GREAT BARRIER REEF
MARINE PARK AUTHORITY

RESEARCH PUBLICATION No. 48

Habitat, Cross Shelf and Regional Patterns in the Distributions and Abundances of Some Coral Reef Organisms on the Northern Great Barrier Reef

with Comment on the Implications for Future Monitoring

B D Mapstone,
A M Ayling and
J H Choat

RESEARCH PUBLICATION No. 48

Habitat, Cross Shelf and Regional Patterns in the Distributions and Abundances of Some Coral Reef Organisms on the Northern Great Barrier Reef

with Comment on the Implications for Future Monitoring

B D Mapstone
Department of Marine Biology
James Cook University

A M Ayling
Sea Research

J H Choat
Department of Marine Biology
James Cook University

A REPORT TO THE GREAT BARRIER REEF MARINE PARK AUTHORITY

ISSN 1037-1508
ISBN 0 642 23044 7

Published March 1998
by the Great Barrier Reef Marine Park Authority

National Library of Australia Cataloguing-in-Publication data:

Mapstone, Bruce D. (Bruce David).
Habitat, cross shelf and regional patterns in the distributions and abundances of some coral reef organisms on the northern Great Barrier Reef, with comment on the implications for future monitoring.

Bibliography.
ISBN 0 642 23044 7.

1. Coral reef biology - Queensland - Great Barrier Reef. 2. Marine organisms - Queensland - Great Barrier Reef. 3. Environmental sampling - Queensland - Great Barrier Reef. 4. Environmental monitoring - Queensland - Great Barrier Reef. I. Ayling, Tony, 1947- . II. Choat, J. H. III. Great Barrier Reef Marine Park Authority (Australia). IV. Title. (Series : Research publication (Great Barrier Reef Marine Park Authority (Australia)) ; no. 48).

577.8809943

GREAT BARRIER REEF
MARINE PARK AUTHORITY

PO Box 1379
Townsville Qld 4810
Telephone (07) 4750 0700

[redacted]

EXECUTIVE SUMMARY

Marine protected areas increasingly are being seen as precautionary mechanisms by which to provide for the conservation of major marine habitats. An underlying principle of the approach is that the protection of representative areas from impacts of human activities will establish patches of healthy habitats in perpetuity and provide refugia from which the wider ecological systems will be replenished. McNeill (1994) pointed out, however, 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 the design and ongoing assessment of marine protected areas require knowledge of the main patterns of distribution of biota in the managed areas and structured monitoring studies tailored to rigorously tests the effectiveness of various levels of protection from human use.

In this report we describe some relatively large-scale patterns in the distributions and abundances of several coral reef organisms on the northern Great Barrier Reef. We considered the degree to which habitat, position across the continental shelf, and region explained variations in abundances. These factors have been invoked as major determinants of pattern in abundances in past studies and we sought to examine the consistency and generality of such models. Our main focus was on the implications of systematic patterns in abundance for the spatial design of sampling and monitoring programmes. Ignorance or inappropriate treatment of strong systematic patterns when designing monitoring and assessment programmes has the potential to cause mistaken conclusions about the merits of future management strategies or the performance of existing strategies.

Our data indicated that strong patterns in abundances were correlated with habitat, shelf position, and regions. Many of these single factor patterns, however, were not consistent among taxa or across other major physical gradients. For example, differences among habitats varied greatly from mid-shelf to outer-shelf reefs, and the effects of shelf position varied among regions for many organisms. The lack of generality of such patterns is contrary to important assumptions underlying much previous work.

Our results have important implications for the design and interpretation of future studies and for the design and assessment of managed protected areas. It is clear 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. It is critical in future studies that sampling be well distributed over major within-reef strata. It is also clear that the successful choice of truly representative areas for the conservation of major biomes on the Great Barrier Reef will require highly structured descriptive information that encompasses a range of bio-physical factors. Strong patterns in abundances can be related to major bio-physical factors, but it is becoming clearer that the relationships are far less static and general than previously thought. Failure to consider the variation in such patterns, that presumably reflect important large-scale processes, may lead to the misrepresentation of important aspects of the Great Barrier Reef in conservation management strategies.

TABLE OF CONTENTS

List of Tables

List of Figures

Acknowledgements

The work presented in this report stems from a great deal of effort by many people. Rob Van Woesik, Robyn Cumming, Richard Birdsey, Ian Butler, Jim Higgs, Brian Cohen, Ian Roderick, Stewart Cairns, and Rachel Webb all participated in field work and data entry. Kerry Bell and Linda Axe also helped with data entry. Terry Ford and Louis Wilson kept the RV Sunbird running and ensured that the work got done. Avril, Xenica, & Bliss Ayling put up with Tony's long absences in the field. Gina Mercer and Lucy supported Bruce through too many late nights and weekends at work to finish the report. Our thanks to you. The work was funded by the Great Barrier Reef Marine Park Authority and the Crown of Thorns Starfish Research Committee. Bruce Mapstone was supported in the earlier stages by a National Research Fellowship.

INTRODUCTION

Recent decades have been characterised by increasing concern for conservation of the global environment, socially, economically and politically (Hendee *et al.* 1990). In particular, the past 30 years has seen a dramatic shift in approach to management of marine resources. Whereas historically access to marine resources was generally assumed, now restrictions on their access and use are commonplace. The development of numerous Marine Environment Protected Areas (MEPAs) encapsulates this recent shift in emphasis (Kelleher & Kenchington 1991).

The motivation for MEPAs typically includes conservation of marine environments and principles of multiple use (Kelleher & Kenchington 1991, Kenchington 1990). In practice, however, the establishment of MEPAs has been somewhat *ad hoc*, with the objectives of their declaration and management couched in generalities, and rarely consistent (McNeill, 1994). In many cases, the features to be conserved are not specified in detail. This is almost certainly reasonable in many (perhaps most) cases initially, because understanding of the function of the target ecological systems is rudimentary at best. We rarely understand completely, for example, the multitude of interactions that are essential for the maintenance of a particular habitat type.

Whatever the overriding objective(s) of a protected area, the extent and nature of features to be conserved must be established at some stage, usually meaning either the use of prior information (such as a resource inventory) or dedicated surveys or monitoring programmes. It is important also to establish a framework of regular, systematic, and carefully designed studies for monitoring the environmental status of the protected area(s) as a means of assessing the degree to which management strategies are ensuring the conservation of those resources.

The declaration of the Great Barrier Reef Marine Park in 1975 (GBR Marine Park Act 1975) arose out of concern about perceived threats to the Great Barrier Reef (GBR) from extractive activities, particularly mining, petroleum exploration and extraction, and fishing (Kenchington 1990). The rationale for the declaration of the Great Barrier Reef Marine Park, then, was firstly the conservation of the Great Barrier Reef as an ecologically valuable resource. Recognising the existing uses of the GBR, and potential benefits from continued use, however, a secondary motivation was to provide for ongoing human use and enjoyment of the GBR, consistent with the conservation of its environmental characteristics. The Act called for the GBR to be zoned for multiple use on a regional basis, but offered no guidance to the demarcation of regions.

Management of the GBR for conservation (as well as multiple use) should include efforts to conserve the full range of bio-geographical characteristics of reef assemblages. Adequate judgement of management strategies with respect to conservation of the GBR environment, therefore, requires sound empirical knowledge of spatial and temporal patterns in the distribution and abundance of organisms on the GBR under 'normal' conditions. The Great Barrier Reef Marine Park Authority (GBRMPA) sought to use existing knowledge of the hydrodynamics and geomorphology of the GBR to define several sections of the GBR Marine Park, which were eventually amalgamated into four major sections for the purposes of zoning and management (GBRMPA 1983, 1985, 1987, 1988, 1992). The GBRMPA adopted a strategy in each section of zoning different areas for different levels of human use, on the premise that ensuring minimum human impact on at least some areas would ensure conservation of the GBR's key features. The choice of particular areas for each zone, however, arose more out of patterns of contemporary human use than from knowledge of key bio-physical features of the ecosystem.

The GBRMPA recently has initiated planning for the protection of a system of 'representative areas' to ensure that samples of major features of the GBR are conserved. This approach necessarily draws more than the zoning approach on knowledge of the distribution and abundance of bio-physical features. Flexibility in allocation of resources to different management regimes should be greatest within relatively homogeneous bio-physical strata of the GBR, and least flexible across such strata. For this to happen, and for 'representative areas' to be chosen sensibly, some knowledge of the systematic patterns in distribution and abundances of reef biota is necessary.

Persistent Systematic Effects on Abundances

Done (1982), Williams (1982), Dinesen (1983), Williams & Hatcher (1983), and Russ (1984), suggested that strong gradients in abundances and/or occurrence of several species exist across the continental shelf of the GBR off Townsville, with inshore, mid-shelf, and shelf-break assemblages being distinct. Strong, predictable patterns in abundances have been observed also in conjunction with the major habitat-types within most reefs (Bradbury *et al.* 1987, Chave & Eckert 1974, Clarke 1977, Done 1983, Done & Potts 1992, Galzin 1987, Helfman 1978, Jones & Chase 1975), whilst latitudinal (regional) patterns in abundances have been observed for some species, but are generally perceived to be less dramatic than the cross-shelf or habitat related patterns (Doherty 1987, Sale *et al.* 1984, Williams *et al.* 1986).

In most cases, however, these systematic patterns have been thoroughly explored at only relatively few locations, and usually not together. It remains unclear how the cross shelf patterns suggested by previous workers relate to habitat-related patterns or regional patterns in abundances. Similarly, the consistency of habitat effects across the continental shelf or among regions is not well documented. Thus, the degree to which these patterns can be accepted as a general basis from which to implement conservation management plans remains uncertain.

Knowledge of systematic patterns in abundances is critical also in the design of monitoring programmes, impact assessment studies, and experimental field projects. This is so especially if systematic patterns across one effect (such as shelf position) are not consistent across other common effects (such as habitats). If important interactions between systematic effects occur, then it will be misleading to invoke general patterns on the basis of sampling within only selected (supposedly 'standardised') strata of any of those effects, as often has been the case. For example, Ayling (1983a,b) and Ayling & Ayling (1984a,b,c, 1985, 1986a,b) sampled reefs along the length of the GBR but sampled only one location on each reef (generally the northern end of the back-reef). The AIMS Long Term Monitoring Programme (AIMS 1992) now in progress (Oliver *et al.* 1995) adopts a sampling strategy similar to that reported by Sale *et al.* (1984) and Doherty (1987), which involved sampling three sites at only one location on the north-eastern margin of each reef. Williams (1982) attempted to standardise community surveys across the continental shelf off Townsville by sampling exposed reef slopes, but was forced by bad weather to confound exposure with reefs. It has been argued that such standardisation of the within-reef location of sampling should provide a satisfactory index of abundances on each reef for comparisons among reefs, regions, and assessment of cross-shelf patterns etc. This argument rests on the assumptions that: i) the relationship between the location sampled and other locations within the same habitat is consistent among reefs and across larger geographic (or temporal) strata; and ii) relationships among habitats are also consistent across reefs and larger-scale effects. The presence of interactions between Habitat and Region and/or Shelf Position would mean that regional or cross-shelf comparisons based on samples from only one Habitat would be prone to provide results that were habitat specific rather than applicable to entire reefs. The nature of interactions between cross-shelf effects, habitat effects, regional effects, and location effects on the GBR have been explored by Mapstone *et al.* (1995) with the data from this study to test the assumptions implicit in many prior sampling programmes.

Thus, a primary objective of this study was to investigate some aspects of spatial pattern in the abundances of a number of reef organisms over a large area of the GBR Marine Park. 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) the choice of areas for explicit conservation should include consideration of as wide a variety of organisms as possible; 2) a monitoring programme (for assessing the status of managed areas) should take into account the status of several species; 3) the optimum sizes of sampling units proved to be the same for several organisms (Mapstone & Ayling 1993); 4) many of the organisms could be efficiently counted concurrently; and 5) 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 desirable to maximise the return from such costs.

Survey of *Acanthaster planci*

Outbreaks of *Acanthaster planci* (crown of thorns, COTS) on the Great Barrier Reef have become the focus of considerable financial, personal, and institutional resources over the past decade (Bradbury *et al.* 1985, Brodie 1992, Endean & Cameron 1990, Moran *et al.* 1988). The economic, management, and potential ecological consequences of *A. planci* outbreaks is of great ongoing concern. It is still unclear whether the phenomenon of widespread explosions of populations of crown of thorns are entirely natural, episodic events or in part the result of anthropogenic perturbations to the reef and neighbouring environments (Brodie 1992). Irrespective of their cause, it is clearly in everyone's interests to describe in detail the dynamics of these events.

One model of the genesis and propagation of crown of thorns outbreaks is that periodically very successful recruitment leads to 'boom' populations on reefs inshore of the ribbon reefs north of Cape Tribulation/Cape Kimberley. These population explosions then generate a wave of recruitment that cascades southward with successive generations. This seems to have been the pattern of the two most recent series of outbreaks (Dight 1992, Moran *et al.* 1988, Moran & De'Ath 1992, but see James & Scandol 1992, Scandol 1994). The southern migration of strong cohorts of starfish has been attributed to the influence of the East Australia Current on dispersal of larvae, and the generally southerly flow of GBR lagoonal water south of the ribbon reef area. The reefs behind the ribbon reefs seem relatively unaffected by the East Australia current, probably because the emergent, near continuous ribbon reefs provide an effective barrier to Coral Sea circulation (Frith *et al.* 1986).

If the above model is true, any large populations of crown of thorns that might appear in the future would be expected to do so first on the reefs north of Cape Tribulation/Cape Kimberley. We have relatively little detailed information, however, about the dynamics of non-outbreak populations or the growth of populations to plague status. The provision of such information would greatly aid our understanding of outbreaks and increase the predictive power of models of their development.

Prior to 1995, when the GBRMPA commenced fine-scale SCUBA counts of *A. planci*, most information about crown of thorns abundance came from rapid manta-tow surveys of reef perimeters (Moran *et al.* 1988). Those methods allowed useful qualitative statements about whether a reef had an outbreak or not, but did not provide reliable or accurate estimates of abundances, particularly at intermediate levels (Fernandez 1990, Fernandez *et al.* 1990, but see De'Ath 1992). From a management perspective, the precise description of population dynamics prior to outbreak conditions would provide a vital ability for managers to predict where and when outbreaks were imminent. In the longer term, better understanding of consistent spatial patterns in *A. planci* outbreaks will provide a better basis for zoning decisions and regulating use of the GBR.

Accordingly, a secondary objective of the study was to document the status of *A. planci* in the mid-north regions of the Cains Section of the GBR Marine Park. We sought to obtain precise estimates of densities of *A. planci* on the reefs north of Cape Tribulation and on those reefs immediately south of Cape Kimberley, where the first 'flow-on' effects of increases in northern populations are likely to be seen under the above model. If sufficient numbers of COTS were observed, we sought to test the hypothesis that COTS outbreaks first arise on reefs behind the shelf-break ribbon reefs north of Cape Kimberley (Dight 1992, but see James & Scandol 1992, Scandol 1994). If few COTS were recorded, our data would provide useful baseline information for future surveys of *A. planci* that might indicate the genesis of further 'booms' in COTS populations. In either case, these data will contribute to an empirical test of the predictions of the model in the event of future increases in numbers of crown of thorns.

The density data we obtained for *A. planci* also provided an important complement to the more qualitative data provided by manta tow surveys of the same areas by AIMS personnel. The two methods were used sequentially, through collaboration with Moran and his co-workers, to provide valuable data for comparison of the methods and validation of the generality of the conclusions drawn about manta tows by Fernandez (1990) and Fernandez *et al.* (1990). Concurrent with counting *A. planci*, we estimated percent coverage and some gross population parameters of hard corals. Given knowledge of the recent history of COTS outbreaks, these data allowed us to compare recovering assemblages with coral assemblages not recently affected by crown of thorns.

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 $14^{\circ}25'$S and $16^{\circ}45'$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.

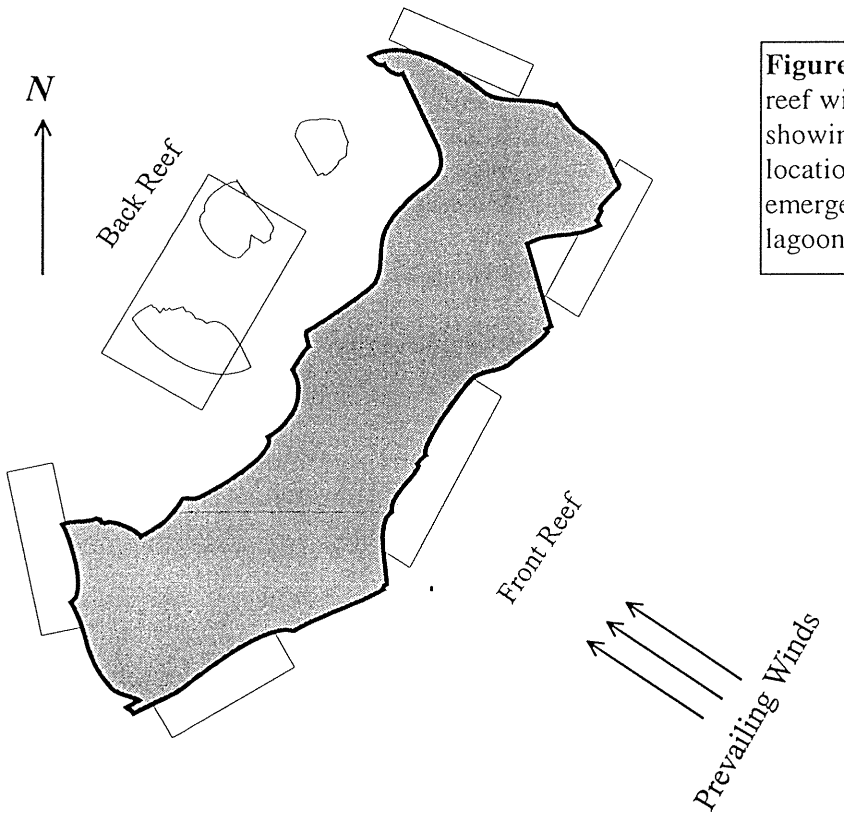


Figure 1: Schematic drawing of reef with back reef bommie field, showing locations of six sample locations. Shaded area indicates emergent reef crest or shallow lagoon.

---

[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°/250m^2)

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°/125m^2)
(massive / sub-massive)

Poritids 21-50cm	(P50)
Poritids 51-100cm	(P100)
Poritids >100cm	(PLg)

20m x 2.5m Transects
(N°/50m^2)

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°/10m^2)

Juvenile Corals
(0-5cmϕ)

Acroporidae	(AcJ)
Faviidae	(FaJ)
Pocilloporidae	(PcJ)
Misc. hard corals	(MCJ)
Soft corals	(SCJ)
Poritidae	
Poritids 0-5cmϕ	(P5)
Poritids 6-20cmϕ	(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 (*Φ*) 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 (*Φ*), 20-50cm*Φ*, and >50cm*Φ*), 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*Φ*, 50<100cm*Φ*, 100-200cm*Φ*, and >200cm*Φ*. 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$5cmΦ) within a belt 25cm either side of the tape. The corals were recorded only by family or higher taxa. Poritid corals of 6<20 cmΦ 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.

---

[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 (β) or Type I error (α). 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 (β) if H_o was not rejected against a critical significance value of α_c. The value of α_c set initially is arbitrary.

v. Iteratively adjust α_c and recalculate β at the revised level of α_c until $\beta=\alpha_c/k$.

vi. Compare the value of α for the observed data (α_o) with the value of α_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 ***r**eef* m in **H**abitat i in **R**egion j with **C**OTS history k.

ε_{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 β), 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	$\sigma_\varepsilon^2 + 6\sigma_{r(RC)}^2 + 24\delta_C^2$	$\mathrm{MS}_{reef(\mathrm{RC})}$
Habitat	1	$\sigma_\varepsilon^2 + 3\sigma_{Hr(RC)}^2 + 36\delta_H^2$	$\mathrm{MS}_{Hr(\mathrm{RC})}$
Region	2	$\sigma_\varepsilon^2 + 6\sigma_{r(RC)}^2 + 24\delta_R^2$	$\mathrm{MS}_{reef(\mathrm{RC})}$
H*R	2	$\sigma_\varepsilon^2 + 3\sigma_{Hr(RC)}^2 + 12\delta_{HR}^2$	$\mathrm{MS}_{Hr(\mathrm{RC})}$
H*C	1	$\sigma_\varepsilon^2 + 3\sigma_{Hr(RC)}^2 + 18\delta_{HC}^2$	$\mathrm{MS}_{Hr(\mathrm{RC})}$
R*C	2	$\sigma_\varepsilon^2 + 6\sigma_{r(RC)}^2 + 12\delta_{RC}^2$	$\mathrm{MS}_{reef(\mathrm{RC})}$
H*R*C	2	$\sigma_\varepsilon^2 + 3\sigma_{Hr(RC)}^2 + 6\delta_{HRC}^2$	$\mathrm{MS}_{Hr(\mathrm{RC})}$
***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	σ_ε^2	-

$^{+}$: δ^2 is used to indicate the variations attributable to fixed effects, as opposed to the variances associated with random variables (σ^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	**$\mathbf{df_0}$**	**$\mathbf{df_1}$**	**MS Estimate^{+}**	**F-ratio Denominator**
Habitat	1	1	$\sigma_\varepsilon^2 + 3\sigma_{Hr(RC)}^2 + 72\delta_H^2$	$\mathbf{MS}_{Hr(\mathbf{RS})}$
Region	2	2	$\sigma_\varepsilon^2 + 6\sigma_{r(RC)}^2 + 48\delta_R^2$	$\mathbf{MS}_{reef(\mathbf{RS})}$
Shelf Pos$^{\mathbf{n}}$	1	1	$\sigma_\varepsilon^2 + 6\sigma_{r(RC)}^2 + 48\delta_C^2$	$\mathbf{MS}_{reef(\mathbf{RS})}$
H*R	2	2	$\sigma_\varepsilon^2 + 3\sigma_{Hr(RC)}^2 + 24\delta_{HR}^2$	$\mathbf{MS}_{Hr(\mathbf{RS})}$
H*S	1	1	$\sigma_\varepsilon^2 + 3\sigma_{Hr(RC)}^2 + 36\delta_{HC}^2$	$\mathbf{MS}_{Hr(\mathbf{RS})}$
R*S	2	2	$\sigma_\varepsilon^2 + 6\sigma_{r(RC)}^2 + 24\delta_{RC}^2$	$\mathbf{MS}_{reef(\mathbf{RS})}$
H*R*S	2	2	$\sigma_\varepsilon^2 + 3\sigma_{Hr(RC)}^2 + 12\delta_{HRC}^2$	$\mathbf{MS}_{Hr(\mathbf{RS})}$
***reef*(RS)**	18	16	$\sigma_\varepsilon^2 + 6\sigma_{r(RC)}^2$	$\mathbf{MS}_{res}$
Hr* (RS)**	18	16	$\sigma_\varepsilon^2 + 3\sigma_{Hr(RC)}^2$	$\mathbf{MS}_{res}$
residual	96	80	σ_ε^2	-

$^{+}$: δ^2 is used to indicate the variations attributable to fixed effects, as opposed to the variances associated with random variables (σ^2)

RESULTS

Effects of Recent COTS Outbreaks

Differences in abundance between mid-shelf reefs which had suffered recent outbreaks of *A. planci* and reefs which had not were evident for several taxa (Table 5, Appendix 2). The direction and magnitude of those differences, however, differed among taxa and often differed between habitats or among regions within taxa. Indeed, the main effect of COTS history was significant and independent of other effects for only six taxa of fish (Fig. 2). No reef-wide effects of COTS history were common to all regions for any of the 21 benthic taxa examined.

Table 5: Summary results of tests by univariate ANOVA for the effects of recent *A. planci* infestation [**COTS**, C], Habitat [**H**], Region [**R**], and reefs [**r(CR)**] and their interactions. *, -: statistical significance and non-significance respectively at $\alpha_c=\beta$, given the ES described in the text. Bold asterisks indicate the terms in analyses that were interpretable without ambiguity. Shaded columns indicate those terms that might indicate effects of *A planci* over more than single reefs.

A: Fishes.

