even (Fig. 8).

In summary, although standardised measures of variation showed large effects of Shelf Position, Habitat, and Region either singly or in combination, those effects were not consistent within or among taxa except in the Cape Flattery region, and no clear generalisations about systematic geographic changes in variability were evident.

## Estimation of Sampling Requirements

### *Allocation of Sampling Effort Within Reefs*

Cost-benefit analyses resulted in very variable predictions of optimum allocation of sampling effort among strata within reefs (Table 6). When analysed by habitat, analyses of most taxa resulted in at least one estimate of 0-1 samples at one (or two) scale(s), with the result that all effort would have been put into increased replication at the other scale(s). Consequently, the distributions of predicted numbers of locations, sites, and transects were generally positively skewed (Table 6).

In both habitats, sampling at sites within locations proved the least productive (in terms of accounting for variance) most often for most taxa (median number of sites  $\sim 1$ ) (Table 6). Whilst locations were of low priority ( $n_{locn} \sim 1$ ) at least once for all taxa except 21-50cm poritids in back-reef habitats, median replication of locations was one in both habitats for only three chaetodontid fishes (*C. plebeius*, *C. trifasciatus*, and *C. vagabundus*), three pomacentrid fishes (*A. curacao*, *C. atripectoralis*, and *P. lacrymatus*), and the clams (*Tridacna* spp.) (Table 6). For most other taxa, our data suggested that about 3-7 locations should be sampled in each habitat (Table 6). The mean of the median recommended replication of locations for those taxa where locations were non-trivial was 5.4 ( $\pm 0.32$  SE,  $n=32$ ) in back-reef habitats and 5.7 ( $\pm 0.39$  SE,  $n=29$ ) in front-reef habitats, under the constraint that sampling effort was dispersed over the entire habitat

For no taxon was the optimum effort to be put into sampling transects consistently trivial. The 10<sup>th</sup> percentile of transect replication was most frequently 3, and no median score was one. Average median optimum replication of transects was less for line intercept data ( $3.28 \pm 0.41$  SE) and counts of poritids ( $3.1 \pm 0.37$  SE) than for counts of small corals ( $5.4 \pm 0.22$  SE), small fishes ( $7.3 \pm 0.70$  SE), or large fishes ( $7.5 \pm 0.60$  SE). The 90<sup>th</sup> percentile estimates of optimum replication at each scale were about 15-18 in most cases, but the consistency among these reflects the number of units at any one scale alone that would be sampled within the limit of one day of sampling per habitat.

When variance estimates and scale-specific costs were averaged across habitats within each reef and cost-benefit calculations done for a limited cost of one day per whole reef, the resultant optimum allocations of effort were more uniform than those within each habitat (Table 6). These values would underestimate the true variance of predicted sample sizes more than habitat-specific values, however, because we averaged more variance and cost estimates before doing the cost-benefit analyses and did not consider the variances within those averaged values in our calculations. Note that the data in table 6C are maxima and minima (rather than upper and lower 10% quantiles), and that for several taxa locations were never trivial (Minimum estimate always  $> 1$ ) in the reef-wide cost-benefit analyses.

**Table 6:** Optimum allocations of effort to sampling locations, sites, and transects within back-reefs (A), front-reefs (B), and over whole reefs (C). Optimum allocations were estimated for the 4 reefs at each shelf position in each region, giving 12 estimates at each scale. 10% = 10<sup>th</sup> percentile value, Med. = median value, 90% = 90<sup>th</sup> percentile.

A: Back-reef		Locations			Sites			Transects		
		10%	Med.	90%	10%	Med.	90%	10%	Med.	90%
Large Fishes	Total Acanthurids	1	7	13	-	-	-	1	3.5	13
	<i>Z. scopas</i>	1	5	10	-	-	-	2	6	17
	Other Acanthurids	1	7	13	-	-	-	1	3.5	16
	All Chaetodonts	1	3.5	14	-	-	-	2	9.5	16
	<i>C. aureofasciatus</i>	1	5	8	-	-	-	3	7	16
	<i>C. baronessa</i>	1	5	10	-	-	-	3	6	16
	<i>C. plebeius</i>	1	1	10	-	-	-	3	10	15
	<i>C. trifasciatus</i>	1	1	11	-	-	-	2	10	15
	<i>C. vagabundus</i>	1	1	8	-	-	-	3	11.5	16
	Other Chaetodonts	1	4.5	13	-	-	-	2	7.5	16
	All Lutjanids	1	6	10	-	-	-	2	5	15
	<i>L. carponotatus</i>	1	7	11	-	-	-	3	5.5	14
	<i>Plectropomus</i> spp.	1	4	11	-	-	-	2	9.5	13
Small Fishes	<i>A. curacao</i>	1	1	8	1	1.5	15	4	6.5	12
	<i>C. atripectoralis</i>	1	1	6	1	1	9	6	11	14
	<i>C. rollandi</i>	1	1	21	1	1.5	12	2	7	13
	Recruit C.r.	1	1	12	1	1	11	3	6	17
	<i>P. lacrymatus</i>	1	1	9	1	1	12	4	10	18
	<i>P. moluccensis</i>	1	5	16	1	1	10	3	6	13
	Recruit P.m.	1	6.5	12	1	1	10	4	5.5	12
	<i>T. lunare</i>	1	3	9	1	1	11	5	8.5	14
Small Corals	Small Acroporids	1	7.5	15	1	1	12	2	5	7
	Small Faviids	1	5	16	1	1	12	3	5.5	16
	Small Pocilloporids	1	1	12	1	1	12	2	5	18
	Misc. Small Hards	1	4.5	10	1	1	9	4	6	17
	Small Soft Corals	1	5	9	1	1	10	3	5.5	19
Poritid Counts	Poritids <6cm	1	9.5	19	1	1	24	1	2	8
	Poritids 6-20cm	1	7.5	21	1	1	8	1	3.5	22
	Poritids 21-50cm	3	8	16	-	-	-	1	2	12
	Poritids 51-100cm	1	7	16	-	-	-	1	2	12
	Poritids >100cm	1	7	13	-	-	-	1	3	12
% Coverage	Total Hard Coral	1	4.5	19	1	1	9	1	3	12
	Acroporidae	1	8	16	1	1	11	1	2	4
	Faviidae	1	1.5	13	1	1	11	1	3	10
	Pocilloporidae	1	4	9	1	1	10	1	2.5	10
	Poritidae	1	5	12	1	2	16	1	2	4
	Misc. Hard Corals	1	5	11	1	1	9	1	3	8
	Dead Standing Coral	1	3.5	9	1	1	4	2	4.5	11
	Soft Corals	1	7.5	13	1	1	7	1	2	10
	Sponges	1	2	11	1	1	8	1	3.5	12
	Total Algae	1	4	12	1	1	11	1	2	10
	Misc. Benthos	<i>L. laevigata</i>	1	8.5	15	-	-	-	1	3
<i>Tridacna</i> spp.		1	1	11	-	-	-	2	10	14

Table 6 (Continued)

B: Front-reef		Locations			Sites			Transects		
		10%	Med.	90%	10%	Med.	90%	10%	Med.	90%
Large Fishes	Total Acanthurids	1	7.5	11	-	-	-	1	3	15
	<i>Z. scopas</i>	1	7.5	12	-	-	-	1	3	14
	Other Acanthurids	1	7	11	-	-	-	1	3	15
	All Chaetodons	1	2.5	9	-	-	-	2	9.5	15
	<i>C. aureofasciatus</i>	1	6	10	-	-	-	2	4	15
	<i>C. baronessa</i>	1	3	9.5	-	-	-	2	8	15.5
	<i>C. plebeius</i>	1	1	7	-	-	-	3	9	15
	<i>C. trifasciatus</i>	1	1	9	-	-	-	3	11	16
	<i>C. vagabundus</i>	1	1	5	-	-	-	5	12	15
	Other Chaetodons	1	5.5	13	-	-	-	2	6.5	15
	All Lutjanids	1	3.5	15	-	-	-	1	9.5	16
	<i>L. carponotatus</i>	1	2	8	-	-	-	4	11.5	16
	<i>Plectropomus</i> spp.	1	2	9	-	-	-	3	11.5	15
Small Fishes	<i>A. curacao</i>	1	1	9	1	1	9	4	8	16
	<i>C. atripectoralis</i>	1	1	7	1	1	2	4	15	17
	<i>C. rollandi</i>	1	7	12	1	1	3	4	5	15
	Recruit <i>C.r.</i>	1	8	13	1	1	8	4	6	13
	<i>P. lacrymatus</i>	1	1	10	1	1	11	4	7	15
	<i>P. moluccensis</i>	1	8.5	14	1	1	2	3	4	13
	Recruit <i>P.m.</i>	1	9	14	1	1	1	3	5	15
	<i>T. lunare</i>	1	5.5	18	1	1	12	3	5.5	10
Small Corals	Small Acroporids	1	1	11	1	5	16	2	4.5	9
	Small Faviids	1	1	10	1	1	14	3	5.5	15
	Small Pocilloporids	1	5	11	1	1	11	3	5	19
	Misc. Small Hards	1	5	12	1	1	10	3	5	16
	Small Soft Corals	1	5	9	1	1	1	4	7	17
Poritid Counts	Poritids <6cm	1	2	33	1	3.5	17	1	3	19
	Poritids 6-20cm	1	5.5	16	1	1	14	2	4	17
	Poritids 21-50cm	1	8	14	-	-	-	1	2	11
	Poritids 51-100cm	1	6	11	-	-	-	2	4	15
	Poritids >100cm	1	6	9	-	-	-	2	5.5	15
% Coverage	Total Hard Coral	1	4	12	1	1	7	1	3	12
	Acroporidae	1	6	13	1	1	12	1	2	10
	Faviidae	1	7.5	13	1	1	10	2	2	8
	Pocilloporidae	1	5	12	1	1.5	9	1	2	5
	Poritidae	1	4	12	1	1	10	1	3	7
	Misc. Hard Corals	1	2	9	1	1	12	2	3	11
	Dead Standing Coral	1	1	8	1	1	1	2	8	12
	Soft Corals	1	7.5	15	1	1	15	1	2	3
	Sponges	1	1	19	1	1	5.5	1	5	12
	Total Algae	1	1	13	1	1	6.5	1	8	12
Misc. Benthos	<i>L. laevigata</i>	1	8.5	14	-	-	-	2	3	15
	<i>Tridacna</i> spp.	1	1	11	-	-	-	2	11.5	15.5

C: Whole Reef	TAXON	Locations			Sites			Transects		
		Min.	Med.	Max.	Min.	Med.	Max.	Min.	Med.	Max.
Large Fishes	Total Acanthurids	6	8.5	11	.	.	.	2	3.5	7
	<i>Z. scopas</i>	5	9	12	.	.	.	2	3	8
	Other Acanthurids	6	8	10	.	.	.	3	4	6
	All Chaetodons	5	7.5	9	.	.	.	4	4	9
	<i>C. aureofasciatus</i>	1	4	9	.	.	.	4	8	15
	<i>C. baronessa</i>	1	7.5	9	.	.	.	3	4.5	15
	<i>C. plebeius</i>	1	5	8	.	.	.	4	8.5	15
	<i>C. trifasciatus</i>	1	3.5	7	.	.	.	6	9	15
	<i>C. vagabundus</i>	1	2.5	10	.	.	.	3	12.5	15
	Other Chaetodons	5	7	11	.	.	.	3	4.5	10
	All Lutjanids	1	7.5	9	.	.	.	3	4.5	21
	<i>L. carponotatus</i>	1	5	10	.	.	.	3	10	14
	<i>Plectropomus</i> spp.	1	6	8	.	.	.	5	7.5	14
Small Fishes	<i>A. curacao</i>	1	3	12	1	4	11	2	6.5	13
	<i>C. atripectoralis</i>	1	3	8	1	1	8	4	6	17
	<i>C. rollandi</i>	1	4	16	1	4.5	9	2	4	4
	Recruit <i>C.r.</i>	1	9	12	1	1	8	2	3	17
	<i>P. lacrymatus</i>	1	5.5	7	1	1.5	14	2	4.5	16
	<i>P. moluccensis</i>	1	11	13	1	1	8	2	4	6
	Recruit <i>P.m.</i>	5	10	12	1	1	2	3	3	6
	<i>T. lunare</i>	1	7.5	12	1	1	2	3	5	14
	Small Corals	Small Acroporids	1	8.5	12	1	1	13	2	3
Small Faviids		1	7.5	10	1	1.5	12	2	3	5
Small Pocilloporids		1	5.5	9	1	1	10	3	4.5	24
Misc. Small Hards		1	6	8	1	2	9	2	6	10
Small Soft Corals		1	3.5	8	1	1	1	4	14.5	19
Poritid Counts	Poritids <6cm	1	8	10	2	2	8	2	2.5	4
	Poritids 6-20cm	7	7.5	11	1	1	1	3	4	5
	Poritids 21-50cm	7	10.5	12	.	.	.	2	2	4
	Poritids 51-100cm	3	10	13	.	.	.	2	3	18
	Poritids >100cm	1	9.5	10	.	.	.	2	3	11
% Coverage	Total Hard Coral	5	6.5	10	1	1	2	2	2	4
	Acroporidae	3	9	12	1	1	4	1	1.5	4
	Faviidae	1	6	12	1	2	10	1	2	3
	Pocilloporidae	1	6.5	9	1	1	7	1	2	3
	Poritidae	1	7.5	11	1	2	10	1	1.5	4
	Misc. Hard Corals	1	4.5	10	1	2.5	11	1	2.5	5
	Dead Standing Coral	1	5.5	8	1	1	1	2	4	10
	Soft Corals	9	11	12	1	1	1	2	2	3
	Sponges	1	8	14	1	1	5	1	2	4
	Total Algae	1	7.5	15	1	1.5	18	1	1	3
Misc. Benthos	<i>L. laevigata</i>	1	10.5	13	.	.	.	2	2.5	14
	<i>Tridacna</i> spp.	1	7	11	.	.	.	3	5.5	11

### *Numbers of Reefs or Locations to be Sampled*

Predictions of the numbers of replicate reefs or locations required in order to detect nominated linear differences among means were highly variable both within and among taxa (Table 7), even though the critical ESs were stipulated in terms of multiples (50%) of existing densities<sup>8</sup>. Had critical ESs been specified as absolute numbers (*e.g.*, differences of 10 fish per 250m<sup>2</sup>), this variation would be expected to increase. Distributions of both predicted sample sizes (Table 7) and predicted detectable Effect Sizes (Table 8) were generally positively skewed, typically with one or two values considerably larger than all others.

There was little pattern to the results of these analyses. Estimates often ranged over more than an order of magnitude, although median values were mostly only about twice the minimum predicted sample sizes (Table 7). For relatively few taxa were median required sample sizes less than 10 reefs, however (Table 7). Sample size requirements generally decreased with increasing taxonomic aggregation before analyses, but family level analyses were not uniformly more consistent than species level analyses. For example, it was predicted that between 19 and 135 reefs would have to be sampled to detect a 50% difference in total lutjanids, but only 3-22 reefs were necessary to detect a similar difference in the densities of *C. trifasciatus* (Table 7).

Predictions of required replication for sampling fishes were generally far more variable in front-reef habitats than in back-reef habitats or over whole reefs (Table 7), although the acanthurids and lutjanids were exceptions. This pattern was not clear for sessile benthos, however, with sampling requirements frequently similar for both habitats and over the whole reef, or greater in back-reefs (Table 7).

As expected, optimising sub-sampling within reefs generally did not affect either the predicted replication of reefs (Table 7) or the Effect Sizes detectable with nominated replication (Table 8). Results based on error variances (MSSs) taken directly from our data were usually very close to those estimated after determining optimum within-reef allocation for most taxa (Tables 8, 9).

The differences between sets of reefs detectable with sample sizes of only four reefs also were highly variable (Table 8). This is to be expected since the results derive from the same estimates of error variance as the estimates of required sample size. Median detectable Effect Sizes for both corals and fishes were mostly between 40% and 150% of existing densities for whole reef data, and ranged up to over 300% with habitat-specific data for some taxa (Table 8). Within taxa, estimated ESs detectable mostly varied over a 2-4-fold range among the data from different regions and shelf positions upon which the estimates were based (Table 8).

Finally, when critical ES was specified as a multiple (1) of within population variance, the sample size needed was 3 reefs for a critical Type I error rate ( $\alpha_c$ ) and estimated potential for Type II error ( $\beta_o$ ) of 0.2 ( $\alpha_c=\beta_o=0.2$ ), 6 reefs at  $\alpha_c=\beta_o=0.1$ , and 8 reefs at  $\alpha_c=\beta_o=0.05$ . As discussed in the methods, this value was constant across all taxa and locations.

