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## RESILIENCE TO LARGE-SCALE DISTURBANCE IN CORAL AND FISH ASSEMBLAGES ON THE GREAT BARRIER REEF

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**Abstract.** Recognition of the complex spatial and temporal variability of abundance and diversity found in many populations has led to a greater focus on the roles of heterogeneity, stochasticity, and disturbance in the structure and persistence of communities. This focus is directly relevant to coral reef communities that are characterized by very high species diversity in a spatially heterogeneous environment, display stochastic variability in community structure at small spatial and temporal scales, and are subject to major disturbances. We monitored coral and fish assemblages over 14 years on fixed sites spread over 80 km of the southern Great Barrier Reef (GBR), Australia, and found evidence of large-scale resilience and predictable recovery of these assemblages. Sometime between November 1987 and October 1989, live coral cover on the shallow northeast flanks of some reefs in the southern GBR decreased from >80% to <10%, probably as a result of storm damage. We compared the fish and benthic communities present in these areas prior to the disturbance (1983–1984) with those present in 1992 and the subsequent changes through to 1998. Hard coral cover increased slowly from 1992 to 1994, then accelerated to be indistinguishable from pre-impact levels by 1998. The response of the coral assemblages was largely due to the predominance of tabulate *Acropora* species and their characteristics of rapid growth and competitive dominance. Patterns of species richness of the fish families Acanthuridae, Chaetodontidae, Scaridae, and Pomacentridae mirrored that of hard coral, except the Pomacentridae had not recovered to pre-impact levels by 1998. Of the 26 fish species analyzed for changes in abundance, 88% decreased after the disturbance, then subsequently increased, with all but two recovering to pre-impact levels by 1998. Although processes such as settlement and immigration are ultimately responsible for replenishment of local populations, our data suggested that habitat plays a strong role in modifying fish assemblages. Thus, both coral and fish assemblages demonstrated resilience to large-scale natural disturbance and predictability in the structure of the assemblages, with most taxa approaching the asymptote of abundance and species richness that existed prior to the disturbance.

**Key words:** coral assemblage; disturbance; Great Barrier Reef; large scale; recovery; reef fish assemblage; resilience.

### INTRODUCTION

As recently as the 1970s, there was still a view among community ecologists that biological systems tended towards equilibrium conditions (see Pimm [1991] for discussion). Although physical disturbances were recognized as having some role in the development of communities, they were considered transient phenomena, not significant enough to disturb an ecosystem's intrinsic march towards a climax community (Odum 1969). However, an increasing number of studies were unable to reconcile the complex spatial and temporal variability of abundance and diversity found in many communities using the prevailing equilibrium

theories (e.g., Doherty 1987). From this awareness came the rapid development of nonequilibrium theory and a greater focus on the role of heterogeneity, stochasticity, and disturbance in structuring communities (e.g., Holling 1973, Paine and Levin 1981, Chesson and Case 1986).

It is now well established that disturbance is a major source of temporal and spatial heterogeneity in the structure and dynamics of natural communities and an agent of natural selection in the evolution of life histories (Pickett and White 1986). Most research however, has focused on terrestrial systems, most notably forests (e.g., Bormann and Likens 1979, Heinzelman 1981). It was not until Connell's (1978) seminal review that nonequilibrium theory was explicitly applied to coral reefs. While there is still some debate over the general validity of the "intermediate disturbance hypothesis" as espoused by Connell (1978), it nevertheless served to highlight the importance of spatial hetero-

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geneity and the significance of extrinsic factors such as disturbance in modifying coral reef community structure (Karlson and Hurd 1993). Current models of community structure now incorporate aspects of patch dynamics, hierarchy theory, and metapopulation stability (see Wu and Loucks [1995]) thereby incorporating a wide range of spatial and temporal scales explicitly linked to heterogeneity, of which disturbance plays a major role. However, empirical studies at large ecological scales are rare, with most studies constrained to small spatial and temporal scales.

A system can be considered stable in the face of a disturbance if (1) it retains a similar structure ("resistance") or (2) it returns to a similar pre-disturbance structure after an initial deviation ("resilience"; Connell and Sousa 1983). Disturbances occur over a range of spatial and temporal scales and with varying intensity. Investigations conducted at small spatial scales have generally concluded that the community is unstable (Sale 1978, Sale and Williams 1982), while studies conducted at larger scales generally consider that communities are stable (Williams and Hatcher 1983). However, the spatial scale at which a reef fish assemblage displays stability will also vary according to the level of larval connectivity in the regional system of assemblages. As reef fish have a highly dispersive larval phase lasting from 10 to 60 d (Brothers et al. 1983) the minimum areas under which assemblages will display stability are likely to be large (Connell and Sousa 1983). This is especially likely in an archipelagic system such as the Great Barrier Reef.

In general, studies of the effects of disturbance on coral reefs have been biased towards sessile organisms, most likely because they are easier to observe and quantify. Most large-scale disturbances (>1 km) affecting coral reefs are due to natural events such as large storms (Lassig 1983, Walsh 1983), crown-of-thorns starfish (COTS) outbreaks (Williams 1986, Hart and Klumpp 1996, Hart et al. 1996), and coral bleaching (Wellington and Victor 1985). Their effects on benthic communities can be extensive (e.g., Colgan 1987, van Woesik et al. 1991, Brown 1997, Connell 1997, Connell et al. 1997). In the case of storms, damage is generally most severe on the windward side of reefs, with corals in the lee often remaining unaffected (Woodley et al. 1981, Connell 1997, Cheal et al. 2002). Damage can vary from removal of entire coral outcrops (over tens to hundreds of meters) in the direct path of the storm to individual colony damage within more sheltered areas (van Woesik et al. 1991, Done 1992). In contrast, COTS outbreaks and bleaching events kill only the living veneer of hard corals, leaving the skeletal structures intact. Irrespective of the disturbance type, effects are always patchy, with partial survival of corals even in areas subject to the most intense disturbance (Done 1992, Connell et al. 1997). Recovery of benthic communities from such disturbances is highly variable and dependent on the interplay of many

factors, e.g., the scale of the disturbance, availability of larval propagules from undamaged areas, and the type of coral community that existed at the time of the disturbance (see Hughes and Connell [1999]). However, in general, recovery is usually slower after acute disturbances that alter not only the coral but also the underlying physical environment than after disturbances that kill or damage only the coral (Connell 1997).