	SOURCE OF VARIATION								
TAXON	Cots	Habitat	Region	H*C	R*C	R*H	R*H*C	r(RC)	H*r(RC)
Large Fishes									
Total Acanthurids	*	-	*	-	-	-	-	-	-
Z. scopas	-	*	*	-	-	*	-	-	-
Other Acanthurids	*	-	*	-	-	-	-	*	-
All Chaetodons	-	-	*	-	-	-	-	-	*
C. aureofasciatus	-	-	*	-	-	-	-	*	-
C. baronessa	-	*	-	-	*	-	-	*	*
C. plebeius	-	-	*	-	*	-	-	-	*
C. trifasciatus	-	-	*	-	-	-	-	*	-
C. vagabundus	-	-	*	-	-	-	-	*	-
Other Chaetodons	-	-	*	-	*	-	-	-	-
All Lutjanids	*	-	*	-	-	-	-	-	-
L. carponotatus	-	-	*	-	-	-	-	*	-
Plectropomus **spp**	-	*	*	-	*	-	*	-	-
Small Fishes									
A. curacao	-	-	-	-	-	-	-	*	*
C. atripectoralis	*	*	*	-	-	*	-	*	-
C. rollandi	-	*	-	-	-	-	-	*	*
Recruit ***C.r.***	-	-	*	*	*	-	-	-	-
P. lacrymatus	-	-	*	-	-	-	-	*	*
P. moluccensis	*	-	*	-	-	-	-	*	-
Recruit ***P.m.***	*	-	*	-	-	*	-	-	-
T. lunare	-	-	*	-	-	-	-	-	*

Table 5 (continued):

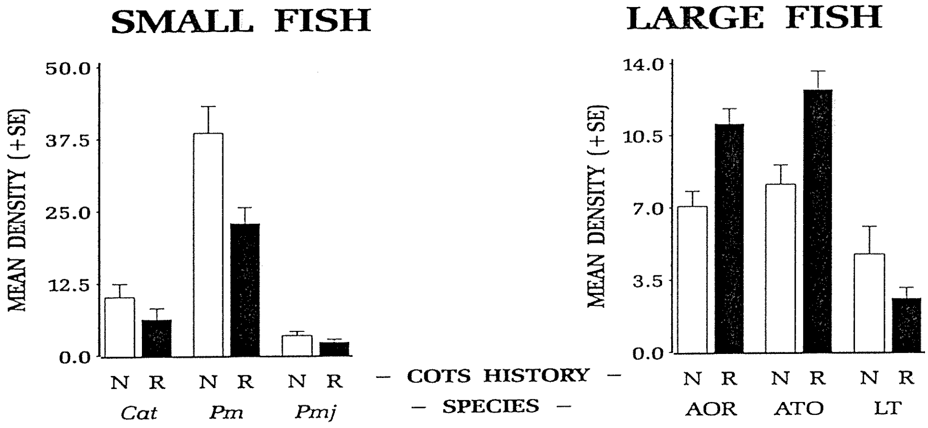
B: Benthic Organisms

	SOURCE OF VARIATION								
TAXON	Cots	Habitat	Region	H*C	R*C	R*H	R*H*C	r(RC)	H*r(RC)
Small Corals									
Small Acroporids	-	-	-	-	-	-	-	-	*
Small Faviids	-	*	-	*	-	-	-	*	*
Small Pocilloporids	-	-	-	-	-	-	-	-	-
Misc. Small Hard	-	*	-	-	-	-	-	-	*
Small Soft Corals	-	-	-	-	-	-	-	-	-
Poritid Counts									
Poritids < 6cm	-	-	-	-	-	-	-	*	*
Poritids 6-20cm	-	-	-	*	-	-	-	-	*
Poritids 21-50cm	-	-	*	-	-	-	-	-	-
Poritids 51-100cm	-	-	-	-	-	-	-	-	*
Poritids >100cm	-	-	-	-	-	*	-	*	-
% Coverage									
Total Hard Coral	-	-	-	-	-	-	-	*	*
Acroporidae	-	*	-	-	-	*	-	*	*
Faviidae	-	*	-	-	-	-	-	-	-
Pocilloporidae	-	-	-	-	-	-	-	*	-
Poritidae	-	-	-	-	-	*	-	*	-
Misc. Hard Coral	-	*	-	-	*	-	-	*	-
Dead Stand Coral	-	-	-	*	-	-	-	*	-
Soft Corals	-	-	-	*	-	-	-	-	*
Sponges	-	-	-	-	-	-	-	-	-
# Intercepts									
Total Hard Coral	-	-	-	*	*	-	-	*	-
Acroporidae	-	*	-	*	*	-	-	-	-
Faviidae	-	*	-	*	-	-	-	*	*
Pocilloporidae	-	*	-	-	*	-	-	*	-
Poritidae	-	*	-	-	-	*	-	*	-
Misc. Hard Coral	-	-	-	-	*	-	-	*	-
Dead Stand Coral	-	-	-	*	-	-	-	*	-
Soft Corals	-	-	-	*	-	-	-	-	*
Sponges	-	-	-	-	-	-	-	-	*
Misc. Benthos									
Tridacna spp	-	-	*	*	-	*	*	-	-
L. laevigata	-	*	*	*	-	*	-	-	-

General Effects of A. planci

Mean densities of the fishes *C. atripectoralis*, adult and recruit *P. moluccensis*, and total lutjanids were significantly less on COTS affected reefs in all regions than on reefs unaffected by COTS in recent years (Fig. 2). The reductions in abundance were about 25% for *C. atripectoralis* and recruit *P. moluccensis*, but about one third for the other two taxa. By contrast, acanthurids were generally more abundant on COTS affected reefs than on unaffected reefs (Fig. 2). The relative magnitude of the difference was similar to that for adult *P. moluccensis* and total lutjanids, but in the opposite direction.

Figure 2: Main effects of recent *A. planci* infestations on biota on mid-shelf reefs. **Abbreviations**: **SE** - Standard Error; **R** - evidence of Recent Cots outbreak; **N** - No evidence of recent COTS outbreak; ***Cat*** - *C. atripectoralis; **Pm** - P. moluccensis;* ***Pmj*** - recruit *P. moluccensis;* **AOR** - Acanthurids other than *Z. scopas;* **ATO** - Total Acanthurids; **LT** - total lutjanids.

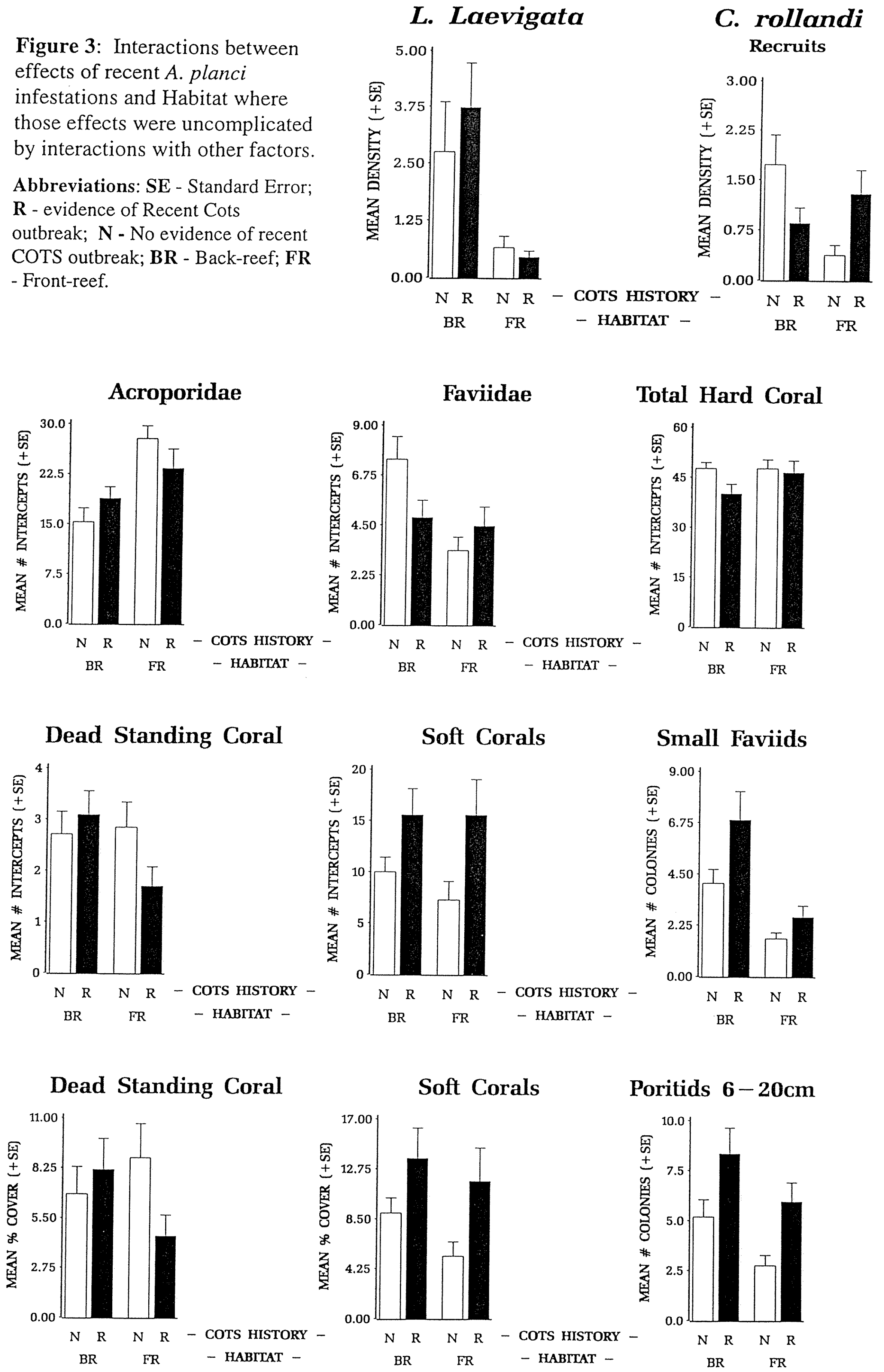


Effects of A. planci Related to Habitat

Effects of COTS history interacted with the effects of Habitat for the asteroid *L. laevigata*, recruitment of the pomacentrid *C. rollandi*, the mean number of patches of faviid corals, acroporid corals, and total hard corals, and the abundance of dead standing corals (both numbers of patches and percent coverage). In each case, the effects of recent COTS history either reversed with change in habitat or were negligible in one habitat (Fig. 3). Counts of recruit *C. rollandi* and faviid corals were greater on COTS affected reefs when only front-reef habitats were considered, but greater on COTS unaffected reefs in back-reef habitats (Fig. 3). The reverse pattern was true for *L. laevigata*, acroporid corals, and dead standing corals, but the confidence in conclusions about *L. laevigata* was very low ($\alpha=\beta=0.34$, Appendix 2). Abundances of soft corals, small faviids, and 6-20cm poritids were 50-100% greater on reefs that had suffered recent COTS infestations than on reefs that had not (Fig. 3), whist overall coral cover was similar on the fronts of both sets of reefs, but slightly greater on COTS-free reefs in back-reef habitats (Fig. 3).

Figure 3: Interactions between effects of recent *A. planci* infestations and Habitat where those effects were uncomplicated by interactions with other factors.

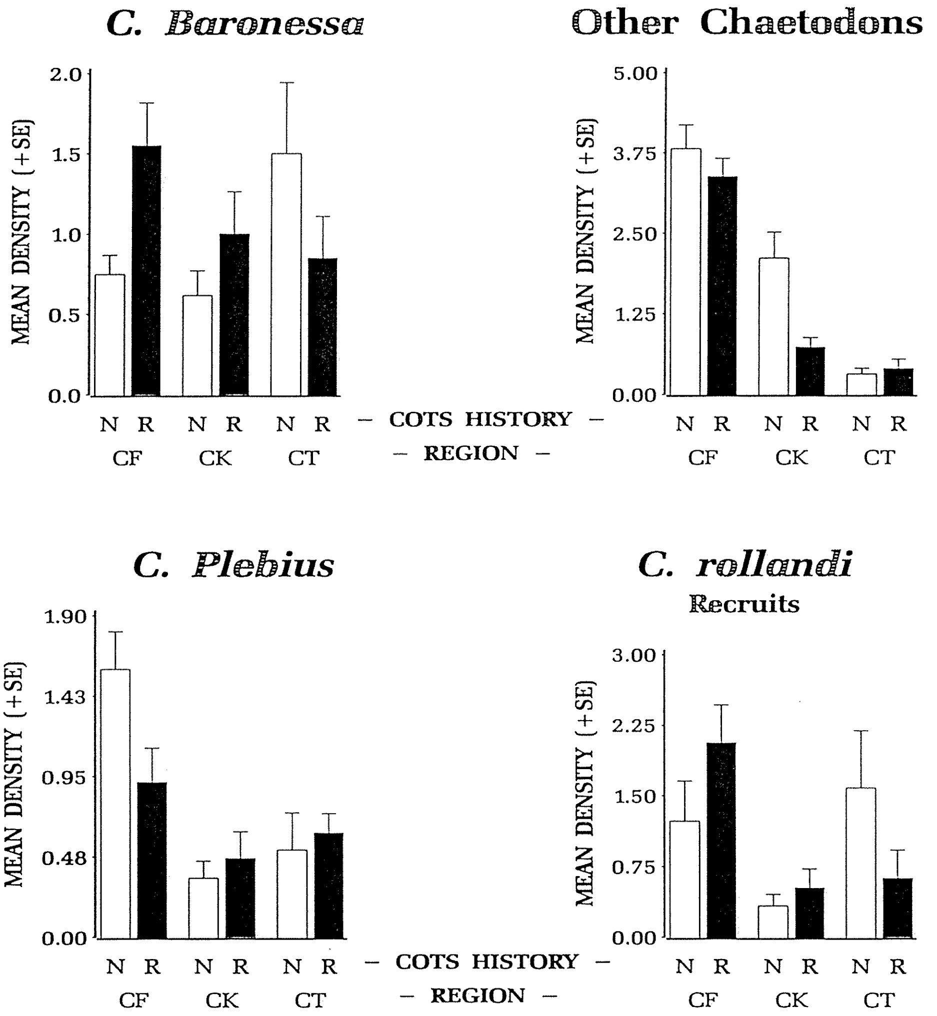
Abbreviations: SE - Standard Error; **R** - evidence of Recent Cots outbreak; **N** - No evidence of recent COTS outbreak; **BR** - Back-reef; **FR** - Front-reef.



Effects of A. planci Related to Region

Differences in abundances correlated with COTS history varied among regions for several taxa (Fig. 4). Miscellaneous chaetodontids and *C. plebeius* were considerably and significantly more abundant on COTS unaffected reefs than on COTS affected reefs in the central and northern regions respectively (Fig. 4), but in other regions the two chaetodontid taxa had similar densities on all reefs. By contrast, *C. baronessa* was more abundant on COTS affected reefs than on unaffected reefs in the northern region, but showed highly variable abundances among reefs in both groups in the central and southern regions, with the result that seemingly large differences in mean abundances could not be discriminated with confidence (Fig. 4). Recent COTS outbreaks apparently affected recruitment by *C. rollandi* in opposite ways in the north and south regions, but neither effect, though apparently large, was statistically significant.

Figure 4: Significant interactions between COTS history and Region on fishes on mid-shelf reefs. **Abbreviations**: SE - Standard Error; **R** - evidence of Recent Cots outbreak; **N** - No evidence of recent COTS outbreak; CF - Cape Flattery; **CK** - Cooktown; **CT** - Cape Tribulation.



C. Baronessa

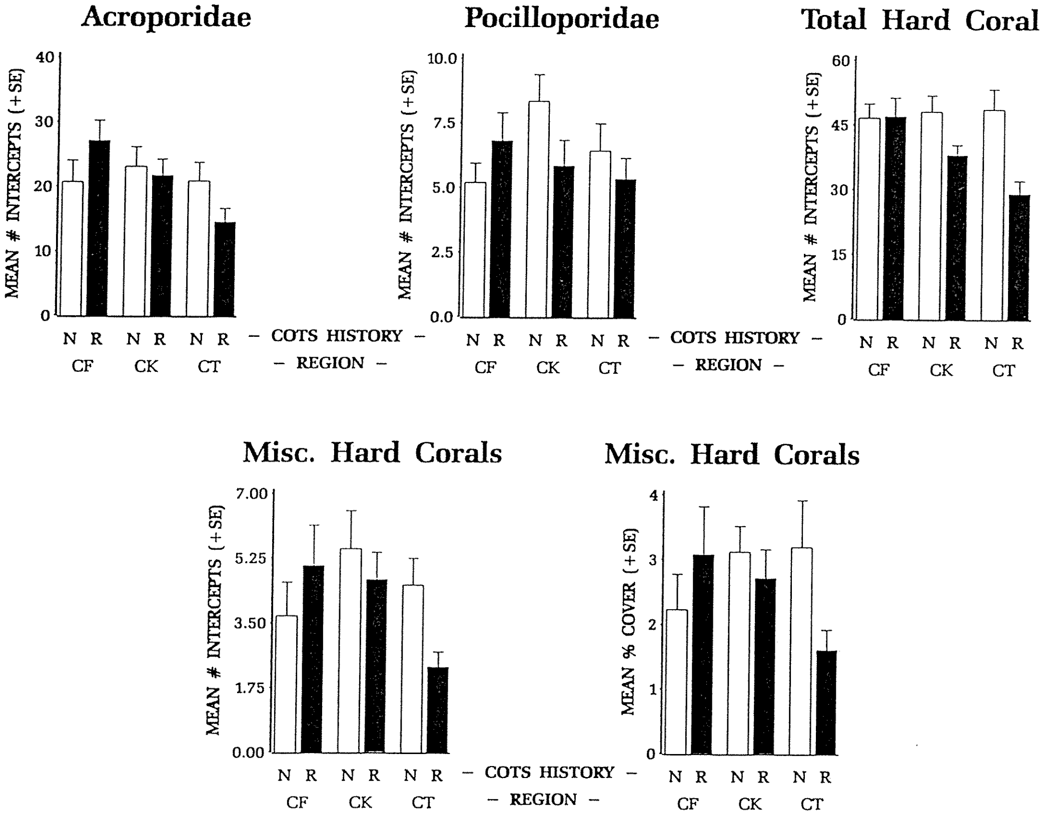
Other Chaetodons

C. Plebius

C. rollandi
Recruits

For all sessile benthic taxa showing significant interaction between COTS history and Region, the measures of abundances (coverage or number of patches) were ranked lower on COTS unaffected reefs in the northern region (off Cape Flattery), but lower on COTS affected reefs in the central and southern regions (Fig. 5). Both percent coverage and numbers of patches of miscellaneous hard corals were significantly higher (by a factor of 2) on COTS unaffected reefs in the Cairns-Cape Tribulation (southern) region, but neither differed significantly between reef type in the central and northern regions, although the rank of the means changed in the northern region (Fig. 5). Apparent differences in the number of pocilloporid colonies were not statistically significant off Cape Flattery and Cape Tribulation, but in the central region there were significantly more colonies per 20m on COTS unaffected reefs than on COTS affected reefs (Fig. 5). When the total numbers of all hard corals were analysed, apparent differences were significant in the central and southern regions, but the effect of recent COTS outbreaks did not affect total coral coverage in the northern region (Fig. 5).

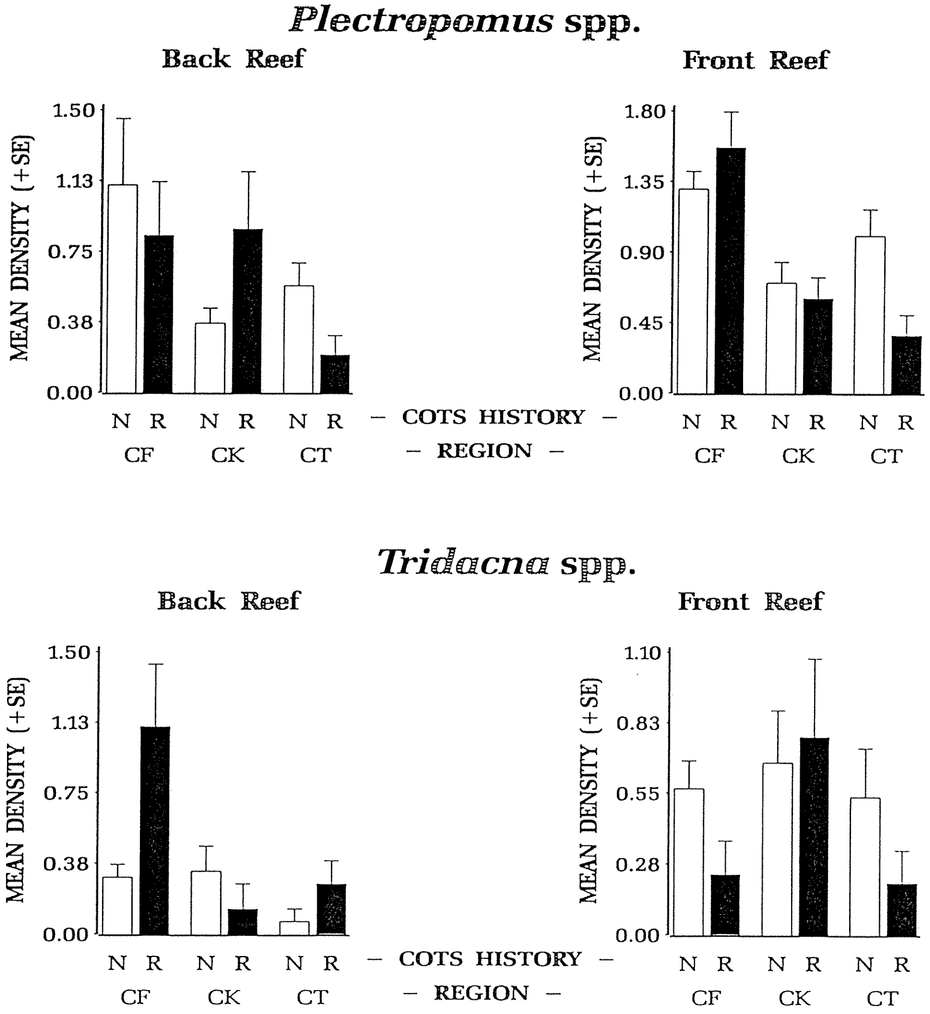
Figure 5: Interactions between COTS history and Region on corals on mid-shelf reefs. **Abbreviations**: **SE** - Standard Error; **R** - evidence of Recent Cots outbreak; **N** - No evidence of recent COTS outbreak; **CF** - Cape Flattery; **CK** - Cooktown; **CT** - Cape Tribulation.



Effects of A. planci Related to Habitat and Region

Plectropomus spp and *Tridacna* spp each exhibited three way interactions between the effects of COTS history, Habitat, and Region (Table 5). Differences in density between COTS affected and unaffected reefs were significant in both habitats off Cape Flattery for *Tridacna* spp., and both habitats off Cape Tribulation for *Plectropomus* spp. COTS effects were also significant for *Plectropomus* spp. in back-reef habitats off Cooktown (Fig. 6). For neither genus, however, were the significant COTS effects consistent among regions or habitats. *Tridacna* spp. were more abundant on the back-reefs of COTS affected reefs than on the back-reefs of COTS unaffected reefs (off Cape Flattery), but the reverse was true when front-reef habitats were considered (Fig. 6). Although coral trout were more abundant in both habitats on COTS unaffected reefs off Cape Tribulation, the reverse was so in back-reef habitats off Cooktown (Fig. 6).

Figure 6: Interactions between COTS history, Habitat, and Region on *Plectropomus* spp. and *Tridacna* spp. on mid-shelf reefs.
Abbreviations: **SE** - Standard Error; **R** - evidence of Recent Cots outbreak; **N** - No evidence of recent COTS outbreak; **CF** - Cape Flattery; **CK** - Cooktown; **CT** - Cape Tribulation.



Summary

In summary, the effects of recent COTS infestation could not be said to be consistent across taxa or even across regions and habitats within most taxa. Although conspicuous differences between COTS affected and COTS unaffected reefs were apparent for some corals, effects of recent COTS outbreaks on most corals were relatively slight when the reefs in the Cairns section were surveyed early in 1990. Some persistent effects were suggested for a few fish taxa.

Comparison of Counts of *A. planci* with Data from Manta Tows

Counts of *A. planci* on the reefs we surveyed were consistently low. We saw a total of only 11 individuals, and no more than 4 on any one reef (Table 6). *A. planci* were observed on 1-2 mid-shelf reefs in each region (Table 6), but not on any outer-shelf reefs. Eight of the 11 individuals were found in back-reef habitats.

The AIMS team observed 2 individuals during manta tows of the same reefs. Our surveys recorded *A. planci* on four reefs where none was recorded on manta tow surveys, whereas the AIMS team recorded one individual on one reef where we saw none. All *A. planci* seen by either team were greater than 15cm in diameter.

Table 6: Total counts of *A. planci* in three size classes (**< 20cm, 21-50cm, >50cm** diameter) from underwater visual searches (**UVS**, this project) and manta tow surveys (**MT**, AIMS) on the 24 reefs we surveyed. Only those reefs where at least one *A. planci* was seen by either team are included. Note that COTS are counted in only two size classes by MT observers, ≤15cm & >15cm diameter. Individuals greater than 15cm were put in the 21-50cm size class below.

			Acanthaster Planci							
			< 20cm		21-50cm		>50cm		TOTAL	
REGION	REEF	HABITAT	UVS	MT	UVS	MT	UVS	MT	UVS	MT
Cape Tribulation	**Hastings**	**Front-reef**	0	0	3	0	0	0	3	0
Cooktown	**Boulder**	**Back-reef**	0	0	1	0	0	0	1	0
	Egret	**Back-reef**	0	0	2	0	2	0	4	0
Cape Flattery	**Eyrie**	**Back-reef**	0	0	2	1	0	0	2	1
	Helsdon	**Back-reef**	0	0	0	1	0	0	0	1
	Lizard	**Back-reef**	0	0	1	0	0	0	1	0
TOTAL			**0**	**0**	9	2	2	**0**	**11**	2

Effects of Habitat

Habitat effects were common in these datasets. For all but one fish (*C. rollandi*), Habitat effects were dependent on other factors, such as Region and Shelf Position, but for several sessile taxa Habitat effects were significant and consistent across other strata.

General Effects of Habitat

The main effects of Habitat were significant, and uncomplicated by interactions with other fixed effects, for *C. rollandi*, counts of dead standing coral, faviids, and juvenile poritids, and both counts and percent coverage of miscellaneous hard corals (Table 7, Fig. 7). In all these cases, abundances were at least 50% greater on back-reefs than on front-reefs (Fig. 7). This was true also for pocilloporid corals (counts), acroporid corals (counts), small faviids, and small miscellaneous corals when only mid-shelf reefs were analysed to consider the effects of COTS infestations. *Chaetodon baronessa* also showed Habitat effects on mid-shelf reefs, but were more abundant on the front-reefs than back-reefs.

Table 7: Summary results of tests by univariate ANOVA for the effects of Shelf Position [**S**], Habitat [**H**], Region [**R**], and reefs [**r(RS)**] and their interactions on abundances of biota. Reef selection for analyses was standardised with respect to COTS history across shelf positions within each region. *, - = statistical significance and non-significance respectively at $\alpha_c = \beta$, given the effect sizes described in the text. Bold asterisks indicate the terms in analyses that were interpretable without ambiguity.