The estimated numbers of "control" locations that would have to be sampled in an impact monitoring programme to detect a difference between a single "impact" location and the average of the control locations equivalent to 50% of the control conditions are shown in Table 9. The differences that might be expected to be detectable after sampling 4 control locations are shown in Table 10. In both cases, estimates were generally larger and more variable in front-reef habitats than back-reef habitats. For only three of the most aggregated taxa (total hard coral coverage, total chaetodonts, & total acanthurids) and coverage by pocilloporid corals were the median sample sizes less than 15 (Table 9) or detectable effects sizes less than 100% of existing abundances (Table 10).

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<sup>8</sup> Specifying ES in this way - as a multiple of existing densities - is analogous to the stipulation of additive ESs for log-transformed data, although we chose not to transform the data for the reasons given earlier.

Table 7: The predicted number of reefs needed to be sampled to detect a 50% change in abundance with  $\alpha=\beta=0.10$ . The change was expressed as a percentage (50%) of existing abundances. 'Whole Reefs', 'Back-reefs', and 'Front-reefs' refer to the scale and habitat over which potential treatments might be applied and from which data hypothesis tests were assessed, as described in text.

TAXON	Whole Reef						Back Reef						Front Reef					
	Data			Optimised			Data			Optimised			Data			Optimised		
	Min.	Med.	Max.	Min.	Med.	Max.	Min.	Med.	Max.	Min.	Med.	Max.	Min.	Med.	Max.	Min.	Med.	Max.
<i>Large Fishes</i>																		
Total Acanthurid	2	4	19	2	4	18	3	5	32	3	5	31	2	4	11	3	3.5	11
<i>Z. scopas</i>	7	11	41	6	11	38	2	41.5	79	5	32	74	11	20.5	41	7	20	37
Other Acanthurids	2	5	17	2	5	17	3	5.5	29	4	5	29	2	4.5	12	3	4	12
All Chaetodonts	2	5.5	9	2	5.5	9	2	4.5	9	3	4	9	4	9	13	4	8.5	14
<i>C. aureofasciatus</i>	12	72.5	274	12	71.5	586	8	21	146	8	19	140	23	68	275	19	73.5	1176
<i>C. baronessa</i>	13	22	60	12	20.5	52	19	25.5	56	11	20	77	25	42	138	19	42.5	349
<i>C. plebeius</i>	9	15	21	8	15.5	36	6	14.5	47	9	23	46	6	33	81	22	28.5	114
<i>C. trifasciatus</i>	3	8	22	5	10	21	2	10.5	26	4	14	24	2	9	32	6	10.5	27
<i>C. vagabundus</i>	10	16.5	96	12	24	222	8	33	93	10	31.5	375	11	14	113	14	30.5	458
Other Chaetodonts	3	10	35	3	10	36	2	8	38	5	7.5	28	3	14.5	43	4	14	53
All Lutjanids	19	29	135	17	27	134	10	68.5	152	31	58	141	4	17	122	9	27.5	123
<i>L. carponotatus</i>	7	97	277	6	135	745	13	180	275	15	297.5	1496	11	34.5	275	14	37	1176
<i>Plectropomus</i> spp.	5	8.5	23	5	10	30	3	16	32	9	15	38	4	16	108	7	21.5	117
<i>Small Fishes</i>																		
<i>A. curacao</i>	9	13	29	6	11.5	26	4	21.5	62	5	17.5	70	3	23	275	3	21	1097
<i>C. atripectoralis</i>	19	26.5	126	10	27.5	102	4	28.5	203	12	28.5	258	25	63.5	275	19	81	878
<i>C. rollandi</i>	10	27.5	42	9	24	36	6	31.5	56	6	25	42	29	49.5	275	15	44	382
Recruit <i>C.r.</i>	10	23	61	6	17	60	13	29.5	61	8	24.5	56	20	47	71	28	34	70
<i>P. lacrymatus</i>	10	35.5	61	9	33.5	92	4	47	100	4	55.5	172	7	44	100	4	40.5	192
<i>P. moluccensis</i>	9	16	35	6	14.5	31	11	20	43	10	14.5	37	7	24.5	186	4	18	204
Recruit <i>P.m.</i>	10	29	94	8	23	86	5	18.5	136	8	26.5	114	7	31	66	7	15	104
<i>T. lunare</i>	5	25.5	46	4	21	43	13	21.5	47	11	25	43	9	15.5	138	4	13	167

Table 7 (Continued).

TAXON	Whole Reef						Back Reef						Front Reef					
	Data			Optimised			Data			Optimised			Data			Optimised		
	Min.	Med.	Max.	Min.	Med.	Max.	Min.	Med.	Max.	Min.	Med.	Max.	Min.	Med.	Max.	Min.	Med.	Max.
<i>Small Corals</i>																		
Misc. Small Hards	8	14.5	25	6	12	23	5	11	23	4	9.5	24	24	32	53	8	21.5	53
Small Acroporids	5	13.5	51	5	10	48	5	14	63	5	11.5	61	4	24.5	46	3	18	40
Small Faviids	5	11	30	5	9.5	29	4	13.5	28	3	10	28	6	16.5	42	3	14	32
Small Pocilloporids	3	6.5	34	3	5.5	32	4	9.5	17	4	9	12	4	11	52	3	9	51
Small Soft Corals	10	25	72	8	26.5	88	18	34	247	11	26	280	4	15	61	8	23	65
<i>Poritid Counts</i>																		
Poritids < 6cm	5	15	40	4	14.5	39	5	18.5	59	3	15.5	58	4	15	66	4	14.5	66
Poritids 6-20cm	6	14	31	4	13	29	3	17.5	33	5	13.5	32	13	24	50	11	24	48
Poritids 21-50cm	5	7.5	24	4	6.5	25	2	16.5	49	3	12	45	6	9.5	24	5	9.5	21
Poritids 51-100cm	5	20	31	5	16	30	3	22	95	6	12	88	3	27	41	15	20	46
Poritids >100cm	15	24.5	60	15	22	73	6	26.5	84	11	21	73	37	69	158	34	63.5	399
<i>% Coverage</i>																		
Total Algae	22	70	136	18	53	131	18	71	249	14	33	292	67	94	202	40	115.5	343
Acroporidae	4	7.5	22	3	7.5	21	2	10.5	24	4	6.5	19	6	9	35	4	9	33
Dead Stand. Corals	9	21.5	42	11	25	59	3	21	33	13	20.5	41	21	94	176	21	177.5	600
Faviidae	5	10.5	15	5	9.5	19	3	11.5	20	6	10	20	5	16.5	36	9	13	34
Misc. Hard Corals	4	10.5	41	5	11	42	3	13.5	36	7	9.5	33	2	13.5	101	5	13	100
Pocilloporidae	3	4	9	3	4	9	5	16.5	34	6	16	23	3	3	7	3	3	5
Poritidae	8	11	28	7	11.5	29	7	24.5	68	6	16.5	69	8	24	64	9	24.5	68
Soft Corals	8	21.5	49	8	19.5	46	10	55.5	155	7	47.5	141	11	24.5	45	6	20	39
Sponges	21	39	122	27	42.5	92	16	37	80	17	39.5	84	49	160	229	61	114	438
Total Hard Coral	3	3.5	13	3	4	13	3	7	16	3	7.5	14	2	4	16	3	4.5	16
<i>Misc. Benthos</i>																		
<i>Tridacna</i> spp.	11	26	30	11	25.5	39	26	35	107	26	32.5	134	5	45	113	12	69	249
<i>L. laevigata</i>	7	129	275	6	113	376	6	93	275	4	73	375	11	63	275	6	74	1097



Table 8: Differences between (2) treatment means detectable at  $\alpha=\beta=0.10$  when 4 reefs were sampled within each treatment. Differences are expressed as multiples of existing mean abundances. 'Whole Reefs', 'Back-reefs', and 'Front-reefs' refer to the scale and habitat over which potential treatments might be applied and from which data hypothesis tests were assessed, as described in text.

TAXON	Whole Reef						Back Reef						Front Reef						
	Data			Optimised			Data			Optimised			Data			Optimised			
	Min.	Med.	Max.	Min.	Med.	Max.	Min.	Med.	Max.	Min.	Med.	Max.	Min.	Med.	Max.	Min.	Med.	Max.	
<i>Large Fishes</i>																			
Total Acanthurids	0.19	0.47	1.20	0.19	0.47	1.18	0.32	0.54	1.57	0.30	0.55	1.56	0.12	0.44	0.90	0.29	0.39	0.90	
<i>Z. scopas</i>	0.67	0.90	1.79	0.61	0.87	1.72	0.10	1.64	2.51	0.52	1.41	2.43	0.89	1.25	1.79	0.70	1.22	1.70	
Other Acanthurids	0.21	0.54	1.14	0.21	0.54	1.12	0.40	0.57	1.50	0.47	0.53	1.50	0.16	0.53	0.94	0.25	0.47	0.93	
<i>All Chaetodonts</i>																			
<i>C. aureofasciatus</i>	0.22	0.57	0.81	0.21	0.56	0.81	0.21	0.48	0.79	0.26	0.47	0.78	0.43	0.77	0.99	0.47	0.76	1.02	
<i>C. baronessa</i>	0.94	2.24	4.70	0.94	2.23	6.88	0.72	1.25	3.43	0.73	1.20	3.36	1.32	2.27	4.71	1.21	2.34	9.75	
<i>C. plebeius</i>	0.97	1.30	2.18	0.94	1.25	2.03	1.21	1.40	2.10	0.91	1.24	2.48	1.40	1.79	3.33	1.21	1.79	5.31	
<i>C. trifasciatus</i>	0.77	1.06	1.28	0.74	1.07	1.69	0.58	1.05	1.93	0.78	1.32	1.90	0.61	1.60	2.54	1.30	1.49	3.03	
<i>C. vagabundus</i>	0.39	0.71	1.30	0.57	0.82	1.26	0.18	0.86	1.43	0.43	1.02	1.35	0.20	0.77	1.58	0.63	0.87	1.44	
Other Chaetodonts	0.86	1.11	2.77	0.94	1.34	4.22	0.73	1.59	2.72	0.83	1.55	5.50	0.87	1.01	3.01	1.03	1.52	6.08	
<i>All Lutjanids</i>																			
<i>Plectropomus</i> spp	0.32	0.83	1.64	0.29	0.83	1.67	0.11	0.72	1.72	0.56	0.70	1.49	0.32	1.04	1.84	0.50	1.02	2.04	
<i>L. carponotatus</i>	1.21	1.50	3.29	1.14	1.43	3.27	0.85	2.33	3.49	1.55	2.15	3.36	0.46	1.12	3.13	0.78	1.41	3.14	
<i>L. carponotatus</i>	0.68	2.64	4.72	0.61	3.03	7.76	1.00	3.66	4.71	1.05	4.48	11.00	0.90	1.65	4.71	1.00	1.71	9.75	
<i>Small Fishes</i>																			
<i>A. curacao</i>	0.54	0.75	1.33	0.51	0.83	1.54	0.26	1.10	1.58	0.78	1.05	1.72	0.48	1.06	2.94	0.69	1.29	3.07	
<i>A. curacao</i>	0.77	0.97	1.49	0.62	0.91	1.41	0.45	1.27	2.21	0.54	1.13	2.35	0.33	1.34	4.71	0.37	1.28	9.42	
<i>C. atripectoralis</i>	1.22	1.42	3.18	0.84	1.45	2.86	0.46	1.45	4.04	0.92	1.46	4.56	1.39	2.21	4.71	1.20	2.52	8.42	
<i>C. rollandi</i>	0.82	1.46	1.82	0.77	1.35	1.68	0.59	1.54	2.10	0.62	1.38	1.81	1.50	1.98	4.71	1.06	1.86	5.55	
Recruit <i>C.r.</i>	0.84	1.32	2.21	0.64	1.13	2.17	0.97	1.48	2.21	0.74	1.33	2.11	1.24	1.93	2.37	1.47	1.64	2.36	
<i>P. lacrymatus</i>	0.86	1.63	2.21	0.81	1.59	2.71	0.46	1.84	2.83	0.46	2.01	3.72	0.65	1.84	2.83	0.43	1.77	3.93	
<i>P. moluccensis</i>	0.80	1.09	1.65	0.64	1.03	1.56	0.87	1.24	1.84	0.85	1.04	1.70	0.66	1.35	3.86	0.41	1.16	4.05	
Recruit <i>P.m.</i>	0.86	1.49	2.74	0.72	1.30	2.62	0.55	1.18	3.30	0.72	1.40	3.02	0.70	1.56	2.30	0.70	1.06	2.89	
<i>T. lunare</i>	0.55	1.41	1.91	0.43	1.27	1.84	0.96	1.28	1.92	0.89	1.39	1.84	0.80	1.06	3.33	0.49	0.99	3.66	

Table 8 (Continued).

TAXON	Whole Reef						Back Reef						Front Reef					
	Data			Optimised			Data			Optimised			Data			Optimised		
	Min.	Med.	Max.	Min.	Med.	Max.	Min.	Med.	Max.	Min.	Med.	Max.	Min.	Med.	Max.	Min.	Med.	Max.
<i>Small Corals</i>																		
Small Acroporids	0.56	0.99	2.00	0.53	0.84	1.95	0.55	1.02	2.23	0.52	0.91	2.20	0.44	1.35	1.91	0.37	1.14	1.78
Small Faviids	0.55	0.89	1.53	0.52	0.80	1.51	0.46	0.98	1.46	0.32	0.84	1.46	0.61	1.09	1.82	0.33	1.00	1.57
Small Pocilloporids	0.36	0.66	1.62	0.32	0.58	1.59	0.48	0.82	1.12	0.43	0.79	0.93	0.44	0.88	2.03	0.25	0.79	2.02
Misc. Small Hard	0.75	1.04	1.39	0.64	0.95	1.33	0.51	0.87	1.31	0.48	0.80	1.34	1.36	1.58	2.04	0.73	1.29	2.05
Small Soft Corals	0.86	1.39	2.40	0.71	1.41	2.66	1.18	1.62	4.46	0.90	1.39	4.75	0.45	1.04	2.20	0.73	1.33	2.27
<i>Poritid Counts</i>																		
Poritids < 6cm	0.52	1.00	1.76	0.44	0.98	1.75	0.52	1.19	2.17	0.39	1.08	2.14	0.41	1.06	2.29	0.48	1.02	2.29
Poritids 6-20cm	0.58	1.02	1.54	0.45	0.96	1.50	0.26	1.15	1.59	0.54	0.99	1.57	0.98	1.36	1.98	0.89	1.36	1.95
Poritids 21-50cm	0.55	0.70	1.36	0.50	0.64	1.37	0.24	1.10	1.97	0.36	0.90	1.89	0.62	0.82	1.37	0.56	0.80	1.28
Poritids 51-100cm	0.54	1.24	1.56	0.55	1.09	1.53	0.39	1.30	2.75	0.58	0.92	2.65	0.36	1.44	1.79	1.06	1.24	1.90
Poritids >100cm	1.06	1.37	2.19	1.07	1.29	2.40	0.61	1.43	2.59	0.88	1.27	2.41	1.70	2.34	3.57	1.62	2.24	5.67
<i>% Coverage</i>																		
Total Hard Coral	0.27	0.43	0.96	0.27	0.45	0.96	0.28	0.66	1.10	0.29	0.68	1.04	0.18	0.45	1.10	0.26	0.49	1.09
Acroporidae	0.43	0.71	1.29	0.37	0.70	1.28	0.15	0.88	1.36	0.47	0.65	1.20	0.61	0.80	1.65	0.45	0.80	1.60
Faviidae	0.51	0.85	1.05	0.54	0.81	1.19	0.32	0.90	1.24	0.58	0.85	1.22	0.57	1.11	1.68	0.79	0.98	1.64
Pocilloporidae	0.39	0.45	0.80	0.36	0.47	0.80	0.53	1.11	1.62	0.61	1.10	1.33	0.27	0.35	0.65	0.28	0.37	0.58
Poritidae	0.73	0.90	1.47	0.70	0.91	1.50	0.69	1.34	2.33	0.59	1.09	2.34	0.75	1.35	2.26	0.78	1.36	2.33
Misc. Hard Coral	0.47	0.87	1.78	0.55	0.90	1.81	0.31	1.00	1.68	0.71	0.82	1.60	0.19	0.98	2.85	0.55	0.97	2.83
Dead Stand Coral	0.77	1.25	1.81	0.87	1.37	2.16	0.29	1.27	1.60	0.95	1.25	1.81	1.27	2.74	3.76	1.27	3.68	6.96
Soft Corals	0.74	1.28	1.96	0.75	1.22	1.91	0.86	2.09	3.53	0.67	1.93	3.37	0.90	1.33	1.88	0.63	1.16	1.76
Sponges	1.26	1.74	3.13	1.43	1.82	2.72	1.10	1.70	2.52	1.13	1.74	2.59	1.96	3.58	4.30	2.20	3.02	5.95
Total Algae	1.29	2.32	3.30	1.15	2.04	3.24	1.15	2.35	4.48	1.02	1.59	4.85	2.31	2.74	4.03	1.76	3.04	5.26
<i>Misc. Benthos</i>																		
<i>Tridacna</i> spp	0.87	1.41	1.52	0.87	1.41	1.74	1.41	1.65	2.93	1.43	1.59	3.27	0.58	1.87	3.01	0.94	2.28	4.48
<i>L. laevigata</i>	0.70	3.21	4.71	0.58	3.00	5.50	0.58	2.72	4.71	0.49	2.41	5.50	0.90	2.24	4.71	0.63	2.43	9.42

**Table 9:** Predicted numbers of control locations required to detect 50% difference between a single impact location and the average of the control locations in front-reef and back-reef habitats.

