

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 chaetodonts, 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 serranid⁵ fishes, greater abundances of soft corals, chaetodontid fishes, and *Chromis* spp⁵ on outer-shelf reefs than on mid-shelf reefs, and greater densities of *Pomacentrus* spp⁵ 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.