A: Fishes

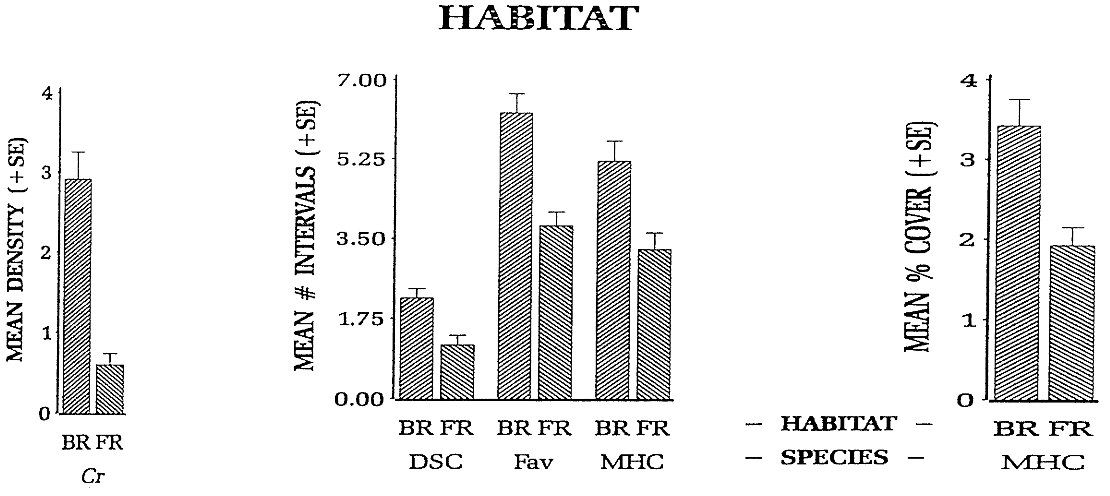
	SOURCE OF VARIATION								
TAXON	Habitat	Region	Shelf	H*R	H*S	R*S	H*R*S	r(RS)	H*r(RS)
Large Fishes									
Total Acanthurids	*	*	*	-	*	*	-	*	*
Z. scopas	*	*	*	*	*	*	*	*	-
Other Acanthurids	*	*	*	-	*	*	-	*	*
All Chaetodons	-	*	-	*	-	*	*	*	-
C. aureofasciatus	-	*	*	-	-	*	-	*	-
C. baronessa	-	*	*	-	*	*	*	-	*
C. plebeius	*	*	-	-	*	-	-	-	-
C. trifasciatus	*	*	*	*	*	-	*	*	-
C. vagabundus	*	-	*	-	-	*	*	*	-
Other Chaetodons	*	*	*	-	*	-	-	*	*
All Lutjanids	*	*	*	*	-	-	-	-	-
L. carponotatus	-	*	*	-	-	*	-	*	-
Plectropomus spp	-	*	*	*	*	-	*	-	-
Small Fishes									
A. curacao	*	-	*	-	*	-	-	*	*
C. atripectoralis	-	*	*	*	*	*	-	-	-
C. rollandi	*	-	*	-	-	-	-	*	*
Recruit *C.r.*	*	*	*	*	*	*	*	-	-
P. lacrymatus	-	*	*	*	*	-	-	*	*
P. moluccensis	-	*	*	*	-	*	*	*	-
Recruit *P.m.*	-	*	*	*	*	*	*	-	-
T. lunare	-	*	*	-	*	*	-	-	-

Table 7: (Continued)

B: Sessile Benthos

TAXON	SOURCE OF VARIATION Habitat	Region	Shelf	H*R	H*S	R*S	H*R*S	r(RS)	H*r(RS)
Small Corals									
Small Acroporids	*	*	*	*	*	*	-	*	*
Small Faviids	*	*	-	*	-	*	-	*	*
Small Pocilloporids	*	*	*	-	*	*	-	*	-
Misc. Small Hard	*	*	*	*	*	*	*	*	-
Small Soft Corals	-	*	*	-	-	*	-	*	*
Poritid Counts									
Poritids < 5cm	*	-	*	-	-	*	-	*	*
Poritids 6-20cm	-	-	*	-	-	*	-	*	*
Poritids 21-50cm	-	-	*	-	*	*	-	-	-
Poritids 51-100cm	*	-	-	-	*	*	*	-	-
Poritids >100cm	*	-	-	-	*	*	*	-	-
% Coverage									
Total Hard Coral	-	-	-	*	*	-	-	*	-
Acroporidae	*	-	-	*	-	-	-	*	*
Faviidae	*	-	-	-	*	-	-	-	-
Pocilloporidae	*	-	*	*	*	*	*	-	-
Poritidae	*	-	-	-	*	-	*	-	*
Misc. Hard Coral	*	-	-	-	-	-	-	*	*
Dead Stand Coral	*	*	*	-	*	*	-	-	*
Soft Corals	-	-	-	-	*	-	-	*	*
Sponges	*	-	*	-	*	-	-	-	*
# Intercepts									
Total Hard Coral	*	*	*	*	*	-	-	*	-
Acroporidae	*	*	*	-	*	-	-	*	*
Faviidae	*	-	-	-	-	*	-	*	*
Pocilloporidae	*	*	*	*	*	*	*	-	-
Poritidae	*	-	*	*	*	*	*	-	*
Misc. Hard Coral	*	-	-	-	-	-	-	*	*
Dead Stand Coral	*	*	*	-	*	*	-	-	*
Soft Corals	-	-	-	-	*	-	-	*	-
Sponges	*	-	*	-	*	-	-	*	*
Misc. Benthos									
Tridacna spp	*	*	*	*	*	-	*	-	-
L. laevigata	*	*	*	*	*	*	*	-	-

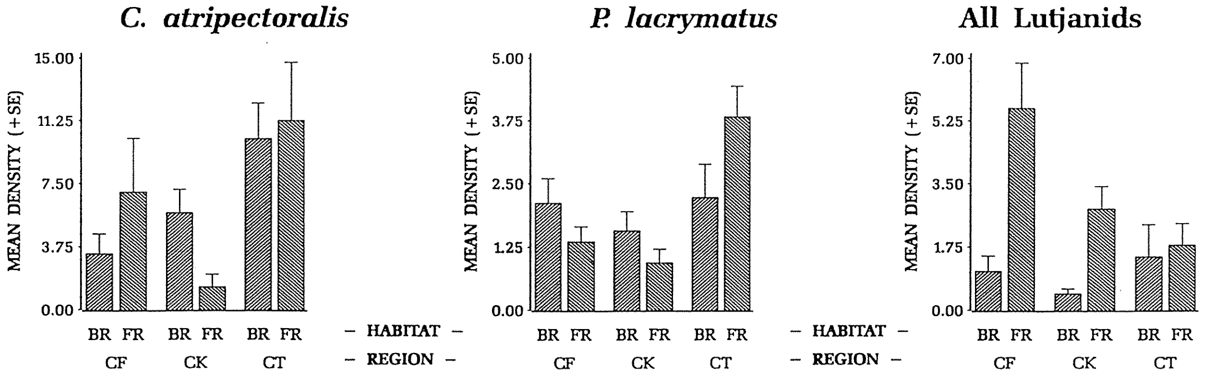
Figure 7: Main effects of Habitat on densities of biota from both shelf positions and all regions. **Abbreviations**: **SE** - Standard Error; **BR** - Back-reef; **FR** - Front-reef; ***Cr*** - *C. rollandi;* **DSC** - Dead Standing Corals; **MHC** - Miscellaneous Hard Corals; **Fav** - Faviidae.



Effects of Habitat Related to Region

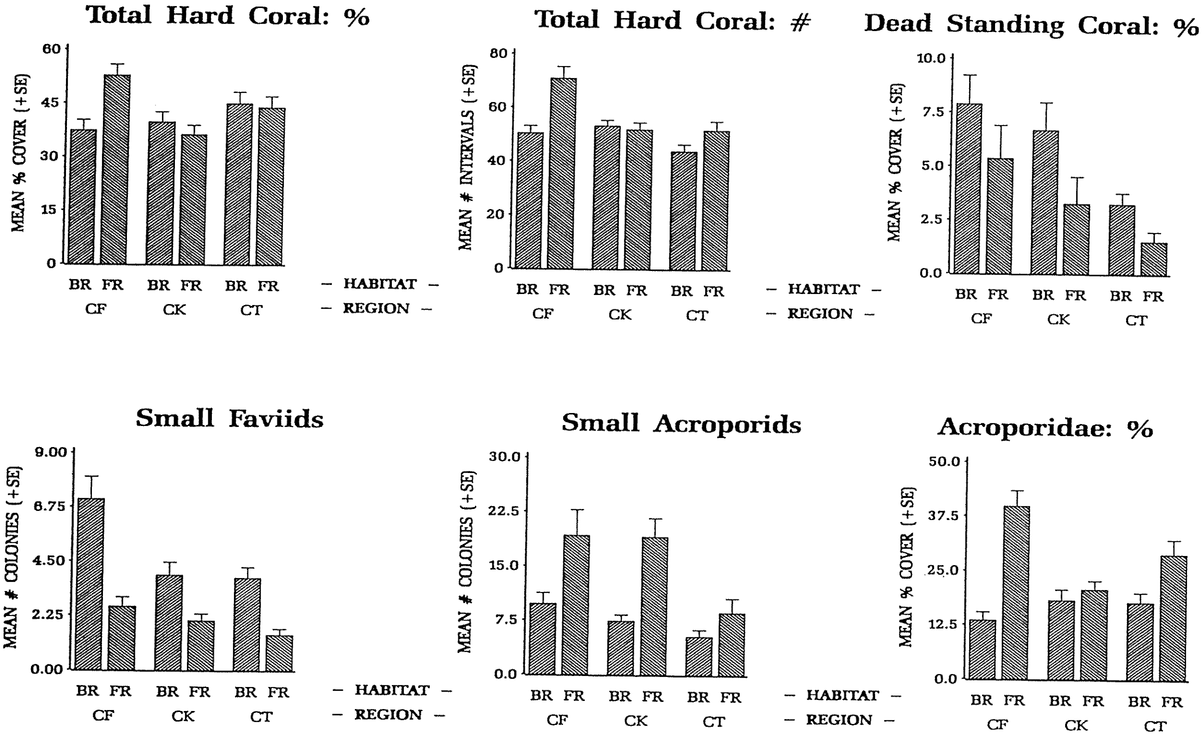
Habitat effects varied with region when averaged over shelf positions for *C. atripectoralis*, and all lutjanids (Fig. 8). Abundances of *C atripectoralis* did not vary with habitat when averaged over shelf positions off Cape Flattery and Cape Tribulation, but off Cooktown, abundances were greater in back-reef habitats. When only the mid-shelf reefs were considered, COTS history affected densities of *C. atripectoralis* consistently in both habitats across all regions (Table 5, Fig. 2), and so it seems unlikely that the result here arose because of confounding between COTS history and region. Similarly, for total counts of lutjanids, COTS effects were consistent with Region and Habitat in the mid-shelf, and so regional effects on Habitat here seem unlikely to have arisen from confounding. When both mid-shelf and outer-shelf reefs were analysed, lutjanids were apparently more abundant on front-reefs in the north and central regions, but similarly abundant in both habitats in the south (Fig. 8). Habitats did not affect significantly the densities of *P. lacrymatus* in any regions, though regional differences were habitat specific (see later).

Figure 8: Habitat comparisons of abundances of fishes in each Region, for taxa with significant H*R interactions based on reefs with similar COTS history at both shelf positions in each region. **Abbreviations**: **SE** - Standard Error; **BR** - Back-reef; **FR** - Front-reef; **CF** - Cape Flattery; **CK** - Cooktown; **CT** - Cape Tribulation.



For sessile benthos, Habitat effects interacted with region for small faviids, small acroporids, total coverage by acroporids, total abundances of hard corals (counts & coverage), and coverage by dead standing corals (Fig. 9). Small faviids and dead standing corals were consistently more abundant in back-reef habitats than in front-reef habitats, but the other taxa were either of similar abundance in both habitats at one or more regions or at greater abundances in front-reef habitats (Fig. 9). The results were consistent whether only mid-shelf data or all data were considered, however, only for coverage by acroporids. For this family, coverage was greater on front-reef slopes in the north and southern regions, but did not differ with habitat off Cooktown (Fig. 9). There were no effects of COTS history on small acroporids on mid-shelf reefs, meaning that the regional differences in Habitat effects for this group were probably not the result of confounded COTS effects. For small faviids and total coral abundances, however, Habitat effects on mid-shelf reefs depended on COTS history (Table 5). This result renders ambiguous the interpretation of the regional variation in Habitat effects in the analyses of reefs from both shelf positions.

Figure 9: Habitat comparisons of abundances of benthos in each Region, for taxa with significant H*R interactions based on reefs with similar COTS history at both shelf positions in each region. **Abbreviations**: SE - Standard Error; **BR** - Back-reef; **FR** - Front-reef; **CF** - Cape Flattery; **CK** - Cooktown; **CT** - Cape Tribulation.



Total Hard Coral: %

Total Hard Coral: #

Dead Standing Coral: %

Small Faviids

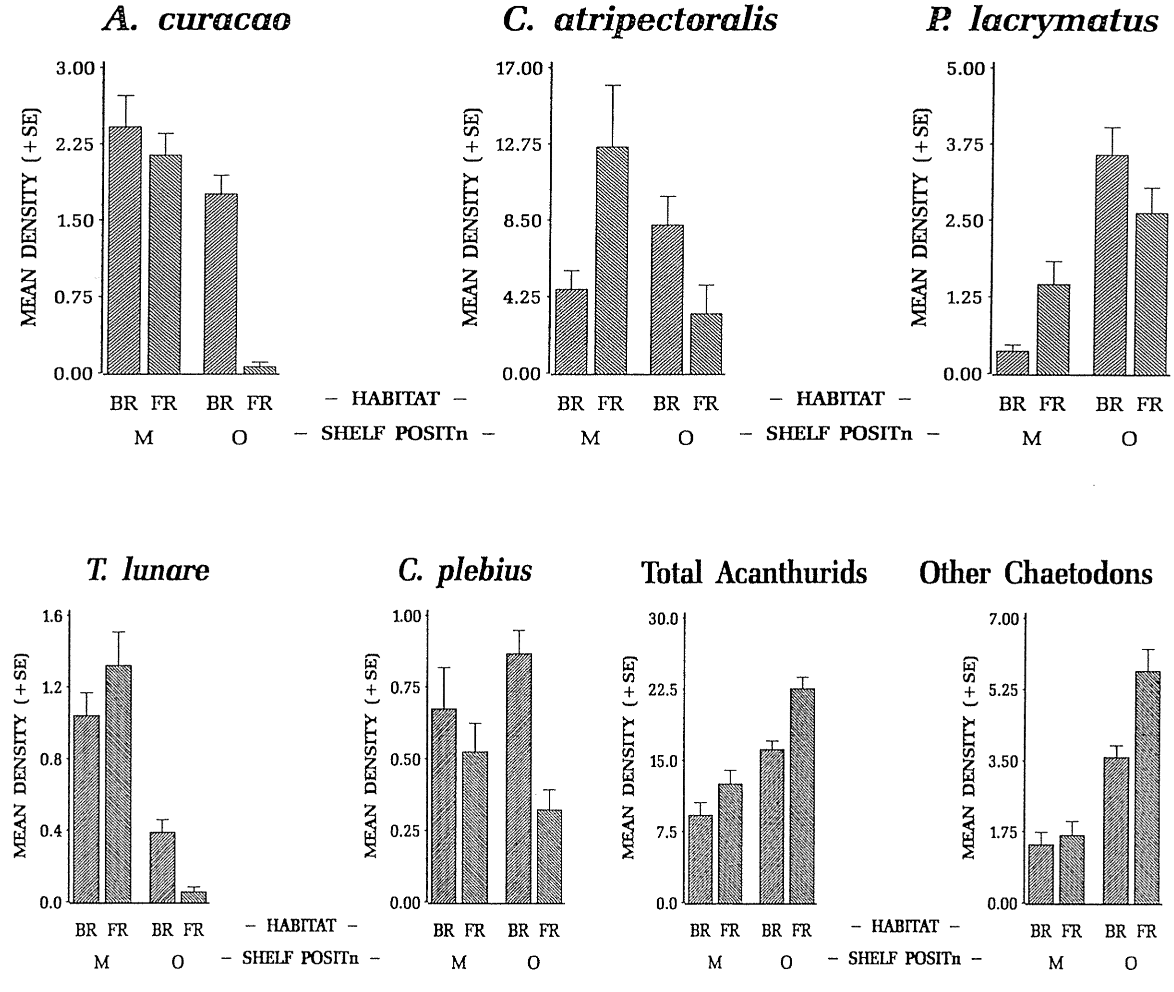
Small Acroporids

Acroporidae: %

Effects of Habitat Related to Shelf Position

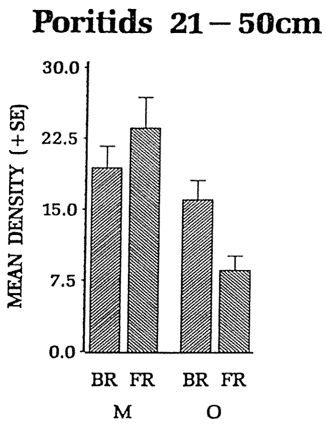
Among the fishes, Habitat effects depended on shelf position for acanthurids, *C. plebeius*, miscellaneous chaetodons, *T. lunare*, *A. curacao*, *C atripectoralis*, *P. lacrymatus* (Fig. 10, Table 7). Where habitats differed, those effects were relatively consistent in nature: abundances were generally greater in front-reef habitats on the mid-shelf reefs, but greater in the back-reef habitats of outer-shelf reefs (Fig. 10). The two exceptions were the acanthurids and miscellaneous chaetodons, both groups being at greater abundances on the front-reefs of outer-shelf reefs (Fig. 10). Differences between habitats within shelf positions were often as great as differences between shelf positions within habitats for these groups.

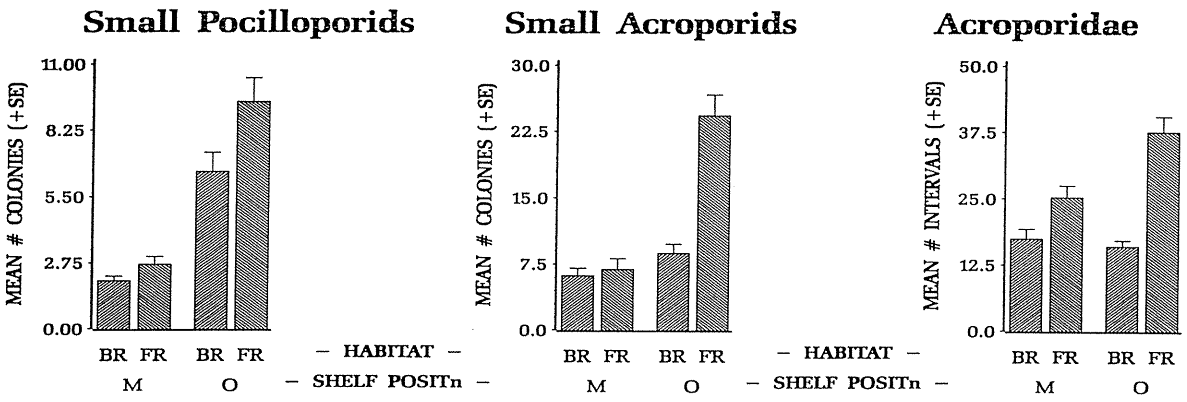
Figure 10: Habitat comparisons of abundances of fishes at each Shelf Position.
Abbreviations: **SE** - Standard Error; **BR** - Back-reef; **FR** - Front-reef; **M**-Mid-shelf; **O**-Outer-shelf.

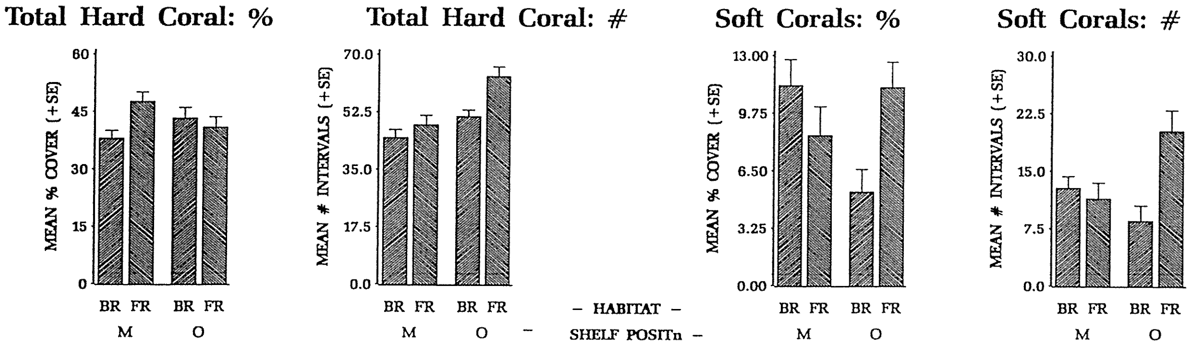


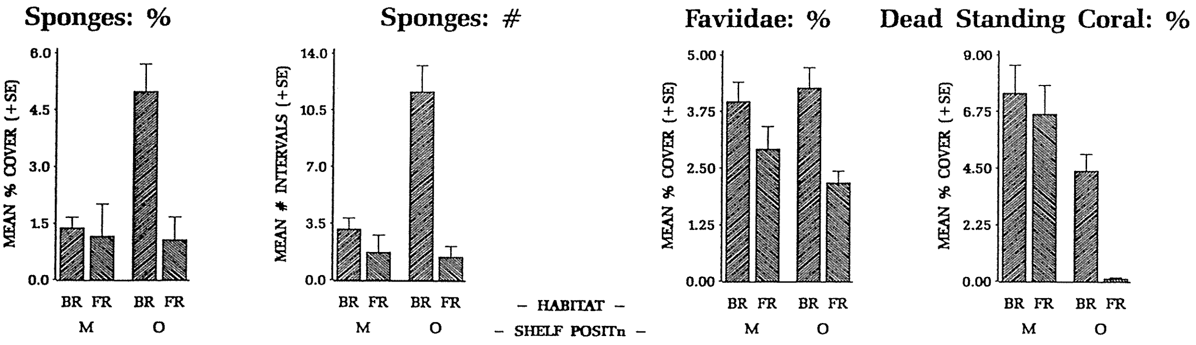
Habitat by Shelf Position interactions were significant for 9 groups of sessile benthos. In most cases, habitat differences were manifest as greater abundances (counts and/or coverage) on front-reef habitats than in back-reef habitats, with these differences being greatest in magnitude and most frequent on outer-shelf reefs (Fig. 11). The few exceptions were striking, however, for the magnitudes of the contrasting patterns: coverage and counts of sponges on mid-shelf reefs were dramatically (~600%) greater in back-reef habitats, as was coverage by dead standing corals on mid-shelf reefs and numbers of 21-50cmΦ poritid corals on outer-shelf reefs (Fig. 11).

Figure 11: Habitat comparisons of abundances of benthos at each Shelf Position. **Abbreviations**: SE - Standard Error; **BR** - Back-reef; **FR** - Front-reef; **M** - Mid-shelf; **O** - Outer-shelf.







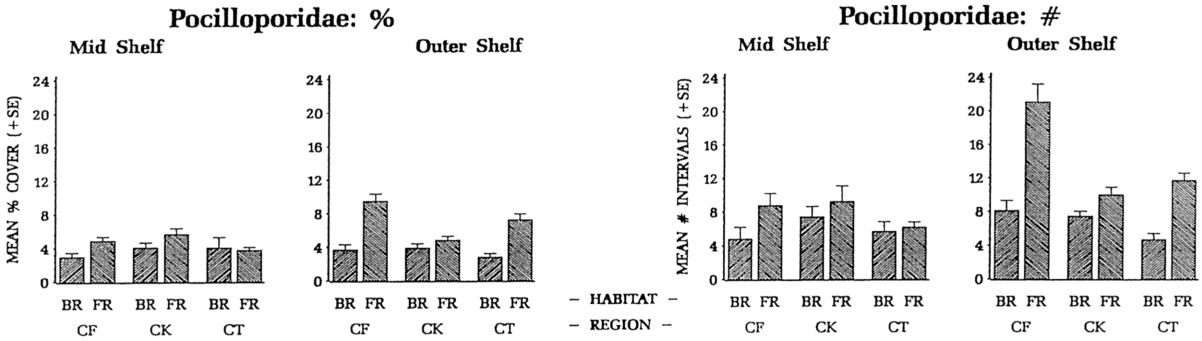


Effects of Habitat Related to Shelf Position and Region

Three way interactions between Habitat, Region, & Shelf Position were statistically significant for several taxa of fishes and benthos (Table 7). Despite these complex interactions, however, four patterns in abundance with habitat were apparent.

Firstly, pocilloporid corals (whether measured by % coverage or number of intercepts), were either of similar abundances in both habitats (on mid-shelf reefs off Cape Tribulation) or significantly more abundant in front-reef habitats than in back-reef habitats (in all other places) (Figure 12).

Figure 12: Habitat comparisons of abundances of pocilloporid corals measured along line intercept transects in each Region at each Shelf Position.
Abbreviations: **SE** - Standard Error; **BR** - Back-reef; **FR** - Front-reef; **FR** - Front-reef; **CF** - Cape Flattery; **CF** - Cape Flattery; **CK** - Cooktown; **CT** - Cape Tribulation.



Secondly, there were several taxa for which abundances were generally either significantly greater on back-reefs than on front-reefs, or relatively similar in both habitats. This group included *L. laevigata*, *Tridacna* spp, total chaetodons, *C. vagabundus*, adult and recruit *P. moluccensis*, juvenile *C. rollandi,* miscellaneous juvenile corals, counts of Poritid corals of 51-100cm*Φ* and > 100cm*Φ*, and coverage and the numbers of intercepts of Poritids (Fig. 13). Note that for the poritids, however, front-reef habitats were ranked above back-reef habitats on mid-shelf reefs off Cooktown, and that difference was statistically significant for the line intercept data (Fig. 13).

Figure 13: Habitat comparisons of abundances of biota in each Region at each Shelf Position for which densities were generally greater in back-reef habitats than in front-reef habitats.
Abbreviations: **SE** - Standard Error; **BR** - Back-reef; **FR** - Front-reef; **FR** - Front-reef; **CF** - Cape Flattery; **CF** - Cape Flattery; **CK** - Cooktown; **CT** - Cape Tribulation.

