# METHODS

## Field Methods & Data Processing[1]

### 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 | *Lizard* | 14:41 | NPZ/2 | ***RE*** |
| | | *Eyrie* | 14:43 | GU | ***NO*** |
| | | *Martin* | 14:45 | GU | ***NO*** |
| | | *Helsdon* | 14:57 | GU | ***RE*** |
| | Outer-shelf | *Hicks* | 14:27 | GU | ***RE*** |
| | | *Day* | 14:30 | GU | ***RE*** |
| | | *Carter* | 14:33 | NPZ | ***RE*** |
| | | *Yonge* | 14:36 | GU | ***RE*** |
| Cooktown *(Northern Boundary)* | Mid-shelf | *Boulder* | 15:25 | GU | ***NO*** |
| | | *Egret* | 15:29 | GU | ***NO*** |
| | | *Endeavour* | 15:46 | GU | ***RE*** |
| | | *Pickersgill* | 15:52 | GU | ***RE*** |
| | Outer-shelf | *Ribbon #4* | 15:26 | NPZ | ***NO*** |
| | | *Ribbon #3* | 15:30 | GU | ***NO*** |
| | | *Ribbon #2* | 15:33 | GU | ***NO*** |
| | | *Lena* | 15:39 | GU | ***NO*** |
| Cape Tribulation *(Northern Boundary)* | Mid-shelf | *Batt* | 16:25 | GU | ***NO*** |
| | | *Hastings* | 16:31 | GU | ***RE*** |
| | | *Michaelmas* | 16:35 | NPZ | ***NO*** |
| | | *Arlington* | 16:42 | GU | ***RE*** |
| | Outer-shelf | *Agincourt 4* | 15:57 | GU | ***RE*** |
| | | *Agincourt 3* | 15:59 | NPZ | ***NO*** |
| | | *St Crispin* | 16:06 | GU | ***NO*** |
| | | *Opal* | 16:13 | GU | ***RE*** |

[1] 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 1984, 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). 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 having suffered COTS outbreaks, none of the outer-shelf reefs in the Cooktown (central) region having been affected, and half of the outer-shelf reefs in the Cape Tribulation (south) region being 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'[2] (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)

[2] 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).

were sampled in December 1989[3]. 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.