GROUP	TAXON	Back-reef			Front-reef		
		10%	Med.	90%	10%	Med.	90%
<i>Large Fish</i>	Total Acanthurid	4	10.5	45	4	13	28
	<i>Z. scopas</i>	13	52.5	412	10	47.5	181
	Other Acanthurid	3	12	51	5	12	25
	All Chaetodons	3	10	35	3	8	41
	<i>C. aureofasciatus</i>	10	31	412	4	82	241
	<i>C. baronessa</i>	35	108	301	22	84	412
	<i>C. plebeius</i>	12	61	181	17	111.5	412
	<i>C. trifasciatus</i>	8	27.5	107	3	27	138
	<i>C. vagabundus</i>	15	75.5	412	27	104	412
	Other Chaetodons	6	28.5	116	5	32.5	116
	All Lutjanids	27	161	412	23	113	335
	<i>L. carponotatus</i>	13	45	412	11	59	241
	<i>Plectropomus</i> spp.	6	70.5	181	5	75.5	138
<i>Small Fish</i>	<i>A. curacao</i>	4	21	102	5	29	330
	<i>C. atripectoralis</i>	25	107	330	40	172	330
	<i>C. rollandi</i>	3	21	172	24	158.5	330
	Recruit <i>C.r.</i>	15	81	209	83	145	330
	<i>P. lacrymatus</i>	11	50	330	8	70	330
	<i>P. moluccensis</i>	4	25	84	8	52	330
	Recruit <i>P.m.</i>	22	69	330	68	143	330
	<i>T. lunare</i>	9	60.5	330	16	50	177
	<i>Small Corals</i>	Small Acroporids	8	27	90	4	24
Small Faviids		4	28	55	10	36.5	110
Small Pocilloporids		3	19	46	6	19	67
Misc. Small Corals		5	26	76	28	85	134
Small Soft Coral		15	46.5	93	10	52	100
<i>Poritid Counts</i>	Poritids < 6cm	10	32	51	5	16.5	53
	Poritids 6-20cm	5	30.5	100	7	19	95
	Poritids 21-50cm	7	31	73	19	51.5	95
	Poritids 51-100c	11	58	156	14	96	225
	Poritids >100cm	19	146	412	30	198	412
<i>% Coverage</i>	Total Hard Coral	3	5.5	21	3	4.5	18
	Acroporidae	9	27.5	70	4	11.5	61
	Faviidae	7	29	114	9	40	205
	Pocilloporidae	4	12	80	5	14.5	34
	Poritidae	7	34.5	82	8	58	133
	Misc. Hard Coral	11	36	87	11	35	93
	Dead Stand Coral	7	41	170	12	120	330
	Soft Corals	6	27.5	95	9	30	91
	Sponges	6	47.5	138	52.5	166.5	330
	Algae	29	148.5	323	50	187.5	330
<i>Misc. Benthos</i>	<i>L. laevigata</i>	13	236.5	412	27	127	412
	<i>Tridacna</i> spp.	19	104	412	27	116	412

**Table 10:** Predicted differences between a single impact location and the average of 4 control locations for hypothetical impact assessments in front-reef and back-reef habitats.

Differences are expressed as multiples of existing mean abundances ( $\approx$  control locations).

GROUP	TAXON	Back-reef			Front-reef			
		10%	Med.	90%	10%	Med.	90%	
Large Fish	Total Acanthurid	0.44	0.92	1.99	0.48	1.04	1.57	
	<i>Z. scopas</i>	1.01	2.15	6.09	0.89	2.04	4.02	
	Other Acanthurid	0.35	0.98	2.13	0.56	0.99	1.47	
	All Chaetodons	0.32	0.91	1.76	0.25	0.78	1.91	
	<i>C. aureofasciatus</i>	0.89	1.65	6.09	0.42	2.71	4.65	
	<i>C. baronessa</i>	1.76	3.11	5.20	1.24	2.74	6.09	
	<i>C. plebeius</i>	1.00	2.32	4.02	1.22	3.16	6.09	
	<i>C. trifasciatus</i>	0.78	1.54	3.10	0.26	1.52	3.51	
	<i>C. vagabundus</i>	1.11	2.59	6.09	1.52	3.04	6.09	
	Other Chaetodons	0.66	1.56	3.22	0.58	1.69	3.22	
	All Lutjanids	1.52	3.79	6.09	1.42	3.18	5.49	
	<i>L. carponotatus</i>	1.03	2.00	6.09	0.94	2.27	4.65	
	<i>Plectropomus</i> spp.	0.61	2.50	4.02	0.57	2.59	3.51	
	Small Fish	<i>A. curacao</i>	0.49	1.34	3.02	0.57	1.58	5.44
		<i>C. atripectoralis</i>	1.48	3.10	5.44	1.88	3.92	5.44
<i>C. rollandi</i>		0.35	1.34	3.92	1.43	3.76	5.44	
Recruit <i>C.r.</i>		1.12	2.68	4.33	2.72	3.60	5.44	
<i>P. lacrymatus</i>		0.93	2.11	5.44	0.76	2.48	5.44	
<i>P. moluccensis</i>		0.48	1.46	2.74	0.78	2.12	5.44	
Recruit <i>P.m.</i>		1.39	2.48	5.44	2.46	3.58	5.44	
<i>T. lunare</i>		0.85	2.27	5.44	1.15	2.09	3.99	
Small Corals	Small Acroporids	0.80	1.53	2.83	0.40	1.44	2.26	
	Small Faviids	0.49	1.57	2.21	0.90	1.79	3.14	
	Small Pocilloporids	0.35	1.27	2.01	0.63	1.27	2.44	
	Misc. Small Corals	0.54	1.51	2.60	1.57	2.76	3.46	
	Small Soft Coral	1.10	2.03	2.88	0.90	2.14	2.99	
Poritid Counts	Poritids < 6cm	0.88	1.67	2.13	0.54	1.19	2.17	
	Poritids 6-20cm	0.51	1.63	2.99	0.70	1.27	2.92	
	Poritids 21-50cm	0.74	1.66	2.55	1.28	2.14	2.91	
	Poritids 51-100c	0.94	2.27	3.74	1.10	2.92	4.50	
	Poritids >100cm	1.26	3.61	6.09	1.61	4.21	6.09	
% Coverage	Total Hard Coral	0.32	0.62	1.33	0.18	0.47	1.23	
	Acroporidae	0.83	1.54	2.49	0.39	0.95	2.32	
	Faviidae	0.70	1.58	3.20	0.82	1.87	4.29	
	Pocilloporidae	0.39	1.00	2.67	0.53	1.11	1.72	
	Poritidae	0.74	1.75	2.70	0.79	2.27	3.45	
	Misc. Hard Coral	0.95	1.78	2.79	0.93	1.75	2.88	
	Dead Standing Co	0.70	1.89	3.90	1.00	3.27	5.44	
	Soft Corals	0.65	1.54	2.91	0.81	1.62	2.84	
	Sponges	0.64	2.04	3.52	2.16	3.86	5.44	
	Total Algae	1.58	3.65	5.38	2.06	4.10	5.44	
Misc. Benthos	<i>L. laevigata</i>	1.03	4.60	6.09	1.52	3.37	6.09	
	<i>Tridacna</i> spp.	1.26	3.04	6.09	1.52	3.22	6.09	

### Location Specific Patterns Among Reefs

Interactions between specific locations and either Shelf Position and/or Region were significant by scalable decision criteria for 7 fishes and 9 benthic taxa in either or both habitats (Table 11). Had a conventional statistical decision criterion ( $\alpha_c=0.05$ ) been used, three additional terms would have been considered significant but the number of taxa for which such interactions were significant would not have increased (Table 12). For four fishes (*C. baronessa*, *Plectropomus* spp., total lutjanids, and juvenile *C. rollandi*) and six benthic taxa (Miscellaneous small corals, percent coverage by acroporids, faviids, and pocilloporids, and counts of *Tridacna* spp. and *L. laevigata*) differences among regions or between shelf positions varied with the location considered (Table 12), whilst for the remaining taxa shelf-positions or regional patterns were consistent across locations. For three fishes (*C. atripectoralis*, juvenile *P. molluccensis*, *T. lunare*) and pocilloporid corals, however, the likelihood of error in these tests was so great ( $\alpha_c=\beta>0.3$ , Table 11) that they should be given little weight.

**Table 11:** Results of hypothesis tests of the effects of sampling at specific locations on inferences about spatial patterns among reefs. Tabulated numbers are the critical significance level used for hypothesis tests and the expected Type II error rate for non-significant results, after Mapstone (1995, 1996). Bold values indicate statistically significant terms by scalable decision criteria, whilst '\*' shows additional terms that would have been significant by a conventional criterion ( $\alpha_c=0.05$ ). Only terms involving Location effects are presented, and shading indicates those terms which, if significant, might represent large scale effects (Region, Shelf Position) that depended on the location sampled within reefs.

TAXON	$\alpha_c=\beta$							
	Locat <sup>n</sup>	BACK-REEFS			FRONT-REEFS			
		L*R	L*S	L*R*S	Locat <sup>n</sup>	L*R	L*S	L*R*S
<i>Large Fish</i>								
Total Acanthurids	0.015	0.026	0.015	0.026	0.035	0.056	0.035	0.056
<i>Z. scopas</i>	0.223	0.268	0.223	0.268	0.014	0.025	0.014	0.025
Other Acanthurids	0.011	0.020	0.011	0.020	0.042	0.066	0.042	0.066
Total Chaetodons	0.061	0.090	0.061	0.090	0.006	0.012	0.006	0.012
<i>C. aureofasciatus</i>	0.000	0.000	0.000	0.000	0.002	0.004	0.002	0.004
<i>C. baronessa</i>	0.102	<b>0.141</b>	<b>0.102</b>	<b>0.141</b>	0.012	0.022	0.012	0.022
<i>C. plebeius</i>	0.129	0.172	0.129	0.172	0.008	0.016	0.008	0.016
<i>C. trifasciatus</i>	0.046	0.071	0.046	0.071	0.083	0.118	0.083	0.118
<i>C. vagabundus</i>	0.049	0.076	0.049	0.076	0.121	0.162	0.121	0.162
Other Chaetodons	0.232	0.278	0.232	0.278	*0.010	0.018	0.010	0.018
Total Lutjanids	0.068	0.100	0.068	0.100	0.173	0.219	0.173	<b>0.219</b>
<i>L. carponotatus</i>	0.010	0.018	0.010	0.018	0.065	0.096	0.065	0.096
<i>Plectropomus</i> spp	<b>0.204</b>	<b>0.250</b>	0.204	0.250	0.047	0.073	0.047	0.073
<i>Small Fish</i>								
<i>A. curacao</i>	0.007	0.014	0.007	0.014	0.014	<b>0.025</b>	0.014	*0.025
<i>C. atripectoralis</i>	0.398	0.422	0.398	0.422	<b>0.270</b>	<b>0.313</b>	0.270	<b>0.313</b>
<i>C. rollandi</i>	0.017	0.029	0.017	0.029	0.009	0.017	0.009	0.017
Juvenile <i>C. rollandi</i>	0.114	<b>0.155</b>	0.114	0.155	0.000	0.001	0.000	0.001
<i>P. lacrymatus</i>	0.002	0.004	0.002	0.004	0.026	0.043	0.026	0.043
<i>P. molluccensis</i>	0.001	0.002	0.001	0.002	0.002	0.004	0.002	0.004
Juvenile <i>P. molluc.</i>	0.022	0.038	0.022	0.038	<b>0.500</b>	<b>0.500</b>	<b>0.500</b>	<b>0.500</b>
<i>T. lunare</i>	0.017	0.029	0.017	0.029	<b>0.394</b>	<b>0.418</b>	<b>0.394</b>	<b>0.418</b>

B: Benthos		$\alpha_c = \beta$						
		BACK-REEFS				FRONT-REEFS		
TAXON	Locat <sup>n</sup>	L*R	L*S	L*R*S	Locat <sup>n</sup>	L*R	L*S	L*R*S
<i>Small Corals</i>								
Small Acroporids	0.012	0.022	0.012	0.022	0.018	0.032	0.018	0.032
Small Faviids	0.003	0.006	0.003	0.006	0.012	0.021	0.012	0.021
Small Pocilloporids	0.045	<b>0.070</b>	<b>0.046</b>	<b>0.070</b>	0.036	0.057	0.036	0.057
Misc. Small Corals	0.028	0.046	*0.028	0.046	0.243	0.287	<b>0.243</b>	<b>0.287</b>
Small Soft Corals	0.000	0.000	0.000	0.000	0.018	0.031	0.018	0.031
<i>Poritids</i>								
Poritids < 6cm	0.002	0.004	0.002	0.004	0.003	0.007	0.003	0.007
Poritids 6-20cm	0.032	0.052	0.032	0.052	0.011	0.021	0.011	0.021
Poritids 21-50cm	0.015	0.026	0.015	0.026	0.244	0.288	0.244	0.288
Poritids 51-100cm	0.051	<b>0.077</b>	0.051	0.077	0.106	0.145	0.106	0.145
Poritids >100cm	<b>0.070</b>	0.102	0.070	0.102	0.005	0.010	0.005	0.010
<i>% Coverage</i>								
Total Hard Corals	0.003	0.006	0.003	0.006	0.001	0.003	0.001	0.003
Acroporidae	<b>0.112</b>	0.152	<b>0.112</b>	0.152	0.002	0.003	0.002	0.003
Faviidae	<b>0.065</b>	0.096	0.065	0.096	0.130	0.172	0.130	<b>0.172</b>
Pocilloporidae	0.034	0.054	0.034	0.054	0.320	<b>0.357</b>	<b>0.320</b>	<b>0.357</b>
Poritidae	0.051	0.077	0.051	0.077	<b>0.064</b>	0.094	0.064	0.094
Misc. Hard Coral	0.024	0.040	0.024	0.041	0.007	0.014	0.007	0.014
Dead Stand. Coral	0.075	0.108	0.075	<b>0.108</b>	0.002	0.005	0.002	0.005
Soft Coral	0.001	0.003	0.001	0.003	0.021	0.036	0.021	0.036
Sponges	0.006	0.012	0.006	0.012	0.105	0.144	0.105	0.144
<i>Benthos</i>								
<i>Tridacna</i> spp	0.019	0.034	0.019	<b>0.034</b>	0.085	<b>0.121</b>	0.085	<b>0.121</b>
<i>L. Laevigata</i>	<b>0.105</b>	0.145	<b>0.105</b>	<b>0.145</b>	0.153	0.199	0.153	0.199

**Table 12:** Statistically significant large scale patterns identified after identifying interactions between Location and either Shelf Position or Region. Comparisons of region or shelf position where no significant differences were found are not presented.