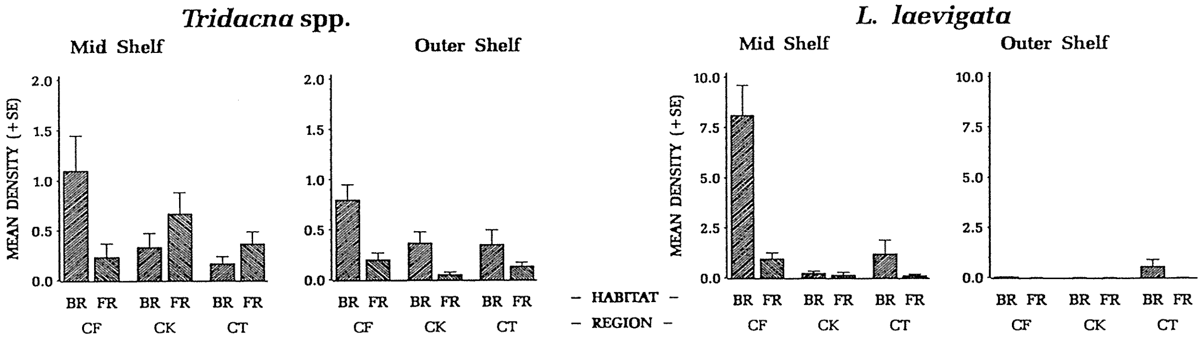
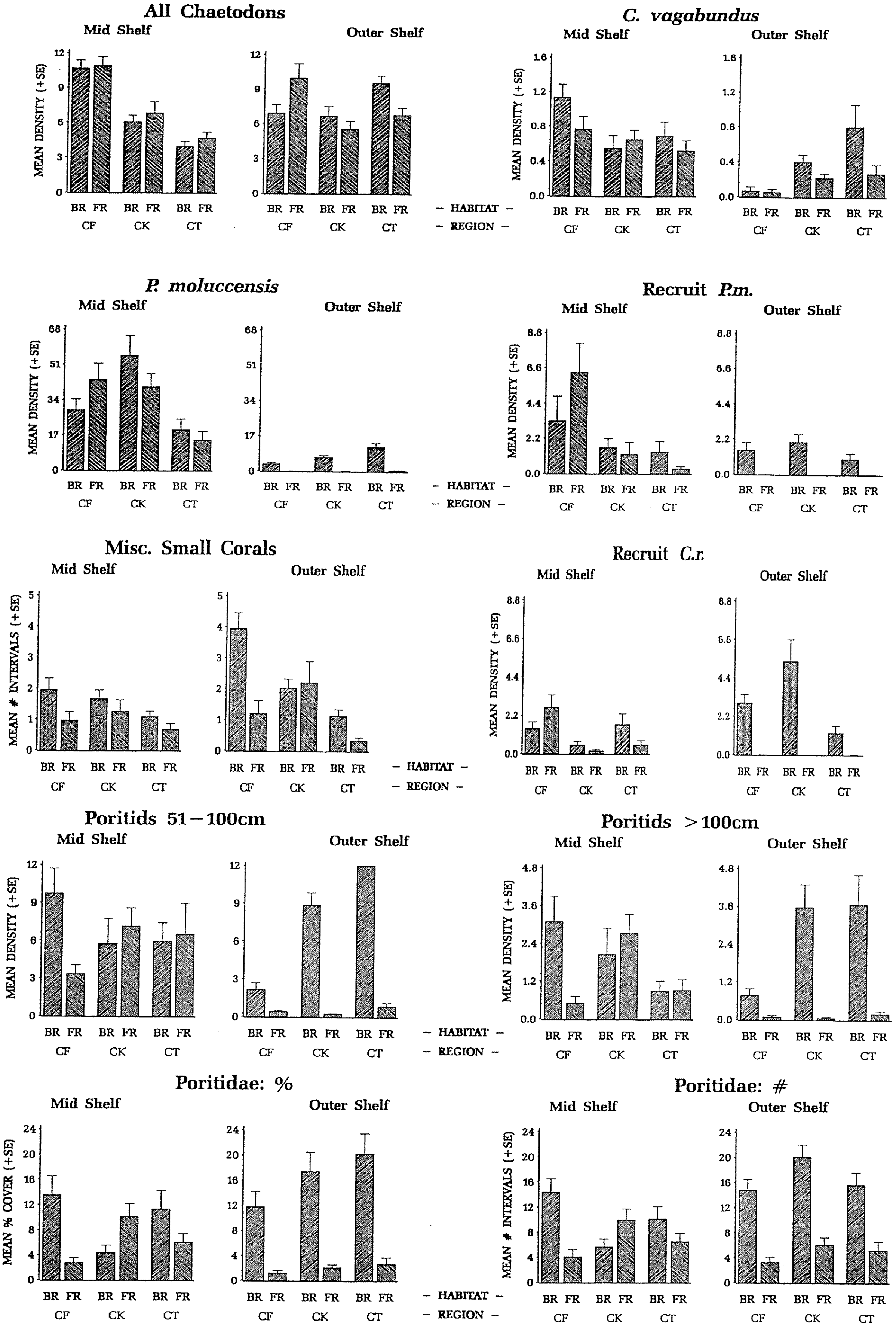


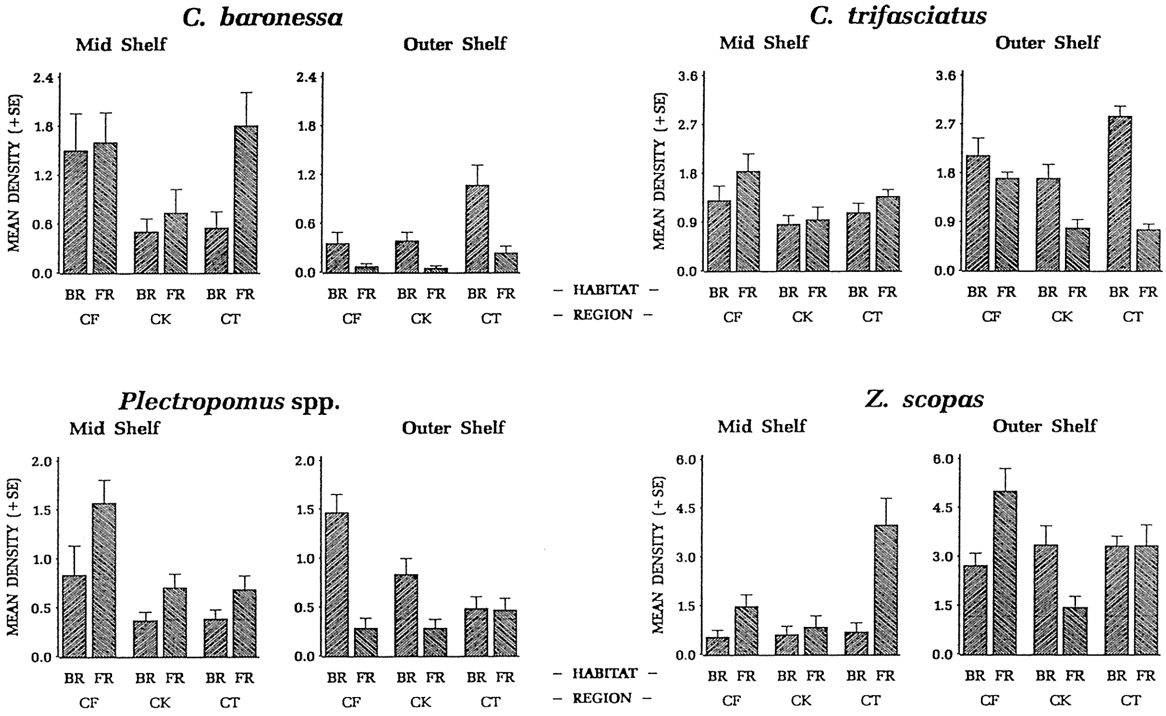
Figure 13: (Continued).



Thirdly, some taxa were apparently (though not always significantly) more abundant in front-reef habitat on mid-shelf reefs, but more abundant in back-reef habitat on outer-shelf reefs. This group included *Plectropomus spp*, *C. baronessa*, and *C trifasciatus* (Fig. 14).

Finally, *Zebrossoma scopas* showed no consistent pattern in habitat related differences in abundances.

Figure 14: Habitat comparisons of abundances of biota in each Region at each Shelf Position where densities tended to be greater in front-reef habitats on mid-shelf reefs but greater in back-reef habitats on outer-shelf reefs.
Abbreviations: **SE** - Standard Error; **BR** - Back-reef; **FR** - Front-reef; **FR** - Front-reef; **CF** - Cape Flattery; **CF** - Cape Flattery; **CK** - Cooktown; **CT** - Cape Tribulation.



Summary

In summary, Habitat effects were generally greater in magnitude and more often statistically significant on outer-shelf reefs than mid-shelf reefs, and in most cases abundances were greater in back-reef habitat than in front-reef habitat on outer-shelf reefs. Abundances tended to be more similar between habitats on mid-shelf reefs off Cooktown than those of Cape Flattery or Cape Tribulation.

Effects of Shelf Position

Cross shelf patterns in mean abundances were indicated for several taxa. Interactions between Shelf Position and Habitat and/or Region were significant for most of these taxa, however (Table 7), and the cross-shelf patterns often were not consistent across habitats and/or regions.

General Effects of Shelf Position

The main effect of Shelf Position was simply interpretable for only two taxa: the pomacentrid *C. rollandi* (adults) and the aggregate counts of lutjanids (Table 7). Estimated densities of both these species were about 50% lower on outer-shelf reefs than on mid-shelf reefs (Fig. 15).

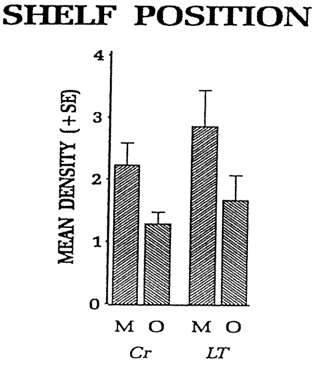
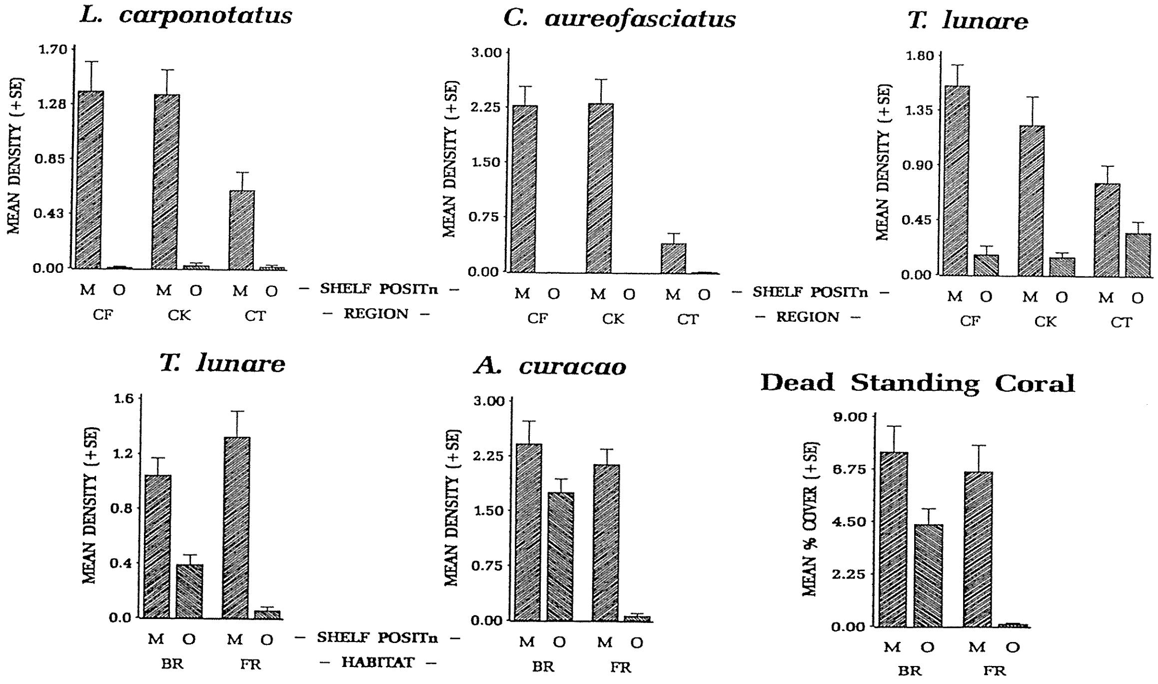


Figure 15: Significant main effects of Shelf Position on the fish *C. rollandi* (*Cr*) and lutjanids (**LT**). **Abbreviations**: **SE** - Standard Error; **M** - Mid-shelf; **O** - Outer-shelf.

Two-way interactions between Shelf Position and Habitat and/or Shelf Position and Region were significant for 9 of the 21 fish taxa analysed, and 10 of 21 taxa of benthos. Despite the significant interactions, however, effects of Shelf Position were consistent across levels of either Habitat or region (and therefore general in nature) for many of these taxa.

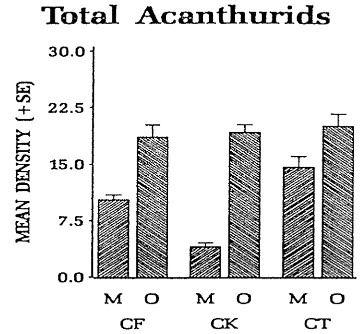
Mean abundances were consistently greater on mid-shelf reefs than on outer-shelf reefs for four fishes (*A. curacao*, *C. aureofasciatus*, *L. carponotatus*, & *T. lunare*) and dead standing corals (Fig. 16).

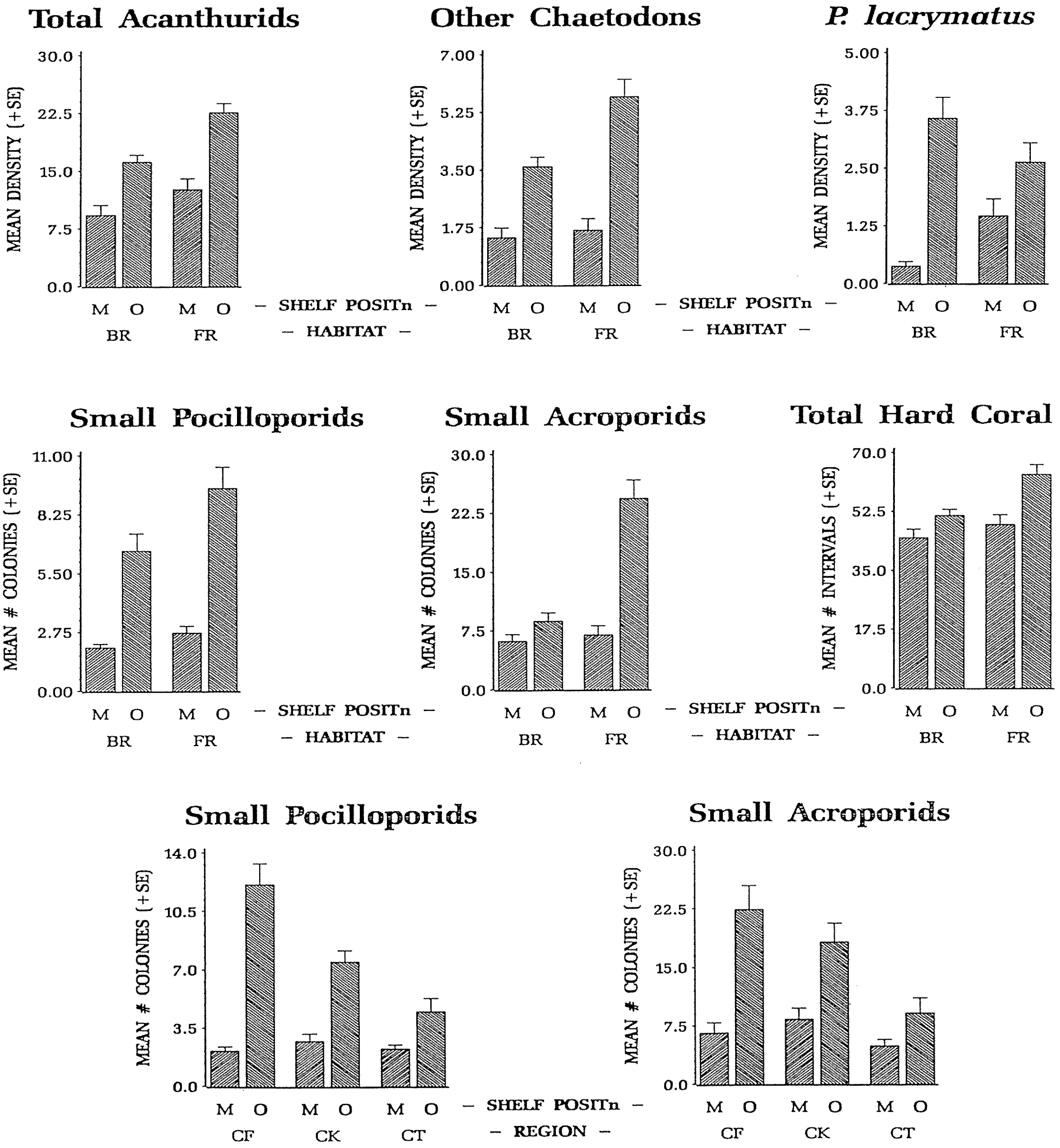
Figure 16: Comparisons of densities of biota between Shelf Position within each Region (top) and Habitat (bottom) where abundances were greater on mid-shelf reefs than on outer-shelf reefs. **Abbreviations**: **SE** - Standard Error; **BR** - Back-reef; **FR** - Front-reef; **CF** - Cape Flattery; **CK** - Cooktown; **CT** - Cape Tribulation; **M** - Mid-shelf; **O** - Outer-shelf.



Abundances were significantly greater on outer-shelf reefs than mid-shelf reefs despite significant interactions with Region and/or Habitat for 3 fish taxa (total acanthurids, miscellaneous chaetodons, & *P. lacrymatus*) and 3 coral groups (small acroporids, small pocilloporids, and total number of hard coral patches) (Fig. 17). For example, despite significant interactions with Region and Habitat, the average numbers of small pocilloporids and small acroporids were 2-6 times as great on outer-shelf reefs as on mid-shelf reefs in all regions (Fig. 17).

Figure 17: Comparisons of densities of biota between Shelf Position within each Region (right) and Habitat (below) where abundances tended to be greater on outer-shelf reefs than on mid-shelf reefs. **Abbreviations**: SE - Standard Error; **BR** - Back-reef; **FR** - Front-reef; **CF** - Cape Flattery; **CK** - Cooktown; **CT** - Cape Tribulation; **M** - Mid-shelf; **O** - Outer-shelf.

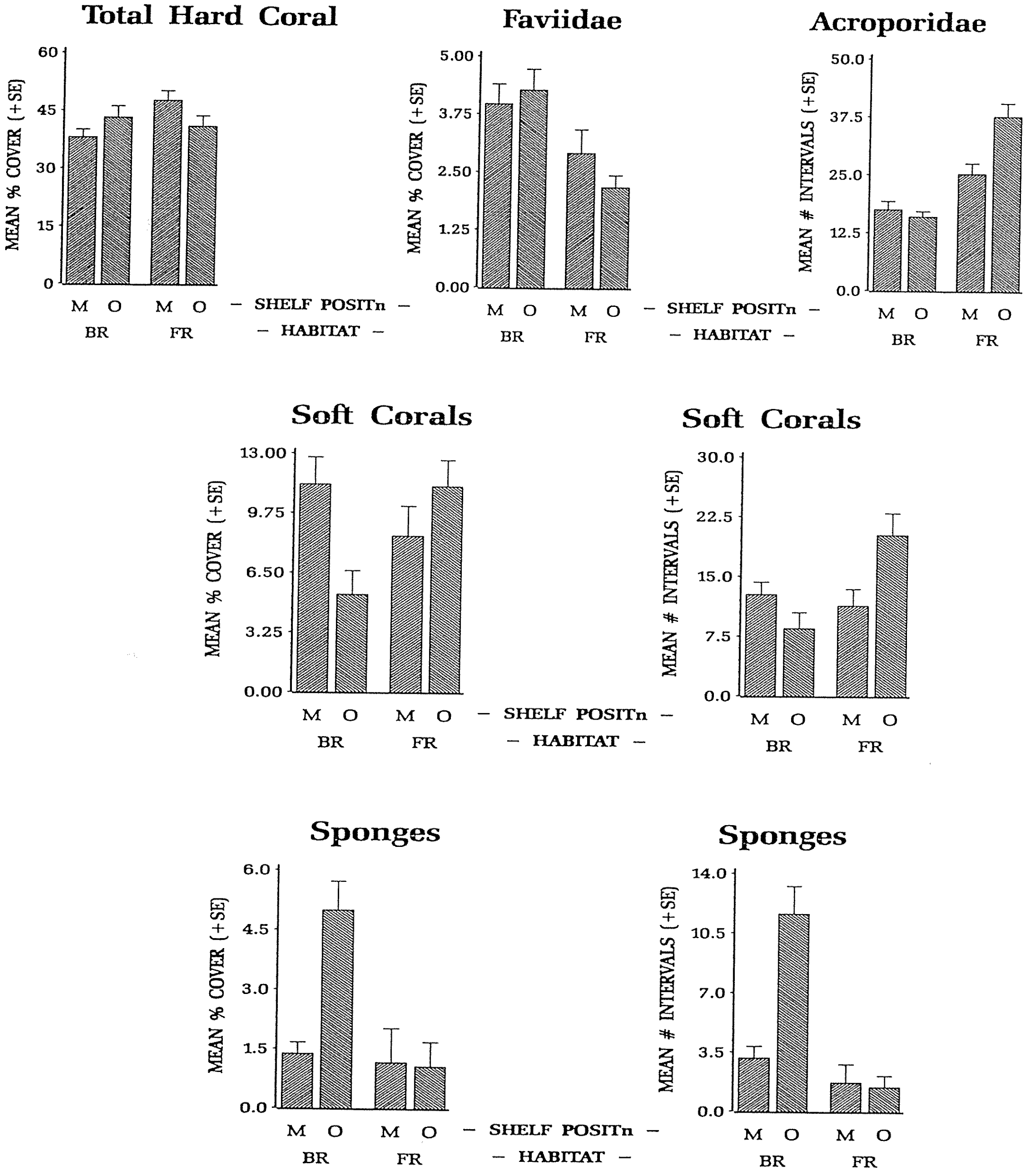




Effects of Shelf Position Related to Habitat

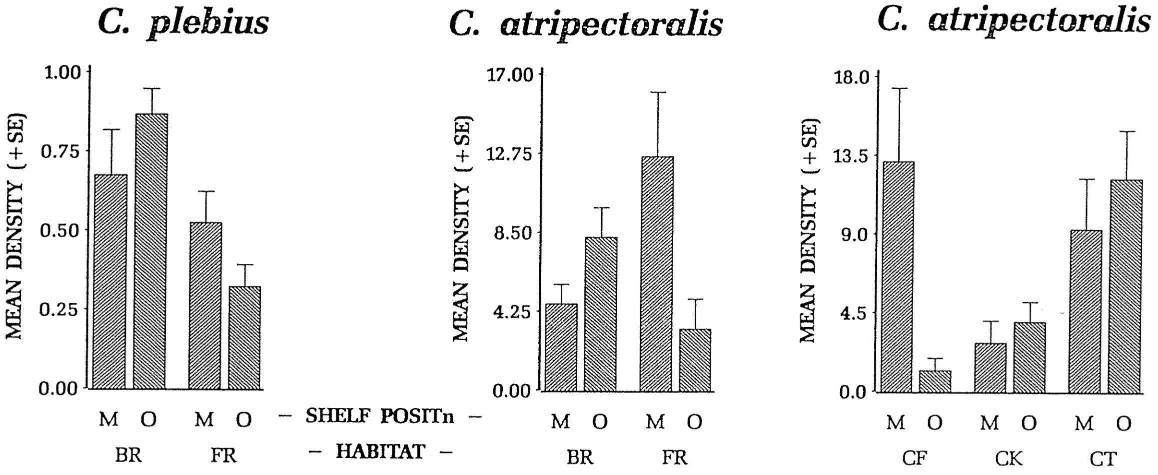
For most of the remaining categories of benthos, abundances were correlated significantly with shelf position in one habitat, but not the other. For acroporids in front-reef habitats, numbers of patches were greater on outer-shelf reefs than on mid-shelf reefs, but in back-reef habitats numbers did not differ significantly with shelf position (Fig. 18). Percent coverage by faviids and all hard corals was greater on average on mid-shelf reefs in front-reef habitats, but did not differ significantly with Shelf Position in back-reef habitats (Fig. 18). Conversely, both coverage and numbers of sponges were about 3.5 times higher in the back-reefs of outer-shelf reefs than in the back-reefs of mid-shelf reefs, but both measures were very similar between shelf positions in the front-reef habitats (Fig. 18). For soft corals, both coverage and numbers in front-reef habitats were greater on outer-shelf reefs, but in back-reefs the reverse was true (Fig. 18).

Figure 18: Comparisons of densities of corals between Shelf Position within each Habitat where the effects of Shelf Position varied with Habitat.
Abbreviations: SE - Standard Error; **BR** - Back-reef; **FR** - Front-reef; **M** - Mid-shelf; **O** - Outer-shelf.



For the remaining 2 fish taxa (*C. atripectoralis* & *C. plebeius*), differences between reefs with shelf position also depended on which habitat or region was considered. Both *C. plebeius* and *C. atripectoralis* were significantly more abundant in outer-shelf back-reef habitats than in mid-shelf back-reef habitats, but significantly less abundant in outer-shelf front-reef habitats than in mid-shelf front-reef habitats (Fig. 19).

Figure 19: Comparisons of densities of fishes between Shelf Position within each Habitat (left) and Region (right) where the effects of Shelf Position reversed with Habitat or Region. **Abbreviations**: **SE** - Standard Error; **BR** - Back-reef; **FR** - Front-reef; **CF** - Cape Flattery; **CK** - Cooktown; **CT** - Cape Tribulation; **M** - Mid-shelf; **O** - Outer-shelf.



Effects of Shelf Position Related to Region

When averaged over both habitats in each region, *C atripectoralis* was significantly (and substantially) more abundant on mid-shelf reefs only in the northern region, off Cape Flattery (Fig. 19). In the other two regions, abundances of *C. atripectoralis* did not differ significantly with shelf position (Fig. 19).

Interactions between the effects of Shelf Position and Region also were significant for several corals (Table 7). Similarly, small soft corals were 5-10 times more abundant on outer-shelf reefs than mid-shelf reefs in the northern and central regions, but did not differ in abundance across the shelf in the southern region (Fig. 20). By contrast, dead standing corals were far more abundant on the mid-shelf of the northern and central regions, but also did not differ with shelf position in the south (Fig. 20). Finally, faviid corals were more abundant on mid-shelf reefs in the northern region, but more abundant on the outer-shelf reefs in the central (for juveniles) and southern regions (for # intervals on line intercept transects) (Fig. 20).