In contrast to coral communities, the role of disturbance in shaping reef fish assemblages is still unclear. Current models of fish assemblage dynamics vary widely, encompassing fish populations as stable and resistant to change at one end of a scale to unstable and highly variable at the other (see review by Jones and Syms [1998]). Evidence of direct disturbance effects on fish assemblages is limited (Bohnsack 1983, Lassig 1983, Walsh 1983), with most of the literature implicating indirect effects through modification of habitat. However, the effects of habitat modification are difficult to predict. Some investigators have found positive correlations between habitat and the abundance and/or diversity of fish (Luckhurst and Luckhurst 1978, Bell and Galzin 1984, Chabanet et al. 1997) while others have found no significant correlations between these variables (Roberts and Ormond 1987, Fowler 1990, Green 1996). More recently, the influence of underlying habitat heterogeneity, rather than coral cover per se, has been implicated as a major determinant of reef fish community structure (Lewis 1997, Syms 1998, Syms and Jones 2000). All three of these cited studies demonstrated that removal of substantial proportions of biogenic habitat (e.g., hard corals) at small scales did not necessarily result in altered fish communities.

Given the increasing evidence that recovery of many hard coral assemblages occurs over decades (Williams 1986, Ninio et al. 2000) and that many reef fish species are long-lived (Choat and Axe 1996, Meekan et al. 1999), there is a need for long-term studies of fish assemblage dynamics at appropriate scales, analogous to recent works on corals (e.g., Done 1992, Hughes 1994, Connell et al. 1997). A dramatic decline in hard coral cover on some reefs of the Capricorn Bunkers region (southern Great Barrier Reef, Australia) between November 1987 and October 1989 provided an opportunity to examine the effects of a large scale disturbance on adult, reef fish assemblages. During this period, benthic cover on the northeast flanks of the most exposed reefs was reduced from >80% to <8% (Doherty et al. 1997, I. R. Miller, A. A. Thompson, V. J. Baker, D. K. Bass, and C. A. Christie, *unpublished manuscript*). An earlier study investigating the effects of this same disturbance on fish recruitment was unable to unequivocally assign any individual event as causing the damage (see Doherty et al. 1997). After consulting weather records from numerous sources Doherty et al. (1997) concluded that a combination of storms over

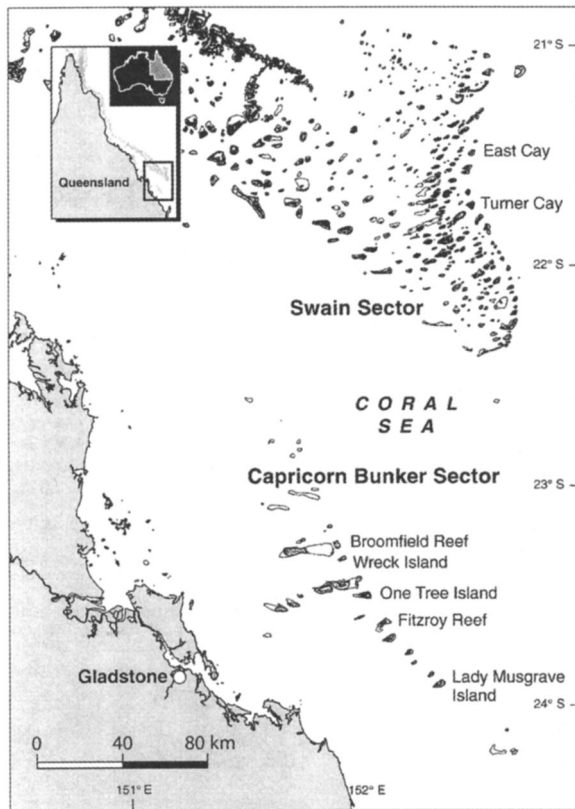


FIG. 1. Location of the seven reefs surveyed at the southern end of the Great Barrier Reef, Australia.

the period in question was the most likely cause of the damage.

In 1992, when hard coral cover was still very low (site mean of 8.2%,  $n = 4$  reefs  $\times$  3 sites; Oliver et al. 1995) a long-term program was implemented to monitor annual changes in adult fish assemblages and benthic assemblage structure on five reefs in the Capricorn Bunker sector. These same reefs had been the focus of two other studies of fish and benthic structure in the 1980s (Doherty et al. 1997). By combining the results of these pre- and post-impact studies, we were able to gain some historical perspective on the effects of the disturbance and the subsequent patterns of recovery. We focused on four questions: (1) What quantifiable changes occurred in the benthos and fish assemblages immediately after the disturbance? (2) In the

years following the disturbance (i.e., between 1992 and 1998), how did the taxa respond? (3) Nine years after the disturbance, how similar were the benthic and fish assemblages to their pre-impact levels? (4) To what extent were changes in the abundance and/or species richness of selected fish taxa correlated with changes in the benthos?

## METHODS

The reefs included in this study were situated in the southern Great Barrier Reef (GBR), Australia. Five reefs were in the Capricorn Bunker sector (Broomfield, Wreck, One Tree Island, Fitzroy, and Lady Musgrave Island) and two reefs were in the Swains sector (East Cay and Turner Cay) (Fig. 1). Although not ideal as controls, the Swains reefs were the closest reefs to the disturbed area that also contained similar fish and benthic assemblages (Williams 1991). Moreover, given the absence of any large-scale coral decline, they were most likely not subject to the same major disturbance.

### Data collection and survey methods

All study sites were located on the shallow northeast flanks of reefs, between the 6- and 12-m depth contours. Sites, and transects within sites, were all fixed, with transects running consecutively  $\sim 5$ –10 m apart. Annual reef surveys were conducted using a variety of comparable, established methods (Table 1). Benthic data on percentage cover of corals and algae were collected using manta-tow surveys, video-transect surveys, and line intercept surveys (Oliver et al. 1995, Doherty et al. 1997, Sweatman et al. 2000) during 1985–1987 and 1989–1998. Data on adult fish abundances and species richness from the families Acanthuridae (surgeonfishes), Chaetodontidae (butterflyfishes), Labridae (wrasses), Pomacentridae (damselfishes), and Scaridae (parrotfishes) were collected using two methods. Pre-disturbance data (1983–1984) were collected during 45-min timed swims using a log<sub>5</sub> abundance scale (Williams 1982) while post-disturbance data (1991–1998) were collected using absolute abundance counts of selected species within transects of fixed size (see Thompson and Mapstone [2002] for a detailed description).

By assuming that estimates of benthic cover were spatially and temporally consistent for each of the methods, overlap between the three different benthic

TABLE 1. Methods used to collect benthic and fish data over the 14-year time span of the study.