HABITAT	TAXON	<u>Shelf Effects</u>			<u>Region Effects</u>		
		Locat <sup>n</sup>	Region	Effect	Locat <sup>n</sup>	Shelf Pos <sup>n</sup>	Effect
Back-reef	<i>Plectropomus</i> spp	-	-	-	North	Both	L<M≈N
		-	-	-	Centre	"	L<M<N
		-	-	-	South	"	L<M≈N
	<i>C. baronessa</i>	Centre	C. Flattery	M>O	Centre	Mid	L≈M<N
		South	C. Flattery	M>O	Centre	Outer	L≈M>N
		"	Cooktown	M>O	South	"	L>M≈N
	<i>Juvenile C. rollandi</i>	-	-	-	Centre	Both	L<M>N
	<i>L. laevigata</i>	North	C. Flattery	M>O	North	Mid	L≈M<N
		Centre	"	M>O	Centre	"	L≈M<N
		South	"	M>O	South	"	L≈M<N
		North	Cooktown	M>O	-	-	-
	<i>Tridacna</i> spp	North	Cooktown	M>O	North	Mid	L<M≈N
		-	-	-	Centre	"	L≈M<N
-		-	-	South	"	L≈M<N	
Acroporids	South	All	M>O	-	-	-	
Front-reef	Total Lutjanids	Centre	Cooktown	M>O	North	Mid	L<M<N
		North	C. Tribulation	M<O	South	Outer	L<M<N
		South	C. Tribulation	M>O	-	-	-
	<i>Tridacna</i> spp	North	Cooktown	M>O	-	-	-
		Centre	"	M>O	-	-	-
		South	"	M>O	-	-	-
		"	C. Tribulation	M>O	-	-	-
	Small Misc. Corals	Centre	C. Flattery	M<O	North	Mid	L<M≈N
		North	Cooktown	M<O	"	Outer	L<M>N
		South	C. Tribulation	M>O	Centre	"	L<M≈N
	Faviidae	Centre	C. Flattery	M>O	South	Mid	L>M<N
		North	Cooktown	M>O	"	Outer	L>M≈N
		South	C. Tribulation	M<O	-	-	-
Pocilloporidae	North	C. Flattery	M<O	South	Mid	L<M>N	
	South	C. Flattery	M<O	North	Outer	L>M<N	
	North	Cooktown	M>O	Centre	"	L>M<N	
	South	Cooktown	M>O	South	"	L<M≈N	
	North	C. Tribulation	M<O	-	-	-	
	Centre	C. Tribulation	M<O	-	-	-	
	South	C. Tribulation	M<O	-	-	-	

## DISCUSSION

In this report we have concentrated on the description of variation in abundances of several coral reef organisms in the Cairns Section of the Great Barrier Reef Marine Park. Our focus was on the implications of variation for the spatial design of sampling and monitoring programmes and the inference of spatial pattern, possibly arising from such effects as area-based management strategies or human impacts on the reef environment. The data we have presented indicate that existing spatial variation is large for most organisms, and that it is unlikely that small or even moderate effects of management strategies, human use, or natural perturbations will be reliably detectable as spatial pattern without considerable expense.

### Scales of Variation

The consistently great heterogeneity at small scales (among transects) suggested that the transects we used were not integrating small-scale patchiness in distributions of organisms (Downing 1979, Elliott 1977, Green 1979). The genesis of such local variation probably lies in such bio-physical features as micro-topography, local inter- and intra-specific interactions, and local hydrodynamics, but will also include counting (methodological) variation (Link *et al.* 1994). It is tempting to suggest the use of larger sampling units to attenuate these large variances, but numerous studies have shown that sampling larger units generally is not the most cost-effective sampling strategy to minimise variances (see Andrew & Mapstone 1987 for review, Downing 1979, Downing & Anderson 1985, Downing & Cyr 1985, Downing *et al.* 1987, Fowler 1987, Mapstone & Ayling 1993, Pringle 1984). If these earlier results are accepted, then it will be necessary to sample many more sampling units than is often used (including in this study) to adequately sample the range of small scale variations and reduce sample variation.

Heterogeneity was reduced greatly at larger scales, even at scales of only small multiples of the size of sampling units (sites). Indeed, the strongest signal from these results was that the scale of our closely spaced sites is perhaps the least important scale to account for when sampling many reef taxa.

Similarity in coefficients of variation for location and reef means suggests as much heterogeneity among distant locations within the same habitats at one reef as among reefs, when measured in the same habitats. Our data suggest that neither of these sources of variation should be disregarded when sampling coral reef populations on the GBR with the intention of deriving results that are not peculiar to a very specific reef or location. We cannot infer what processes might be most influential at either of these scales from these simple descriptions of patterns. The similarity in magnitudes of variation among locations and among reefs over such a diversity of circumstances (regions, shelf positions, habitats), however, suggests that the key processes driving populations at each scale are either the same and/or produce the same magnitudes of effects on abundances.

The absence of clear or consistent pattern in CV's across larger-scale systematic effects such as Habitat, Shelf Position, or Region indicates that although such very large-scale factors might affect the abundances of some taxa, they generally neither attenuate or exacerbate apparently stochastic processes within such strata. Although some consistent changes in CV, were observed with Habitat, they were taxon specific and involved few taxa. Accordingly, there is no clear advantage (on the basis of empirical sampling characteristics alone) to favouring particular habitats, shelf positions or regions for ecological, monitoring, or management studies of most taxa where reduced stochastic variation in sample data is desirable. It is noteworthy also that there was considerable consistency among taxa in the relative magnitudes of scale-related variation, and in the characteristics of predicted sampling requirements. Hence, whilst there were some taxa that were conspicuously poor candidates for monitoring studies, there were no clear candidates that would provide sensitive measures of impacts (based on their sampling characteristics alone).

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## Predictions of Future Sampling Requirements

### *Sub-sampling Reefs*

Predictions of 'optimal' allocations of effort across sub-sampling hierarchies within reefs were highly variable, both among and within taxa. Predicted sample sizes needed to detect nominated effects, or the sizes of effects expected to be seen with limited sampling, were similarly variable. Cochran (1963), Winer (1971) and Winer *et al.* (1991) noted that such predictions would be uncertain because of their derivation from ratios of estimated (rather than known) variances. None of these authors, or others we know of, however, indicated the severity of such uncertainty, although McArdle (pers. com.) speculated that the predictions would be highly variable. Mapstone (1995, 1996) and Keough & Mapstone (1995) provide examples where the variations in cost-benefit procedures and sample size predictions are evident, but in most discussions of these procedures the uncertainty of the predicted sampling strategies are ignored (Andrew & Mapstone 1987, Bross & Cowell 1987, Cohen 1988, Downing 1979, Downing *et al.* 1987, Fryer & Nicholson 1993, Gerrodette 1987, Green 1989, Kenelly & Underwood 1984, 1985, Kennelly *et al.* 1993, Millard & Lettenmaier 1986, Peterman 1990, Prihoda 1983, Sokal & Rohlf 1981, Taylor & Gerrodette 1993, Underwood 1981, Zar 1984, Zedaker *et al.* 1993). It is clear from our analyses that if such procedures are to be interpreted realistically, and the strengths and limitations of proposed sampling schemes truthfully depicted, the uncertainty associated with the predictions cannot be ignored.

Despite such uncertainty, however, some generalisations can be inferred from our data. Firstly, sites were often not included in projected sub-sampling within habitats & reefs. This result is consistent with relatively small variation among sites discussed above. Secondly, sampling multiple locations and transects was consistently important. These results indicate that strategies such as those adopted by Sale *et al.* (1984), Doherty (1987), and in the AIMS Long Term Monitoring Programme (AIMS 1992, Oliver *et al.* 1995), where several closely spaced sites were sampled with multiple transects but no 'location scale' sampling was done, are almost certainly inefficient.

To the extent that our results can be extended to general recommendations, we recommend that at least 5-6 locations within habitats or reefs be sampled in future studies for most organisms. Doing so would not only ensure adequate coverage of the sampling space with which many studies (such as those just cited) are concerned (Hurlbert 1984), but also be likely to efficiently estimate the variances within reefs and/or habitats. The remaining available effort should then be put into sampling several transects within each location. It is likely that sampling multiple sites in close proximity will be useful only for studies where the experimental units are site-scale or location-scale. In the case of location-scale effects, sub-sampling at multiple sites will be likely to provide a well behaved error term in analyses, whereas sampling only transects, even many of them, might not (see also McArdle *et al.* 1990).

It is clear also from our data that optimising sub-sampling of experimental units by cost-benefit procedures is unlikely to affect substantially the expected power of statistical tests. This is to be expected from the algebra of the non-centrality parameters for tests since the numbers of sub-samples at all levels appear in both the numerator and denominator of the noncentrality parameters from which power is calculated, but we know of no empirical investigations of this subject. Very poor representation of experimental units (*i.e.*, poor precision of estimates for each unit) through highly inadequate sub-sampling might be expected to influence power, but in our results both optimised and non-optimised results provided relatively similar results. This may reflect the fact that both sets of calculations were based on fairly similar cost-constraints (1 vs 1.5-2 days per reef), and relatively large total numbers of sub-sampling units (~15).

These results have important implications for the design and interpretation of future studies, especially with respect to the role and scope of pilot studies. Our data do not provide the sought-after prescription of a 'best' allocation of sampling effort across different spatial scales, or a clear and unequivocal guide to the replication needed to assess either management strategies or human impacts on the GBR environment (Mapstone *et al.* 1989). Indeed, the analyses we present demonstrate that

such messages are likely to be unavailable or flawed in ecological field studies. At best, we can provide some guidelines on the scales that are (empirically) likely to require least emphasis in future sampling programmes, and insights into the reliability of predictions of required sample sizes to detect nominated effects.

It is clear also that the hitherto recommended approach of doing small pilot studies to fine-tune sampling strategies for larger programmes should be reconsidered. We do not suggest that prior information is unnecessary for designing major sampling programmes, but we suggest that pilot estimates should be treated more cautiously than they have been previously. For such pilot estimates of variance to be sufficiently robust to provide sound predictions of future sampling (Andrew & Mapstone 1987, Elliott 1977, Fairweather 1991, Green 1979, Kennelly *et al.* 1993, Keough & Mapstone 1995, Mapstone 1988, Underwood 1981, 1991, 1993, 1996), they will almost certainly need to be larger and more specifically targeted at deriving multiple estimates of variance (rather than precise estimates of means) than is now considered appropriate (McArdle *et al.* 1990, Underwood 1991). The tendency to view the predictive results of such pilot studies as definite also is clearly misguided. We have demonstrated that predictions of 'optimum' allocations of effort, sample sizes, and statistical power are highly variable. The careful design of field studies from pilot data will require explicit consideration of that uncertainty (Keough & Mapstone 1995, Mapstone 1995, 1996).

### *Replication of Experimental Units*

Our data illustrate that only large magnitude spatial patterns in ecological effects are likely to be detectable with good certainty by most sampling programmes, given current conventional standards for critical Type I error rates. For tests of large scale phenomena such as management actions (zoning), effects of fishing, or gross geographical effects, visual surveys of four reefs within a given category are likely to detect median effects of only about 50-100% of existing abundances at best. In several cases, particularly for small fishes counted within small transects and abundances of sessile benthos, our methods would be sensitive to only gross changes in abundances of about 75-150% of standing stocks if only four replicate reefs were sampled in each 'treatment' condition, even when the test criterion was set larger than that used by convention ( $\alpha=0.1$  vs  $\alpha=0.05$ ). Considered in terms of the expected numbers of reefs needed in a sample to detect more moderate effects, equivalent to 50% of standing abundances, our data indicate that replication will have to be great in order to ensure good confidence (Power = 0.9) of detecting systematic effects on abundances. Even with relatively liberal significance criteria (by conventional standards  $\alpha=0.1$  would be considered liberal), in excess of 10 reefs or locations would need to be sampled to realise 90% power in 50% or more cases. These results generally held whether sampling was only within selected habitats or over whole reefs. Although it would clearly be more efficient to sample some taxa in one habitat than in the other, there was no consistent evidence that measuring reef-wide effects would be more economic in either front reef or back reef environments for all or most groups.

A corollary of these results is that, with current approaches, looking for subtle spatial effects on reef organisms will be expensive. If relatively moderate effects are considered important, then either: i) very many reefs or locations will have to be sampled; ii) it will be necessary to reconsider our dogmatic adherence to low Type I error rates in the interests of constructing more balanced inferences about results, whatever they might be; or iii) alternative approaches to sampling and monitoring studies will be required. Such alternatives will be discussed at the end of the document.

Finally, it is clear from these data that the use of predictive power analyses must be regarded with greater caution than so far suggested in the literature (Andrew & Mapstone 1987, Bernstein & Zalinski 1983, Fairweather 1991, Peterman 1990, but see Mapstone 1995, 1996, Keough & Mapstone 1995). Single (point) estimates of sample sizes, detectable effect sizes, or statistical power (or  $\beta=1$ -power) should be interpreted cautiously unless accompanied by statements of confidence. The highly skewed distributions of such estimates we observed indicate that single estimates have a high likelihood of underestimating the true means (of power, effect size, or sample size calculations) and thus may result in inadequate sampling. Adjustment for such potential errors can only be made by

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considering the uncertainty around estimated sample sizes etc., which means that multiple estimates of variances will be required (see also Underwood 1991, 1993, 1996). Again, this suggests the need for larger pilot studies that deliver better, multiple estimates of variance.

The implications of these conclusions are two fold. Firstly, the conventional approaches to sampling or funding strategies may need re-thinking, particularly where strong inferences will be made from either 'positive' or 'negative' results (Hayes 1987, Millard 1987). It may be better in future studies to do (and fund) large 'pilot' studies to gain sound impressions of the merits of proceeding with subsequent studies, given that those subsequent studies are likely to be constrained by *reduced* funding. If the substantive pilot studies indicate that the proposed future project is weak, then funding should be refused or the approach modified. Secondly, it is likely to be inefficient to adopt an approach for assessing management strategies in which the effects of management are compared only periodically, and where inferences of success or failure rely on the detection of spatial pattern, unless dramatic effects of management are expected (Alcala 1988, Russ 1989, 1984a). In so far as there has been a 'strategy' for assessing the effectiveness of the management of the Great Barrier Reef Marine Park to date, it seems to be based on just such an approach (Mapstone *et al.*, 1990). This is likely to be uninformative in the GBR region because the spatial effects of different zoning strategies seem likely to be slight relative to background variation (*e.g.*, see Ayling *et al.* 1991, Ayling & Ayling 1991, 1992a).

### Sampling to Represent Reef Status and Large Scale Pattern

The existence of strong interactions between effects of shelf position and/or habitat and/or region (see also Mapstone *et al.* 1995) emphasise the need to sample comprehensively around reefs and across gross geographic clines when an objective of sampling is to monitor the status of the GBR or sections of it, or to examine the effects of any one of these factors on abundances. Further, it was clear from our data that several of the habitat, shelf position, or regional patterns evident in data from entire reefs were not consistent across locations within reefs. It apparently has been assumed in a number of past studies that standardising the location of restricted sampling within reefs provided security for the inference of among reef patterns (AIMS 1992, Dinesen 1983, Done 1982, Doherty 1987, Mapstone 1988, Sale *et al.* 1986, Williams 1982). For such an argument to provide a legitimate basis for inference of cross-shelf, habitat, regional, or (probably) temporal patterns among reefs, the effects of each of these factors would have to be consistent across each of the others, and among reefs. This is clearly not so, at least in the Cairns section of the GBR Marine Park.

Oliver *et al.* (1995) clearly identify this limitation in the AIMS Long Term Monitoring Programme, in which only a restricted (standardised) location is sampled on each reef. Throughout their text, however, they refer to the data by reefs ("for brevity") and the conclusions they reached after the first year of monitoring refer mainly to cross-shelf and regional patterns in abundances. Given the data we have presented, some caveats should be considered when interpreting the results of such studies. Most importantly, it should be specified exactly what the within-reef sampling space was and conclusions about larger scale pattern should be restricted to those within-reef strata (at the expense of brevity, if necessary). For the future monitoring of reef organisms, therefore, we recommend stratification across both habitat and shelf position to depict accurately effects of either factor on abundances of most organisms.

### Future Directions

Our results indicate that the high levels of existing (natural?) spatial heterogeneity in the GBR system mean that even large differences in abundances associated with human impacts cannot be taken to signal unequivocally important environmental impacts. This does not mean, however, that human impacts of smaller magnitude than natural variation are unimportant, though they may be difficult to detect (Bence *et al.* 1996, Kingsford & Gray 1996, Nisbet *et al.* 1996, Raimondi & Reed 1996, Stewart-Oaten 1996). Whilst the importance of localised, low frequency impacts might be assessed sensibly in relation to natural spatial variability, chronic or large scale impacts of relatively small

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magnitudes might be considerably more important than natural disturbances of large magnitude but low frequency. Our data suggest, however, that unless human activities, including management strategies, generate very strong signals, they are unlikely to be recognisable in space over the great existing spatial variations in abundances.

For assessments of human impacts and management strategies to be fruitful, alternative approaches to monitoring will be necessary, which allow separation of the spatial variations inherent in the system from temporal changes in abundances that might arise from management strategies or low-level human impacts. It might be expected, therefore, that frequent (annual or sub-annual) repeated measures of different management units will provide more sensitive tests of the effects of management regimes on reef-associated organisms (Green 1989, Keough & Mapstone 1995). Such an approach seems likely to be more productive than occasional spatial comparisons because of the long-lived and sessile or relatively sedentary characteristics of many reef organisms, and recent developments in analyses of such temporal data. A key assumption of such an approach, however, is that sampling and observation biases are relatively stable through time (Thompson & Mapstone in press, Mapstone, Neale & Christie in prep). A repeated measures approach to monitoring is being taken in the AIMS LTM Programme, although with severe restrictions on the spatial coverage of sampling within reefs (Oliver *et al.* 1995), and has been recommended for impact assessment studies for some time (Green 1989, Keough & Mapstone 1995, Mapstone 1990, Mapstone *et al.* 1989, 1992).