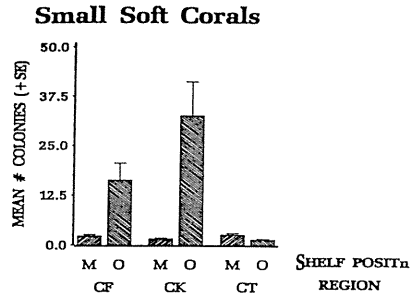
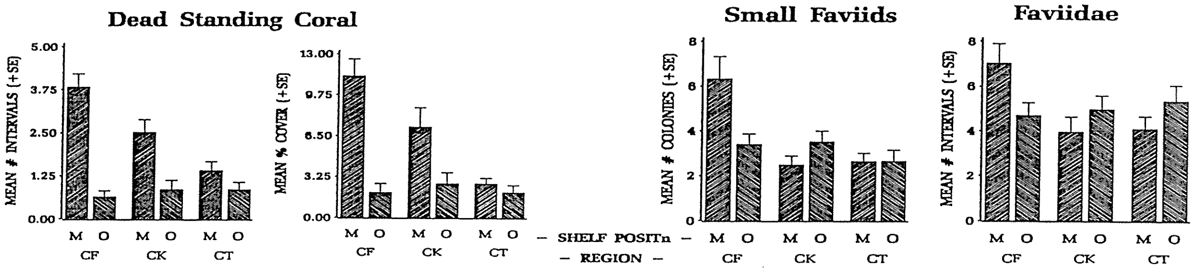
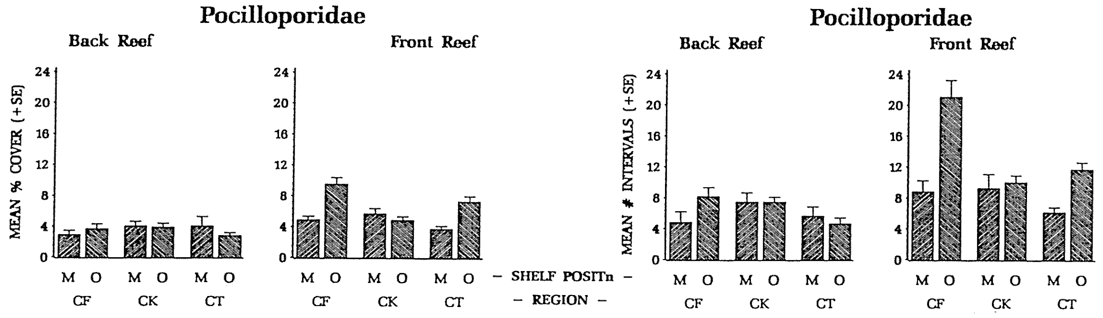


Figure 20: Comparisons of densities of corals between Shelf Position within each Region where interactions between Shelf Position and Region were significant. **Abbreviations**: **SE** - Standard Error; **BR** - Back-reef; **FR** - Front-reef; **M** - Mid-shelf; **O** - Outer-shelf.



Effects of Shelf Position Related to Habitat and Region

Three-way interactions among Shelf Position, Region, and Habitat were also significant for several taxa (Table 7). When effects of Shelf Position were significant for pocilloporid corals or miscellaneous small corals, abundances (numbers of colonies and coverage) were always greater on outer-shelf reefs than mid-shelf reefs (Fig. 21). For each habitat, however, Shelf Position had no effect in at least one region (Fig. 21). The same pattern was apparent for the acanthurid *Z. scopas*.



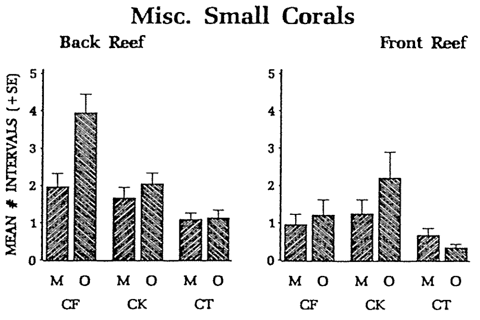
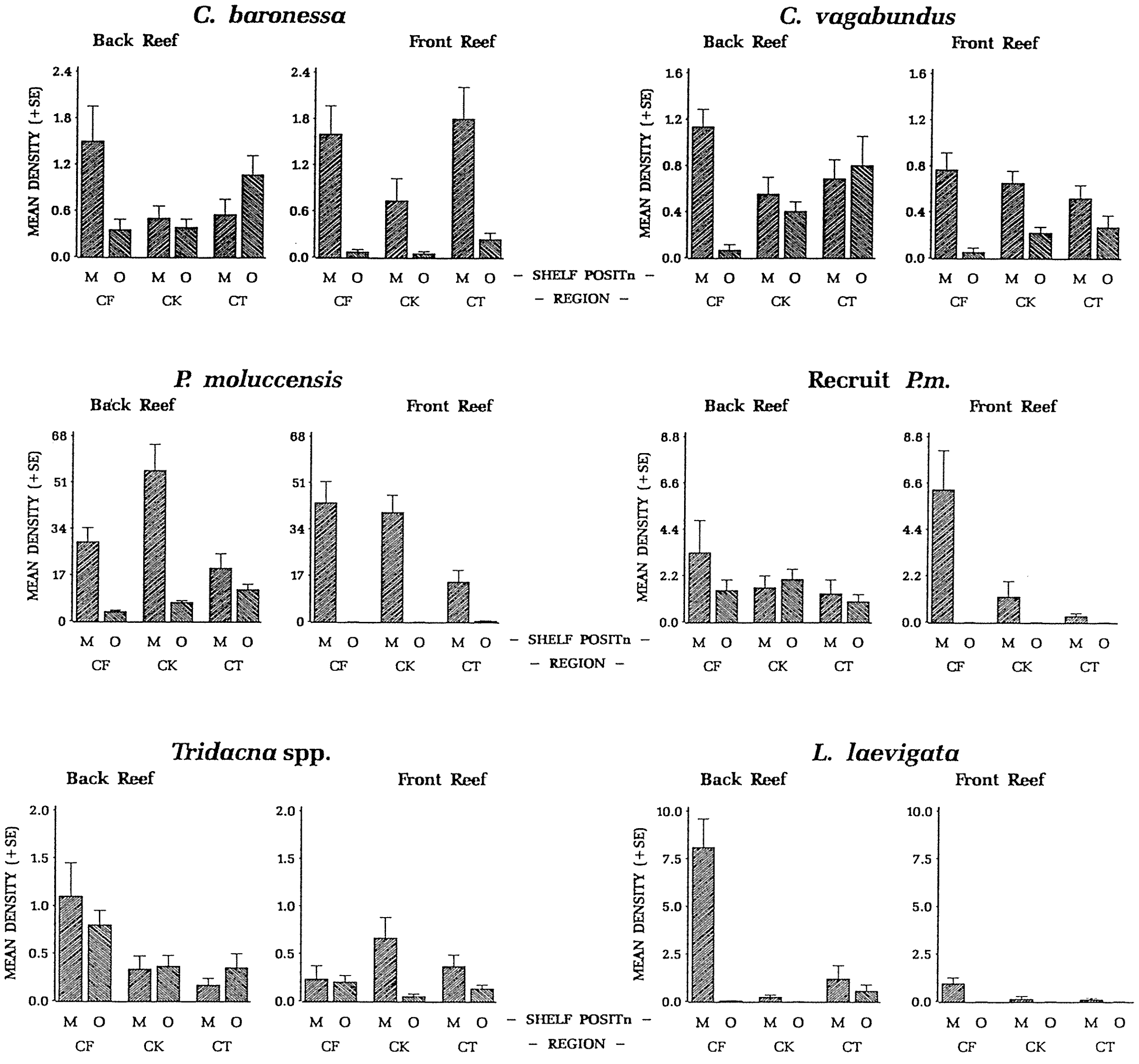


Figure 21: Comparisons of densities of biota between Shelf Position within each Region and Habitat where abundances on outer-shelf reefs were greater than or similar to those on mid-shelf reefs. **Abbreviations**: **SE** - Standard Error; **BR** - Back-reef; **FR** - Front-reef; **M** - Mid-shelf; **O** - Outer-shelf.

The reverse pattern (mid-shelf > outer-shelf when significantly different) was apparent for the chaetodons *C. baronessa* and *C. vagabundus*, recruit and adult *P. moluccensis*, *L. laevigata*, and clams (*Tridacna* spp) (Fig. 22). Though typically very large where they did occur, in no case were these differences significant for both habitats in all regions.

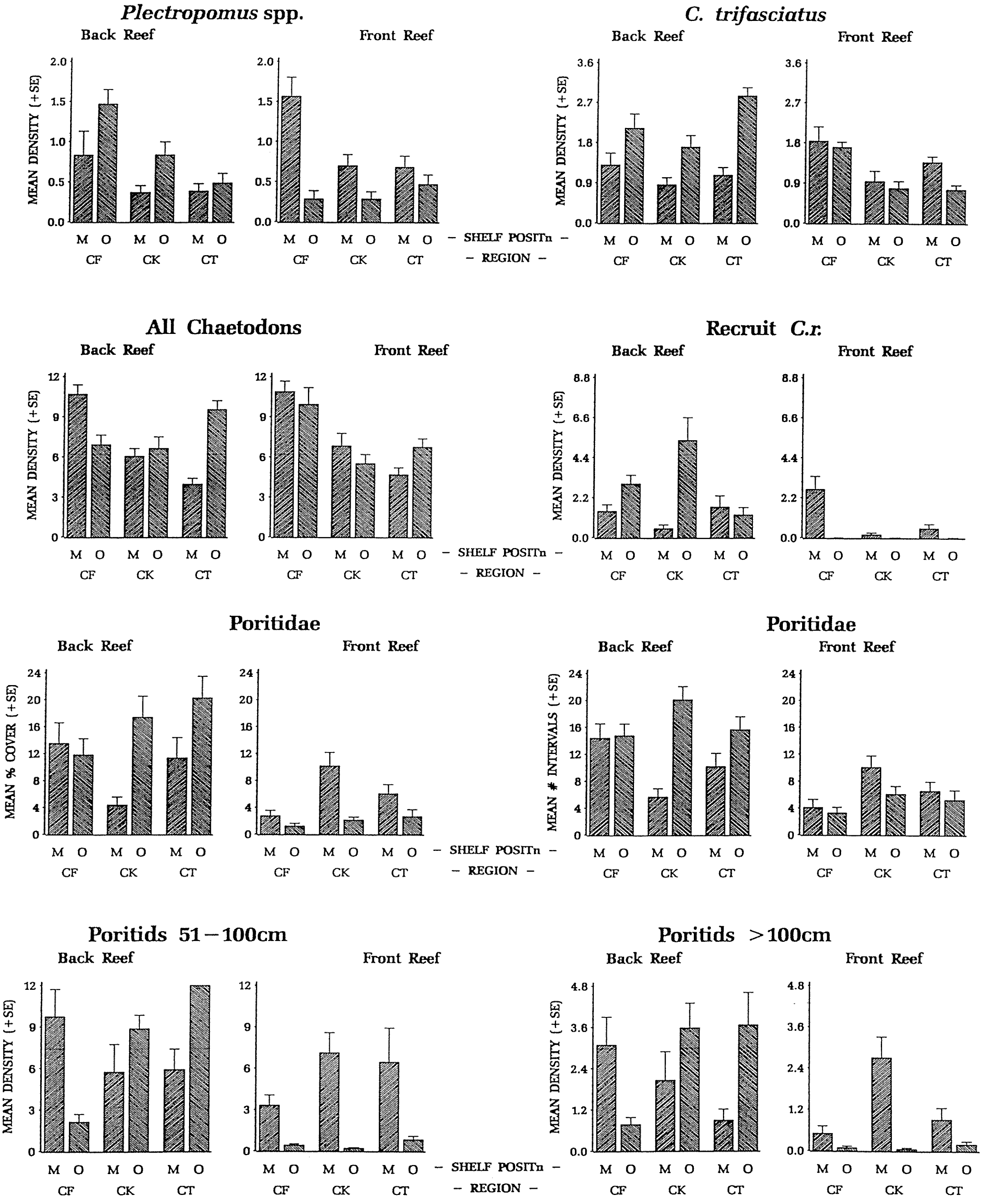
Figure 22: Comparisons of densities of biota between Shelf Position within each Region and Habitat where abundances on mid-shelf reefs were greater than or similar to those on outer-shelf reefs. **Abbreviations**: SE - Standard Error; **BR** - Back-reef; **FR** - Front-reef; **M** - Mid-shelf; **O** - Outer-shelf.



Mid-shelf reefs usually had greater numbers of coral trout (*P. leopardus*), the chaetodon *C. trifasciatus*, and recruit *C. rollandi* (Fig. 23) in front-reef habitats, but outer-shelf reefs had the greater abundances of these species in back-reef habitats (Fig. 23). This was also true for numbers and coverage of poritid corals, although when considered by size class, large poritids (51-100cm & > 100cm) were more abundant in back-reefs of mid-shelf reefs only in the Cape Flattery (northern) region (Fig. 23). Again, these patterns were not obvious in all regions, however, with no effect of Shelf Position for each habitat in at least one region for each taxon. Finally, when considered at family level, the chaetodons were significantly more abundant in both habitats on outer-shelf reefs than on mid-shelf reefs off Cape Tribulation, but were more abundant on mid-shelf reefs in back-reef habitats off Cape Flattery (Fig. 23).

Figure 23: Comparisons of densities of biota between Shelf Position within each Region and Habitat where contrasts between shelf positions reversed with Habitat and/or region.

Abbreviations: **SE** - Standard Error; **BR** - Back-reef; **FR** - Front-reef; **M** - Mid-shelf; **O** - Outer-shelf.



Summary

In summary, Shelf Position influenced the abundances of many taxa. In most cases the differences were large (larger > 2*smaller), suggesting strong cross shelf effects. The patterns were frequently habitat dependent, however, and often of unequal strength in all regions.

Differences Among Regions

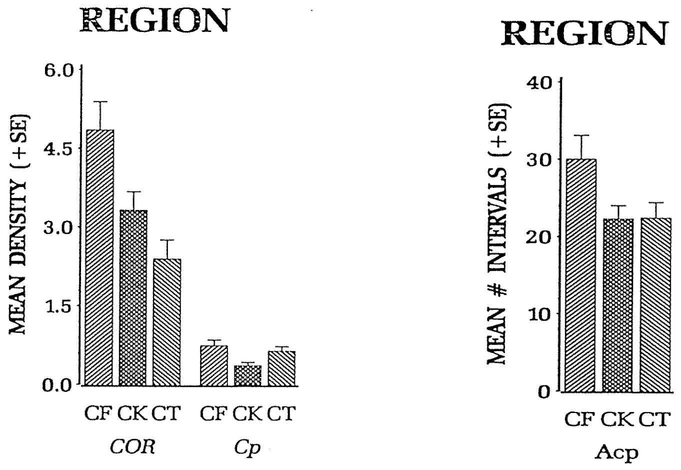
General Differences Among Regions

Main effects of Region were clear for only two fishes (*C. plebeius* and miscellaneous chaetodons) and Acroporid corals (# intervals) (Table 7).

For miscellaneous chaetodons, there was a strong north-south decline in abundance, with declines of about 30% from one region to the next (Fig. 24). This pattern was consistent within both COTS affected and COTS unaffected reefs on the mid-shelf (Fig. 4), and thus is probably not simply the result of the different COTS histories of reefs analysed from different regions. *C. plebeius* was equally abundant, however, in the northern and southern regions, but at lower abundance (by about 30%) in the middle region (Fig. 24). Since only COTS affected reefs from the northern (Cape Flattery) region were included in these analyses, and COTS history had a strong effect on *C. plebeius* there (Fig. 4), it is unclear how much of the apparent regional variation in densities of *C. plebeius* arises because of confounding of regions with COTS history.

Acroporid corals were most abundant in the north, but of almost identical abundance in the Cooktown and Cape Tribulation regions (Fig. 24). Again, comparison of the results from all mid-shelf reefs (Fig. 5) with those from the reefs selected from both shelf positions (Fig. 24) indicates ambiguity in the interpretation of this result.

Figure 24: Comparisons of abundances among regions averaged over Shelf Position and Habitat.
Abbreviations: **SE** - Standard Error; **CF** - Cape Flattery; **CK** - Cooktown; **CT** - Cape Tribulation; ***COR*** - Miscellaneous chaetodons; ***Cp*** - C. plebeius; **Acp** - Acroporid corals.

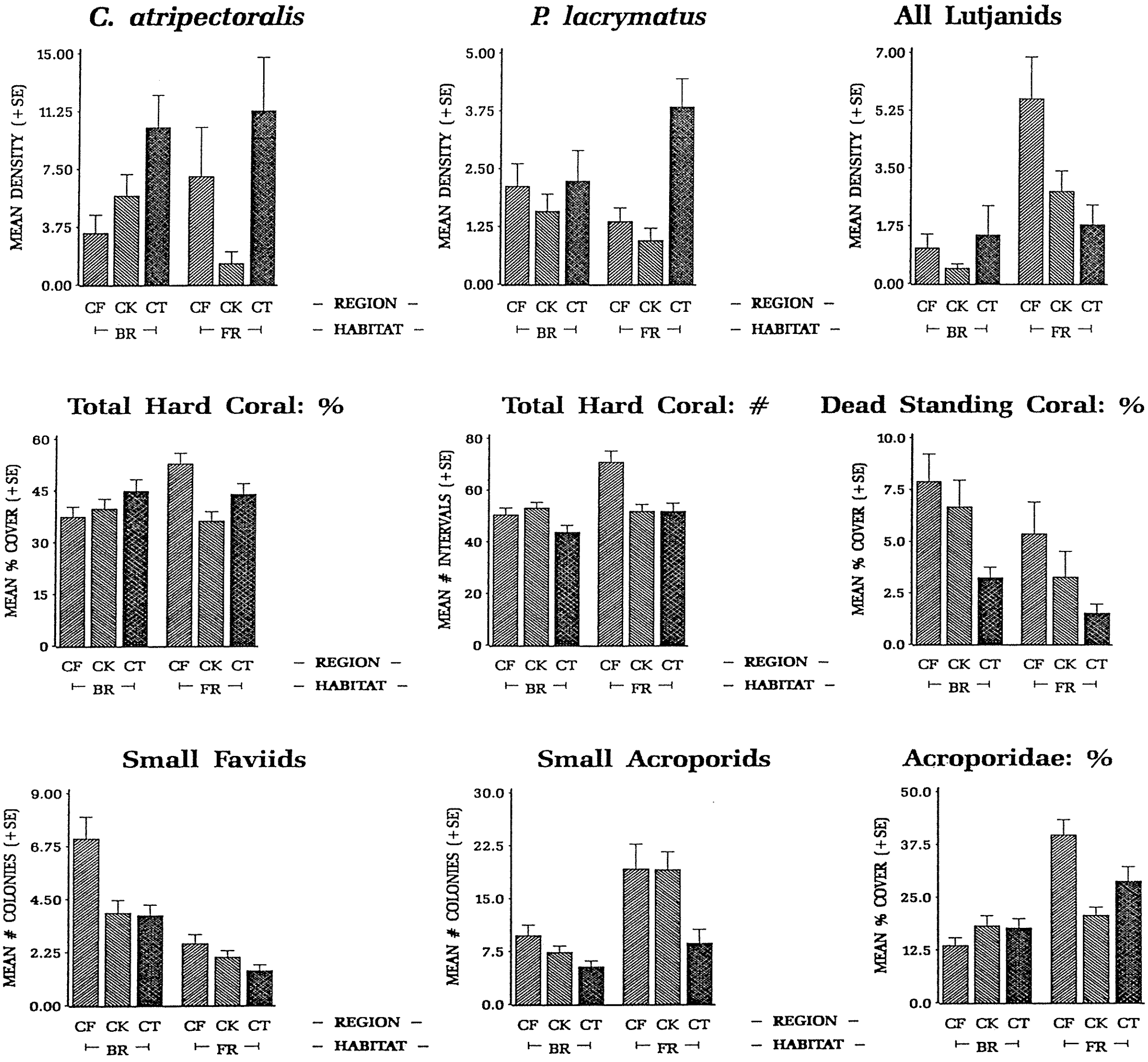


Differences Among Regions Related to Habitat

Regional effects varied with habitat for the fishes *C. atripectoralis*, *P. lacrymatus*, total lutjanids, and the benthic taxa small faviids and acroporids, % coverage of acroporids and total hard corals, and the number of intercepts of total hard coral and dead standing coral (Fig. 25). Abundances of the two pomacentrid fishes were greater in the south than in the mid and north regions, in both habitats for *C. atripectoralis* but only in the front-reef for *P. lacrymatus* (Fig. 25). These results were likely to reflect true regional variation since: i) COTS history had no effect on the abundances of *P. lacrymatus* (Table 5); and ii) regional variation in abundances of *C. atripectoralis* was consistent across both COTS affected and unaffected reefs in the mid-shelf (Table 5).

For the corals and lutjanid fishes, the regional effects were mostly evident in only one habitat, but in all cases abundances were significantly greater off Cape Flattery than in the other two regions, which differed significantly only for acroporid % coverage (Fig. 25). The meaning of results for small faviids and dead standing corals was unclear because of the presence of strong (habitat specific) COTS effects for these taxa on mid-shelf reefs, without any evidence on those reefs of regional effects (Table 5). For the remaining taxa, however, the results were unlikely to have resulted from confounding COTS history with region because either COTS did not affect the abundances of those taxa, or regional effects on mid-shelf reefs were uniform across COTS history (Table 5). Note that the decreasing north-south trend in the back-reef habitats for juvenile acroporids was opposite to the trend for total Acropora coverage.

Figure 25: Comparisons of abundances among regions for each habitat, averaged over Shelf Position. **Abbreviations**: **SE** - Standard Error; **BR** - Back-reef; **FR** - Front-reef; **CF** - Cape Flattery; **CK** - Cooktown; **CT** - Cape Tribulation.

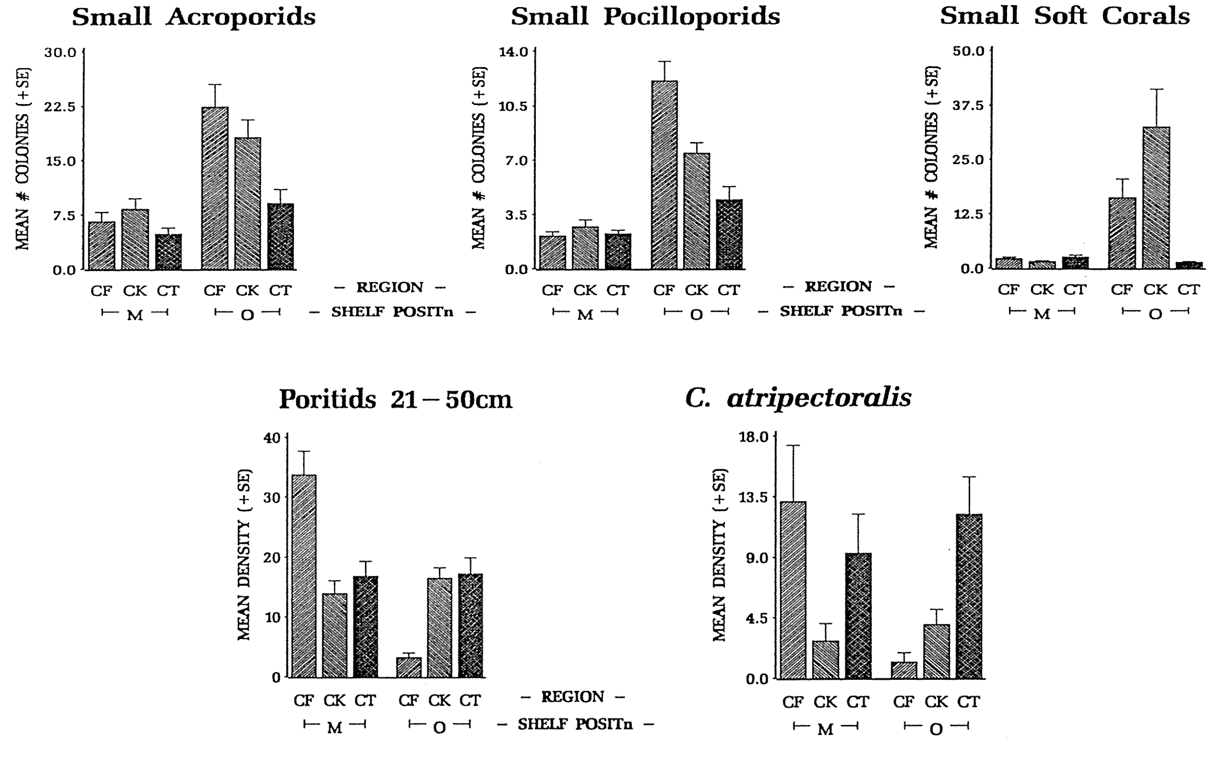


Differences Among Regions Related to Shelf Position

Effects of Shelf Position on regional patterns in abundance were evident for several taxa, but again regional effects on outer-shelf reefs should be interpreted cautiously because of the confounding effects of COTS history (above).

Regional differences in abundances on outer-shelf reefs were apparent for only one fish (*C. atripectoralis*), and for only three of the six taxa of benthos for which Shelf position by Region interactions were significant (Table 7). Numbers of small acroporids and pocilloporids decreased significantly from north to south on the outer-shelf, but were of relatively uniform abundance regionally on the mid-shelf (Fig. 26). Small soft corals, however, were at greatest abundance on outer-shelf reefs off Cooktown (with no recent COTS infestations), significantly lower abundance off Cape Flattery (where all included reefs were COTS affected), and very scarce on outer-shelf reefs of Cape Tribulation (even numbers of COTS affected and unaffected reefs) (Fig. 26). Poritid corals (21-50cm Φ) were at lowest abundance in the south, but equally abundant in the central and northern regions, whilst the damselfish *C. atripectoralis* showed a north-south increasing trend on outer-shelf reefs (south>mid>north). Both the poritids and the pomacentrid were most abundant on northern mid-shelf reefs and least in the central region (Fig. 26). There was no conspicuous correspondence between COTS history and these outer-shelf regional patterns in abundances.