Group	1984	1985–1987	1988	1989	1990	1991	1992	1993	1994–1998
Benthos		LI, MT		MT		MT	MT, VT	LI, MT, VT	MT, VT
Fish	Log <sub>5</sub>						LTM	LTM	LTM

Notes: Key to abbreviations: LI, line intercept (three sites,  $5 \times 40$  m transects per site); MT, manta tow (2-min tows along northeast perimeter); VT, video transects (three sites,  $5 \times 50$  m transects per site); Log<sub>5</sub>, timed swims using an abundance scale (three 45-min swims with abundance categories: 1 = 1, 2 = 2–5, 3 = 6–25, 4 = 26–125, up to 7); LTM, absolute transect counts (three sites,  $5 \times 50$  m transects; Pomacentridae counted along 1 m wide strip; all other species counted along a 5 m wide strip). See *Methods: Data collection and survey methods* for references on each method.

survey methods provided the necessary comparative information for inter-calibration. However, unlike the benthic data collections, there was no overlap between the fish census methods used, so a dedicated calibration study was undertaken to enable direct comparison of the two methods. Fixed sites at four reefs within the central GBR were initially surveyed using absolute abundance counts and then resurveyed within 24 h using the  $\log_5$  abundance scale. The absolute abundance estimates were then converted to the  $\log_5$  abundance scale to correspond with the timed swims. Both data sets were then averaged to reef level (i.e., northeast flanks). This calibration data set was then included in the analysis of the fish data from the Capricorn Bunker sector in order to interpret differences between the two counting methods.

Several additional criteria were used to determine which fish species were included in the analyses of changes in abundance: (1) Comparison of the two methods of data collection was conducted in the central GBR, and some of the species found in the Capricorn Bunker and Swains sectors in the southern GBR were not present. Therefore, only those species that existed in both regions could be part of the full analysis (i.e., pre- and post-impact) of the disturbance data sets. (2) For the remaining species present only in the southern GBR, those that occurred on at least two of the Capricorn Bunker reefs were included. These species could only be analyzed for post-impact effects. (3) The caveat for inclusion in either of the first two criteria was sufficient abundance and replication through time to make any analysis worthwhile. In practice, this meant occurrence over at least three consecutive years in the study and relative consistency in abundance between years. Borderline inclusions were checked for normality and where residuals were highly non-normal they were excluded from further investigation.

#### *Statistical analyses*

Mixed linear models were fitted independently to the benthic and fish data. Estimates of cover, species richness, and abundance were obtained using restricted maximum likelihood as implemented in the SAS MIXED procedure (Littell et al. 1996). The models included (1) the fixed effects of method and the polynomial for the change of benthic cover, species richness, and fish abundance over time, for the periods before and after the disturbance, and (2) the random effects for the polynomial over time for each reef (details are presented in the Appendix). The adjusted means for benthic cover were estimated by averaging across reefs for the video transects methodology. Adjusted means for fish abundance and species richness were calculated by combining the parameter estimates from the model to reflect the mean for a given year using the 45-min timed swim.

Besides examining changes in the benthos and fish independently, we also tested for significant relation-

ships between the amount of benthic cover and fish abundance, using only data from the post-impact period (i.e., collected with one method). Prior to any analysis, estimates of fish abundance were summed to site and benthic cover averaged to site. Fish abundance was then transformed using  $\log(x + 1)$  and benthic cover transformed using the empirical logit of McCullagh and Nelder (1989). Fish abundance was modeled using a mixed linear model incorporating sampling design effects such as reef and site differences. The remaining variability in fish abundance was then partitioned between the benthic categories of hard coral, soft coral, turf algae, and a residual. The residual was then partitioned into a temporal trend and random error. This approach removed variability from the response due to known factors such as design effects and benthic cover. Any remaining variability that could be related to temporal trends indicated that fish abundance reacted to some other cue not accounted for by the benthic categories. If no significant temporal trend remained, we concluded that the trends in the benthic categories accounted for the trends in fish abundance. Although this conclusion implies that benthic abundance and fish abundance were related, it does not necessarily indicate that a given benthic category caused the observed changes.

## RESULTS

### *Changes in benthic assemblages*

In the years immediately preceding the disturbance, the benthic assemblages on the northeast flanks of reefs in the Capricorn Bunkers sector were characterized by very high cover of hard corals (>80% in 1987), especially tabulate *Acropora* (Fig. 2a, b). As a result of the disturbance the benthic assemblages were altered dramatically, with mean hard coral cover reduced to <10%. The only hard corals remaining were the more robust and encrusting types. On the most affected reefs at One Tree Island and Lady Musgrave Island, the benthos was reduced to scoured pavement (Fig. 3a). For five years following the disturbance, hard coral cover remained low and turf algae dominated the benthos. However, between 1992 and 1996 hard coral cover began to increase exponentially (Figs. 2a, 3b), returning to pre-disturbance levels by 1998 (1987 vs. 1998,  $P = 0.135$ ; Fig. 3c), with tabulate *Acropora* again dominant. Soft corals also declined after the disturbance, but had returned to their low yet stable pre-impact levels by 1995 (Fig. 2a). By way of comparison, coral cover data collected prior to and following a major crown-of-thorns-starfish outbreak in the central GBR showed a similar pattern of decline and recovery to this study (Fig. 2a, c).

### *Changes in fish assemblages*

*Species richness.*—In 1983, approximately five years prior to the disturbance, species richness of the fish

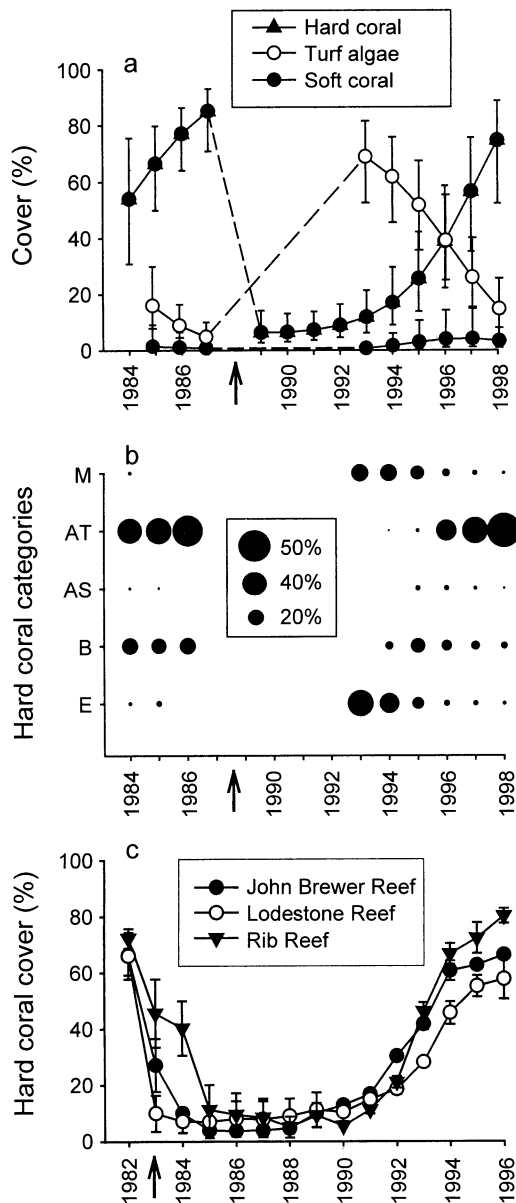


FIG. 2. (a) Percent cover of hard coral, soft coral, and turf algae on five reefs in the Capricorn Bunker sector. Values are estimated means and 95% confidence intervals calculated from the mixed linear models. (b) The relative contribution of the main hard coral morphologies to total coral cover in the Capricorn Bunker sector. Coral codes: M, massive; AT, *Acropora* tabulates; AS, *Acropora* submassives; B, branching; E, corals encrusting. (c) Percent cover of hard coral from three reefs in the central Great Barrier Reef subject to a crown-of-thorns outbreak in 1983–1984 (means  $\pm$  1 SE) (D. McB. Williams, unpublished data). In each panel, the arrow indicates the timing of the disturbance.