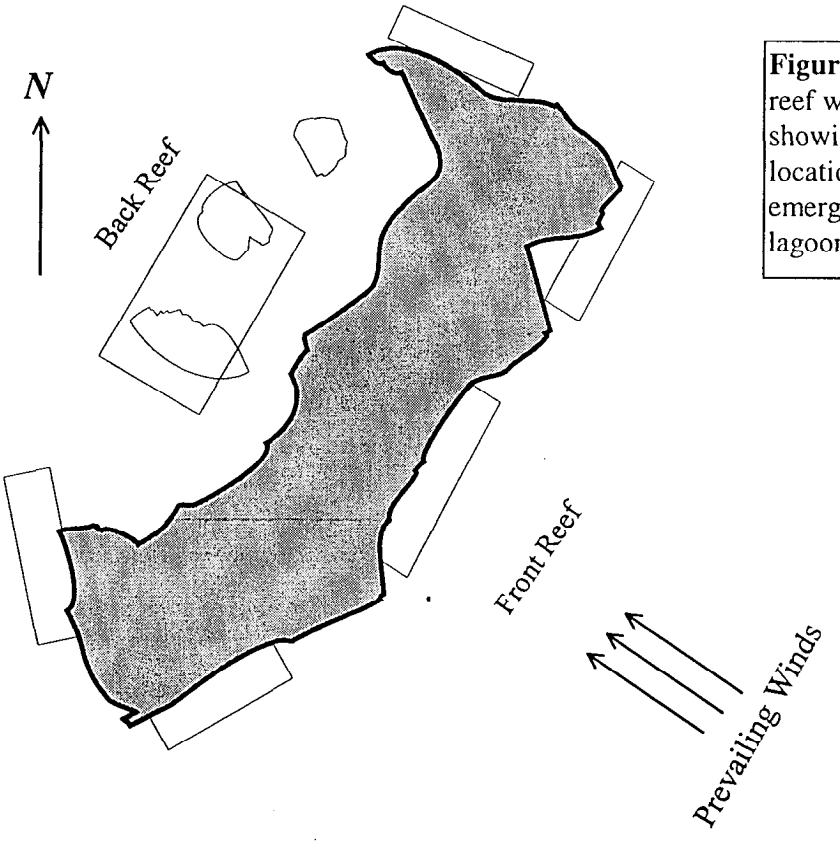


**Figure 1**: Schematic drawing of reef with back reef bommie field, showing locations of six sample locations. Shaded area indicates emergent reef crest or shallow lagoon.

[3] 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 2nd and 3rd survey of these reefs (Van Woesik *et al.* 1991, Done *et al.* 1992). Because of the considerable habitat damage caused by the cyclone, the 3rd survey is not considered here. Thus, only the 2nd (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).

**Taxa Surveyed**

The taxa and substratum categories recorded are given in Appendix 1, and the pooled groups analysed are listed in Table 2. Throughout the report, densities of taxa are expressed as means per transect. The units of density vary among taxa, therefore, as indicated in Table 2.

**Table 2**: Taxa and/or size classes of organisms analysed in the report. Abbreviations used for each taxon in figures later in the report are given in parentheses. Units of abundance are indicated for each transect size. Organisms with very low abundances could not be analysed statistically and are not listed in this table. See Appendix 1 for the complete list of taxa counted.

**50m x 5m Transects**
**(N°/250m²)**

**Large Fishes**

**Acanthuridae**
- *Zebrassoma scopas* (*Zs*)
- Other acanthurids (AOR)
- Total acanthurids (ATO)

**Chaetodontidae**
- *C. aureofasciatus* (*Ca*)
- *C. baronessa* (*Cb*)
- *C. plebeius* (*Cp*)
- *C. trifasciatus* (*Ct*)
- *C. vagabundus* (*Cv*)
- Other chaetodons (COR)
- Total chaetodons (CTO)

**Lutjanidae**
- *L. carponotatus* (*Lc*)
- Total lutjanids (LT)

**Serranidae**
- *Plectropomus* spp. (*Psp*)

**Benthos**

**Ophidiasteridae**
- *Linckia laevigata* (*Ll*)

**Tridacnidae**
- *Tridacna* spp. (*Tsp*)

**50m x 2.5m Transects**
**Poritidae (N°/125m²)**
**(massive / sub-massive)**
- Poritids 21-50cm (P50)
- Poritids 51-100cm (P100)
- Poritids >100cm (PLg)

**20m x 2.5m Transects**
**(N°/50m²)**
**Small Fishes**

**Labridae**
- *Thalassoma lunare* (*Tl*)

**Pomacentridae**
- *Amblyglyphidodon curacao* (*Ac*)
- *Chromis atripectoralis* (*Cat*)
- *Chrysiptera rollandi* (*Cr*)
- Recruit *C. rollandi* (*Crj*)
- *Plectroglyphidodon lacrymatus* (*Pl*)
- *Pomacentrus moluccensis* (*Pm*)
- Recruit *P. moluccensis* (*Pmj*)

**20m x 0.5m Transects**
**(N°/10m²)**
**Juvenile Corals**
(0-5cm$\phi$)
- Acroporidae (AcJ)
- Faviidae (FaJ)
- Pocilloporidae (PcJ)
- Misc. hard corals (MCJ)
- Soft corals (SCJ)

**Poritidae**
- Poritids 0-5cm$\phi$ (P5)
- Poritids 6-20cm$\phi$ (P20)

**20m Line Transects**
**(%, N°/20m)**
**Sessile Benthos**

**Hard Corals**
- Acroporidae (Acp)
- Faviidae (Fav)
- Pocilloporidae (Poc)
- Poritidae (Por)
- Misc. hard corals (MHC)
- Total hard coral (THC)
- Dead stand. coral (DSC)

**Soft Corals**
- Total soft coral (Sof)

**Sponges**
- All sponges (Spo)

**Algae**
- Total algae (Alg)

## 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 (≤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$5cm$\Phi$) within a belt 25cm either side of the tape. The corals were recorded only by family or higher taxa. Poritid corals of 6<20 cm$\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$^+$ 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.