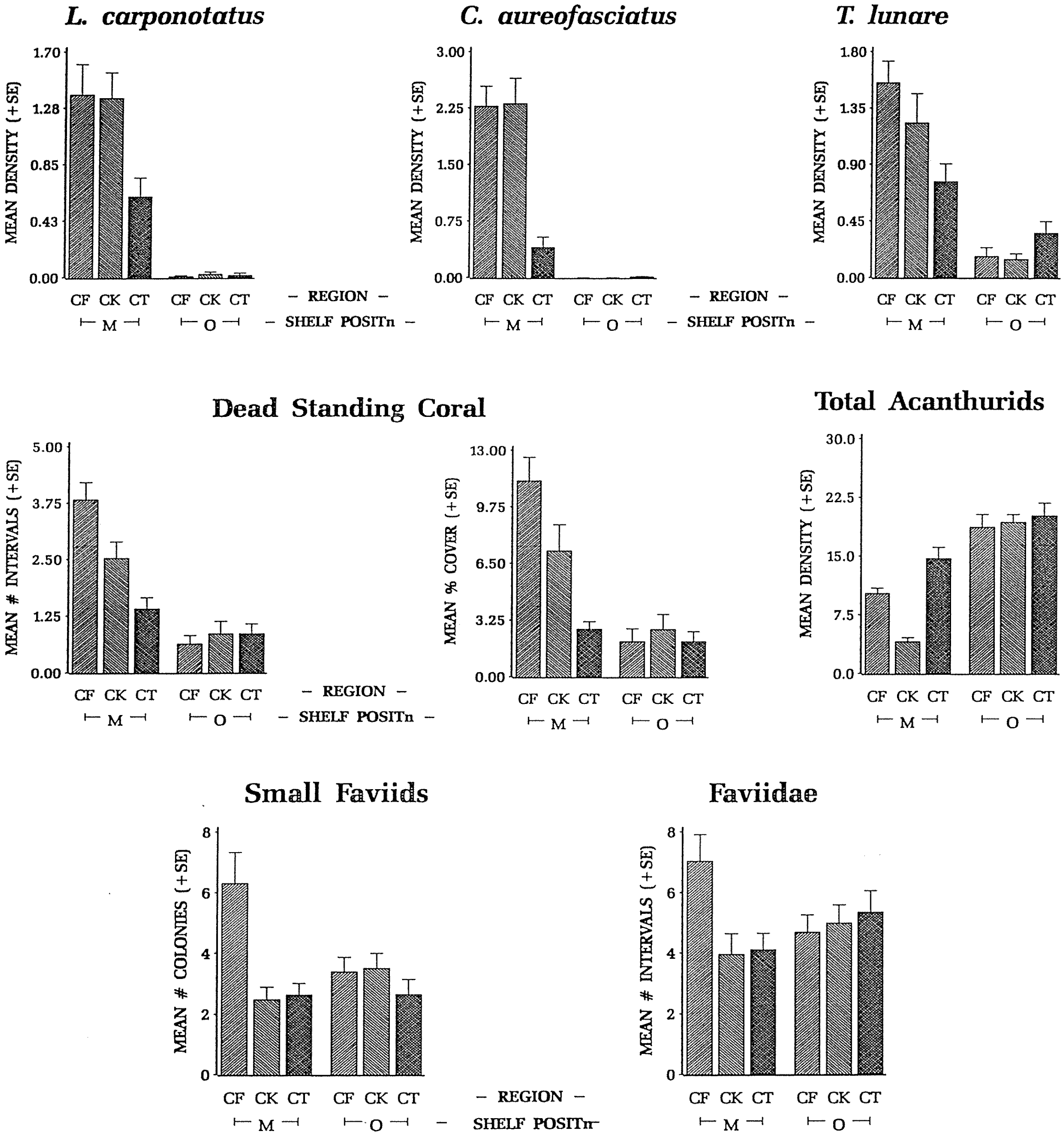
Figure 26: Comparisons of abundances among regions for each shelf position, where regional differences occurred on outer-shelf reefs.
Abbreviations: **SE** - Standard Error; **CF** - Cape Flattery; **CK** - Cooktown; **CT** - Cape Tribulation; **M** - Mid-shelf; **O** - Outer-shelf.



Four other fishes (*C. aureofasciatus*, *L. carponotatus*, *T. lunare,* and total acanthurids) and three sessile groups (juvenile faviids, numbers of faviid intercepts, and dead standing coral) had relatively similar abundances in all regions on outer-shelf reefs but varied regionally on mid-shelf reefs (Fig. 27). With the exception of total acanthurids, these variations were all from highest abundances in the north to lowest in the south. Dead standing coral decreased by about 2/3, whilst the Faviidae (juveniles and totals) decreased over the gradient by about 30%. The regional patterns for all fishes were consistent across COTS affected and unaffected reefs on the mid-shelf (Table 5). Although the shelf-position averaged regional patterns for the coral taxa were not logically related to the regional pattern of COTS history, there were no regional effects for the same taxa when analysed on the mid-shelf reefs alone (Table 5).

Figure 27: Comparisons of abundances among regions for each shelf position, where regional differences occurred only on mid-shelf reef.

Abbreviations: **SE** - Standard Error; **BR** - Back-reef; **FR** - Front-reef; **CF** - Cape Flattery; **CK** - Cooktown; **CT** - Cape Tribulation; **M** - Mid-shelf; **O** - Outer-shelf.

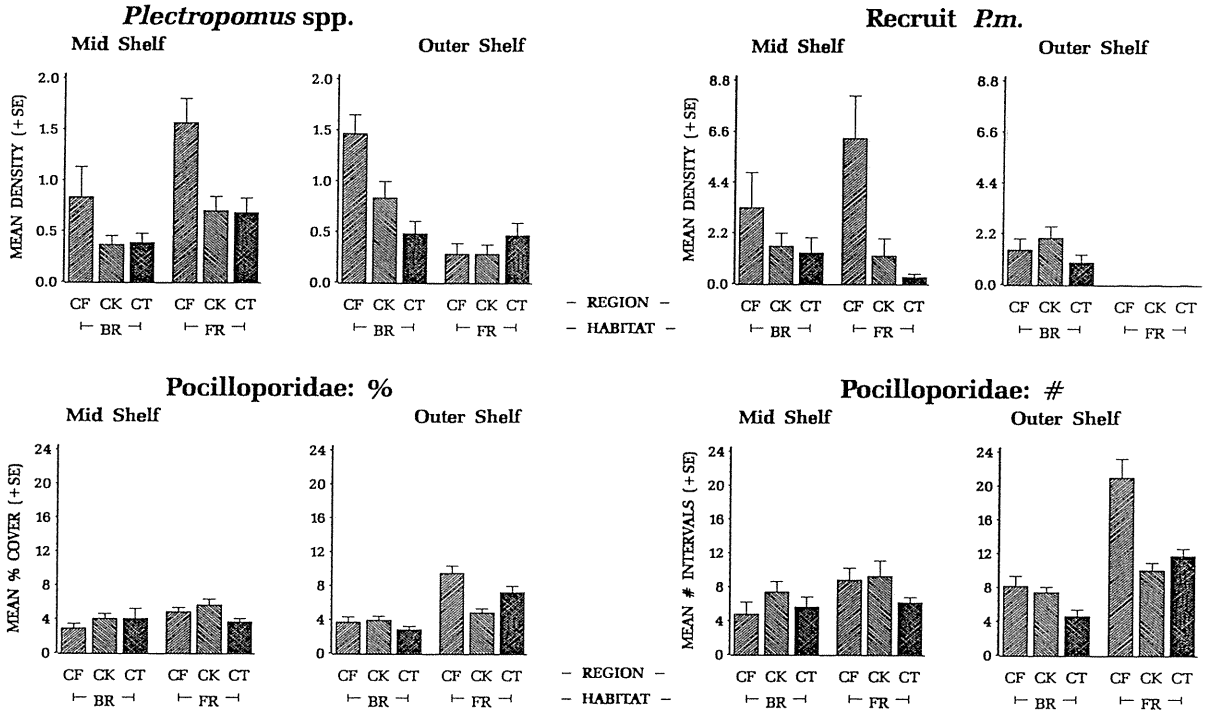


Differences Among Regions Related to Habitat and Shelf Position

Region effects within interactions of Region, Habitat, and Shelf Position were often inconsistent between habitats and shelf positions. Nevertheless, three categories of pattern were identifiable.

Firstly, *Plectropomus* spp, recruit *P. moluccensis,* and pocilloporid corals were either significantly more abundant in the northern region than the central and/or southern regions, or else differed little among regions (Fig. 28). These results were either consistent with those from all mid-shelf reefs (Fig. 5 - pocilloporids, Fig. 6 - *P. leopardus*), or contrary to that expected if they reflected differential COTS history across regions (*P. moluccensis* - abundances expected to be least on COTS affected reefs, *i.e.* off Cape Flattery; see Fig. 2).

Figure 28: Comparisons of abundances among regions for each habitat at each shelf position where abundances tended to decline from north to south.
Abbreviations: **SE** - Standard Error; **BR** - Back-reef; **FR** - Front-reef; **CF** - Cape Flattery; **CK** - Cooktown; **CT** - Cape Tribulation; **M** - Mid-shelf; **O** - Outer-shelf.



***Plectropomus* spp.**

Recruit *P.m.*

Pocilloporidae: %

Pocilloporidae: #

Secondly, abundances of miscellaneous small corals, total chaetodons, *C. vagabundus*, *C. baronessa*, and *C. trifasciatus* showed regional patterns that were relatively consistent across shelf positions but differed with habitats, or were consistent across habitats but differed with shelf position (Fig. 29). For miscellaneous small corals, abundances in back-reef habitats declined north-south (as for the above taxa), but in front-reef habitats abundances were ordered Cooktown > Cape Flattery > Cape Tribulation (Fig. 29). Total abundances of chaetodons and abundances of *C. vagabundus* declined north-south in all habitats on mid-shelf reefs, but increased north-south on outer-shelf reefs, in both habitats for *C. vagabundus*, but in only back-reef habitats for total chaetodons. With the exception of the front-reefs of mid-shelf reefs, the same pattern was apparent for *C. baronessa* (Fig. 29). *C. trifasciatus* had lowest abundances in the Cooktown region, and greatest abundances off Cape Flattery in both habitats at both shelf positions (Fig. 29). None of these patterns were conspicuously consistent in any straightforward way with apparent COTS effects, though the possibility that they arose because of regional variations in the manifestation of COTS effects cannot be ruled out.

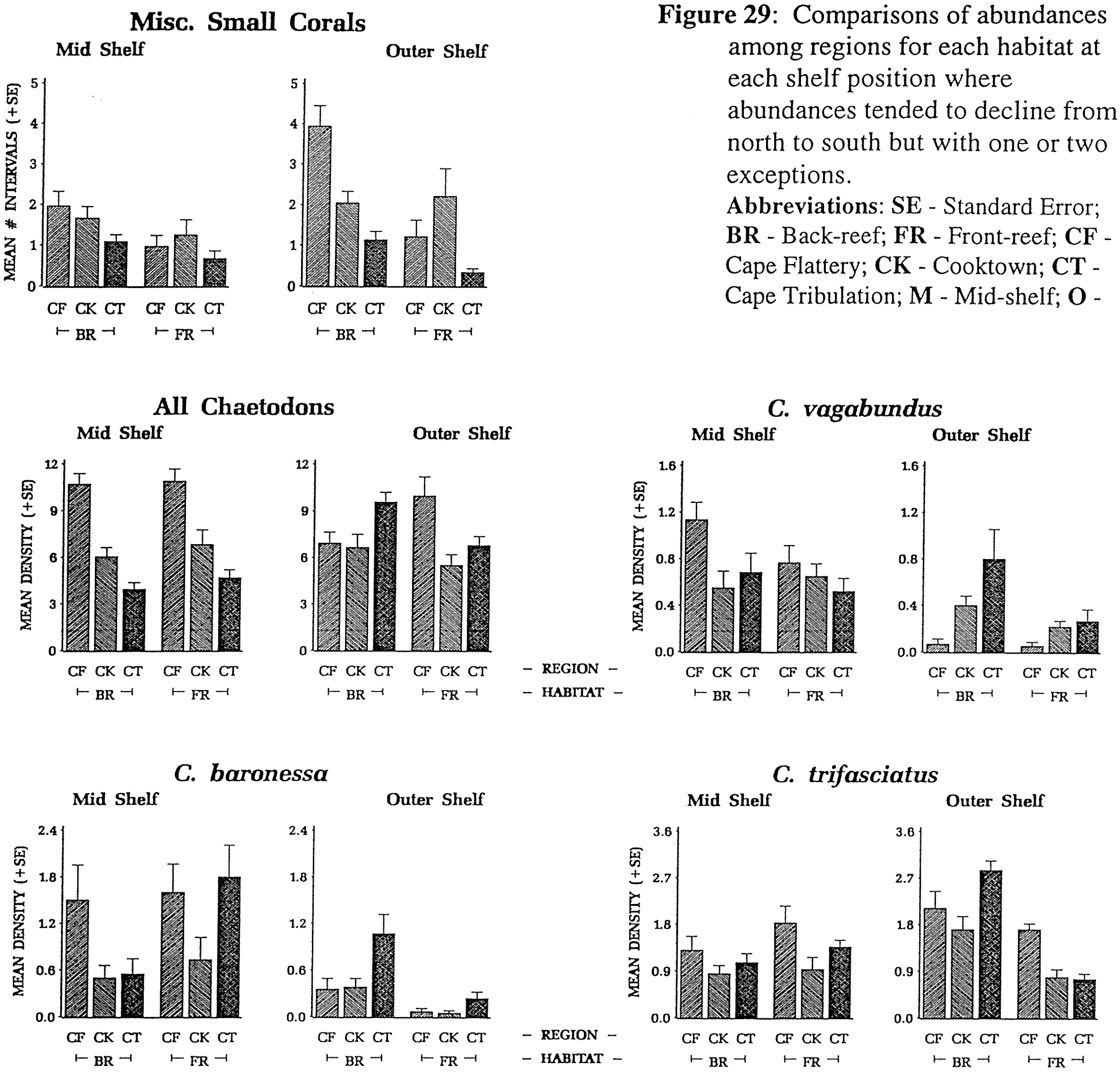


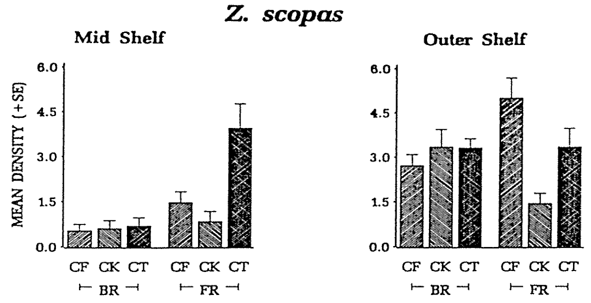
Figure 29: Comparisons of abundances among regions for each habitat at each shelf position where abundances tended to decline from north to south but with one or two exceptions.
Abbreviations: SE - Standard Error; **BR** - Back-reef; **FR** - Front-reef; **CF** - Cape Flattery; **CK** - Cooktown; **CT** - Cape Tribulation; **M** - Mid-shelf; **O** -

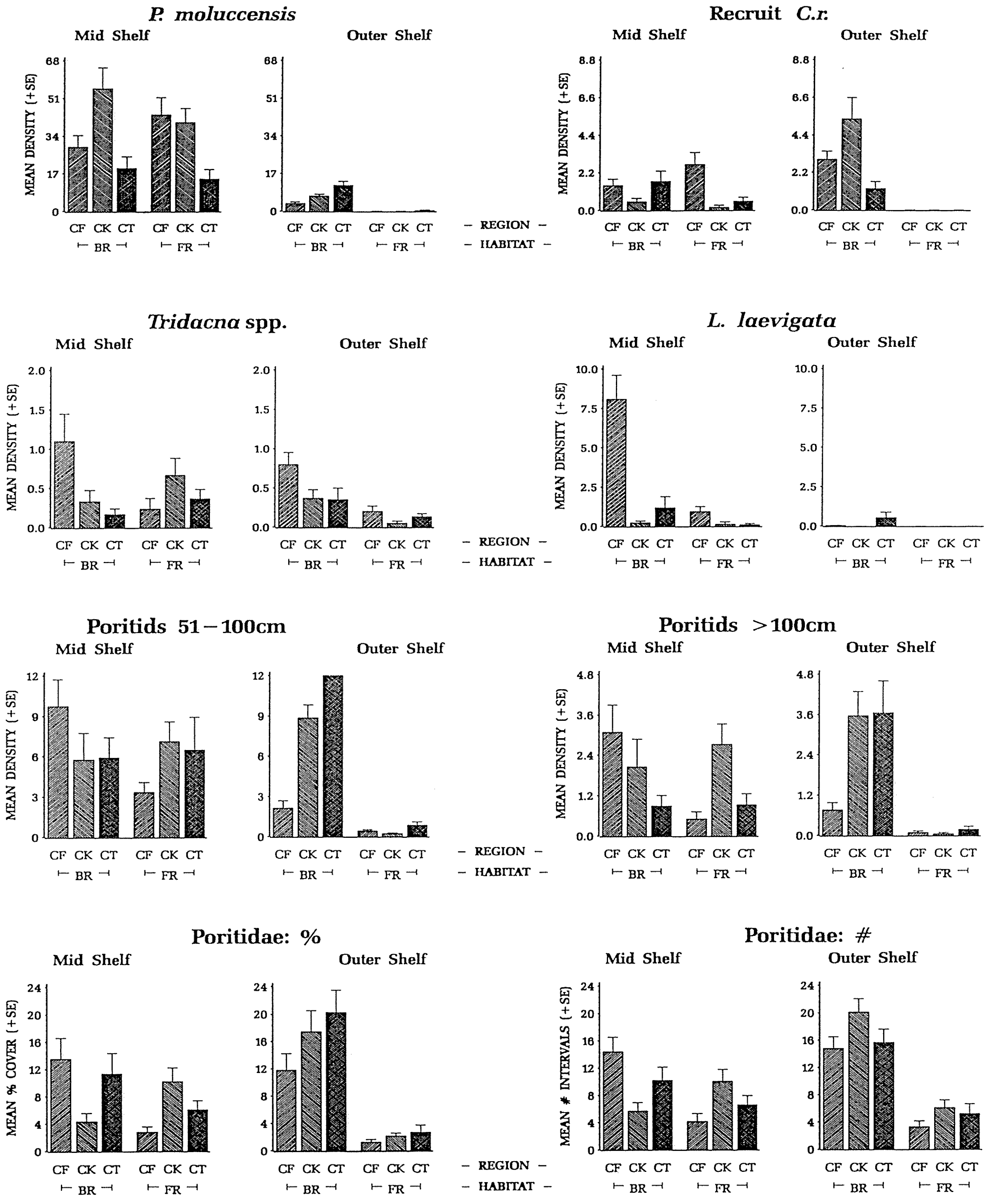
Finally, for adult *P. moluccensis*, Recruit *C. rollandi*, *Z. scopas*, *Linckia laevigata*, *Tridacna* spp, and poritid corals, at least three different regional patterns were evident in the four Habitat-Shelf Position combinations (Fig. 30). Abundances of *Z. scopas* were relatively uniform across regions in back-reef habitats at both shelf positions, but showed strong shelf-position specific patterns in front-reef habitats (Fig. 30). Tridacnid clams declined in abundance from north to south in back-reef habitats, but also showed regional patterns that varied with shelf position in front-reef habitats (Fig. 30). The remaining taxa had regional variations in abundances specific to each habitat in each shelf position (Fig. 30).

Summary

In summary, regional variations in abundances were relatively common, but tended to be of smaller magnitude than variations across habitats or shelf-positions. Declining abundances from north to south was the most common pattern of regional variation, but was typically restricted to single habitats or in only one shelf position. The degree to which such regional variation was a product of regional patterns in prior infestations by *A. planci* (Table 1), however, cannot be determined categorically from our data.

Figure 30: Comparisons of abundances among regions for each habitat at each shelf position where regional patterns in abundances were highly variable across habitats and shelf positions.
Abbreviations: **SE** - Standard Error; **BR** - Back-reef; **FR** - Front-reef; **CF** - Cape Flattery; **CK** - Cooktown; **CT** - Cape Tribulation; **M** - Mid-shelf; **O** - Outer-shelf.





DISCUSSION

Abundances of *Acanthaster planci*

There was no evidence in our data of large numbers of *Acanthaster planci* in the Cairns Section of the GBR Marine Park in early 1990. If populations of COTS were beginning to increase in size in this area then either: i) they were doing so in areas beyond our survey, such as deep reef slopes; or ii) such increases were at an early stage and most individuals were very small and cryptic, or unavailable to observers (Fernandez 1990, Fernandez *et al* 1990). Given the low numbers of COTS we observed, we were unable to test any hypotheses about the genesis of the *A. planci* 'boom' phenomenon.

The manta tow data provided by AIMS for the same reefs sampled at the same time were consistent with our results in so far as they recorded no evidence of large populations of COTS. It is noteworthy, however, that the diver surveys found more *A. planci* on more reefs than the manta tow surveys. Given these observations, and the work of Fernandez (1990) & Fernandez *et al.* (1990), serious consideration should be given for future surveys of *A. planci* being by diver searches of the substratum. Such surveys could be tailored to the same time-table as current Manta Tow surveys, but have the advantages of: i) being more likely to record COTS at an earlier size, when they are still secretive (though not cryptic); ii) being more likely to detect increases in COTS abundances at an earlier stage of population growth; and iii) facilitate the collection of other quantitative data concurrently.

Persistent Effects of Past *A. planci* Outbreaks

Effects on Fishes

Although several fishes showed differences between COTS affected and unaffected reefs, consistent with lasting effects of COTS, the effect was not consistent among taxa. The greater densities of *P. moluccensis* (adults and recruits) and *C. atripectoralis* on COTS unaffected reefs might be expected since these species settle only into live corals (Eckert 1985, Mapstone 1988, pers. obs.), often of the taxa most preferred by *A. planci*. *P. moluccensis* is long lived (Fowler 1990, Mapstone 1988, Sale *et al* 1986) and survival after settlement is apparently not affected by the life or death of 'home' corals (Mapstone 1988). Hence, severe degradation of coral abundances as a result of COTS infestations might be expected to have an effect on populations of these species, but lagged by several years because the direct effect would be on larval settlement rather than post-settlement survivorship. With rapid recovery of coral cover (perhaps within 5 years, T. Done pers. com.), such effects also might be expected to be temporary.

The greater abundances of acanthurids on COTS affected reefs also has a feasible causal relationship with COTS infestations. Many acanthurids recruit into rubble (K. Clemments pers. com.) and browse over non-living substrata, which would be expected to increase because of COTS activity. Thus, suitable settlement and feeding habitat would increase after *A. planci* infestations, and may have resulted in increased abundances of these grazing fishes over several years.

Plausible explanations for the COTS-related patterns in abundances of other fishes are not as clear, however. Only one other species (*Lutjanus carponotatus*) showed a clear general pattern (greater densities on COTS unaffected reefs), but there is no conspicuous link between the abundance of this carnivore/piscivore and past infestations of reefs by *A. planci*, except perhaps through shortage of the juvenile prey fishes of *L. carponotatus* (pers. obs.) that normally inhabit live corals.

Patterns in population densities of chaetodons, coral trout, and recruit *Chrysiptera rollandi* related to past COTS infestation were less clear-cut. It would be expected that the corallivorous chaetodontids would be among the fishes most affected by widespread coral mortality, but such an effect was region dependent, often absent, and in some cases opposite to expectation (e.g., the chaetodon *C. baronessa*). Similarly, although a clear mechanism exists for coral mortality following COTS infestation to affect recruitment by *Chrysiptera rollandi* (because the pomacentrid recruits only into rubble), *C. rollandi* recruitment was greater on COTS affected reefs than unaffected reefs only in back-reef habitats and in the southern region. In front-reef habitats, and off Cape Flattery, the pattern in recruitment was opposite to that expected, and there were no strong effects apparent for adult *C. rollandi*. Densities of coral trout were even less consistently related to COTS history.

Effects on Benthos

The main consistent effects of recent COTS infestations on corals was that abundances of soft corals, small faviids, and small poritids were more abundant on COTS affected reefs. This may reflect opportunistic recruitment of these corals into damaged substrata. There was strong regional variation in the effects of past COTS infestations on other live corals in 1990. Coral coverage of most taxa either did not differ with COTS history, or showed greater coverage on COTS affected reefs off Cape Flattery but increasingly greater coverage on COTS unaffected reefs in the central and southern regions. This pattern is consistent with the history of COTS outbreaks in the Cairns Section, since outbreaks were earlier (by 1-2 years) in the north than in the south (Moran *et al.* 1988), and reefs in the Cape Flattery Region have had longer to recover from COTS effects than the central and southern region reefs. If this explanation is true, then it is expected that most gross effects of past COTS outbreaks on the reefs we sampled would have disappeared by about 1993.

Interestingly, effects of COTS history were most often manifest in records of the numbers of intercepts of live corals, rather than in measures of percent coverage. This trend could have arisen because interval data were less variable at small scales than coverage data, or because re-growth and/or recruitment of corals following COTS infestations had resulted in high coral cover comprising many colonies, whereas in the absence of recent disturbance by COTS coral assemblages of similar coverage were comprised of fewer, larger colonies (Connell 1978). Such an explanation would hold only in the northern region, however, since in the central and southern regions there were no significant effects of COTS history on coverage, but generally greater numbers of intercepts (= colonies or fragments of colonies) on COTS unaffected reefs. If such a pattern in numbers of patches arose because COTS affected reefs in these regions were at an earlier stage of recovery, we would have expected to see a lower percent coverage and/or higher numbers of colonies on them than on the COTS unaffected reefs. Only for miscellaneous corals were effects evident for both numbers of patches and percent coverage. Patterns in numbers of patches and cover paralleled each other, suggesting that patch size was not affected by past COTS infestation, possibly indicating in turn that whole colonies rather than only parts of corals in this group were lost to *A. planci*.

Although there were significant effects of COTS history on *L. laevigata* and *Tridacna* spp., the effects were not consistent across habitats or regions (respectively), and difficult to interpret in any causal way.

Systematic Spatial Effects

Our examination of systematic geographic patterns in abundances indicated that such patterns were far more variable and less predictable than previous work had suggested. The patterns we observed have important implications for future sampling or monitoring studies. In discussing these effects, we will not attempt to explore in detail the processes that might have precipitated those patterns, but rather briefly comment on the implications of the patterns for future work. The multi-variate classification of communities from different shelf positions, habitats, and regions will be reported elsewhere (Mapstone & De'Ath, in prep. a, b).

Effects of Habitat

Only four taxa showed consistent effects of gross habitat categories on abundances. Although habitat effects were statistically significant for many taxa, the effects were not consistent among shelf positions and/or regions. Under these circumstances it is difficult to ascribe general importance to the habitat categories we adopted, except to say that because their effects were variable, it cannot be assumed that sampling in only single habitats adequately represents other large scale geographic patterns.