families Acanthuridae, Chaetodontidae, Scaridae, and Pomacentridae was similar between the Capricorn Bunker and Swains sectors. By 1992, three years after the disturbance, the species richness of all four families had fallen significantly within the Capricorn Bunker sector

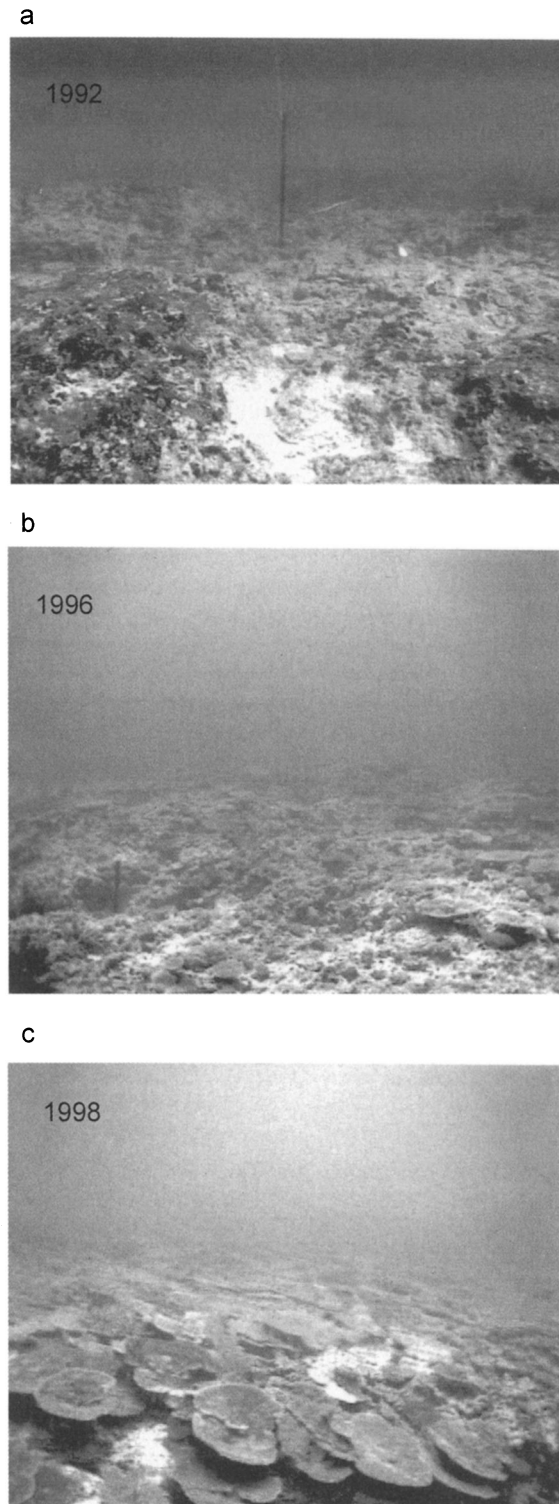


FIG. 3. Video frames of the beginning of Site 1 at One Tree Reef in the Capricorn Bunker sector from (a) 1992, (b) 1996, and (c) 1998. This reef was one of the most badly damaged during the disturbance, and this sequence illustrates the rapid regrowth of corals.

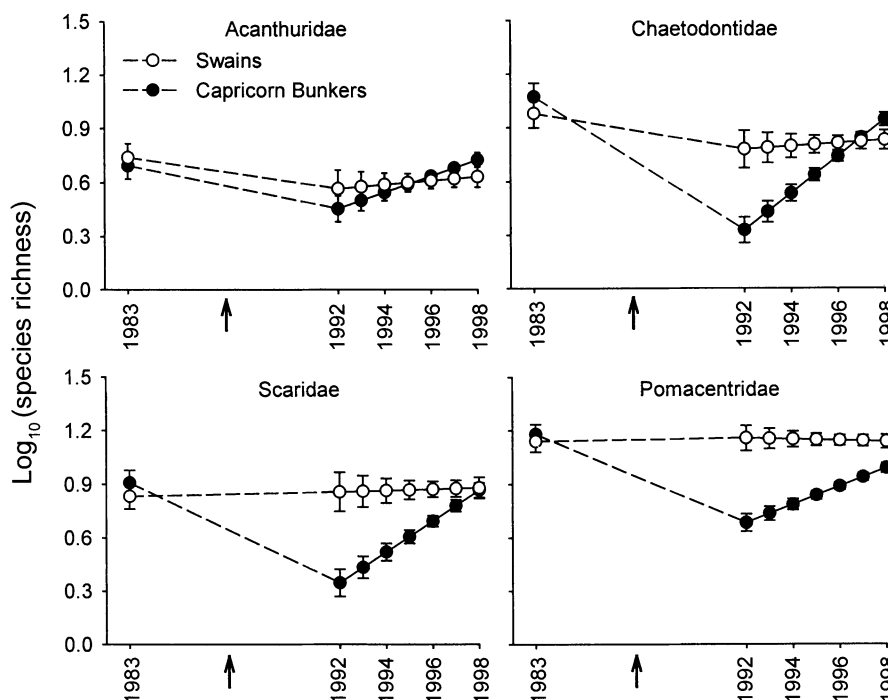


FIG. 4. Species richness of Acanthuridae, Chaetodontidae, Scaridae, and Pomacentridae in the Capricorn Bunker and Swains sectors between 1983 and 1998. No data were available between 1984 and 1991. Values are estimated means and standard errors calculated from the mixed linear models. Arrows indicate the timing of the disturbance.

(Fig. 4). This decrease was not mirrored in the Swains reefs, where species richness values remained stable over the entire period of this study (Fig. 4). The Chaetodontidae suffered the greatest decrease, with species richness falling by 83% from an estimated mean of 12 species in 1983 to two species in 1992 ( $P = 0.0001$ ). Also strongly affected were the Scaridae and Pomacentridae, with a 75% and 67% drop, respectively ( $P = 0.0001$  for both). The Acanthuridae did not fare as badly, with a 40% drop ( $P = 0.0075$ ) in species richness over the same period. Seven years later, recovery was complete for three of the four families, with species richness levels in 1998 not significantly different from pre-disturbance levels. The Acanthuridae had actually recovered their pre-impact levels by 1995, while the Chaetodontidae and Scaridae did not recover their pre-impact richness until 1998. The Pomacentridae were slow to recover, with species richness levels in 1998 still significantly less ( $\sim 35\%$ ) than before the disturbance.