We have not considered here the potential for sequential data from the same units (*e.g.*, reefs) analysed as repeated measures to detect temporal shifts in abundances and thus test the effects of management strategies or human impacts more sensitively than simple spatial analyses. Smaller scale empirical studies (Kaly *et al.* 1993a,b, Mapstone 1990, Mapstone *et al.* 1989, 1992), and theoretical work (Mapstone *et al.* 1994), however, suggest that such an approach will provide far more sensitive tests of impacts and/or management. Additional data concerning temporal variation (diel, tidal, lunar, and longer term) in abundances of reef associated fish have been collected by W. Richards and Reef Biosearch (in 1988-89), Choat (1982-present), and within the AIMS LTM Project. These data would provide a reasonable basis for investigating the merits of repeated measures analyses of fish abundances at local scales, where abundances of fish would be expected to vary relative to times taken to survey sampling units and because of short-term movement. There are few data, however, that would allow for repeated measures analyses at the scale of whole reefs or substantive strata of them, which would be the scales at which most management strategies should be assessed (but see Ayling & Ayling 1992b, 1993, 1994, 1995). Again, such investigations would imply a substantial shift from historical approaches to assessing the effectiveness of management strategies & protected areas, along the lines of the work done over the last decade in impact assessment studies. In view of the result of this study, we suggest that consideration of such a shift is necessary for the robust and informative assessment of the effectiveness of the GBRMPA strategy of managing the GBR Marine Park by zoning.

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## APPENDIX 1: TAXA SURVEYED

Table A1.1: Taxa and size classes counted on at least one belt transect of the nominated size.  
Selected taxa only were counted on belt transects.

50m x 5m	Transects	20m x 2.5m Transects	20m x 0.5m Transects
<b>Fishes</b> <b>Acanthuridae</b> <i>Zebrassoma scopas</i> Other acanthurids  <b>Chaetodontidae</b> <i>C. aureofasciatus</i> <i>C. baronessa</i> <i>C. plebeius</i> <i>C. rainfordi</i> <i>C. trifasciatus</i> <i>C. vagabundus</i> <i>Chemon rostratus</i> Other chaetodons  <b>Lethrinidae (Total)</b>  <b>Lutjanidae</b> <i>Lutjanus bohar</i> <i>L. carponotatus</i> <i>L. fulviflamma</i> <i>L. gibbus</i> <i>L. quinqilineatus</i>  <b>Serranidae</b> <i>Plectropomus laevis</i> <i>P. leopardus</i>	<b>Benthos</b> <b>Acanthasteridae</b> <i>A. planci</i> <20cm <i>A. planci</i> 21-50cm <i>A. planci</i> >50cm  <b>Ophidiasteridae</b> <i>Linckia laevigata</i>  <b>Tridacnidae</b> <i>T. gigas</i> ≤ 20cm <i>T. gigas</i> > 20cm <i>T. derasa</i> ≤ 20cm <i>T. derasa</i> > 20cm	<b>Labridae</b> <i>Thalassoma lunare</i>  <b>Pomacentridae</b> <i>Amblyglyphidodon curacao</i> <i>Chromis atripectoralis</i> <i>Chrysiptera rollandi</i> Recruit <i>C. rollandi</i> <i>Plectroglyphidodon dickii</i> <i>P. lacrymatus</i> <i>Pomacentrus moluccensis</i> Recruit <i>P. moluccensis</i>	<b>Juvenile Coral (&lt;5cm<math>\phi</math>)</b> Acroporidae Faviidae Pocilloporidae Misc. hard corals  Soft corals  <b>Poritidae</b> Poritidae 0-5cm $\phi$ Poritidae 6-20cm $\phi$  <b>50m x 2.5m Transects</b>  <b>Poritidae</b> (massive / sub-massive) <b>Poritidae</b> Poritids 21-50cm Poritids 51-100cm Poritids 101-200cm Poritids >200cm

**Table A1.2:** Taxa or substarta encountered under line intercept transects. All taxa or substrata encountered were resolved as far as possible in the field. # Obs. = the number of transects out of 808 on which each taxon or substratum was recorded.

Family / Genus	Species	# Obs.	Family / Genus	Species	# Obs.
<b>Pocilloporidae</b>			<b>Oculinidae</b>		
	<i>Palanastrea ramosa</i>	1		<i>Achrehelia horrescens</i>	2
	<i>Pocillopora damicornis</i>	522		<i>Galaxea astreata</i>	54
	<i>eydouxi</i>	102		<i>fascicularis</i>	228
	<i>verrucosa</i>	320		spp.	39
	<i>Seriatopora hystrix</i>	439			
	<i>Stylophora pistillata</i>	611			
<b>Acroporidae</b>			<b>Acroporidae (cont)</b>		
	<i>Acropora aculeus</i>	129		<i>Acropora palifera</i>	257
	<i>acuminata</i>	7		<i>pallida</i>	1
	<i>anthoceris</i>	44		<i>palmerae</i>	6
	<i>aspera</i>	8		<i>paniculata</i>	35
	<i>austera</i>	103		<i>plating form</i>	63
	<i>azurea</i>	49		<i>polystoma</i>	56
	<i>brueggemanni</i>	44		<i>pulchra</i>	3
	<i>carduus</i>	51		<i>robusta</i>	138
	<i>caroliniona</i>	2		<i>samoensis</i>	12
	<i>cerialis</i>	316		<i>sarmentosa</i>	153
	<i>clathrata</i>	20		<i>secale</i>	148
	<i>cuneata</i>	3		<i>selago</i>	144
	<i>cytherea</i>	168		<i>subglabra</i>	7
	<i>danai</i>	25		<i>subulata</i>	93
	<i>dendrum</i>	4		<i>tenuis</i>	226
	<i>digitifera</i>	167		<i>valenciennesi</i>	18
	<i>divaricata</i>	77		<i>valida</i>	15
	<i>donei</i>	23		<i>vaughani</i>	8
	<i>echinata</i>	2		<i>verweyi</i>	28
	<i>elseyi</i>	174		<i>willisae</i>	72
	<i>florida</i>	153		<i>yongei</i>	90
	<i>formosa</i>	243		<i>tortuosa</i>	2
	<i>gemmifera</i>	216		spp. #1	2
	<i>grandis</i>	58		spp. #2	1
	<i>granulosa</i>	4		unident. juvenils	175
	<i>horrida</i>	8		branching form	4
	<i>humilis</i>	174		clumping form	76
	<i>hyacinthus</i>	321		staghorn form	11
	<i>latistella</i>	53		remnants / bases	12
	<i>listeri</i>	14		<i>Anacropora puertogaleraea</i>	1
	<i>longicyathus</i>	101		spp.	1
	<i>loripes</i>	295		<i>Astreopora gracilis</i>	1
	<i>lutkeni</i>	54		<i>myrophthalma</i>	69
	<i>microclados</i>	181		spp.	124
	<i>microthalma</i>	52		<i>Montipora aequituberculata</i>	1
	<i>millepora</i>	243		<i>encrusting habit</i>	434
	<i>monticulosa</i>	57		<i>explanate habit</i>	88
	<i>nana</i>	59		<i>foliose habit</i>	10
	<i>nasuta</i>	366		<i>incrassata</i>	7
	<i>nobilis</i>	191		<i>tuberculosa</i>	1
				massive/submas.	156

Table A1.2: continued.

Family / Genus	Species	# Obs.	Family / Genus	Species	# Obs.
<b>Poritidae</b>			<b>Agariscidae</b>		
<i>Alveopora</i>	<i>spongiosa</i>	1	<i>Coeloseris</i>	<i>mayeri</i>	137
	spp.	2	<i>Gardinoseris</i>	<i>planulata</i>	9
<i>Goniopora</i>	spp.	114	<i>Leptoseris</i>	spp.	2
<i>Porites</i>	<i>annae</i>	85	<i>Pachyseris</i>	<i>rugosa</i>	10
	<i>cylindrica</i>	106		<i>speciosa</i>	20
	<i>encrusting habit</i>	48		spp.	1
	<i>lichen</i>	94	<i>Pavona</i>	<i>cactus</i>	4
	<i>massive habit</i>	571		<i>decussata</i>	19
	<i>nigrescens</i>	128		<i>explanulata</i>	11
	<i>rus</i>	36		<i>minuta</i>	6
	<i>vaughani</i>	4		spp.	1
	spp.	142		<i>varians</i>	115
				<i>venosa</i>	34
<b>Siderasteridae</b>			<b>Merulinidae</b>		
<i>Coscinarea</i>	<i>columna</i>	34	<i>Hydnophora</i>	<i>exesa</i>	50
	<i>exesa</i>	13		<i>microconos</i>	20
	spp.	12		<i>rigida</i>	58
<i>Psammocora</i>	<i>contigua</i>	19		spp.	1
	<i>digitata</i>	19	<i>Merulina</i>	<i>ampliata</i>	38
	<i>haimeana</i>	6		<i>scabricula</i>	13
	spp.	11		spp.	37
	<i>superfiscialis</i>	7	<i>Paraclavarina</i>	<i>triangularis</i>	6
<i>Pseudosiderastrea</i>	<i>tayamai</i>	6	<i>Scapophyllia</i>	<i>cylindrica</i>	8
<b>Fungiidae</b>			<b>Mussidae</b>		
<i>Fungia</i>	<i>concinna</i>	1	<i>Acanthastrea</i>	<i>echinata</i>	47
	<i>danai</i>	1		spp.	11
	<i>echinata</i>	5	<i>Lobophyllia</i>	<i>corymbosa</i>	15
	<i>fungites</i>	6		<i>diminuta</i>	2
	<i>simplex</i>	11		<i>hemprichii</i>	104
	spp.	7		<i>pachysepta</i>	13
(= <i>Ctenactis</i> )	<i>simplex/echin.</i>	205		<i>recta</i>	3
<i>Halomitra</i>	<i>pileus</i>	8		spp.	54
<i>Heliofungia</i>	<i>actiniformis</i>	2	<i>Scolymia</i>	<i>australiens</i>	1
<i>Herpolitha</i>	<i>limax</i>	8		spp.	1
	<i>weberi</i>	3		<i>vitieus</i>	1
<i>Lithophyllon</i>	<i>edwardsi</i>	1	<i>Symphyllia</i>	<i>agaricia</i>	2
<i>Podabacia</i>	spp.	2		<i>radians</i>	21
<i>Polyphyllia</i>	<i>talpini</i>	6		<i>recta</i>	76
<i>Sandolitha</i>	<i>robusta</i>	21		spp.	43
<b>Pectinidae</b>			<b>Carvophyllidae</b>		
<i>Echinophyllia</i>	<i>aspera</i>	19	<i>Euphyllia</i>	<i>divisa</i>	1
	<i>echinoporoides</i>	6	<i>Physogyra</i>	<i>lichtensteini</i>	6
	<i>orpheensis</i>	5	<i>Plerogyra</i>	<i>sinuosa</i>	4
	spp.	10	<b>Dendrophyllidae</b>		
<i>Mycedium</i>	<i>elephantotus</i>	33	<i>Turbinaria</i>	<i>frondens</i>	2
<i>Oxypora</i>	<i>lacera</i>	14		<i>mesenterina</i>	6
	spp.	2		<i>peltata</i>	5
<i>Pectinia</i>	<i>alcicornis</i>	15		<i>reniformis</i>	6
	<i>lactuca</i>	2		spp.	5
	<i>paeonia</i>	3		<i>stellulata</i>	31
	spp.	1		spp.	5

Table A1.2: continued.

Family / Genus	Species	# Obs.	Family / Genus	Species	# Obs.	
<b>Faviidae</b>			<b>Faviidae (cont)</b>			
<i>Australogyra</i>	<i>zelli</i>	19	<i>Favites</i>	<i>abditata</i>	100	
<i>Barabattoia</i>	<i>amicorum</i>	34		<i>chinensis</i>	25	
<i>Caulastrea</i>	<i>furcata</i>	2		<i>complanata</i>	44	
<i>Cyphastrea</i>	<i>chalcidicum</i>	29		<i>flexuosa</i>	53	
	<i>japonicus</i>	13		<i>halicora</i>	47	
	<i>microphthalma</i>	49		<i>pentagonia</i>	13	
	<i>serailia</i>	107		<i>rotundata</i>	1	
	spp.	33		<i>russelli</i>	26	
<i>Diploastrea</i>	<i>heliopora</i>	122		spp.	66	
<i>Echinopora</i>	<i>gemmacea</i>	29	<i>Goniastrea</i>	<i>aspera</i>	113	
	<i>horrida</i>	143		<i>australiensis</i>	27	
<i>Echinopora</i>	<i>lamellosa</i>	171		<i>edwardsi</i>	62	
	<i>mammiformis</i>	30		<i>favulus</i>	17	
	spp.	29		<i>palauensis</i>	4	
<i>Favia</i>	<i>favus</i>	47		<i>pectinata</i>	93	
	<i>laxa</i>	24		<i>retiformis</i>	213	
	<i>lizardensis</i>	115		spp.	56	
	<i>matthai</i>	102		<i>Leptastrea</i>	<i>bewickensis</i>	1
	<i>maxima</i>	13			<i>inaequalis</i>	17
	<i>pallida</i>	96	<i>pruinosa</i>		5	
	<i>rotumana</i>	9	<i>purpurea</i>		21	
	<i>rotundata</i>	18	spp.		30	
	<i>speciosa</i>	55	<i>transversa</i>		101	
		spp.	77	<i>Leptoria</i>	<i>phrygia</i>	114
		<i>stelligera</i>	152		<i>Montastrea</i>	<i>annuligera</i>
	<i>Platygyra</i>	<i>daedalea</i>	41	<i>curta</i>		107
		<i>lamellosa</i>	40	<i>magnistellata</i>		49
		<i>pini</i>	42	spp.		4
		<i>sinensis</i>	79	<i>valenciennesi</i>	17	
		spp.	35	<i>Oulophyllia</i>	<i>bennettae</i>	7
<i>Plesiastrea</i>	<i>versiposa</i>	7	<i>crispa</i>		13	
<b>Helioporidae</b>			<i>Millepora</i>	spp.	52	
<i>Heliopora</i>	<i>coerulea</i>	5		<i>tenella</i>	87	
<b>Tubiporidae</b>				encrusting habit	129	
<i>Tubipora</i>	<i>musica</i>	39	hydroids		26	



Table A1.2: continued

Family / Genus	Species	# Obs.	Family / Genus	Species	# Obs.	
<b>Order Alcyonacia</b>			<b>Sponges</b>		448	
<i>Alcyonaria</i>	spp.	21	<b>Algae</b>	<i>Amphiroa</i>	spp.	29
<i>Anthelia</i>	spp.	17		<i>Caulerpa</i>	spp.	38
<i>Asterospicularia</i>	spp.	14		<i>Chlorodesmis</i>	spp.	30
<i>Briarium</i>	spp.	78		<i>Galaxea</i>	spp.	1
<i>Capnella</i>	spp.	140		<i>Halimeda</i>	spp.	201
<i>Cladiella</i>	spp.	5		<i>Turbinaria</i>	spp.	31
<i>Clavularia</i>	spp.	14			encrusting habit	4
<i>Efflatournaria</i>	spp.	195			red form	2
<i>Lobophyton</i>	spp.	286			turfing habit	23
<i>Pachyclavularia</i>	spp.	12				
<i>Paralemnalia</i>	spp.	15	<b>Tridacnidae</b>			
<i>Parerythropodium</i>	spp.	14	<i>Tridacna</i>	<i>crocea</i>	12	
<i>Sarcophyton</i>	spp.	341		<i>gigas</i>	2	
<i>Sinularia</i>	spp.	519		<i>maxima</i>	6	
<i>Xenia</i>	spp.	169		<i>squamosa</i>	1	
various Nephthiids	spp.	153		spp.	2	
Unident. soft corals		88		non tridacnids	2	
<b>Misc. Benthos</b>			<b>Dead Substrata</b>			
anemones		36	cyclone peeled sub.		49	
ascidians		83	dead standing coral		63	
bryozoans		1		rubble	359	
crinoids		14		sand	91	
gorgonians		207				
sea urchins		2				
zoanthsids		145				

## APPENDIX 2: RESULTS OF ANOVAs FOR CVs

**Table A2.1:** Results of ANOVAs to test for effects of Habitat, Shelf Position, and Region and their interactions on Coefficients of Variation among reefs for fishes. The analytical models for each taxon are described in the text.