These results are at odds with most published accounts of habitat effects on abundances, which have generally claimed great generality for such effects (Bouchon-Navaro 1980, Bradbury *et al.* 1987, Chave & Eckert 1974, Clarke 1977, Done 1983, Galzin 1987, Gladfelter & Gladfelter 1978, Harmelin-Vivien 1977, Helfman 1978, Jones 1968, Jones & Chase 1975). Potential reasons for such discrepancies include: i) we considered different habitat strata to most other studies, where the habitats considered typically related to changes with depth down reef slopes; ii) we considered the effects of habitat in many places and across other potentially influential variables, whereas others usually have considered habitat characteristics at only one place or within one environmental situation (*e.g.*, windward reefs); or iii) we have concentrated on species-specific patterns whereas others have considered community-level patterns related to habitat type. Irrespective of the basis of the lack of generality in our results, it suggests that generalisations about the role of habitat in determining abundances of reef organisms should be considered carefully, even within single species. The complex patterns we observed suggest also that the features of habitat (or exposure) that do influence abundances either are not consistent across other geographic gradients or their effects are tempered by processes operating over those other gradients.

Effects of Shelf Position

Effects of Shelf Position were considerably more consistent within taxa across other geographic strata than effects of either Habitat or Region. Generalisations about the direction of Shelf Position effects on abundances were supported for many of the taxa we considered. It should be noted, however, that the magnitudes of cross-shelf patterns in abundances of these taxa frequently varied among regions. For these taxa, our results generally concurred with those of earlier studies of cross-shelf distribution and/or abundances (Dinesen 1983, Done 1982, Russ 1984, Williams 1982), and the results from the first year of work in the AIMS Long Term Monitoring (LTM) Project (total lutjanids, *A. curacao*[5], *P. lacrymatus*[5], total acanthurids).

For several other taxa, habitat or region dependence of cross-shelf patterns was conspicuous. For these taxa, generalisations about cross shelf patterns based on sampling in only a single habitat category, as has been common in the past, will certainly be misleading. For example, data from single front-reef locations sampled in the AIMS LTM Programme were used to assert no cross-shelf pattern in abundances of total hard coral cover and serranid[5] fishes, greater abundances of soft corals, chaetodontid fishes, and *Chromis* spp[5]. on outer-shelf reefs than on mid-shelf reefs, and greater densities of *Pomacentrus* spp[5] on mid shelf reefs than on outer shelf reefs. For each of these taxa, however, the cross-shelf patterns we observed varied in direction and magnitude with the habitat and/or region considered. It seems likely that previous assertions that reefs in different shelf positions support different assemblages of fishes and corals will be shown to have some generality, but it seems equally likely that the cross-shelf classification of communities will be considerably improved if habitat is included as an explanatory variable.

Effects of Region

Regional variations in abundances were common in our data, but were rarely consistent over habitat and/or shelf position. Because of the confounding of region with prior COTS infestations, especially on outer-shelf reefs, we cannot generally relate regional variations to the past progress of COTS infestations, although a pattern of declining abundances from north to south was the most common regional pattern observed.

---

[5] Note that in the AIMS project these species were not analysed separately and the similarity or difference between our results and the AIMS results reflect the concurrence (or lack thereof) between their genus-level analyses and our species-level analyses.

It seems unlikely that the magnitudes of regional effects that we observed would arise from gross climatic influences over such a restricted latitudinal range, especially in the tropics. A north-south decline in abundances correlates approximately with the exposure of the reefs we surveyed to human use, but since several taxa did not show these patterns and the patterns were not restricted to the same habitat or shelf position for all (or most) taxa, it seems unlikely that the decline would have arisen from human impacts. The one feasible exception might be the decline in abundances of some chaetodontids, which are sought after as aquarium fishes by a fishery which has its greatest activity in the Cairns-Cape Tribulation region. For these fishes, it might be feasible that the regional patterns in abundances reflected the effects of the fishery, though detailed fleet and catch data would be needed to examine such an hypothesis further.

There is also a major change in the structure of the reef matrix between our central and southern regions, with the disappearance of the string of ribbon reefs that characterise the shelf break to the north. The relationship of this structural discontinuity to other oceanographic features has been discussed in relation to the genesis and spread of COTS outbreaks (Dight 1992, James & Scandol 1992), but it is not clear how (or why) these features might have precipitated the regional patterns in abundances we observed. Again, with respect to future surveys, the key feature to note is that the regional patterns were often habitat and/or shelf position dependent, and sampling in one shelf position, habitat, or location (within each reef) is unlikely to depict accurately patterns at other shelf positions, habitats, or over entire reefs.

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 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 (Mapstone *et al.* 1995). 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.

REFERENCES

AIMS 1992. Draft proposal for the Long Term Monitoring of the Great Barrier Reef. Australian Institute of Marine Science.

Ayling A.M. 1983a. *Distribution and abundance of coral trout species (Plectropomus spp) in the Cairns section of the Great Barrier Reef Marine Park.* **Unpublished Report to GBRMPA.**

Ayling A.M. 1983b. *Distribution and abundance of coral trout species (Plectropomus spp) in the Townsville and Whitsunday areas of the Great Barrier Reef.* **Unpublished Report to GBRMPA.**

Ayling A.M., and A.L. Ayling. 1984a. *Determination of the most accurate survey size and method for visual counting of coral trout (Plectropomus spp.).* **Unpublished Report to the GBRMPA.** 9pp.

Ayling A.M., and A.L. Ayling. 1984b. *Distribution and abundance of coral trout species (Plectropomus spp) in the Swain Group of : Southern Section of the Great Barrier Reef*. **Unpublished Report to GBRMPA.**

Ayling A.M., and A.L. Ayling. 1984c. *A biological survey of selected reefs in the Far-North Section of the Great Barrier Reef Marine Park.* **Unpublished Report to GBRMPA.**

Ayling A.M., and A.L. Ayling. 1985. *A biological survey of selected reefs in the Central Section of the Great Barrier Reef Marine Park.* **Unpublished Report to GBRMPA.**

Ayling A.M., and A.L. Ayling. 1986a. *A biological survey of selected reefs Capricorn Section of the Great Barrier Reef Marine Park.* **Unpublished Report to GBRMPA.** 61pp.

Ayling A.M., and A.L. Ayling. 1986b. *Coral Trout Survey Data.* **Unpublished Report to GBRMPA.** 212pp

Bouchon-Navaro Y. 1980. Quantitative distribution of the Chaetodontidae on a fringing reef of the Jordanian coast (Gulf of Aqaba, Red Sea). *Tethys.* **9**:247-251.

Bradbury, R.H., T.J. Done, S.A. English, D.A. Fisk, P.J. Moran, R.E. Reichelt, & D.McB. Williams. 1985. The crown of thorns: coping with uncertainty. *Search*, **16**: 106-109.

Bradbury, R.H., R.E. Reichelt, D.L. Meyer, and R.A. Birtles. 1987. Patterns in the distribution of the crinoid community at Davies Reef on the central Great Barrier Reef. *Coral Reefs*, **5**:189-196.

Brodie, J.E. 1992. Enhancement of larval and juvenile survival and recruitment in Acanthaster planci from the effects of terrestrial runoff: a review. *Aust. J. Mar. Freshwater Res.*, **43**: 459-74.

Chave, E.H., and D.B. Eckert. 1974. Ecological aspects of the distributions of fishes at Fanning Island. *Pac. Sci.*, **28**:297-317.

Clarke R.D. 1977. Habitat distribution and species diversity of chaetodontid and pomacentrid fishes near Bimini, Bahamas. *Mar. Biol.* **40**:277-289.

Connell, J.H. 1978. Diversity in tropical rainforests and coral reefs. *Science* **199**: 1302-1310.

Day R.W., and G.P. Quinn. 1989. Comparisons of treatments after an analysis of variance in ecology. *Ecol. Monogr.*, **59**: 433-463

De'Ath, G. 1992. Sightability as an indicator of bias in manta tow surveys of Acanthaster planci: comment on Fernandes, Marsh, Moran and Sinclair. *Coral Reefs*, **11**: 1-3.

Dight 1992. PhD Thesis. James Cook University.

Dinesen, Z.D. 1983. Patterns in the distibution of soft corals across the central Great Barrier Reef. *Coral Reefs,* **1**:229-236.

Doherty P.J. 1987. The replenishment of populations of coral reef fishes, recruitment surveys, and the problems of variability manifest on multiple scales. *Bull. Mar. Sci.*, **41**:411-422.

Done, T.J. 1982. Patterns in the distribution of coral communities across the central Great Barrier Reef. *Coral Reefs*, **1**:95-107.

Done T.J. 1983. Coral zonation: Its nature and significance, pp107-147 in *Perspectives on coral reefs*, D.J. Barnes Ed. Australian Inst. Mar. Sci.

Done, T.J., A.M. Ayling, & R. Van Woesik. 1992. *Broad scale effects of Cyclone Ivor in the Cairns Section of the Great Barrier Reef.* **Report to GBRMPA**.

Done, T.J., & D.C. Potts. 1992. Influences of habitat and natural disturbances on contributions of massive *Porites* to reef communities. *Mar. Biol.*, **114**: 479-493.

Eckert, G.J. 1985. Settlement of coral reef fishes to different natural substrata and at different depths. *Proc. 5th Int. Coral Reef Congress*, Tahiti 1985. pp. 385-390.

Endean, R., & A. Cameron. 1990. *Acanthaster planci population outbreaks*. pp 419-437 in: Dubinsky, Z. (ed) **Ecosystems of the World: Coral reefs**. Elsevier Press, Amsterdam.

Fernandez L.1990. Effect of the distribution and density of target organisms on manta tow estimates of their abundance. *Coral Reefs*, **9**:161-165.

Fernandez L., H. Marsh, P.J. Moran, and D.F. Sinclair. 1990. Bias in manta tow surveys of *Acanthaster planci. Coral Reefs*, **9:**155-160.

Fowler, A.J. 1990. Validation of annual growth increments in the otoliths of a small tropical coral reef fish. *Mar. Ecol. Prog. Ser.*, **64**: 25-38.

Frith, C.A., J.M. Leis, & B. Goldman. 1986. Currents in the Lizard Island region of the Great Barrier reef Lagoon and their relevance to potential movements of larvae. *Coral Reefs*, **5**: 81-92.

Galzin R. 1987. Structure of fish communities of French Polynesian coral reefs. I. Spatial scales. *Mar. Ecol. Prog. Ser.*, **41**:129-136.

GBRMPA. 1983. Cairns Section Zoning Plan.

GBRMPA. 1985. Far Northern Section Zoning Plan.

GBRMPA. 1987. Central Section Zoning Information.

GBRMPA. 1988. Mackay/Capricorn Section Zoning Information.

GBRMPA. 1992. Cairns Section and Cairns Marine Park Zoning Plans.

Gladfelter, W.B., and E.H. Gladfelter. 1978. Fish community structure as a function of habitat structure on West Indian patch reefs. *Rev. Biol. Trop.*, **26**(Suppl.):65-84.

Green, D.G., R.H. Bradbury, and R.E. Reichelt. 1987. Patterns of predictability in coral reef community structure. *Coral Reefs*, **6**:27-34.

Harmelin-Vivien M.L. 1977. Ecological distributions of fishes on the outer slope of Tulear Reef (Madagascar). *Proceedings of the 3rd Int. Coral Reef Symp.*, **1**:289-296.

Helfman, G.S. 1978. Patterns of community structure in fishes: Summary and overview. *Env. Biol. Fish.*, **3:**129-148.

Hendee J.C., G.H. Stanky, and R.C. Lucas. 1990. *Wilderness Management.* North American Press. 546pp.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.*, **54**:187-211.

James, M.K. & J.P. Scandol. 1992. Larval dispersal simulations: correlations with crown-of-thorns outbreaks database. *Aus. J. Mar. Freshwater Res.*, **43**: 569-582.

Jones R.S. 1968. Ecological relationships in Hawaiian and Johnston Island Acanthuridae (Surgeonfishes). *Micronesica.* **4**:309-361.

Jones R.S., and J.A. Chase 1975. Community structure and distribution of fishes in an enclosed high island lagoon in Guam. *Micronesica*, **11**:127-148.

Kelleher, G., and R. A. Kenchington. 1991. *Guidelines for establishing marine protected areas.* **Great Barrier Reef Marine Park Authority**. 90pp.

Kenchington, R. A. 1990. *Managing Marine Environments.* **Taylor & Francis,** New York. 248pp.

McArdle B.H., K.J. Gaston, & J.H. Lawton. 1990. Variation in the size of animal populations: Patterns, problems and artefacts. *J. Anim. Ecol.*, **59**,439-454.

McNeill, S. E. 1994. The selection and design of Marine Protected Areas: Australia as a case study. **Biodiversity & Conservation, 3**:586-605.

Mapstone B.D. 1988. *The determination of patterns in the abundance of Pomacentrus moluccensis Bleeker on the southern Great Barrier Reef.* PhD Thesis, University of Sydney. 240pp.

Mapstone B. D. 1992. *Flexible Decision Rules for Hypothesis Testing in Environmental Science.* **Abstracts of International Environmental Biometrics Conference**, Vol. 2. Sydney. December 1992.

Mapstone B.D. 1995. Scalable decision rules in environmental impact assessment: effect size, Type I, and Type II errors, *Ecological Applications*, **5**:401-410.

Mapstone B.D.1996. Scalable decision criteria in environmental impact assessment: effect size, Type I, and Type II errors, pp 67-82 in Schmitt R. J. and C. W. Osenberg (eds). *The Design of Ecological Impact Assessment Studies: Conceptual Issues and Application in Coastal Marine Habitats.* Academic Press.

Mapstone, B. D. & A. M. Ayling. 1993. An Investigation of optimum methods and unit sizes for the visual estimation of abundances of some coral reef organisms. **Report to the GBRMPA**. 70pp.

Mapstone, B. D., A. M. Ayling , and J. H. Choat. 1995. *Scales and Magnitudes of Variation in Population Densities of Some Coral Reef Organisms: Implications for the Design of Sampling and Monitoring Procedures.* **Report to the GBRMPA**. Townsville. 77pp.

Mapstone, B.D., A.M. Ayling, & R. Van Woesik. (in prep.) Quantitative records of the effects of a tropical cyclone on the structure and biota of three reefs on the Great Barrier reefs.

Mapstone, B. D., J. H. Choat, H. Marsh, A. M. Ayling. 1989. An Investigation of scales and magnitudes of variability in population densities of some coral reef organisms: Stage II in The Development of Long Term Monitoring Procedures, incorporating an initial survey of *Acanthaster planci* and Corals Following *A. planci* Outbreaks on Reefs in the Cairns Section, GBR. **Proposal to the GBRMPA and COTSREC.**

Mapstone, B.D., & G. De'Ath (in prep. a). Multivariate classifications of benthic assemblages by habitat, cross-shelf position, and region on the Great Barrier Reef.

Mapstone, B.D., & G. De'Ath. (in prep. b). Patterns of association among sessile benthos on 24 reefs on the Great Barrier Reef: Structure or Randomness?

Moran, P.J., R.H. Bradbury, & R.E. Reichelt. 1988. Distribution of recent outbreaks of crown of thorns starfish (*Acanthaster planci*) along the Great Barrier reef: 1985-86. *Coral Reefs*, **7**:125-137.

Moran P.J., & G. De'Ath. 1992. Estimates of the abundances of the crown-of-thorns starfish *Acanthaster planci* on outbreaking and non-outbreaking populations on reefs within the Great Barrier Reef. *Mar. Biol.*, **113**: 509-516.

Oliver, J., G. De'Ath, T. Done, D. Williams, M. Furnas, and P. Moran (eds). 1995. *Long term monitoring of the Great Barrier Reef - Status Report Number 1.* Australian Institute of Marine Science. Townsville. 121pp.

Russ, G.R. 1984. Distribution and abundances of herbivorous grazing fishes in the central Great Barrier Reef. I. Levels of variability across the entire continental shelf. II Patterns of zonation of mid-shelf and outer-shelf reefs. *Mar. Ecol. Prog. Ser.* **20**: 23-44.

Sale, P.F., P.J. Doherty, G.J. Eckert, W.A. Douglas, and D.J. Ferrell. 1984. Large scale spatial and temporal variation in recruitment to fish populations on coral reefs. *Oecologia* (Berlin), **64**:191-198.

Sale P. F., G. J. Eckert, D. J. Ferrell, A. J. Fowler, T. A. Jones, B. D. Mapstone and W. J. Steel. 1986. *Aspects of the demography of seven species of coral reef fishes, with recommendations for their management.* **Report to The Great Barrier Reef Marine Park Authority**. 65pp

SAS. 1990. *SAS Procedures Guide.* SAS Institute. 705pp.

SAS. 1992 *SAS Technical Report P229 - SAS/STAT Software: Changes and Enhancements.* SAS Institute. 620pp.

Scandol, J.P. 1994. PhD Thesis, James Cook University.

Underwood A.J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. Oceanogr. *Mar. Biol. Ann. Rev.*, **19**:513-605.

Van Woesik, R., A.M. Ayling, & B.D. Mapstone. 1991. Impact of tropical cyclone Ivor on the Great Barrier Reef, Australia. *J. Coast. Res.*, **7**: 551-558.

Williams, D.McB. 1982. Patterns in the distribution of fish communities across the central Great Barrier Reef. *Coral Reefs*, **1**:35-43.

Williams D.McB., and A.I. Hatcher. 1983. Structure of fish communities on outer slopes of inshore, mid-shelf and outer shelf reefs of the Great Barrier Reef. *Mar. Ecol. Prog. Ser.*, **10**:239-250.

Williams, D.McB., G. Russ, and P.J. Doherty. 1986. Reef fish: large-scale distribution and recruitment. *Oceanus*, **29**:76-82.

Winer B.J. 1971. *Statistical Principles in Experimental Design.* McGraw-Hill Kogakusha, Tokyo.

Winer B.J., D.R. Brown, and K.M. Michels. 1992. *Statistical Principles in Experimental Design.* 3rd Ed. McGraw-Hill Kogakusha, Tokyo. 1057pp.

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.

<table>
<tr><th colspan="2">50m x 5m Transects</th><th>20m x 2.5m Transects</th><th>20m x 0.5m Transects</th></tr>
<tr><td rowspan="3">**Fishes**
Acanthuridae
Zebrassoma scopas
Other acanthurids

Chaetodontidae
C. aureofasciatus
C. baronessa
C. plebeius
C. rainfordi
C. trifasciatus
C. vagabundus
Chemon rostratus
Other chaetodons

Lethrinidae (Total)

Lutjanidae
Lutjanus bohar
L. carponotatus
L. Fulviflamma
L. gibbus
L. quinqilineatus

Serranidae
Plectropomus laevis
P. leopardus</td><td rowspan="3">**Benthos**
Acanthasteridae
A. planci <20cm
A. planci 21-50cm
A. planci >50cm

Ophidiasteridae
Linckia laevigata

Tridacnidae
T. gigas ≤ 20cm
T. gigas > 20cm
T. derasa ≤ 20cm
T. derasa > 20cm</td><td rowspan="3">**Labridae**
Thalassoma lunare

Pomacentridae
Amblyglyphidodon curacao
Chromis atripectoralis
Chrysiptera rollandi
Recruit *C. rollandi*
Plectroglyphidodon dickii
P. lacrymatus
Pomacentrus moluccensis
Recruit *P. moluccensis*</td><td>**Juvenile Coral** (<5cmϕ)
Acroporidae
Faviidae
Pocilloporidae
Misc. hard corals

Soft corals

Poritidae
Poritidae 0-5cmϕ
Portitidae 6-20cmϕ</td></tr>
<tr><th>50m x 2.5m Transects</th></tr>
<tr><td>**Poritidae**
(massive / sub-massive)
Poritidae
Poritids 21-50cm
Poritids 51-100cm
Poritids 101-200cm
Poritids >200cm</td></tr>
</table>

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

Table A1.2: continued.

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

Table A1.2: continued.

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

Table A1.2: continued

Family / *Genus*	Species	# Obs.
Order Alcyonacia		
Alcyonaria	spp.	21
Anthelia	spp.	17
Asterospicularia	spp.	14
Briarium	spp.	78
Capnella	spp.	140
Cladiella	spp.	5
Clavularia	spp.	14
Efflatournaria	spp.	195
Lobophyton	spp.	286
Pachyclavularia	spp.	12
Paralemnalia	spp.	15
Parerythropodium	spp.	14
Sarcophyton	spp.	341
Sinularia	spp.	519
Xenia	spp.	169
various Nephthiids	spp.	153
Unident. soft corals		88
Misc. Benthos		
anemones		36
ascidians		83
bryozoans		1
crinoids		14
gorgonians		207
sea urchins		2
zoanthids		145

Family / *Genus*	Species	# Obs.
Sponges		448
Algae		
Amphiroa	spp.	29
Caulerpa	spp.	38
Chlorodesmis	spp.	30
Galaxea	spp.	1
Halimeda	spp.	201
Turbinaria	spp.	31
	encrusting habit	4
	red form	2
	turfing habit	23
Tridacnidae		
Tridacna	*crocea*	12
	gigas	2
	maxima	6
	squamosa	1
	spp.	2
non tridacnids		2
Dead Substrata		
cyclone peeled sub.		49
dead standing coral		63
rubble		359
sand		91

APPENDIX 2: RESULTS OF ANOVAs FOR DENSITIES

Table A2.1: Results of univariate ANOVAs to test for effects of *A. planci* on midshelf reefs. Only non-pooled terms from analyses are shown.

A: Miscellaneous Large Fish

SPECIES	SOURCE	df	F	α	$\alpha_{c=\beta}$	Infer
Plectropomus spp	Habitat	1,63	5.394	0.023	0.106	*
	Region	2,62	12.914	0.000	0.175	*
	R*C	2,62	3.247	0.046	0.175	*
	R*H*C	2,60	2.132	0.127	0.175	*
All Lutjanids	Region	2,8	1.835	0.221	0.329	*
	COTS	1,8	1.597	0.242	0.329	*
L. carponotatus	Region	2,8	2.485	0.145	0.188	*
	H*C	1,58	4.594	0.036	0.014	-
Total Acanthurids	Habitat	1,8	5.404	0.049	0.008	-
	Region	2,8	11.226	0.005	0.099	*
	R*H	2,8	2.568	0.138	0.075	-
	COTS	1,8	12.008	0.009	0.020	*
	H*r(R*C)	6,48	1.746	0.131	0.124	-
Z. scopas	Habitat	1,8	14.276	0.005	0.036	*
	Region	2,54	8.526	0.001	0.085	*
	R*H	2,8	5.521	0.031	0.119	*
	COTS	1,54	3.065	0.086	0.007	-
	R*C	2,54	2.297	0.110	0.085	-
	H*r(R*C)	6,54	1.406	0.229	0.168	-
Other Acanthurids	Region	2,8	5.382	0.033	0.125	*
	COTS	1,8	7.197	0.028	0.042	*
	H*C	1,58	5.451	0.023	0.000	-

B: Chaetodontids

SPECIES	SOURCE	df	F	α	$\alpha_{c=\beta}$	Infer
All Chaetodons	Region	2,6	38.045	0.000	0.107	*
	R*C	2,6	1.880	0.232	0.107	-
	H*r(R*C)	6,48	3.072	0.013	0.173	*
C. aureofasciatus	Region	2,6	7.586	0.023	0.132	*
	COTS	1,6	4.769	0.072	0.050	-
	R*C	2,6	1.774	0.248	0.132	-
C. baronessa	Habitat	1,10	3.412	0.094	0.122	*
	R*C	2,6	2.866	0.134	0.173	*
	H*r(R*C)	6,48	2.980	0.015	0.244	*
C. plebeius	Region	2,54	14.008	0.000	0.139	*
	R*C	2,54	3.506	0.037	0.139	*
	H*r(R*C)	6,54	2.180	0.059	0.274	*
C. trifasciatus	Habitat	1,59	3.425	0.069	0.025	-
	Region	2,8	1.974	0.201	0.214	*
C. vagabundus	Region	2,8	2.057	0.190	0.199	*
	R*H	2,56	1.691	0.194	0.109	-
	COTS	1,8	2.258	0.171	0.138	-
Other Chaetodons	Region	2,64	77.368	0.000	0.033	*
	COTS	1,66	7.010	0.010	0.000	-
	R*C	2,64	3.922	0.025	0.033	*

Table A2.1 (Continued)

C: Small Fish

SPECIES	SOURCE	df	F	α	$\alpha_{c=\beta}$	Infer
A. curacao	Region	2,8	1.811	0.224	0.163	-
	H*C	1,10	7.004	0.024	0.017	-
	H*r(R*C)	6,48	1.409	0.231	0.281	*
C. atripectoralis	Habitat	1,57	8.003	0.006	0.244	*
	Region	2,8	5.326	0.034	0.317	*
	R*H	2,56	1.447	0.244	0.264	*
	COTS	1,8	1.494	0.256	0.314	*
C. rollandi	Habitat	1,10	8.679	0.015	0.058	*
	H*r(R*C)	6,48	2.303	0.049	0.219	*
Rec. *C. rollandi.*	Region	2,62	6.089	0.004	0.087	*
	R*H	2,62	1.588	0.212	0.087	-
	H*C	1,62	9.829	0.003	0.009	*
	R*C	2,62	3.361	0.041	0.087	*
P. moluccensis	Region	2,8	4.137	0.058	0.187	*
	COTS	1,8	5.274	0.051	0.120	*
	H*C	1,58	5.412	0.024	0.020	-
Rec. *P. moluccensis*	Region	2,64	20.914	0.000	0.198	*
	R*H	2,62	1.926	0.154	0.198	*
	COTS	1,66	2.611	0.111	0.143	*
P. lacrymatus	Habitat	1,10	5.857	0.036	0.005	-
	Region	2,8	3.599	0.077	0.079	*
	H*r(R*C)	6,48	2.184	0.061	0.097	*
T. lunare	Habitat	1,10	1.552	0.241	0.150	-
	Region	2,56	4.521	0.015	0.188	*
	H*r(R*C)	6,54	1.641	0.154	0.258	*

D: Benthos Counts

SPECIES	SOURCE	df	F	α	$\alpha_{c=\beta}$	Infer
L. laevigata	Habitat	1,64	28.429	0.000	0.335	*
	Region	2,64	30.128	0.000	0.326	*
	R*H	2,62	14.555	0.000	0.328	*
	H*C	1,64	1.395	0.242	0.335	*
Tridacna spp	Region	2,62	2.672	0.077	0.122	*
	R*H	2,60	4.857	0.011	0.122	*
	H*C	1,62	4.825	0.032	0.036	*
	R*H*C	2,60	3.999	0.023	0.122	*
Poritids 21-50cm	Region	2,66	13.288	0.000	0.168	*
	H*C	1,66	2.290	0.135	0.096	-
Poritids >100cm	Region	2,8	1.709	0.241	0.186	-
	R*H	2,8	4.690	0.045	0.128	*
	COTS	1,8	2.589	0.146	0.119	-
	H*r(R*C)	6,48	1.590	0.171	0.137	-