**Abundance.**—While the abundance of fishes on the disturbed Capricorn Bunker reefs varied markedly over the study period, only two species showed significant changes on the reference (Swains) reefs (Table 2). One species of herbivorous damselfish (*Chrysiptera rex*) decreased in abundance during 1992–1998, and one species of planktivorous damselfish (*Pomacentrus coelestis*) was significantly lower in abundance at the beginning than at the end of the study. Importantly, no species differed in abundance on the reference reefs

between the pre-disturbance count in 1983 and the first count post-disturbance in 1992.

On the impact (Capricorn Bunker) sites, 11 of 19 species analyzed for pre- and post-impact changes decreased significantly in abundance following the disturbance: 1/4 acanthurids (*Ctenochaetus* spp.); 2/3 chaetodontids (*Chaetodon rainfordii*, *C. trifascialis*); 3/3 scarids (*Scarus chameleon*, *S. globiceps*, *S. psittacus*); 4/4 labrids (*Gomphosus varius*, *Halichoeres hortulanus*, *Hemigymnus fasciatus*, *H. melapterus*); and 1/5 pomacentrids (*Pomacentrus lepidogenys*). Only one species, *Pomacentrus coelestis*, increased in abundance following the loss of live coral (Table 2).

Over the “recovery” period from 1992 to 1998, 59% of fish taxa increased in abundance as coral cover increased from less than 10% to over 70%. This increase included all but one (*Halichoeres hortulanus*) of the 11 species that decreased following the disturbance, plus four species whose abundance prior to the disturbance was unknown (*Acanthurus nigrofasciatus*, *Chaetodon kleinii*, *C. plebius*, and *Pomacentrus bankanensis*). Four species showed no significant change in abundance during the entire study (*Naso unicornis*, *Pomacentrus wardi*, *Chrysiptera rex*, and *Neopomacentrus azysron*). Another four species whose abundance prior to the disturbance was also unknown showed no change in the recovery phase (*Chaetodon flaviviridis*, *Scarus sordidus*, *Chromis nitida*, and *Pomacentrus australis*). Only two species declined in abundance during

TABLE 2. Comparisons between pre- and post-impact fish abundance levels for the Capricorn Bunker reefs (impact) and the Swains reefs (reference).

Family and species	Trophic group	Capricorn Bunker			Swains		
		1983–1992	1983–1998	1992–1998	1983–1992	1983–1998	1992–1998
Acanthuridae							
<i>Acanthurus dussumieri</i>	su	NS	NS	0.0034↓	NS	NS	NS
<i>A. nigrofuscus</i>	lc	...	...	0.0019↑	...	...	NS
<i>Ctenochaetus</i> spp.	su	0.0001↓	0.0017↓	0.0418↑	NS	NS	NS
<i>Naso unicornis</i>	lc	NS	NS	NS	NS	NS	NS
<i>Zebrasoma scopas</i>	lc	NS	NS	0.0101↑	NS	NS	NS
Chaetodontidae							
<i>Chaetodon citrinellus</i>	si	NS	NS	0.0041↑	NS	NS	NS
<i>C. flavirostris</i>	si	...	...	NS	...	...	NS
<i>C. kleini</i>	si	...	...	0.0001↑	...	...	NS
<i>C. plebius</i>	cf	...	...	0.004↑	...	...	NS
<i>C. rainfordi</i>	si	0.0001↓	0.0498↓	0.0001↑	NS	NS	NS
<i>C. trifascialis</i>	cf	0.0009↓	NS	0.0001↑	NS	NS	NS
Scaridae							
<i>Scarus chameleon</i>	sp	0.0071↓	NS	0.008↑	NS	NS	NS
<i>S. globiceps</i>	sp	0.0012↓	NS	0.041↑	NS	NS	NS
<i>S. psittacus</i>	sp	0.0054↓	NS	0.0028↑	NS	NS	NS
<i>S. sordidus</i>	sp	...	...	NS	...	...	NS
Labridae							
<i>Gomphosus varius</i>	mi	0.0001↓	NS	0.0001↑	NS	NS	NS
<i>Halochoeres hortulanus</i>	si	0.0172↓	NS	NS	NS	NS	NS
<i>Hemigymnus fasciatus</i>	si	0.0017↓	NS	0.0091↑	NS	NS	NS
<i>H. melapterus</i>	si	0.0011↓	NS	0.0015↑	NS	NS	NS
Pomacentridae							
<i>Chromis nitida</i>	zp	...	...	NS	...	...	NS
<i>Chrysiptera rex</i>	sc	NS	NS	NS	NS	NS	0.0245↓
<i>Neopomacentrus azyron</i>	zp	NS	NS	NS	NS	NS	NS
<i>Pomacentrus bankanensis</i>	sc	...	...	0.0015↑	...	...	NS
<i>P. coelestis</i>	zp	0.0075↑	NS	0.0733↓	NS	0.0001↓	NS
<i>P. lepidogenys</i>	om	0.0016↓	NS	0.0084↑	NS	NS	NS
<i>P. wardi</i>	sc	NS	NS	NS	NS	NS	NS

Notes: Significance is at  $P \leq 0.05$ . Key: NS, not significant; ..., no data available; ↓↑, direction of significant change. Trophic codes (after Williams [1983]): cf, hard coral feeder; mi, motile invertebrate feeder; lc, large cropper (algae); om, small omnivore; sc, small cropper (algae); sp, scraper (algae); zp, small zooplankton feeder; su, sucker (algae); si, sessile invertebrate feeder.

the period 1992–1998 (*Acanthurus dussumieri* and *Pomacentrus coelestis*).

By 1998, the abundance of only one species and one species group (*Chaetodon rainfordi* and *Ctenochaetus* spp.) differed significantly from their pre-disturbance levels (Fig. 5). While the *Ctenochaetus* group appeared to be some way from complete recovery, the pre-disturbance abundance counts were inflated by the inclusion of *Acanthurus nigrofuscus* among the *Ctenochaetus* spp. While it was not possible to separate *A. nigrofuscus* from the pre-impact counts the naturally high abundance of this species implies that recovery would have been nearly complete by 1998 for the *Ctenochaetus* spp.

#### Rates of recovery

The first post-disturbance counts began 3–4 years after the loss of coral, when coral cover was still very low. The timing of increases in fish abundance post-disturbance varied among species, with little or no consistent patterns within families or genera (Fig. 5). A few species maintained significant increases in rates of change over an extended period of five or more years (*Chaetodon kleinii*, *C. trifascialis*, *C. rainfordi*, and *Gomphosus varius*), while other species showed significant increases only over a relatively brief period (*Chaetodon plebius*, *Scarus psittacus*, *Hemigymnus melapterus*, *H. fasciatus*, and *Pomacentrus lepidogenys*). By the end of the study in 1998, 50% of species

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FIG. 5. Abundance of selected fish species from reefs in the Capricorn Bunker and Swains sectors between 1983 and 1998. No data were available between 1984 and 1991. Values are estimated means and standard errors as calculated by the mixed linear models. Horizontal lines along the x-axis link years where the rate of change was significantly greater than 0 (at  $P < 0.05$ ) in the Capricorn Bunker sector. Arrows indicate the timing of the disturbance.