# Statistical Methods

## Preliminary Treatment 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.

To examine larger scale systematic patterns in abundances, we averaged all data (4 or 5 counts) within locations and used the three location means within each combination of Habitat and reef as data for analyses. We adopted this strategy because: i) we were not interested at this stage in differences among locations (or sites) within reefs; and ii) averaging to that level provided data that better satisfied the assumptions of the ANOVA models we used. These means were expected to be (and were) approximately normally distributed (because of the Central Limit Theorem), and generally proved to be homoscedastic[4]. Accordingly, data were not transformed for analyses. With only three location means per cell, we did not test formally the distribution of the data but we examined residual plots to verify that a) variances were relatively homogeneous, and b) there were no conspicuous signs of systematic variation persistent after fitting a Shelf x Habitat x Region x reef(S,R) linear model to location means. Because of the hierarchical structure of sampling within reefs, the F-ratios for the larger scale (fixed) effects of interest in ANOVAs of these means were the same as those that would be calculated had the site and transect level data been retained.

## Hypothesis Testing Approach

We have focused on inferential hypothesis testing throughout this report, generally in the context of univariate Analyses of Variance (ANOVA). We did so because: i) we were more interested in testing specific hypotheses about already predicted patterns than in exploring the data for new or novel (multi-variate) pattens for future testing; 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. The multi-variate patterns in these data and the implications for management and monitoring of multi-variate associations at different taxonomic and spatial scales will be reported elsewhere (Mapstone & De'Ath in prep a,b).

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.

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[4] 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. Further, 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).

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 abundances of organisms might suggest to management agencies that cross-shelf position was relatively unimportant in the choice of reefs to protect from fishing. Alternatively, inferring significant cross shelf patterns in density would suggest stratifying protection, such that reefs were protected in different shelf positions. Erroneous advice of either type could result in poor management of the fished stock, but 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 $H_o$ 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 1990, 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).

## Spatial Patterns in Mean Abundances

We compared mean abundances of organisms across Shelf Positions, Habitats, Regions, and between groups of reefs subject to different histories of COTS infestation. In all cases, we were testing hypotheses about apparently structural phenomena that have been suggested as determinants of abundance for some reef biota. For such effects to be considered important, we required that they have an effect on abundances at least as large as the variation among the largest random elements within the effect. Accordingly, we stipulated the critical ES as that which resulted in the sum of the squared deviations among the population means being at least as large as the variance at the next smallest (random) scale. For example, for Shelf Position effects to be considered noteworthy, the sum of squared deviations between Shelf Position means should have an expected value at least as large as the average variance among reefs within Shelf Position (or COTS) and Region effects. This was our criterion for an effect size of importance in Mapstone's (1995, 1996) procedures. We had no interest in resolving differences among individual reefs, and so restricted our *a posteriori* analyses to the (fixed) effects and their interactions.

Spatial patterns in abundances were considered in two steps.