Table A2.1 (Continued)

E: Small Corals

SPECIES	SOURCE	df	F	α	$\alpha_{c=\beta}$	Infer
Acroporids	COTS	1,10	5.951	0.035	0.027	-
Faviids	Habitat	1, 8	22.812	0.001	0.023	*
	Region	2, 8	3.895	0.066	0.193	*
	R*H	2, 8	2.794	0.120	0.103	-
	COTS	1, 8	2.150	0.181	0.129	-
	H*r(R*C)	6,48	4.793	0.001	0.199	*
Pocilloporids	COTS	1,58	4.172	0.046	0.000	-
	H*r(R*C)	6,54	2.285	0.049	0.043	-
Misc. Corals	Habitat	1,10	6.282	0.031	0.054	*
	Region	2, 8	1.799	0.226	0.168	-
	H*r(R*C)	6,48	1.367	0.247	0.217	-
Soft Corals	H*C	1,58	2.926	0.092	0.000	-

F: Benthic Coverage

SPECIES	SOURCE	df	F	α	$\alpha_{c=\beta}$	Infer
Total Hard Coral	Habitat	1.10	11.158	0.007	0.003	-
	H*r(R*C)	6,48	2.218	0.057	0.149	*
Acroporidae	Habitat	1, 8	17.652	0.003	0.019	*
	R*H	2, 8	5.737	0.028	0.098	*
	H*C	1, 8	4.022	0.080	0.019	-
	H*r(R*C)	6,48	2.523	0.033	0.176	*
Faviidae	Habitat	1,66	2.569	0.114	0.114	*
	H*C	1,66	1.397	0.241	0.114	-
	R*C	2,64	1.688	0.193	0.181	-
Pocilloporidae	Habitat	1,10	2.100	0.178	0.143	-
	Region	2,54	1.469	0.239	0.135	-
	COTS	1,54	2.868	0.096	0.051	-
	R*C	2,54	1.800	0.175	0.135	-
	H*r(R*C)	6,54	2.347	0.044	0.191	*
Poritidae	R*H	2, 8	5.212	0.036	0.166	*
	COTS	1,58	3.506	0.066	0.019	-
	H*r(R*C)	6,54	2.194	0.058	0.212	*
Misc. Hard Corals	Habitat	1,10	6.757	0.027	0.051	*
	H*C	1,10	3.616	0.086	0.051	-
	R*C	2,54	2.865	0.066	0.110	*
	H*r(R*C)	6,54	1.599	0.165	0.288	*
Dead Standing Coral	Region	2,54	17.847	0.000	0.083	*
	H*C	1,10	1.785	0.211	0.115	-
	R*C	2,54	1.652	0.201	0.083	-
	H*r(R*C)	6,54	4.255	0.001	0.214	*
Soft Corals	Habitat	1,59	3.910	0.053	0.000	-
	Region	2, 8	2.288	0.164	0.174	*

Table A2.1 (Continued)

G: Intercepts

SPECIES	SOURCE	df	F	α	$\alpha_{c=\beta}$	Infer
Total Hard Coral	Region	2,54	8.848	0.000	0.062	*
	COTS	1,54	4.038	0.049	0.001	-
	R*C	2,54	11.208	0.000	0.062	*
	H*r(R*C)	6,54	3.099	0.011	0.156	*
Acroporidae	Habitat	1, 8	15.698	0.004	0.012	*
	Region	2,54	3.549	0.036	0.063	*
	R*H	2, 8	3.009	0.106	0.085	-
	H*C	1, 8	3.483	0.099	0.012	-
	R*C	2,54	3.475	0.038	0.063	*
	H*r(R*C)	6,54	1.514	0.191	0.152	-
Faviidae	Habitat	1, 8	6.377	0.036	0.060	*
	Region	2, 8	2.959	0.109	0.186	*
	R*H	2, 8	1.970	0.202	0.141	-
	H*C	1, 8	4.358	0.070	0.060	-
	H*r(R*C)	6,48	1.910	0.098	0.198	*
Pocilloporidae	Habitat	1,10	5.451	0.042	0.077	*
	R*C	2,54	3.104	0.053	0.096	*
	H*r(R*C)	6,54	2.625	0.026	0.123	*
Poritidae	Habitat	1, 8	3.041	0.119	0.123	*
	R*H	2, 8	5.357	0.033	0.189	*
	H*C	1, 8	2.076	0.188	0.123	-
	H*r(R*C)	6,54	2.828	0.018	0.184	*
Misc. Hard Corals	Habitat	1,10	6.405	0.030	0.130	*
	Region	2,54	2.708	0.076	0.127	*
	H*C	1,10	3.322	0.098	0.130	*
	R*C	2,54	3.127	0.052	0.127	*
	H*r(R*C)	6,54	2.727	0.022	0.206	*
Dead Standing Coral	Region	2, 8	13.172	0.003	0.119	*
	H*C	1,10	1.639	0.229	0.118	-
	H*r(R*C)	6,48	4.007	0.002	0.219	*
Soft Corals	Region	2, 8	3.005	0.106	0.140	*
Sponges	Region	2, 8	1.662	0.249	0.106	-

Table A2.2: Results of univariate ANOVA to test for effects on abundance of Shelf Position, Region, and Habitat. Only non-pooled terms from analyses are shown.

A: Miscellaneous Large Fish

SPECIES	SOURCE	df	F	α	$\alpha_{c=\beta}$	**Infer**
Plectropomus **spp.**	Shelf	1,16	1.175	0.295	0.304	*
	H*S	1,94	36.517	0.000	0.262	*
	Region	2,16	9.452	0.002	0.211	*
	R*H	2,94	2.189	0.118	0.155	*
	R*H*S	2,94	7.961	0.001	0.155	*
All Lutjanids	Habitat	1,97	14.544	0.000	0.071	*
	Shelf	1,16	2.507	0.133	0.309	*
	Region	2,16	2.208	0.142	0.218	*
	R*H	2,97	3.825	0.025	0.150	*
L. carponotatus	Shelf	1,18	44.935	0.000	0.229	*
	Region	2,18	2.371	0.122	0.124	*
	R*S	2,18	2.376	0.121	0.124	*
Total Acanthurids	Habitat	1,18	12.736	0.002	0.026	*
	Shelf	1,14	36.949	0.000	0.246	*
	H*S	1,16	1.898	0.187	0.223	*
	Region	2,14	4.437	0.032	0.143	*
	R*S	2,14	3.410	0.062	0.143	*
	H*r(R*S)	14,80	2.036	0.025	0.090	*
Z. scopas	Habitat	1,18	6.620	0.019	0.040	*
	Shelf	1,18	24.900	0.000	0.254	*
	H*S	1,18	4.686	0.044	0.231	*
	Region	2,18	4.127	0.033	0.151	*
	R*H	2,18	6.922	0.006	0.125	*
	R*S	2,18	2.159	0.144	0.151	*
	R*H*S	2,18	4.932	0.020	0.125	*
	H*r(R*S)	18,96	1.604	0.074	0.054	-
Other Acanthurids	Habitat	1,18	11.060	0.004	0.019	*
	Shelf	1,14	26.771	0.000	0.252	*
	H*S	1,16	5.705	0.030	0.209	*
	Region	2,14	2.829	0.093	0.150	*
	R*S	2,14	2.998	0.082	0.150	*
	H*r(R*S)	14,80	1.823	0.049	0.102	*

Table A2.2 (Continued)

B: Chaetodons

SPECIES	SOURCE	df	F	α	$\alpha_{c=\beta}$	Infer
All Chaetodons	Region	2,19	11.460	0.001	0.148	*
	R*H	2,19	2.738	0.090	0.099	*
	R*S	2,18	7.335	0.005	0.152	*
	R*H*S	2,18	4.121	0.034	0.100	*
	H*r(R*S)	18,96	1.607	0.073	0.071	-
C. aureofasciatus	Shelf	1,18	32.975	0.000	0.205	*
	H*S	1,116	2.568	0.112	0.106	-
	Region	2,18	4.727	0.022	0.100	*
	R*S	2,18	4.811	0.021	0.100	*
C. baronessa	Shelf	1,14	21.090	0.000	0.225	*
	H*S	1,14	8.493	0.011	0.239	*
	Region	2,14	3.434	0.061	0.121	*
	R*S	2,14	3.004	0.082	0.121	*
	R*H*S	2,14	2.534	0.115	0.135	*
	H*r(R*S)	14,80	2.266	0.012	0.079	*
C. plebeius	Habitat	1,113	13.487	0.000	0.026	*
	H*S	1,110	4.766	0.031	0.223	*
	Region	2,113	6.255	0.003	0.112	*
	R*S	2,112	1.721	0.184	0.112	-
C. trifasciatus	Habitat	1,114	13.240	0.000	0.022	*
	Shelf	1,20	6.423	0.020	0.274	*
	H*S	1,114	39.556	0.000	0.218	*
	Region	2,20	5.513	0.012	0.173	*
	R*H	2,114	5.760	0.004	0.108	*
	R*H*S	2,114	4.249	0.017	0.108	*
C. vagabundus	Habitat	1,115	8.008	0.005	0.015	*
	Shelf	1,18	14.010	0.001	0.281	*
	R*H	2,115	1.678	0.191	0.099	-
	R*S	2,18	4.892	0.020	0.182	*
	R*H*S	2,114	2.700	0.071	0.099	*
Other Chaetodons	Habitat	1,16	8.407	0.010	0.036	*
	Shelf	1,14	23.767	0.000	0.265	*
	H*S	1,14	4.329	0.056	0.225	*
	Region	2,14	4.937	0.024	0.165	*
	R*S	2,14	1.716	0.216	0.165	-
	R*H*S	2,14	2.283	0.139	0.121	-
	H*r(R*S)	14,80	1.757	0.060	0.099	*

Table A2.2 (Continued)

C: Small Fish

SPECIES	SOURCE	df	F	α	$\alpha_{c=\beta}$	Infer
A. curacao	Habitat	1.22	17.205	0.000	0.008	*
	Shelf	1,18	20.601	0.000	0.220	*
	H*S	1,20	8.430	0.009	0.192	*
	R*S	2,18	1.602	0.229	0.115	-
	H*r(R*S)	18,96	2.147	0.009	0.113	*
C. atripectoralis	Shelf	1,110	1.636	0.204	0.333	*
	H*S	1,110	10.868	0.001	0.333	*
	Region	2,110	5.198	0.007	0.245	*
	R*H	2,110	1.500	0.228	0.245	*
	R*S	2,110	5.818	0.004	0.245	*
C. rollandi	Habitat	1,23	31.337	0.000	0.016	*
	Shelf	1,18	3.630	0.073	0.229	*
	R*S	2,18	2.328	0.126	0.124	-
	H*r(R*S)	18,96	2.095	0.011	0.029	*
Recruit *C.r.*	Habitat	1,108	25.796	0.000	0.056	*
	Shelf	1,108	1.373	0.244	0.248	*
	H*S	1,108	19.428	0.000	0.248	*
	Region	2,108	2.817	0.064	0.139	*
	R*H	2,108	3.267	0.042	0.139	*
	R*S	2,108	7.432	0.001	0.139	*
	R*H*S	2,108	5.637	0.005	0.139	*
P. moluccensis	Habitat	1,94	6.765	0.011	0.000	-
	Shelf	1,14	72.604	0.000	0.209	*
	H*S	1,94	2.303	0.132	0.131	-
	Region	2,14	5.486	0.017	0.105	*
	R*H	2,94	6.863	0.002	0.039	*
	R*S	2,14	9.105	0.003	0.105	*
	R*H*S	2,94	4.025	0.021	0.039	*
Recruit *P.m.*	Habitat	1,94	3.055	0.084	0.014	-
	Shelf	1,14	14.686	0.002	0.246	*
	H*S	1,94	9.475	0.003	0.207	*
	Region	2,14	8.958	0.003	0.143	*
	R*H	2,94	3.270	0.042	0.098	*
	R*S	2,14	8.599	0.004	0.143	*
	R*H*S	2,94	4.641	0.012	0.098	*
P. lacrymatus	Shelf	1,20	18.893	0.000	0.219	*
	H*S	1,20	6.336	0.020	0.191	*
	Region	2,20	4.445	0.025	0.113	*
	R*H	2,20	3.588	0.047	0.086	*
	H*r(R*S)	18,96	2.359	0.004	0.059	*
T. lunare	Shelf	1,136	71.124	0.000	0.244	*
	H*S	1,134	7.139	0.008	0.245	*
	Region	2,136	2.371	0.097	0.134	*
	R*S	2,136	6.490	0.002	0.134	*

Table A2.2 (Continued)

D: Benthos Counts

SPECIES	SOURCE	df	F	α	$\alpha_{c=\beta}$	Infer
L. laevigata	Habitat	1.108	41.591	0.000	0.147	*
	Shelf	1,108	54.394	0.000	0.300	*
	H*S	1,108	32.139	0.000	0.300	*
	Region	2,108	29.220	0.000	0.200	*
	R*H	2,108	18.585	0.000	0.200	*
	R*S	2,108	37.349	0.000	0.200	*
	R*H*S	2,108	24.252	0.000	0.200	*
Tridacna	Habitat	1,94	11.230	0.001	0.017	*
	Shelf	1,16	3.048	0.100	0.243	*
	H*S	1,94	3.493	0.065	0.211	*
	Region	2,16	4.906	0.022	0.139	*
	R*H	2,94	10.096	0.000	0.101	*
	R*H*S	2,94	3.208	0.045	0.101	*
Poritids 21-50cm	Shelf	1,136	21.521	0.000	0.243	*
	H*S	1,134	8.732	0.004	0.243	*
	R*S	2,136	29.217	0.000	0.133	*
Poritids 51-100cm	Shelf	1,136	21.521	0.000	0.243	*
	H*S	1,134	8.732	0.004	0.243	*
	R*S	2,136	29.217	0.000	0.133	*
Poritids >100cm	Habitat	1,116	29.684	0.000	0.013	*
	H*S	1,114	10.715	0.001	0.207	*
	Region	2,19	2.002	0.163	0.153	-
	R*S	2,18	2.807	0.087	0.156	*
	R*H*S	2,114	10.673	0.000	0.097	*

Table A2.2 (Continued)

E: Small Corals

SPECIES	SOURCE	df	F	α	$\alpha_{c=\beta}$	Infer
Acroporids	Habitat	1.20	25.092	0.000	0.037	*
	Shelf	1,18	29.888	0.000	0.245	*
	H*S	1,20	20.732	0.000	0.228	*
	Region	2,18	6.544	0.007	0.140	*
	R*H	2,20	2.367	0.120	0.122	*
	R*S	2,18	3.392	0.056	0.140	*
	H*r(R*S)	18,96	2.070	0.013	0.075	*
Faviids	Habitat	1,21	45.625	0.000	0.005	*
	Region	2,19	3.604	0.047	0.144	*
	R*H	2,21	3.397	0.053	0.076	*
	R*S	2,18	2.650	0.098	0.146	*
	H*r(R*S)	18,96	2.021	0.015	0.110	*
Pocilloporids	Habitat	1,118	12.003	0.001	0.016	*
	Shelf	1,18	55.833	0.000	0.266	*
	H*S	1,116	4.555	0.035	0.211	*
	Region	2,18	8.272	0.003	0.164	*
	R*S	2,18	9.167	0.002	0.164	*
Misc. Corals	Habitat	1,114	19.052	0.000	0.063	*
	Shelf	1,18	4.466	0.049	0.295	*
	H*S	1,114	1.638	0.203	0.253	*
	Region	2,18	8.355	0.003	0.199	*
	R*H	2,114	6.860	0.002	0.144	*
	R*S	2,18	2.045	0.158	0.199	*
	R*H*S	2,114	2.867	0.061	0.144	*
Soft Corals	Shelf	1,18	7.939	0.011	0.197	*
	Region	2,18	2.826	0.086	0.092	*
	R*S	2,18	3.202	0.065	0.092	*
	H*r(R*S)	18,96	15.754	0.000	0.081	*

Table A2.2 (Continued)

F: Benthic Coverage

SPECIES	SOURCE	**df**	**F**	α	$\alpha_{c=\beta}$	**Infer**
Total Hard Coral	Habitat	1.114	4.453	0.037	0.000	-
	H*S	1,114	12.083	0.001	0.134	*
	R*H	2,114	12.096	0.000	0.041	*
	R*S	2,18	2.014	0.162	0.150	-
	R*H*S	2,114	2.385	0.097	0.041	-
Acroporidae	Habitat	1,21	32.492	0.000	0.008	*
	R*H	2,21	8.834	0.002	0.084	*
	R*S	2,18	1.826	0.190	0.140	-
	H*r(R*S)	18,96	2.194	0.008	0.050	*
Faviidae	Habitat	1,141	14.139	0.000	0.085	*
	H*S	1,134	1.545	0.216	0.267	*
Pocilloporidae	Habitat	1,132	39.060	0.000	0.052	*
	Shelf	1,132	8.655	0.004	0.245	*
	H*S	1,132	12.203	0.001	0.245	*
	Region	2,132	1.642	0.198	0.135	-
	R*H	2,132	4.077	0.019	0.135	*
	R*S	2,132	5.813	0.004	0.135	*
	R*H*S	2,132	4.875	0.009	0.135	*
Poritidae	Habitat	1,18	30.926	0.000	0.092	*
	H*S	1,18	11.779	0.003	0.268	*
	Region	2,115	1.883	0.157	0.108	-
	R*H	2,18	1.710	0.209	0.166	-
	R*S	2,114	1.501	0.227	0.108	-
	R*H*S	2,18	3.694	0.045	0.166	*
	H*r(R*S)	18,114	1.914	0.021	0.086	*
Misc. Hard Corals	Habitat	1,19	10.179	0.005	0.075	*
	H*r(R*S)	14,80	1.977	0.030	0.196	*
Dead Standing Coral	Habitat	1,22	4.913	0.037	0.046	*
	Shelf	1,114	50.145	0.000	0.166	*
	H*S	1,20	2.056	0.167	0.243	*
	Region	2,114	13.201	0.000	0.063	*
	R*S	2,114	13.158	0.000	0.063	*
	H*r(R*S)	18,114	3.437	0.000	0.041	*
Soft Corals	H*S	1,20	9.074	0.007	0.178	*
	Region	2,21	1.785	0.192	0.146	-
	H*r(R*S)	18,96	1.931	0.022	0.047	*
Sponges	Habitat	1,22	7.242	0.013	0.042	*
	Shelf	1,18	4.174	0.056	0.250	*
	H*S	1,20	5.952	0.024	0.232	*
	R*S	2,18	1.699	0.211	0.145	-
	H*r(R*S)	18,96	1.895	0.025	0.028	*

Table A2.2 (Continued)

G: Intercepts

SPECIES	SOURCE	df	F	α	$\alpha_{c=\beta}$	Infer
Total Hard Coral	Habitat	1.14	11.627	0.004	0.020	*
	Shelf	1,14	6.395	0.024	0.254	*
	H*S	1,14	2.984	0.106	0.206	*
	Region	2,14	4.159	0.038	0.152	*
	R*H	2,14	4.489	0.031	0.102	*
	R*S	2,14	1.969	0.176	0.151	-
	R*H*S	2,14	2.410	0.126	0.102	-
	H*r(R*S)	14,80	1.363	0.191	0.099	-
Acroporidae	Habitat	1,16	39.250	0.000	0.028	*
	Shelf	1,16	1.971	0.179	0.256	*
	H*S	1,16	8.533	0.010	0.217	*
	Region	2,16	2.173	0.146	0.153	*
	R*H	2,16	2.235	0.139	0.112	-
	H*r(R*S)	14,80	1.783	0.056	0.087	*
Faviidae	Habitat	1,21	14.517	0.001	0.051	*
	Region	2,19	1.919	0.174	0.127	-
	R*H	2,21	1.597	0.226	0.135	-
	R*S	2,18	3.347	0.058	0.132	*
	H*r(R*S)	18,96	2.385	0.004	0.070	*
Pocilloporidae	Habitat	1,108	43.032	0.000	0.052	*
	Shelf	1,108	21.717	0.000	0.245	*
	H*S	1,108	13.485	0.000	0.245	*
	Region	2,108	9.743	0.000	0.136	*
	R*H	2,108	6.615	0.002	0.136	*
	R*S	2,108	7.992	0.001	0.136	*
	R*H*S	2,108	2.375	0.098	0.136	*
Poritidae	Habitat	1,18	35.625	0.000	0.105	*
	Shelf	1,114	7.218	0.008	0.218	*
	H*S	1,18	11.949	0.003	0.275	*
	R*H	2,18	1.957	0.170	0.175	*
	R*S	2,114	3.326	0.039	0.107	*
	R*H*S	2,18	3.951	0.038	0.175	*
	H*r(R*S)	18,114	2.131	0.009	0.062	*
Misc. Hard Corals	Habitat	1,19	9.100	0.007	0.127	*
	H*r(R*S)	14,80	2.113	0.019	0.120	*
Dead Standing Coral	Habitat	1,23	9.728	0.005	0.050	*
	Shelf	1,114	87.364	0.000	0.168	*
	Region	2,114	10.831	0.000	0.064	*
	R*S	2,114	15.694	0.000	0.064	*
	H*r(R*S)	18,114	3.286	0.000	0.050	*
Soft Corals	Habitat	1,22	5.410	0.030	0.014	-
	H*S	1,20	8.557	0.008	0.202	*
	Region	2,21	2.155	0.141	0.140	-
	H*r(R*S)	18,96	1.742	0.045	0.045	-
Sponges	Habitat	1,22	18.388	0.000	0.016	*
	Shelf	1,20	6.355	0.020	0.230	*
	H*S	1,20	10.123	0.005	0.207	*
	H*r(R*S)	18,96	3.042	0.000	0.030	*

Table A2.3: Taxa for which variance in abundance among reefs within region and COTS history was non-trivial (and, therefore, not pooled).

SPECIES	df	F	α	$\alpha_{c=\beta}$	Infer
All Lutjanids	6,48	1.600	0.168	0.162	-
L. carponotatus	6,48	2.588	0.030	0.173	*
Total Acanthurids	6,48	1.922	0.096	0.057	-
Other Acanthurids	6,48	3.663	0.004	0.044	*
All Chaetodons	6,48	1.656	0.153	0.089	-
C. aureofasciatus	6,48	3.817	0.003	0.089	*
C. baronessa	6,48	1.885	0.103	0.147	*
C. trifasciatus	6,48	2.552	0.032	0.205	*
C. vagabundus	6,48	3.069	0.013	0.146	*
A. curacao	6,48	5.025	0.000	0.183	*
C. atripectoralis	6,48	1.759	0.128	0.164	*
C. rollandi	6,48	2.787	0.021	0.125	*
P. moluccensis	6,48	2.362	0.044	0.120	*
P. lacrymatus	6,48	3.856	0.003	0.041	*
Poritids >100cm	6,48	2.885	0.018	0.065	*
Coverage					
Total Hard Coral	6,48	7.827	0.000	0.073	*
Acroporidae	6,48	4.723	0.001	0.092	*
Soft Corals	6,48	7.651	0.000	0.076	*
Sponges	6,48	1.788	0.122	0.076	-
Intercepts					
Faviidae	6,48	3.742	0.004	0.108	*
Dead Standing Coral	6,48	1.616	0.163	0.126	-
Soft Corals	6,48	4.765	0.001	0.040	*
Sponges	6,48	2.620	0.028	0.060	*
Small Corals					
Acroporids	6,48	2.637	0.027	0.063	*
Faviids	6,48	14.417	0.000	0.109	*
Misc. Corals	6,48	2.034	0.079	0.124	*
Soft Corals	6,48	3.576	0.005	0.000	-

Table A2.4: Taxa for which variance in abundance among reefs within region and shelf position was non-trivial (and, therefore, not pooled).

SPECIES	df	F	α	$\alpha_{c=\beta}$	Infer
Plectropomus spp	14,80	1.617	0.093	0.029	-
All Lutjanids	14,80	1.879	0.041	0.005	-
L. carponotatus	18,96	2.603	0.001	0.010	*
Total Acanthurids	14,80	2.673	0.003	0.026	*
Z. scopas	18,96	2.236	0.006	0.011	*
Other Acanthurids	14,80	3.052	0.001	0.032	*
All Chaetodons	18,96	3.296	0.000	0.016	*
C. aureofasciatus	18,96	6.069	0.000	0.001	*
C. baronessa	14,80	1.869	0.043	0.021	-
C. trifasciatus	18,96	2.288	0.005	0.067	*
C. vagabundus	18,96	2.537	0.002	0.027	*
Other Chaetodons	14,80	3.082	0.001	0.030	*
A. curacao	18,96	3.252	0.000	0.034	*
C. rollandi	18,96	2.739	0.001	0.004	*
P. moluccensis	14,80	3.439	0.000	0.001	*
Recruit *P.m.*	14,80	1.639	0.087	0.001	-
P. lacrymatus	18,96	3.940	0.000	0.012	*
Tridacna	14,80	1.656	0.082	0.014	-
Poritids >100cm	18,96	2.073	0.012	0.004	-
Coverage					
Total Hard Coral	18,96	7.072	0.000	0.011	*
Acroporidae	18,96	4.442	0.000	0.010	*
Misc. Hard Corals	14,80	4.270	0.000	0.089	*
Soft Corals	18,96	5.583	0.000	0.009	*
Sponges	18,96	2.286	0.005	0.004	-
Intercepts					
Total Hard Coral	14,80	2.703	0.003	0.030	*
Acroporidae	14,80	2.883	0.001	0.025	*
Faviidae	18,96	2.092	0.012	0.016	*
Misc. Hard Corals	14,80	3.436	0.000	0.041	*
Soft Corals	18,96	3.356	0.000	0.008	*
Sponges	18,96	3.757	0.000	0.005	*
Small Corals					
Acroporids	18,96	2.690	0.001	0.018	*
Faviids	18,96	5.847	0.000	0.032	*
Pocilloporids	18,96	2.155	0.009	0.018	*
Misc. Corals	18,96	1.708	0.051	0.062	*
Soft Corals	18,96	10.895	0.000	0.020	*