TAXON	SOURCE	df	REEFS		
			$\alpha$	$\alpha_{c=\beta}$	Infer
<b>Large Fish</b>					
<i>Plectropomus</i> Spp	HABITAT	1,2	0.490	0.140	-
	REGION	2,2	0.682	0.199	-
	SHELF	1,2	0.534	0.140	-
	H*R	2,2	0.367	0.199	-
	S*H	1,2	0.497	0.140	-
	S*R	2,2	0.350	0.199	-
	<hr/>				
All Lutjanids	HABITAT	1,2	0.523	0.140	-
	REGION	2,2	0.201	0.199	-
	SHELF	1,2	0.066	0.140	*
	H*R	2,2	0.500	0.199	-
	S*H	1,2	0.523	0.140	-
	S*R	2,2	0.201	0.199	-
<hr/>					
<i>L. carponotatus</i> (MS only)	HABITAT	1,2	0.341	0.293	-
	REGION	2,2	0.300	0.229	-
<hr/>					
Total Acanthurids	HABITAT	1,2	0.166	0.140	-
	REGION	2,2	0.370	0.199	-
	SHELF	1,2	0.181	0.140	-
	H*R	2,2	0.582	0.199	-
	S*H	1,2	0.074	0.140	*
	S*R	2,2	0.402	0.199	-
<hr/>					
<i>Z. scopas</i>	HABITAT	1,2	0.541	0.140	-
	REGION	2,2	0.392	0.199	-
	SHELF	1,2	0.170	0.140	-
	H*R	2,2	0.449	0.199	-
	S*H	1,2	0.106	0.140	*
	S*R	2,2	0.619	0.199	-
<hr/>					
Other Acanthurids	HABITAT	1,2	0.160	0.140	-
	REGION	2,2	0.159	0.199	*
	SHELF	1,2	0.145	0.140	-
	H*R	2,2	0.490	0.199	-
	S*H	1,2	0.153	0.140	-
	S*R	2,2	0.507	0.199	-

Table A2.1 (Continued).

TAXON	SOURCE	df	REEFS		
			$\alpha$	$\alpha_{\epsilon=\beta}$	Infer
All Chaetodons	HABITAT	1,2	0.010	0.140	*
	REGION	2,2	0.049	0.199	*
	SHELF	1,2	0.121	0.140	*
	H*R	2,2	0.028	0.199	*
	S*H	1,2	0.824	0.140	-
	S*R	2,2	0.080	0.199	*
<i>C. aureofasciatus</i> (MS only, N&C)	HABITAT	1,1	0.142	0.303	*
	REGION	1,1	0.116	0.303	*
<i>C. baronessa</i>	HABITAT	1,2	0.001	0.140	*
	REGION	2,2	0.019	0.199	*
	SHELF	1,2	0.003	0.140	*
	H*R	2,2	0.007	0.199	*
	S*H	1,2	0.005	0.140	*
	S*R	2,2	0.005	0.199	*
<i>C. plebeius</i>	HABITAT	1,2	0.422	0.140	-
	REGION	2,2	0.399	0.199	-
	SHELF	1,2	0.459	0.140	-
	H*R	2,2	0.728	0.199	-
	S*H	1,2	0.766	0.140	-
	S*R	2,2	0.584	0.199	-
<i>C. trifasciatus</i>	HABITAT	1,2	0.933	0.140	-
	REGION	2,2	0.021	0.199	*
	SHELF	1,2	0.049	0.140	*
	H*R	2,2	0.020	0.199	*
	S*H	1,2	0.536	0.140	-
	S*R	2,2	0.174	0.199	*
<i>C. vagabundus</i>	HABITAT	1,2	0.492	0.140	-
	REGION	2,2	0.549	0.199	-
	SHELF	1,2	0.842	0.140	-
	H*R	2,2	0.763	0.199	-
	S*H	1,2	0.747	0.140	-
	S*R	2,2	0.723	0.199	-
Other Chaetodons	HABITAT	1,2	0.247	0.140	-
	REGION	2,2	0.682	0.199	-
	SHELF	1,2	0.824	0.140	-
	H*R	2,2	0.514	0.199	-
	S*H	1,2	0.846	0.140	-
	S*R	2,2	0.499	0.199	-

Table A2.1 (Continued).

TAXON	SOURCE	df	REEFS		
			$\alpha$	$\alpha_{c=\beta}$	Infer
<b>Small Fish</b>					
<i>A. curacao</i> (2 Regions only)	HABITAT	1,1	0.840	0.250	-
	REGION	1,1	0.601	0.250	-
	SHELF	1,1	0.987	0.250	-
	H*R	1,1	0.424	0.250	-
	S*H	1,1	0.299	0.250	-
	S*R	1,1	0.502	0.250	-
<i>C. atripectoralis</i>	HABITAT	1,2	0.854	0.140	-
	REGION	2,2	0.886	0.199	-
	SHELF	1,2	0.629	0.140	-
	H*R	2,2	0.672	0.199	-
	S*H	1,2	0.536	0.140	-
	S*R	2,2	0.741	0.199	-
<i>C. rollandi</i> (MS & OS-B only)	HAB-SH	2,4	0.342	0.148	-
	REGION	2,4	0.980	0.148	-
<i>Recruit C.r.</i> (MS & OS-B only)	HAB-SH	2,4	0.923	0.148	-
	REGION	2,4	0.898	0.148	-
<i>P. lacrymatus</i>	HABITAT	1,2	0.450	0.140	-
	REGION	2,2	0.257	0.199	-
	SHELF	1,2	0.296	0.140	-
	H*R	2,2	0.185	0.199	*
	S*H	1,2	0.169	0.140	-
	S*R	2,2	0.655	0.199	-
<i>P. moluccensis</i> (MS & OS-B only)	HAB-SH	2,4	0.396	0.148	-
	REGION	2,4	0.429	0.148	-
<i>Recruit P.m.</i> (MS & OS-B only)	HAB-SH	2,4	0.294	0.148	-
	REGION	2,4	0.126	0.148	*
<i>T. lunare</i> (MS & OS-B only)	HAB-SH	2,4	0.045	0.148	*
	REGION	2,4	0.473	0.148	-

**Table A2.2:** Results of ANOVAs to test for effects of Habitat, Shelf Position, and Region and their interactions on Coefficients of Variation among locations, sites, and transects for fishes. The analytical models for each taxon are described in the text.

TAXON	SOURCE	df	SCALE										
			LOCATIONS			SITES			TRANSECTS				
			$\alpha$	$\alpha_{c=\beta}$	Infer	$\alpha$	$\alpha_{c=\beta}$	Infer	$\alpha$	$\alpha_{c=\beta}$	Infer		
<b>Large Fish</b>													
<i>Plectropomus</i> Spp.	HAB.	1,34	0.862	0.001	-				0.245	0.001	-		
	REGn.	2,34	0.712	0.002	-				0.143	0.002	-		
	SHELF	1,34	0.306	0.001	-				0.370	0.001	-		
	H*R	2,34	0.580	0.002	-				0.339	0.002	-		
	S*H	1,34	0.146	0.001	-				0.419	0.001	-		
	S*R	2,34	0.799	0.002	-				0.680	0.002	-		
	S*H*R	2,34	0.031	0.002	-				0.022	0.002	-		
All Lutjanids	HAB.	1,35	0.485	0.001	-				0.028	0.001	-		
	REGn.	2,35	0.234	0.002	-				0.019	0.002	-		
	SHELF	1,35	0.688	0.001	-				0.217	0.001	-		
	H*R	2,35	0.610	0.002	-				0.978	0.002	-		
	S*H	1,35	0.080	0.001	-				0.362	0.001	-		
	S*R	2,35	0.647	0.002	-				0.211	0.002	-		
	S*H*R	2,35	0.991	0.002	-				0.910	0.002	-		
<i>L. carponotatus</i> (MS only)	HAB	1,16	0.124	0.022	-				0.016	0.022	*		
	REGn.	2,16	0.111	0.037	-				0.542	0.037	-		
	H*R	2,16	0.249	0.037	-				0.991	0.037	-		
Total Acanthurids	HAB.	1,36	0.798	0.001	-				0.227	0.001	-		
	REGn.	2,36	0.609	0.002	-				0.429	0.002	-		
	SHELF	1,36	0.292	0.001	-				0.039	0.001	-		
	H*R	2,36	0.462	0.002	-				0.683	0.002	-		
	S*H	1,36	0.175	0.001	-				0.054	0.001	-		
	S*R	2,36	0.066	0.002	-				0.268	0.002	-		
	S*H*R	2,36	0.523	0.002	-				0.591	0.002	-		
<i>Z. scopas</i>	HAB.	1,35	0.428	0.001	-				0.417	0.001	-		
	REGn.	2,35	0.241	0.002	-				0.968	0.002	-		
	SHELF	1,35	0.011	0.001	-				0.235	0.001	-		
	H*R	2,35	0.031	0.002	-				0.734	0.002	-		
	S*H	1,35	0.822	0.001	-				0.866	0.001	-		
	S*R	2,35	0.627	0.002	-				0.695	0.002	-		
	S*H*R	2,35	0.651	0.002	-				0.941	0.002	-		
Other Acanthurids	HAB.	1,36	0.594	0.001	-				0.277	0.001	-		
	REGn.	2,36	0.317	0.002	-				0.556	0.002	-		
	SHELF	1,36	0.551	0.001	-				0.068	0.001	-		
	H*R	2,36	0.283	0.002	-				0.531	0.002	-		
	S*H	1,36	0.703	0.001	-				0.097	0.001	-		
	S*R	2,36	0.056	0.002	-				0.390	0.002	-		
	S*H*R	2,36	0.757	0.002	-				0.491	0.002	-		

Table A2.2 (Continued).

TAXON	SOURCE	df	LOCATIONS			SITES			TRANSECTS		
			$\alpha$	$\alpha_{c=\beta}$	Infer	$\alpha$	$\alpha_{c=\beta}$	Infer	$\alpha$	$\alpha_{c=\beta}$	Infer
All Chaetodons	HAB.	1,36	0.988	0.001	-			0.378	0.001	-	
	REGn.	2,36	0.777	0.002	-			0.001	0.002	*	
	SHELF	1,36	0.368	0.001	-			0.726	0.001	-	
	H*R	2,36	0.330	0.002	-			0.957	0.002	-	
	S*H	1,36	0.717	0.001	-			0.231	0.001	-	
	S*R	2,36	0.800	0.002	-			0.005	0.002	-	
	S*H*R	2,36	0.582	0.002	-			0.009	0.002	-	
<i>C. aureofasciatus</i> (MS only, N&C)	HAB.	1,12	0.163	0.047	-			0.455	0.047	-	
	REGn.	1,12	0.394	0.047	-			0.661	0.047	-	
	H*R	1,12	0.965	0.047	-			0.408	0.047	-	
<i>C. baronessa</i>	HAB.	1,31	0.040	0.002	-			0.909	0.002	-	
	REGn.	2,31	0.058	0.003	-			0.214	0.003	-	
	SHELF	1,31	0.006	0.002	-			0.425	0.002	-	
	H*R	2,31	0.454	0.003	-			0.347	0.003	-	
	S*H	1,31	0.559	0.002	-			0.271	0.002	-	
	S*R	2,31	0.564	0.003	-			0.439	0.003	-	
	S*H*R	2,31	0.473	0.003	-			0.917	0.003	-	
<i>C. plebeius</i>	HAB.	1,33	0.656	0.001	-			0.142	0.001	-	
	REGn.	2,33	0.448	0.003	-			0.482	0.003	-	
	SHELF	1,33	0.508	0.001	-			0.628	0.001	-	
	H*R	2,33	0.659	0.003	-			0.118	0.003	-	
	S*H	1,33	0.094	0.001	-			0.135	0.001	-	
	S*R	2,33	0.588	0.003	-			0.976	0.003	-	
	S*H*R	2,33	0.757	0.003	-			0.289	0.003	-	
<i>C. trifasciatus</i>	HAB.	1,36	0.852	0.001	-			0.894	0.001	-	
	REGn.	2,36	0.104	0.002	-			0.120	0.002	-	
	SHELF	1,36	0.205	0.001	-			0.086	0.001	-	
	H*R	2,36	0.456	0.002	-			0.022	0.002	-	
	S*H	1,36	0.850	0.001	-			0.002	0.001	-	
	S*R	2,36	0.314	0.002	-			0.875	0.002	-	
	S*H*R	2,36	0.544	0.002	-			0.237	0.002	-	
<i>C. vagabundus</i>	HAB.	1,31	0.650	0.002	-			0.746	0.002	-	
	REGn.	2,31	0.040	0.003	-			0.027	0.003	-	
	SHELF	1,31	0.572	0.002	-			0.108	0.002	-	
	H*R	2,31	0.839	0.003	-			0.971	0.003	-	
	S*H	1,31	0.736	0.002	-			0.508	0.002	-	
	S*R	2,31	0.381	0.003	-			0.255	0.003	-	
	S*H*R	2,31	0.500	0.003	-			0.851	0.003	-	
Other Chaetodons	HAB.	1,36	0.555	0.001	-			0.168	0.001	-	
	REGn.	2,36	0.313	0.002	-			0.005	0.002	-	
	SHELF	1,36	0.461	0.001	-			0.002	0.001	-	
	H*R	2,36	0.407	0.002	-			0.824	0.002	-	
	S*H	1,36	0.340	0.001	-			0.861	0.001	-	
	S*R	2,36	0.240	0.002	-			0.270	0.002	-	
	S*H*R	2,36	0.519	0.002	-			0.179	0.002	-	

Table A2.2 (Continued).

TAXON	SOURCE	df	SCALE								
			LOCATIONS			SITES			TRANSECTS		
			$\alpha$	$\alpha_{c=\beta}$	Infer	$\alpha$	$\alpha_{c=\beta}$	Infer	$\alpha$	$\alpha_{c=\beta}$	Infer
<b>Small Fish</b>											
<i>A. curacao</i> (2 Regions only)	HAB.	1,19	0.979	0.012	-	0.293	0.012	-	0.012	0.012	*
	REGn.	1,19	0.180	0.012	-	0.607	0.012	-	0.877	0.012	-
	SHELF	1,19	0.579	0.012	-	0.196	0.012	-	0.309	0.012	-
	H*R	1,19	0.054	0.012	-	0.586	0.012	-	0.996	0.012	-
	S*H	1,19	0.293	0.012	-	0.640	0.012	-	0.130	0.012	-
	S*R	1,19	0.904	0.012	-	0.661	0.012	-	0.844	0.012	-
	S*H*R	1,19	0.932	0.012	-	0.382	0.012	-	0.131	0.012	-
<i>C. atripectoralis</i>	HAB.	1,26	0.080	0.003	-	0.217	0.003	-	0.908	0.003	-
	REGn.	2,26	0.025	0.006	-	0.913	0.006	-	0.165	0.006	-
	SHELF	1,26	0.103	0.003	-	0.887	0.003	-	0.237	0.003	-
	H*R	2,26	0.443	0.006	-	0.195	0.006	-	0.724	0.006	-
	S*H	1,26	0.795	0.003	-	0.038	0.003	-	0.026	0.003	-
	S*R	2,26	0.012	0.006	-	0.121	0.006	-	0.410	0.006	-
	S*H*R	2,26	0.025	0.006	-	0.814	0.006	-	0.338	0.006	-
<i>C. rollandi</i> (MS only)	HAB.	1,17	0.230	0.020	-	0.088	0.020	-	0.026	0.020	-
	REGn.	2,17	0.862	0.033	-	0.449	0.033	-	0.071	0.033	-
	H*R	2,17	0.628	0.033	-	0.728	0.033	-	0.379	0.033	-
<i>ROut</i>	REGn.	2, 9	0.971	0.117	-	0.280	0.117	-	0.962	0.117	-
<i>Recruit C.r.</i> (MS only) (OS Backs only)	HAB.	1,17	0.195	0.020	-	0.645	0.020	-	0.003	0.020	*
	REGn.	2,17	0.750	0.033	-	0.221	0.033	-	0.064	0.033	-
	H*R	2,17	0.407	0.033	-	0.112	0.033	-	0.030	0.033	*
	REGn.	2, 9	0.291	0.117	-	0.984	0.117	-	0.335	0.117	-
<i>P. lacrymatus</i>	HAB.	1,31	0.391	0.002	-	0.931	0.002	-	0.950	0.002	-
	REGn.	2,31	0.125	0.003	-	0.146	0.003	-	0.321	0.003	-
	SHELF	1,31	0.389	0.002	-	0.176	0.002	-	0.012	0.002	-
	H*R	2,31	0.664	0.003	-	0.242	0.003	-	0.333	0.003	-
	S*H	1,31	0.862	0.002	-	0.372	0.002	-	0.847	0.002	-
	S*R	2,31	0.805	0.003	-	0.717	0.003	-	0.081	0.003	-
	S*H*R	2,31	0.987	0.003	-	0.880	0.003	-	0.959	0.003	-
<i>P. moluccensis</i> (MS only) (OS Backs only)	HAB.	1,18	0.416	0.017	-	0.726	0.017	-	0.516	0.017	-
	REGn.	2,18	0.454	0.029	-	0.672	0.029	-	0.291	0.029	-
	H*R	2,18	0.105	0.029	-	0.503	0.029	-	0.611	0.029	-
	REGn.	2, 9	0.358	0.117	-	0.713	0.117	-	0.114	0.117	*
<i>Recruit P.m.</i> (MS only) (OS Backs only)	HAB.	1,16	0.600	0.022	-	0.499	0.022	-	0.160	0.022	-
	REGn.	2,16	0.343	0.037	-	0.445	0.037	-	0.185	0.037	-
	H*R	2,16	0.204	0.037	-	0.704	0.037	-	0.954	0.037	-
	REGn.	2, 8	0.222	0.133	-	0.653	0.133	-	0.275	0.133	-
<i>T. lunare</i> (MS only)	HAB.	1,18	0.339	0.017	-	0.718	0.017	-	0.304	0.017	-
	REGn.	2,18	0.394	0.029	-	0.164	0.029	-	0.151	0.029	-
	H*R	2,18	0.530	0.029	-	0.713	0.029	-	0.918	0.029	-
	REGn.	2, 9	0.378	0.117	-	0.134	0.117	-	0.128	0.117	-

**Table A2.3:** Results of ANOVAs to test for effects of Habitat, Shelf Position, and Region and their interactions on Coefficients of Variation among reefs for benthos.