### *Effects of Recent Infestations by A. planci*

Firstly, the effects of COTS history was considered on mid-shelf reefs alone. Outer-shelf reefs were not included because of the previously mentioned confounding between region and COTS history on the outer-shelf (Table 1). Thus, the analyses of COTS effects involved four-factor ANOVAs for each 'analysable' taxon (Table 2). The factors considered were Habitat (front- & back-reef), Region (Cape Flattery, Cooktown, Cape Tribulation), COTS history (± recent outbreak), and reef(R*C) (2 reefs per R*C combination). Habitat, Region, and COTS history were considered fixed effects and reefs were considered random variables. The analytical model was:

$$y_{ijkmn} = \mu_{....} + \mathbf{H}_{i...} + \mathbf{R}_{.j..} + \mathbf{C}_{..k.} + \mathbf{HR}_{ij..} + \mathbf{HC}_{i.k.} + \mathbf{RC}_{.jk.} + \mathbf{HRC}_{ijk.} + r(\mathbf{RC})_{.jkm} + \mathbf{H}r(\mathbf{RC})_{ijkm} + \varepsilon_{ijkmn}$$

where:

$\mu_{....}$ is the population grand mean abundance over all factors;
$y_{ijkmn}$ is the $n^{th}$ location mean on *reef* $m$ in **H**abitat $i$ in **R**egion $j$ with **C**OTS history $k$.
$\varepsilon_{ijkmn}$ is a random normal error associated with each location mean.

The degrees of freedom, expected mean squares, and F-ratio denominators are given in Table 3. Hypothesis tests proceeded from the highest order interactions down to the main effects, with reef and Habitat*reef effects being tested first. At each test, numerator and denominator sources of variation were pooled whenever possible to increase the power of subsequent tests. Pooling occurred if either: i) the estimate of variation attributable to the term being tested was zero ($F \leq 1$); or ii) $F > 1$ but the term was non-significant with either a) $\alpha_o > 0.25$ (irrespective of $\beta$), or b) $\alpha_o > 0.1$ and $\beta < 0.05$.

**Table 3**: Structure of ANOVA to test for effects of COTS history, Habitat, and Region on abundances of biota.

| Source of Variation | df | MS Estimates* | F-ratio Denominator |
|---|---|---|---|
| **COTS** | 1 | $\sigma_\varepsilon^2 + 6\sigma_{r(RC)}^2 + 24\delta_C^2$ | $MS_{reef(RC)}$ |
| **Habitat** | 1 | $\sigma_\varepsilon^2 + 3\sigma_{Hr(RC)}^2 + 36\delta_H^2$ | $MS_{Hr(RC)}$ |
| **Region** | 2 | $\sigma_\varepsilon^2 + 6\sigma_{r(RC)}^2 + 24\delta_R^2$ | $MS_{reef(RC)}$ |
| **H*R** | 2 | $\sigma_\varepsilon^2 + 3\sigma_{Hr(RC)}^2 + 12\delta_{HR}^2$ | $MS_{Hr(RC)}$ |
| **H*C** | 1 | $\sigma_\varepsilon^2 + 3\sigma_{Hr(RC)}^2 + 18\delta_{HC}^2$ | $MS_{Hr(RC)}$ |
| **R*C** | 2 | $\sigma_\varepsilon^2 + 6\sigma_{r(RC)}^2 + 12\delta_{RC}^2$ | $MS_{reef(RC)}$ |
| **H*R*C** | 2 | $\sigma_\varepsilon^2 + 3\sigma_{Hr(RC)}^2 + 6\delta_{HRC}^2$ | $MS_{Hr(RC)}$ |
| ***reef*(RC)** | 6 | $\sigma_\varepsilon^2 + 6\sigma_{r(RC)}^2$ | $MS_{res}$ |
| **H*r (RC)** | 6 | $\sigma_\varepsilon^2 + 3\sigma_{Hr(RC)}^2$ | $MS_{res}$ |
| ***residual*** | 48 | $\sigma_\varepsilon^2$ | - |

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

### *Effects of Shelf Position, Habitat, and Region*

Data from all 24 reefs were analysed to assess the effects of Shelf Position, Habitat, and Region on abundances of biota. The analytical model was identical in form to that described above for the 'COTS analyses', except that COTS effects were replaced by Shelf Position and there were (potentially) four reefs per Shelf Position * Region combination. The model was thus:

$$y_{ijkmn} = \mu_{....} + \mathbf{H}_{i...} + \mathbf{R}_{.j..} + \mathbf{S}_{..k.} + \mathbf{HR}_{ij..} + \mathbf{HS}_{i.k.} + \mathbf{RS}_{.jk.} + \mathbf{HRS}_{ijk.} + r(\mathbf{RS})_{.jkm} + \mathbf{H}r(\mathbf{RS})_{ijkm} + \varepsilon_{ijkmn}$$

and the analytical structure is given in Table 4.