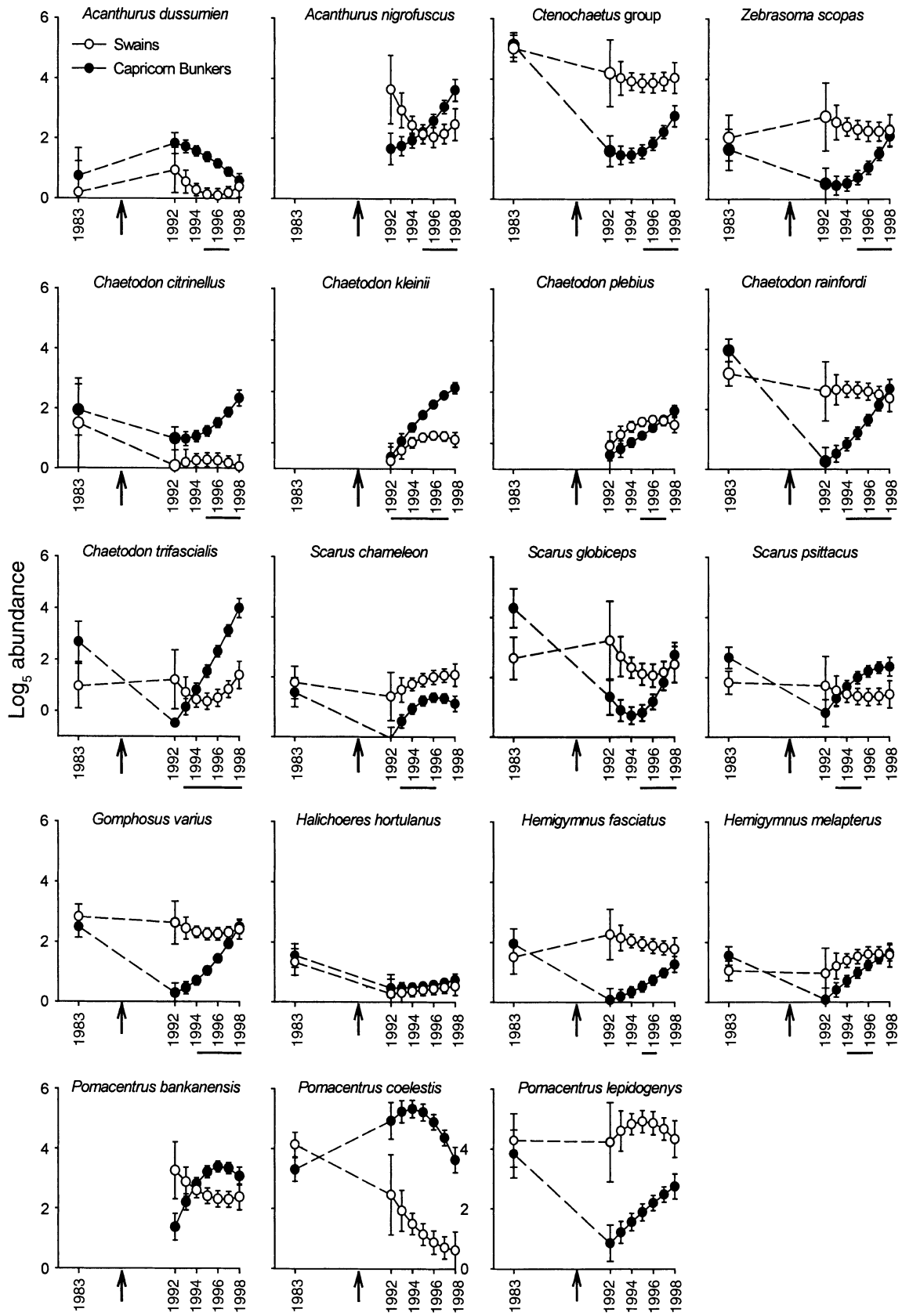


TABLE 3. Relative abundance of those species accounting for 90% of the total abundance of chaetodontids and pomacentrids for 1984 (pre-impact), 1992 (immediate post-impact), and 1998 (nine years post-impact).

Family and species	Relative abundance (%)					
	Pre-disturbance 1984		Post-disturbance			
			1992		1998	
	LM	OT	LM	OT	LM	OT
Chaetodontidae						
<i>Chaetodon auriga</i>	...	...	3.7	28.57	...	...
<i>C. baronessa</i>	...	1.87	...	...	...	...
<i>C. citrinellus</i>	4.95	1.87	29.63	28.57	8.76	...
<i>C. flaviviridis</i>	3.2	4.1	7.41	14.29	...	8.26
<i>C. kleinii</i>	3.49	4.1	14.81	28.57	13.92	7.8
<i>C. lineolatus</i>	...	...	3.7	...	...	...
<i>C. melannotus</i>	...	11.94	...	...	...	6.42
<i>C. ornatissimus</i>	...	...	...	...	4.12	...
<i>C. pelewensis</i>	5.82	...	18.52	...	...	...
<i>C. plebeius</i>	4.08	6.34	...	...	...	5.96
<i>C. rainfordi</i>	27.66	35.45	...	...	6.19	27.52
<i>C. trifascialis</i>	27.66	18.66	...	...	46.91	37.16
<i>C. trifasciatus</i>	5.82	5.22	...	...	4.64	...
<i>C. unimaculatus</i>	2.33	...	...	...	...	...
<i>C. vagabundus</i>	...	...	7.41	...	...	...
<i>Forcipiger</i> spp.	4.95	...	14.81	...	4.64	...
Pomacentridae						
<i>Chromis atripectoralis</i>	46.85	19.18	...	...	...	...
<i>Neopomacentrus azysron</i>	25.55	17.97	3.18	...	3.47	...
<i>Pomacentrus coelestis</i>	14.85	25.52	77.57	98.77	75.07	80.92
<i>P. moluccensis</i>	4.92	...	...	...	...	...
<i>P. lepidogenys</i>	3.73	...	6.54	...	9.07	...
<i>C. nitida</i>	...	35.56	...	...	...	8.78
<i>C. margaritifera</i>	...	...	2.06	...	...	...
<i>P. bankanensis</i>	Not included in census		5.42	...	4.13	6.03

Notes: Data are for Lady Musgrave (LM) and One Tree (OT) Island reefs. Ellipses (---) indicate that no individuals were counted.

were still increasing significantly. The one exception to the consistently positive rate of recovery was *P. coelestis*, which declined significantly in abundance from 1996 to 1997.