TAXON	SOURCE	df	VARIABLE								
			% COVER			INTERCEPTS			JUVENILES		
			$\alpha$	$\alpha_{c=\beta}$	Infer	$\alpha$	$\alpha_{c=\beta}$	Infer	$\alpha$	$\alpha_{c=\beta}$	Infer
Total Hard Coral	HABITAT	1,2	0.706	0.140	-	0.673	0.140	-			
	REGION	2,2	0.400	0.199	-	0.510	0.199	-			
	SHELF	1,2	0.541	0.140	-	0.158	0.140	-			
	H*R	2,2	0.787	0.199	-	0.131	0.199	*			
	S*H	1,2	0.270	0.140	-	0.132	0.140	*			
	S*R	2,2	0.128	0.199	*	0.167	0.199	*			
Acroporidae	HABITAT	1,2	0.451	0.140	-	0.833	0.140	-	0.826	0.140	-
	REGION	2,2	0.460	0.199	-	0.829	0.199	-	0.883	0.199	-
	SHELF	1,2	0.724	0.140	-	0.934	0.140	-	0.597	0.140	-
	H*R	2,2	0.764	0.199	-	0.830	0.199	-	0.776	0.199	-
	S*H	1,2	0.447	0.140	-	0.863	0.140	-	0.872	0.140	-
	S*R	2,2	0.638	0.199	-	0.920	0.199	-	0.219	0.199	-
Faviidae	HABITAT	1,2	0.967	0.140	-	0.541	0.140	-	0.860	0.140	-
	REGION	2,2	0.908	0.199	-	0.885	0.199	-	0.362	0.199	-
	SHELF	1,2	0.812	0.140	-	0.343	0.140	-	0.403	0.140	-
	H*R	2,2	0.789	0.199	-	0.536	0.199	-	0.295	0.199	-
	S*H	1,2	0.678	0.140	-	0.824	0.140	-	0.180	0.140	-
	S*R	2,2	0.739	0.199	-	0.696	0.199	-	0.289	0.199	-
Pocilloporidae	HABITAT	1,2	0.069	0.140	*	0.283	0.140	-	0.826	0.140	-
	REGION	2,2	0.389	0.199	-	0.792	0.199	-	0.800	0.199	-
	SHELF	1,2	0.190	0.140	-	0.345	0.140	-	0.827	0.140	-
	H*R	2,2	0.704	0.199	-	0.592	0.199	-	0.896	0.199	-
	S*H	1,2	0.545	0.140	-	0.717	0.140	-	0.840	0.140	-
	S*R	2,2	0.715	0.199	-	0.509	0.199	-	0.416	0.199	-
Poritidae	HABITAT	1,2	0.759	0.140	-	0.159	0.140	-			
	REGION	2,2	0.217	0.199	-	0.187	0.199	*			
	SHELF	1,2	0.937	0.140	-	0.551	0.140	-			
	H*R	2,2	0.475	0.199	-	0.151	0.199	*			
	S*H	1,2	0.285	0.140	-	0.466	0.140	-			
	S*R	2,2	0.238	0.199	-	0.439	0.199	-			
Misc. Hard Corals	HABITAT	1,2	0.720	0.140	-	0.613	0.140	-	0.609	0.140	-
	REGION	2,2	0.459	0.199	-	0.456	0.199	-	0.322	0.199	-
	SHELF	1,2	0.589	0.140	-	0.839	0.140	-	0.734	0.140	-
	H*R	2,2	0.787	0.199	-	0.648	0.199	-	0.655	0.199	-
	S*H	1,2	0.528	0.140	-	0.463	0.140	-	0.596	0.140	-
	S*R	2,2	0.504	0.199	-	0.537	0.199	-	0.599	0.199	-



Table A2.3 (continued)

TAXON	SOURCE	df	VARIABLE								
			% COVER			INTERCEPTS			JUVENILES		
			$\alpha$	$\alpha_{c=\beta}$	Infer	$\alpha$	$\alpha_{c=\beta}$	Infer	$\alpha$	$\alpha_{c=\beta}$	Infer
Dead Standing Coral	HABITAT	1,2	0.623	0.140	-	0.607	0.140	-			
	REGION	2,2	0.829	0.199	-	0.629	0.199	-			
	SHELF	1,2	0.363	0.140	-	0.193	0.140	-			
	H*R	2,2	0.636	0.199	-	0.798	0.199	-			
	S*H	1,2	0.174	0.140	-	0.101	0.140	*			
	S*R	2,2	0.599	0.199	-	0.653	0.199	-			
Soft Corals	HABITAT	1,2	0.037	0.140	*	0.114	0.140	*	0.552	0.140	-
	REGION	2,2	0.797	0.199	-	0.860	0.199	-	0.839	0.199	-
	SHELF	1,2	0.128	0.140	*	0.126	0.140	*	0.469	0.140	-
	H*R	2,2	0.051	0.199	*	0.052	0.199	*	0.564	0.199	-
	S*H	1,2	0.059	0.140	*	0.087	0.140	*	0.777	0.140	-
	S*R	2,2	0.154	0.199	*	0.139	0.199	*	0.570	0.199	-
Sponges	HABITAT	1,2	0.138	0.140	*	0.480	0.140	-			
	REGION	2,2	0.089	0.199	*	0.121	0.199	*			
	SHELF	1,2	0.038	0.140	*	0.359	0.140	-			
	H*R	2,2	0.059	0.199	*	0.103	0.199	*			
	S*H	1,2	0.082	0.140	*	0.798	0.140	-			
	S*R	2,2	0.058	0.199	*	0.081	0.199	*			
All Algae	HABITAT	1,2	0.482	0.140	-	0.276	0.140	-			
	REGION	2,2	0.500	0.199	-	0.283	0.199	-			
	SHELF	1,2	0.482	0.140	-	0.352	0.140	-			
	H*R	2,2	0.812	0.199	-	0.704	0.199	-			
	S*H	1,2	0.157	0.140	-	0.096	0.140	*			
	S*R	2,2	0.812	0.199	-	0.238	0.199	-			

Table A2.3 (continued)

<b>Poritids</b>								
<b>SOURCE</b>	<b>df</b>	$\alpha$	$\alpha_{c=\beta}$	<b>Infer</b>	$\alpha$	$\alpha_{c=\beta}$	<b>Infer</b>	
		<u>&lt;6cm<math>\Phi</math></u>			<u>51-100cm<math>\Phi</math></u>			
HABITAT	1,2	0.825	0.140	-	0.410	0.140	-	
REGION	2,2	0.665	0.199	-	0.327	0.199	-	
SHELF	1,2	0.252	0.140	-	0.377	0.140	-	
H*R	2,2	0.302	0.199	-	0.672	0.199	-	
S*H	1,2	0.269	0.140	-	0.914	0.140	-	
S*R	2,2	0.251	0.199	-	0.209	0.199	-	
		<u>6-20cm<math>\Phi</math></u>			<u>&gt;100cm<math>\Phi</math></u>			
HABITAT	1,2	0.349	0.140	-	0.622	0.140	-	
REGION	2,2	0.971	0.199	-	0.109	0.199	*	
SHELF	1,2	0.663	0.140	-	0.487	0.140	-	
H*R	2,2	0.593	0.199	-	0.647	0.199	-	
S*H	1,2	0.644	0.140	-	0.468	0.140	-	
S*R	2,2	0.493	0.199	-	0.088	0.199	*	
		<u>21-50cm<math>\Phi</math></u>						
HABITAT	1,2	0.324	0.140	-				
REGION	2,2	0.573	0.199	-				
SHELF	1,2	0.925	0.140	-				
H*R	2,2	0.759	0.199	-				
S*H	1,2	0.631	0.140	-				
S*R	2,2	0.121	0.199	*				
<b>Benthos</b>								
		<u>Tridacna Spp.</u>			<u>L. laevigata</u>			
HABITAT	1,2	0.737	0.140	-	0.500	0.303	-	
REGION	2,2	0.119	0.199	*	0.500	0.303	-	
SHELF	1,2	0.091	0.140	*				
H*R	2,2	0.158	0.199	*				
S*H	1,2	0.094	0.140	*				
S*R	2,2	0.574	0.199	-				

**Table A2.4:** Results of ANOVAs to test for effects of Habitat, Shelf Position, and Region and their interactions on Coefficients of Variation among locations, sites, and transects for benthos. The same model applied to all analyses, as described in the text.

TAXON	SOURCE	df	SCALE									
			LOCATIONS			SITES			TRANSECTS			
			$\alpha$	$\alpha_{c=\beta}$	Infer	$\alpha$	$\alpha_{c=\beta}$	Infer	$\alpha$	$\alpha_{c=\beta}$	Infer	
<b>% Cover</b>												
<b>Total Hard Coral</b>	HABITAT	1,36	0.729	0.001	-	0.289	0.001	-	0.333	0.001	-	
	REGION	2,36	0.876	0.002	-	0.557	0.002	-	0.086	0.002	-	
	SHELF	1,36	0.243	0.001	-	0.211	0.001	-	0.003	0.001	-	
	H*R	2,36	0.547	0.002	-	0.205	0.002	-	0.507	0.002	-	
	S*H	1,36	0.511	0.001	-	0.776	0.001	-	0.107	0.001	-	
	S*R	2,36	0.161	0.002	-	0.003	0.002	-	0.011	0.002	-	
	S*H*R	2,36	0.271	0.002	-	0.803	0.002	-	0.478	0.002	-	
	<b>Acroporidae</b>											
HABITAT	1,36	0.090	0.001	-	0.145	0.001	-	0.052	0.001	-		
REGION	2,36	0.120	0.002	-	0.196	0.002	-	0.933	0.002	-		
SHELF	1,36	0.871	0.001	-	0.214	0.001	-	0.002	0.001	-		
H*R	2,36	0.474	0.002	-	0.045	0.002	-	0.050	0.002	-		
S*H	1,36	0.501	0.001	-	0.254	0.001	-	0.595	0.001	-		
S*R	2,36	0.947	0.002	-	0.416	0.002	-	0.358	0.002	-		
S*H*R	2,36	0.986	0.002	-	0.741	0.002	-	0.543	0.002	-		
<b>Faviidae</b>												
HABITAT	1,36	0.088	0.001	-	0.432	0.001	-	0.446	0.001	-		
REGION	2,36	0.117	0.002	-	0.384	0.002	-	0.556	0.002	-		
SHELF	1,36	0.041	0.001	-	0.622	0.001	-	0.181	0.001	-		
H*R	2,36	0.250	0.002	-	0.954	0.002	-	0.194	0.002	-		
S*H	1,36	0.189	0.001	-	0.629	0.001	-	0.927	0.001	-		
S*R	2,36	0.030	0.002	-	0.302	0.002	-	0.139	0.002	-		
S*H*R	2,36	0.509	0.002	-	0.702	0.002	-	0.419	0.002	-		
<b>Pocilloporidae</b>												
HABITAT	1,36	0.266	0.001	-	0.682	0.001	-	0.000	0.001	*		
REGION	2,36	0.155	0.002	-	0.887	0.002	-	0.050	0.002	-		
SHELF	1,36	0.383	0.001	-	0.302	0.001	-	0.459	0.001	-		
H*R	2,36	0.176	0.002	-	0.257	0.002	-	0.107	0.002	-		
S*H	1,36	0.207	0.001	-	0.261	0.001	-	0.193	0.001	-		
S*R	2,36	0.219	0.002	-	0.194	0.002	-	0.572	0.002	-		
S*H*R	2,36	0.052	0.002	-	0.336	0.002	-	0.281	0.002	-		
<b>Poritidae</b>												
HABITAT	1,36	0.358	0.001	-	0.675	0.001	-	0.028	0.001	-		
REGION	2,36	0.077	0.002	-	0.056	0.002	-	0.620	0.002	-		
SHELF	1,36	0.840	0.001	-	0.320	0.001	-	0.359	0.001	-		
H*R	2,36	0.700	0.002	-	0.727	0.002	-	0.063	0.002	-		
S*H	1,36	0.552	0.001	-	0.481	0.001	-	0.221	0.001	-		
S*R	2,36	0.833	0.002	-	0.297	0.002	-	0.224	0.002	-		
S*H*R	2,36	0.444	0.002	-	0.302	0.002	-	0.836	0.002	-		

Table A2.4 (Continued).

TAXON	SOURCE	df	LOCATIONS			SITES			TRANSECTS		
			$\alpha$	$\alpha_{c=\beta}$	Infer	$\alpha$	$\alpha_{c=\beta}$	Infer	$\alpha$	$\alpha_{c=\beta}$	Infer
<b>% Cover</b>											
Misc. Hard Corals	HABITAT	1,36	0.792	0.001	-	0.561	0.001	-	0.154	0.001	-
	REGION	2,36	0.278	0.002	-	0.324	0.002	-	0.592	0.002	-
	SHELF	1,36	0.394	0.001	-	1.000	0.001	-	0.635	0.001	-
	H*R	2,36	0.553	0.002	-	0.024	0.002	-	0.825	0.002	-
	S*H	1,36	0.542	0.001	-	0.566	0.001	-	0.034	0.001	-
	S*R	2,36	0.682	0.002	-	0.987	0.002	-	0.640	0.002	-
	S*H*R	2,36	0.508	0.002	-	0.607	0.002	-	0.487	0.002	-
	Dead Standing Coral	HABITAT	1,31	0.251	0.002	-	0.742	0.002	-	0.000	0.002
REGION		2,31	0.918	0.003	-	0.090	0.003	-	0.472	0.003	-
SHELF		1,31	0.205	0.002	-	0.117	0.002	-	0.000	0.002	*
H*R		2,31	0.315	0.003	-	0.746	0.003	-	0.971	0.003	-
S*H		1,31	0.052	0.002	-	0.204	0.002	-	0.004	0.002	-
S*R		2,31	0.101	0.003	-	0.436	0.003	-	0.908	0.003	-
S*H*R		2,31	0.900	0.003	-	0.526	0.003	-	0.611	0.003	-
Soft Corals		HABITAT	1,36	0.912	0.001	-	0.285	0.001	-	0.649	0.001
	REGION	2,36	0.198	0.002	-	0.646	0.002	-	0.095	0.002	-
	SHELF	1,36	0.312	0.001	-	0.095	0.001	-	0.307	0.001	-
	H*R	2,36	0.297	0.002	-	0.500	0.002	-	0.406	0.002	-
	S*H	1,36	0.291	0.001	-	0.745	0.001	-	0.170	0.001	-
	S*R	2,36	0.321	0.002	-	0.155	0.002	-	0.069	0.002	-
	S*H*R	2,36	0.223	0.002	-	0.490	0.002	-	0.042	0.002	-
	Sponges	HABITAT	1,32	0.856	0.002	-	0.471	0.002	-	0.000	0.002
REGION		2,32	0.592	0.003	-	0.053	0.003	-	0.489	0.003	-
SHELF		1,32	0.764	0.002	-	0.107	0.002	-	0.500	0.002	-
H*R		2,32	0.096	0.003	-	0.758	0.003	-	0.155	0.003	-
S*H		1,32	0.988	0.002	-	0.395	0.002	-	0.071	0.002	-
S*R		2,32	0.680	0.003	-	0.439	0.003	-	0.796	0.003	-
S*H*R		2,32	0.681	0.003	-	0.491	0.003	-	0.512	0.003	-
Algae		HABITAT	1,30	0.690	0.002	-	0.844	0.002	-	0.493	0.002
	REGION	2,30	0.741	0.004	-	0.992	0.004	-	0.586	0.004	-
	SHELF	1,30	0.353	0.002	-	0.236	0.002	-	0.077	0.002	-
	H*R	2,30	0.444	0.004	-	0.728	0.004	-	0.834	0.004	-
	S*H	1,30	0.488	0.002	-	0.636	0.002	-	0.140	0.002	-
	S*R	2,30	0.051	0.004	-	0.706	0.004	-	0.590	0.004	-
	S*H*R	2,30	0.972	0.004	-	0.085	0.004	-	0.044	0.004	-

Table A2.4 (Continued).