For those taxa which showed significant effects of COTS history, only those mid-shelf reefs in each region that had the same COTS history as outer-shelf reefs in the same region were included in analyses of Shelf Position* Region * Habitat. Hence, when COTS effects were present, only COTS affected mid-shelf reefs were included for the northern (Cape Flattery) region, only COTS unaffected reefs were included in the central (Cooktown) region, and all reefs were included in the southern (Cape Tribulation) region (see Table 1). This meant that the cross shelf comparison was not confounded in any way by effects of COTS history, but, for those taxa affected by COTS on mid-shelf reefs, regional effects would be completely confounded with COTS history. Interpretation of such regional effects was tentative, therefore, and made in the context of comparisons between results obtained for mid-shelf reefs alone (above) with those for both outer and mid-shelf reefs. *A posteriori* and pooling procedures were the same as those described previously.

**Table 4**: Structure of ANOVA to test for effects of Habitat, Region, and Shelf Position on abundances of biota. The degrees of freedom shown as $\mathbf{df_0}$ are for the balanced analysis in the absence of significant COTS effects on mid-shelf reefs. Where COTS effects were significant, analyses were unbalanced across Shelf Positions and Regions (with only 2 mid-shelf reefs included for the Cape Flattery and Cooktown regions), and degrees of freedom were those shown in $\mathbf{df_1}$. **MS Estimates** are shown for the balanced model only.

| Source of Variation | $df_0$ | $df_1$ | MS Estimate* | F-ratio Denominator |
|---|---|---|---|---|
| **Habitat** | 1 | 1 | $\sigma^2_\varepsilon + 3\sigma^2_{Hr(RC)} + 72\delta^2_H$ | $MS_{Hr(RS)}$ |
| **Region** | 2 | 2 | $\sigma^2_\varepsilon + 6\sigma^2_{r(RC)} + 48\delta^2_R$ | $MS_{reef(RS)}$ |
| **Shelf Pos$^n$** | 1 | 1 | $\sigma^2_\varepsilon + 6\sigma^2_{r(RC)} + 48\delta^2_C$ | $MS_{reef(RS)}$ |
| **H*R** | 2 | 2 | $\sigma^2_\varepsilon + 3\sigma^2_{Hr(RC)} + 24\delta^2_{HR}$ | $MS_{Hr(RS)}$ |
| **H*S** | 1 | 1 | $\sigma^2_\varepsilon + 3\sigma^2_{Hr(RC)} + 36\delta^2_{HC}$ | $MS_{Hr(RS)}$ |
| **R*S** | 2 | 2 | $\sigma^2_\varepsilon + 6\sigma^2_{r(RC)} + 24\delta^2_{RC}$ | $MS_{reef(RS)}$ |
| **H*R*S** | 2 | 2 | $\sigma^2_\varepsilon + 3\sigma^2_{Hr(RC)} + 12\delta^2_{HRC}$ | $MS_{Hr(RS)}$ |
| ***reef*(RS)** | 18 | 16 | $\sigma^2_\varepsilon + 6\sigma^2_{r(RC)}$ | $MS_{res}$ |
| **H*r (RS)** | 18 | 16 | $\sigma^2_\varepsilon + 3\sigma^2_{Hr(RC)}$ | $MS_{res}$ |
| ***residual*** | 96 | 80 | $\sigma^2_\varepsilon$ | - |

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