#### Changes in community structure

The butterflyfishes (Chaetodontidae) and damselfishes (Pomacentridae) underwent changes in community structure as a result of the severe loss of coral cover. The pre-disturbance communities of butterflyfish on Lady Musgrave Island and One Tree Island reefs (the two most heavily impacted reefs) were dominated by *Chaetodon rainfordi* and *C. trifascialis* (Table 3). Both species were absent in the first surveys post-disturbance, but by 1998, *C. trifascialis* was again numerically dominant on both reefs while *C. rainfordi* had recovered its numerical dominance on One Tree Island, but not Lady Musgrave Island. In 1992, when coral cover was very low, *C. citrinellus* was the numerically dominant butterflyfish on both reefs while *C. auriga* and *C. kleinii* were also dominant at One Tree Island. This dominance of a different suite of butterflyfish species during the years immediately following the disturbance was due to the absence of previously

dominant species rather than any positive numerical response by the remaining species. Nevertheless, both *C. citrinellus* and *C. kleinii* increased in abundance from 1992 to 1998 (Fig. 5) as live coral cover increased, but their relative dominance in the butterflyfish assemblage decreased (Table 3).

Prior to the disturbance, the most numerically abundant damselfishes on Lady Musgrave Island and One Tree Island reefs were *Chromis atripectoralis*, *Neopomacentrus azysron*, *Pomacentrus coelestis*, and *Chromis nitida*, although the latter species was only present on One Tree Island (Table 3). By 1992, these species had either disappeared completely or been reduced to a minor proportion of the surviving assemblage. At the end of this study in 1998, the situation remained mostly unchanged from 1992, with minor recovery of these species or none at all. The one exception to this pattern was *P. coelestis*, which actually increased in abundance after the disturbance and remained the overwhelmingly abundant damselfish for the remainder of this study.

#### Fish-habitat correlations

For those families and genera investigated, the majority of variation in the data was due to sampling-

TABLE 4. Percentage of variation in the abundances of dominant families and genera of reef fishes accounted for by benthic cover and temporal trends in the multiple regression model.

Family or genus	Overall effects		Within benthic/temporal effects			
	Blocking	Benthic/ temporal	Hard coral	Soft coral	Turf algae	Temporal trend
Acanthuridae	94.7	2.9	NS	NS	NS	NS
Chaetodontidae	63.6	36.4	86.5	NS	NS	NS
Scaridae	75.6	24.4	84.2	1.7	10.7	4.1
Labridae	74	26	81	5	8	NS
<i>Chromis</i>	64	36	76	NS	10.6	NS
<i>Pomacentrus</i> (minus <i>P. coelestis</i> )	83.7	16.3	NS	45.9	25.2	NS

Note: NS, not significant.

design effects, although there were considerable family differences in the strength of this relationship (Table 4). Benthic variables and/or temporal trends explained very little of the variation in abundance of the Acanthuridae, with >90% of the variation attributable to sampling-design effects. For the Chaetodontidae, Labridae, and Scaridae, 36%, 26%, and 24% of the variation in abundance, respectively, could be explained by benthic/temporal trends, with most of the variation (>80%) directly attributable to changes in hard coral cover alone. For the Chaetodontidae, changes in hard coral cover explained virtually all the variation (86.5%), whereas for the Labridae and Scaridae, a small but significant correlation was also present with soft coral and turf algae. Furthermore, the temporal trends for the Scaridae were significant, suggesting a trend in abundance over time divorced from the effects of the benthic variables investigated. Of the two damselfish genera examined, benthic/temporal trends explained over twice as much of the variation in abundance of *Chromis* compared with *Pomacentrus*. For *Chromis*, 76% of this variation was explained by hard coral cover and 10% by turf algae. *Pomacentrus* showed no correlation with hard coral cover but rather an association with soft coral and turf algae.

#### DISCUSSION

Benthic and fish assemblages in the southern GBR displayed a high degree of resilience to major storm activity. Despite catastrophic habitat losses, within 10 years hard coral cover and the species richness and abundance of most fish taxa had recovered to be virtually indistinguishable from pre-impact values. Given that these assemblages were situated on various reefs spread over 80 km, the coherency in response to the disturbance event at this scale provides supporting evidence of stability at large scales of space and time and suggests substantial resilience of meta-reef systems to natural disturbance (see also Bythell et al. [2000] and Ninio and Meekan [2002]). The decadal time frame of this response was similar to benthic and fish community recovery periods in other studies (Connell 1997, Ninio et al. 2000, Sano 2000).

#### Resiliency in coral assemblages

The loss of live coral cover on the northeast reef slopes of the Capricorn Bunker reefs in the late 1980s was extreme: from >80% cover to <10%. Although damage was recorded to other reef zones, it was minimal in more protected areas (see I. R. Miller, A. A. Thompson, V. J. Baker, D. K. Bass, and C. A. Christie, *unpublished manuscript*). This "patchiness" in storm damage is common and results in undamaged areas remaining as sources for future renewal of the damaged areas (Bythell et al. 2000, Ninio et al. 2000). The extent of the damage was most likely due to the vulnerable state of the reefs immediately prior to the disturbance: a combination of high percentage cover of coral and the dominance of relatively fragile tabulate acroporid corals. The proportion of cover lost during a severe storm is usually greater the higher the cover just before the storm (Connell et al. 1997), and the morphological form of tabulate corals makes them especially susceptible to the shearing forces generated by wave action from such storms (Massel and Done 1993).

Recovery of hard corals was negligible until 1995, when cover increased rapidly, reaching pre-impact levels by 1998. The recovery of the hard coral community was precipitated by two factors. First, large areas of undamaged reef (i.e., northern flanks and back reef zones) with high coral cover provided a substantial source of new recruits for recolonization. Second, the regenerating assemblages were dominated by tabulate *Acropora* species. The characteristics of rapid growth and competitive dominance in these species ensured that, once started, coral recovery was relatively quick (Stimson 1985, Baird and Hughes 2000). However, despite overall hard coral cover recovering to pre-impact levels by the end of the study, branching corals were still underrepresented compared to the late 1980s. Hence overall structural heterogeneity in 1998 remained below pre-impact levels.

In the absence of anthropogenic effects, coral assemblages subject to acute "natural" disturbances have been found to recover to previous levels of cover within a decade (Connell 1997). One of us (D. McB. Williams) monitored fish and coral assemblages on reef slopes

dominated by tabulate *Acropora* species in the central section of the Great Barrier Reef, following a crown-of-thorns outbreak in 1982/1983. Recovery of coral cover to pre-impact levels took 12 years and, similar to our observations, initial recovery was slow but accelerated greatly after seven years. Hard corals also recovered from an extensive COTS outbreak at Iriomote Island in Japan over a similar period of time (Sano 2000).