TAXON	SOURCE	df	LOCATIONS			SITES			TRANSECTS		
			$\alpha$	$\alpha_{c=\beta}$	Infer	$\alpha$	$\alpha_{c=\beta}$	Infer	$\alpha$	$\alpha_{c=\beta}$	Infer
<b>Intercepts</b>											
Total Hard	HABITAT	1,36	0.521	0.001	-	0.859	0.001	-	0.120	0.001	-
Coral	REGION	2,36	0.228	0.002	-	0.033	0.002	-	0.345	0.002	-
	SHELF	1,36	0.717	0.001	-	0.867	0.001	-	0.986	0.001	-
	H*R	2,36	0.710	0.002	-	0.546	0.002	-	0.263	0.002	-
	S*H	1,36	0.883	0.001	-	0.764	0.001	-	0.627	0.001	-
	S*R	2,36	0.230	0.002	-	0.426	0.002	-	0.303	0.002	-
	S*H*R	2,36	0.707	0.002	-	0.183	0.002	-	0.565	0.002	-
	Acroporidae	HABITAT	1,36	0.654	0.001	-	0.244	0.001	-	0.149	0.001
REGION		2,36	0.244	0.002	-	0.298	0.002	-	0.865	0.002	-
SHELF		1,36	0.463	0.001	-	0.450	0.001	-	0.073	0.001	-
H*R		2,36	0.550	0.002	-	0.118	0.002	-	0.284	0.002	-
S*H		1,36	0.886	0.001	-	0.904	0.001	-	0.470	0.001	-
S*R		2,36	0.924	0.002	-	0.594	0.002	-	0.870	0.002	-
S*H*R		2,36	0.722	0.002	-	0.997	0.002	-	0.454	0.002	-
Faviidae	HABITAT	1,36	0.204	0.001	-	0.737	0.001	-	0.563	0.001	-
	REGION	2,36	0.112	0.002	-	0.471	0.002	-	0.103	0.002	-
	SHELF	1,36	0.228	0.001	-	0.064	0.001	-	0.187	0.001	-
	H*R	2,36	0.652	0.002	-	0.918	0.002	-	0.198	0.002	-
	S*H	1,36	0.129	0.001	-	0.827	0.001	-	0.215	0.001	-
	S*R	2,36	0.609	0.002	-	0.173	0.002	-	0.077	0.002	-
	S*H*R	2,36	0.448	0.002	-	0.901	0.002	-	0.118	0.002	-
Pocilloporidae	HABITAT	1,36	0.222	0.001	-	0.967	0.001	-	0.002	0.001	-
	REGION	2,36	0.143	0.002	-	0.981	0.002	-	0.179	0.002	-
	SHELF	1,36	0.409	0.001	-	0.475	0.001	-	0.113	0.001	-
	H*R	2,36	0.154	0.002	-	0.544	0.002	-	0.078	0.002	-
	S*H	1,36	0.488	0.001	-	0.283	0.001	-	0.198	0.001	-
	S*R	2,36	0.236	0.002	-	0.201	0.002	-	0.403	0.002	-
	S*H*R	2,36	0.392	0.002	-	0.566	0.002	-	0.556	0.002	-
Poritidae	HABITAT	1,36	0.126	0.001	-	0.126	0.001	-	0.007	0.001	-
	REGION	2,36	0.009	0.002	-	0.042	0.002	-	0.775	0.002	-
	SHELF	1,36	0.437	0.001	-	0.335	0.001	-	0.727	0.001	-
	H*R	2,36	0.472	0.002	-	0.195	0.002	-	0.056	0.002	-
	S*H	1,36	0.729	0.001	-	0.536	0.001	-	0.085	0.001	-
	S*R	2,36	0.761	0.002	-	0.217	0.002	-	0.218	0.002	-
	S*H*R	2,36	0.772	0.002	-	0.471	0.002	-	0.739	0.002	-

Table A2.4 (Continued).

TAXON	SOURCE	df	LOCATIONS			SITES			TRANSECTS		
			$\alpha$	$\alpha_{c=\beta}$	Infer	$\alpha$	$\alpha_{c=\beta}$	Infer	$\alpha$	$\alpha_{c=\beta}$	Infer
<b>Intercepts</b>											
Misc. Hard	HABITAT	1,36	0.493	0.001	-	0.315	0.001	-	0.016	0.001	-
Corals	REGION	2,36	0.545	0.002	-	0.208	0.002	-	0.112	0.002	-
	SHELF	1,36	0.734	0.001	-	0.477	0.001	-	0.679	0.001	-
	H*R	2,36	0.815	0.002	-	0.483	0.002	-	0.282	0.002	-
	S*H	1,36	0.523	0.001	-	0.700	0.001	-	0.172	0.001	-
	S*R	2,36	0.995	0.002	-	0.809	0.002	-	0.202	0.002	-
	S*H*R	2,36	0.778	0.002	-	0.785	0.002	-	0.015	0.002	-
	Dead Standing Coral	HABITAT	1,31	0.715	0.002	-	0.793	0.002	-	0.000	0.002
REGION		2,31	0.898	0.003	-	0.230	0.003	-	0.281	0.003	-
SHELF		1,31	0.173	0.002	-	0.265	0.002	-	0.000	0.002	*
H*R		2,31	0.402	0.003	-	0.902	0.003	-	0.995	0.003	-
S*H		1,31	0.022	0.002	-	0.177	0.002	-	0.014	0.002	-
S*R		2,31	0.262	0.003	-	0.609	0.003	-	0.607	0.003	-
S*H*R		2,31	0.879	0.003	-	0.593	0.003	-	0.685	0.003	-
Soft Corals	HABITAT	1,36	0.511	0.001	-	0.709	0.001	-	0.585	0.001	-
	REGION	2,36	0.621	0.002	-	0.057	0.002	-	0.077	0.002	-
	SHELF	1,36	0.109	0.001	-	0.227	0.001	-	0.096	0.001	-
	H*R	2,36	0.911	0.002	-	0.294	0.002	-	0.375	0.002	-
	S*H	1,36	0.087	0.001	-	0.978	0.001	-	0.183	0.001	-
	S*R	2,36	0.029	0.002	-	0.058	0.002	-	0.232	0.002	-
	S*H*R	2,36	0.076	0.002	-	0.379	0.002	-	0.009	0.002	-
Sponges	HABITAT	1,32	0.724	0.002	-	0.067	0.002	-	0.004	0.002	-
	REGION	2,32	0.397	0.003	-	0.396	0.003	-	0.152	0.003	-
	SHELF	1,32	0.649	0.002	-	0.063	0.002	-	0.875	0.002	-
	H*R	2,32	0.167	0.003	-	0.406	0.003	-	0.154	0.003	-
	S*H	1,32	0.774	0.002	-	0.240	0.002	-	0.205	0.002	-
	S*R	2,32	0.898	0.003	-	0.717	0.003	-	0.605	0.003	-
	S*H*R	2,32	0.710	0.003	-	0.340	0.003	-	0.506	0.003	-
All Algae	HABITAT	1,30	0.637	0.002	-	0.724	0.002	-	0.845	0.002	-
	REGION	2,30	0.922	0.004	-	0.947	0.004	-	0.657	0.004	-
	SHELF	1,30	0.560	0.002	-	0.340	0.002	-	0.172	0.002	-
	H*R	2,30	0.517	0.004	-	0.766	0.004	-	0.826	0.004	-
	S*H	1,30	0.723	0.002	-	0.845	0.002	-	0.160	0.002	-
	S*R	2,30	0.040	0.004	-	0.677	0.004	-	0.724	0.004	-
	S*H*R	2,30	0.904	0.004	-	0.130	0.004	-	0.065	0.004	-

Table A2.4 (Continued).

TAXON	SOURCE	df	LOCATIONS			SITES			TRANSECTS		
			$\alpha$	$\alpha_{c=\beta}$	Infer	$\alpha$	$\alpha_{c=\beta}$	Infer	$\alpha$	$\alpha_{c=\beta}$	Infer
<b>Small Corals</b>											
Acroporids	HABITAT	1,36	0.078	0.001	-	0.727	0.001	-	0.540	0.001	-
	REGION	2,36	0.149	0.002	-	0.188	0.002	-	0.282	0.002	-
	SHELF	1,36	0.430	0.001	-	0.946	0.001	-	0.027	0.001	-
	H*R	2,36	0.687	0.002	-	0.560	0.002	-	0.552	0.002	-
	S*H	1,36	0.971	0.001	-	0.246	0.001	-	0.023	0.001	-
	S*R	2,36	0.256	0.002	-	0.053	0.002	-	0.092	0.002	-
	S*H*R	2,36	0.431	0.002	-	0.056	0.002	-	0.156	0.002	-
Faviids	HABITAT	1,36	0.892	0.001	-	0.223	0.001	-	0.381	0.001	-
	REGION	2,36	0.052	0.002	-	0.197	0.002	-	0.493	0.002	-
	SHELF	1,36	0.480	0.001	-	0.691	0.001	-	0.581	0.001	-
	H*R	2,36	0.328	0.002	-	0.004	0.002	-	0.081	0.002	-
	S*H	1,36	0.398	0.001	-	0.764	0.001	-	0.398	0.001	-
	S*R	2,36	0.805	0.002	-	0.851	0.002	-	0.099	0.002	-
	S*H*R	2,36	0.929	0.002	-	0.318	0.002	-	0.675	0.002	-
Pocilloporids	HABITAT	1,36	0.648	0.001	-	0.616	0.001	-	0.166	0.001	-
	REGION	2,36	0.399	0.002	-	0.251	0.002	-	0.126	0.002	-
	SHELF	1,36	0.297	0.001	-	0.207	0.001	-	0.001	0.001	-
	H*R	2,36	0.168	0.002	-	0.345	0.002	-	0.413	0.002	-
	S*H	1,36	0.912	0.001	-	0.314	0.001	-	0.016	0.001	-
	S*R	2,36	0.279	0.002	-	0.000	0.002	*	0.628	0.002	-
	S*H*R	2,36	0.677	0.002	-	0.028	0.002	-	0.448	0.002	-
Misc. Hard Corals	HABITAT	1,36	0.147	0.001	-	0.459	0.001	-	0.140	0.001	-
	REGION	2,36	0.179	0.002	-	0.563	0.002	-	0.648	0.002	-
	SHELF	1,36	0.509	0.001	-	0.985	0.001	-	0.270	0.001	-
	H*R	2,36	0.415	0.002	-	0.910	0.002	-	0.045	0.002	-
	S*H	1,36	0.589	0.001	-	0.773	0.001	-	0.237	0.001	-
	S*R	2,36	0.878	0.002	-	0.904	0.002	-	0.790	0.002	-
	S*H*R	2,36	0.743	0.002	-	0.396	0.002	-	0.392	0.002	-
Soft Corals	HABITAT	1,36	0.828	0.001	-	0.028	0.001	-	0.000	0.001	*
	REGION	2,36	0.083	0.002	-	0.932	0.002	-	0.061	0.002	-
	SHELF	1,36	0.628	0.001	-	0.227	0.001	-	0.022	0.001	-
	H*R	2,36	0.464	0.002	-	0.967	0.002	-	0.550	0.002	-
	S*H	1,36	0.638	0.001	-	0.640	0.001	-	0.414	0.001	-
	S*R	2,36	0.566	0.002	-	0.739	0.002	-	0.055	0.002	-
	S*H*R	2,36	0.375	0.002	-	0.641	0.002	-	0.435	0.002	-

Table A2.4 (Continued).

TAXON	SOURCE	df	LOCATIONS			SITES			TRANSECTS		
			$\alpha$	$\alpha_{c=\beta}$	Infer	$\alpha$	$\alpha_{c=\beta}$	Infer	$\alpha$	$\alpha_{c=\beta}$	Infer
<b>Poritids</b>											
Poritids <6cm	HABITAT	1,36	0.178	0.001	-	0.599	0.001	-	0.025	0.001	-
	REGION	2,36	0.047	0.002	-	0.461	0.002	-	0.033	0.002	-
	SHELF	1,36	0.412	0.001	-	0.328	0.001	-	0.001	0.001	-
	H*R	2,36	0.023	0.002	-	0.863	0.002	-	0.682	0.002	-
	S*H	1,36	0.780	0.001	-	0.101	0.001	-	0.150	0.001	-
	S*R	2,36	0.645	0.002	-	0.665	0.002	-	0.131	0.002	-
	S*H*R	2,36	0.330	0.002	-	0.330	0.002	-	0.354	0.002	-
	Poritids 6-20	HABITAT	1,36	0.333	0.001	-	0.650	0.001	-	0.368	0.001
REGION		2,36	0.774	0.002	-	0.598	0.002	-	0.219	0.002	-
SHELF		1,36	0.892	0.001	-	0.117	0.001	-	0.004	0.001	-
H*R		2,36	0.392	0.002	-	0.844	0.002	-	0.794	0.002	-
S*H		1,36	0.852	0.001	-	0.729	0.001	-	0.330	0.001	-
S*R		2,36	0.994	0.002	-	0.848	0.002	-	0.046	0.002	-
S*H*R		2,36	0.322	0.002	-	0.648	0.002	-	0.750	0.002	-
Poritids 21-50		HABITAT	1,36	0.584	0.001	-				0.000	0.001
	REGION	2,36	0.090	0.002	-				0.000	0.002	*
	SHELF	1,36	0.139	0.001	-				0.003	0.001	-
	H*R	2,36	0.628	0.002	-				0.041	0.002	-
	S*H	1,36	0.816	0.001	-				0.003	0.001	-
	S*R	2,36	0.183	0.002	-				0.000	0.002	*
	S*H*R	2,36	0.114	0.002	-				0.853	0.002	-
	Poritids 51-100	HABITAT	1,36	0.744	0.001	-				0.037	0.001
REGION		2,36	0.052	0.002	-				0.587	0.002	-
SHELF		1,36	0.238	0.001	-				0.081	0.001	-
H*R		2,36	0.620	0.002	-				0.267	0.002	-
S*H		1,36	0.728	0.001	-				0.056	0.001	-
S*R		2,36	0.908	0.002	-				0.745	0.002	-
S*H*R		2,36	0.195	0.002	-				0.227	0.002	-
Poritids >100		HABITAT	1,30	0.124	0.002	-				0.693	0.002
	REGION	2,30	0.014	0.004	-				0.423	0.004	-
	SHELF	1,30	0.013	0.002	-				0.697	0.002	-
	H*R	2,30	0.610	0.004	-				0.405	0.004	-
	S*H	1,30	0.865	0.002	-				0.406	0.002	-
	S*R	2,30	0.898	0.004	-				0.619	0.004	-
	S*H*R	2,30	0.276	0.004	-				0.744	0.004	-



Table A2.4 (Continued).

TAXON	SOURCE	df	LOCATIONS			SITES			TRANSECTS		
			$\alpha$	$\alpha_{c=\beta}$	Infer	$\alpha$	$\alpha_{c=\beta}$	Infer	$\alpha$	$\alpha_{c=\beta}$	Infer
<b>Benthos</b>											
<i>L. laevigata</i> (MS, 2 Reg only)	HABITAT	1,11	0.927	0.054	-				0.289	0.054	-
	REGION	1,11	0.744	0.054	-				0.430	0.054	-
	H*R	1,11	0.492	0.054	-				0.367	0.054	-
<b><i>Tridacna Spp</i></b>											
	HABITAT	1,29	0.116	0.002	-				0.764	0.002	-
	REGION	2,29	0.077	0.004	-				0.489	0.004	-
	SHELF	1,29	0.019	0.002	-				0.418	0.002	-
	H*R	2,29	0.708	0.004	-				0.404	0.004	-
	S*H	1,29	0.678	0.002	-				0.909	0.002	-
	S*R	2,29	0.386	0.004	-				0.343	0.004	-
	S*H*R	2,29	0.973	0.004	-				0.248	0.004	-