The rate and maximum extent of recovery from disturbance is usually a function of the history of previous damage and recovery (Connell et al. 1997, Hughes and Connell 1999). Large-scale disturbance may therefore be a regular feature on the northeast flanks of the Capricorn Bunker reefs. Drilling and monitoring studies have shown that there is little windward accretion on reefs within the Capricorn Bunkers, indicative of a high-energy environment (Davies and Marshall 1979, 1980). Moreover, recent examination of detrital ridges on a series of sites spanning the length of the Great Barrier Reef has also indicated that highly destructive storms are much more common than was previously thought (Nott and Hayne 2001).

#### *Resiliency in fish assemblages*

Given the removal of such a large amount of coral from the northeast reef flanks, it is not surprising there was such a significant impact on the fish assemblages. Recent studies have indicated that habitat structure exerts significant influence on reef fish assemblage composition, rather than coral cover per se (see Lewis [1997], Syms [1998], Syms and Jones [2000]). However, these studies did not encounter a situation where live coral cover was providing most of the habitat. They found the underlying reef matrix was more influential in determining fish assemblage structure and as such moderated disturbance effects to live coral. However, as hard corals provided most of the structure on the northeast flanks of the Capricorn Bunker reefs (see Fig. 3), their removal should have had much greater effects on the fish assemblage than if underlying substrate was providing most of the complexity. Our results support this conclusion, but unfortunately, the lack of underlying structural heterogeneity also means that the role of habitat vs. coral per se was confounded and the relative roles of these two factors could not be separated.

Although our results clearly showed the extent of the response by the fish community to the disturbance, observational studies cannot easily separate the relative influences of processes such as recruitment, competition, predation, and migration in the recovery process. Nevertheless, inferences can still be made. A separate study of the same disturbance and its effects on fish recruitment, to the same reef areas as in our study, found that by 1995–1996 recruitment of most fish was neither lower, nor less diverse, than during the pre-impact period (Doherty et al. 1997). However our re-

sults indicated that a large part of the changes we observed occurred after 1996; hence recruitment alone would not have been sufficient to generate a full recovery of the fish assemblages.

Post-recruitment processes also have great potential to significantly influence patterns established at settlement (see Jones [1991] and Hixon [1991] for a review). From 1996 onwards, the recovering benthic assemblages (principally hard coral cover) were increasing biogenic habitat at an exponential rate. This growth in turn provided an increasingly greater diversity and abundance of refuges for fish. As the strength of ecological interactions can be mediated by habitat (Hixon and Beets 1993, Caley and St John 1996, Friedlander and Parrish 1998), reduced post-recruitment mortality rates via competition and predation may have allowed for the coexistence of more individuals and species, subsequently enhancing the recovery process. This situation would also encourage immigration by juveniles and adults of those species that were able to do so (Walsh 1983, Ault and Johnson 1998). Regardless of the relative roles of settlement and immigration post-settlement, our data suggest a strong role of habitat in the recolonization process. Although the majority of variation in fish abundances was due to sampling design effects, between 20% and 40% of the variance was explainable by changes in the benthos. This is comparable to the amount of variation explained by experimental factors in similar studies conducted at much smaller scales (e.g., Lewis 1997, Syms and Jones 2000). Live coral acts as shelter and/or provides a food source either directly or indirectly by creating favorable conditions for other prey items to flourish. Scarids (parrotfishes), for example, use live coral principally as shelter (Randall et al. 1990). The increased coral cover after 1996 would have allowed species within this family to take advantage of the substantial feeding grounds still remaining by providing them with the necessary shelter from predation (see Hart et al. [1996]). Chaetodontids (butterflyfishes) are foremost among those species with strong affinities to coral, with some species recruiting, feeding, and sheltering in live coral (Allen et al. 1998). Because of their affiliations these taxa could also be expected to be very sensitive to gross changes in coral cover, as was the case in this study.

Of the families investigated, the Pomacentridae (damselfishes) demonstrated the most varied responses. They were also the only family that had not recovered to pre-impact levels by the end of this study. This lagged recovery may be due, in part, to the small-scale site attachment typical of most of the family (Randall et al. 1990). Between 1995 and 2000 overall species richness of fish assemblages on the disturbed areas in the Capricorn Bunkers increased from 76 to 92 (Sweatman et al. 2001) with approximately 40% of this increase within the Pomacentridae alone. Some species, such as *Chromis tripteralis*, which were abundant prior to

the disturbance, require branching corals for shelter as adults (Randall et al. 1990). Although total hard coral cover had recovered by 1998, branching corals were still only present in small amounts. These results are consistent with the idea of finer scale habitat changes happening more slowly through time, to provide the diversity of microhabitats necessary for the reestablishment and survival of a highly diverse family.

### Conclusions

Although the evolving view of coral reefs is about large-scale patterns and processes, these concepts are still mostly derived from the assembly and integration of smaller scale observations (Buddemeier and Fautin 2002). This study is one of the first to provide evidence, on a relatively large scale (14 years and tens of kilometers), of parity with much of the current theory on how marine communities are structured. The essentially stochastic nature of the disturbance, its variable effects in space and time, and the ultimate recovery of the benthic and fish assemblages to a documented, relatively stable state could all be accommodated under the theories of hierarchical patch dynamics (Wu and Loucks 1995), landscape ecology (Hobbs 1994), or metapopulation dynamics (Hanski 1998). Local devastation of parts of reefs is buffered at a metapopulation level by the connectivity within and between individual reefs (Doherty 1991, Fowler et al. 1992). These local populations and assemblages are at differing stages in a temporal continuum, the sum of which confers stability at larger scales. The asymptotic recovery trajectories of the coral and fish assemblages imply a ceiling beyond which increases will not continue. While this asymptote will vary within stochastically defined bounds (Connell and Sousa 1983), it is most likely set by processes operating at regional spatial scales and evolutionary temporal scales (Cornell and Karlson 1996, Caley 1997). While caution must be applied to extrapolating the results of this study beyond the system studied, we believe that similar results to studies from other systems and studies conducted at smaller scales offer evidence for generality of these results.

On a precautionary note, while similar resilience to large natural disturbances might be expected in other relatively healthy archipelagic reef systems, this outcome may not necessarily be the case in more isolated systems or those impacted by anthropogenic disturbances. The poor health of many of the world's coral reefs, due to a combination of overfishing, destructive fishing practices, and large-scale natural disturbance events like bleaching, storms, and disease (Wilkinson 1999), raises questions about the long-term resilience of coral reefs. Studies investigating the interplay of natural and anthropogenic factors over appropriately large scales of space and time (e.g., Hughes 1994) are necessary to understand and prevent future degradation of reefs.

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## APPENDIX

Details of the mixed linear models that were fitted independently to the benthic and fish data are available in ESA’s Electronic Data Archive: *Ecological Archives* E085-053-A1.