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Rapid increase in coral cover on an isolated coral reef, the Ashmore Reef National Nature Reserve, north-western Australia

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Abstract. Against a background of coral reef ecosystem decline, understanding the propensity for coral communities to recover after acute disturbances is fundamental to forecasting and maintaining resilience. It may be expected that offshore reef ecosystems are less affected by anthropogenic disturbances compared with reefs closer to population centres, but that recovery may be slower on isolated reefs following disturbances. To test the hypothesis that community recovery is slow in isolated locations, we measured changes in coral cover and relative abundance of coral genera over a 4 year period (2005–09) at Ashmore Reef, north Western Australia, following severe bleaching. The percent cover of hard coral tripled, from 10.2% (±1.46 s.e.) in 2005 to 29.4% (±1.83 s.e.) in 2009 in all habitats (exposed and lagoonal) and depth zones (2–5 and 8–10 m), and the percent cover of soft corals doubled, from 4.5% (+0.63 s.e.) in 2005 to 8.3% (+1.4 s.e.) in 2009. Significant shifts in the taxonomic composition of hard corals were detected. Our results imply that coral recovery in isolated locations can occur rapidly after an initial delay in recruitment, presumably through the interacting effects of self-recruitment and reduced exposure to additive impacts such as coastal pollution.

Additional keywords: Alcyoniina, coral bleaching, coral recovery, resilience, Scleractinia, temporal dynamics.

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Introduction

Coral reefs throughout the world are increasingly subject to multiple, often cumulative, threatening processes. In the long term, global climate change is regarded as the greatest threat to the viability of tropical coral reefs (Anthony *et al.* 2011). However, in the short term, local pollution, exploitation and habitat modification threaten the health and survival of coral reefs, particularly in the areas close to urban centres and large human populations (Cleary *et al.* 2006; van der Meij *et al.* 2010; Richards and Beger 2011). The cumulative effects of anthropogenic disturbance, natural disturbances and climate change are predicted to exacerbate the vulnerability of coral reefs and accelerate the rate at which widespread changes in ecosystem structure and functioning take place (Hoegh-Guldberg 2011).

Coral reefs isolated from urban centres are expected to provide critical refuges for the survival of coral reef organisms, although they are not immune from the large-scale effects of global climate change (Graham *et al.* 2010). In fact, isolated offshore coral reefs may be much more susceptible to climatic disturbances (compared with coastal reefs) because of limited opportunity for larval replenishment from nearby reefs (Graham *et al.* 2006; Smith *et al.* 2008). Isolated reefs are increasingly being shown to rely primarily on self-replenishment (Ayre and Hughes 2004; Underwood *et al.* 2009) and the extent to which the protection of these reefs from anthropogenic disturbances offsets the limitations imposed by isolation is unknown (Hughes *et al.* 2010).

Offshore coral reefs on the north-west shelf of Australia are isolated from urban centres and removed from coastal influences. However, like many other reefs in the Indian Ocean (Graham *et al.* 2006), reefs on the north-west shelf experienced severe bleaching in 1998 and 2003, culminating in devastating losses of coral cover (>80%) at Scott Reef (Smith *et al.* 2008). After 6 years (in 2005), the recovery of coral cover at Scott Reef

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was moderate but incomplete and an obvious shift in community structure had taken place (Smith *et al.* 2008). Most notably, there was a decline in the relative abundance of the previously dominant reef-building coral family Acroporidae and relative increases of massive corals within the Poritidae and Faviidae families (Smith *et al.* 2008).

The extent to which the 1998 bleaching event impacted Ashmore Reef has not been specifically documented. However, sea surface temperatures (derived from satellite information) show that corals at Ashmore Reef were exposed to abnormally high water temperatures during the first quarter of 2003 (NOAA 2010). A marine survey in 2003 concluded that coral cover declined between 2000 and 2003 as a result of coral bleaching (Rees *et al.* 2003). The purpose of this study was to assess the current status of coral communities at Ashmore Reef, to examine the extent of recent recovery and to ultimately forecast the resilience of coral assemblages at this isolated offshore reef. More specifically, we tested the hypothesis that coral recovery is slow at this isolated location, and we expected to find little change in coral cover at Ashmore Reef in the 4 years since 2006.

Materials and methods

Study sites and sampling protocol

Ashmore Reef (12°17′S, 123°02′E) is an exposed open-ocean platform reef on the north-western edge of the Sahul Shelf in north-west Australia, ~350 km from the Kimberley coastline. The reef boundary encloses an area of ~583 km^2 with three small vegetated islands (East, Middle and West Islands), several sand cays, two lagoons and extensive reef flats covering an area of 239 km^2 (Fig. 1). The nearest reef systems include the fringing reefs of Roti (Timor) ~150 km to the north and Scott Reef, ~220 km to the south-west.

Throughout the last decade (1999–2009), three field surveys that aimed to quantify coral cover and composition (Skewes *et al.* 1999; Kospartov *et al.* 2006; Richards *et al.* 2009) have been conducted at Ashmore Reef. From 2005 onwards, a standard methodology was established. The methods used in 1999 were inconsistent with later methods; the 1999 results are therefore used here to provide a qualitative background against which we discuss recent community changes.

In 2005 and 2009, three replicate 50 m point-intercept transects, with 100 uniformly distributed points (50 cm apart) per transect were used to estimate benthic cover, as utilised in extensive regional surveys of coral reef habitats on the Great Barrier Reef and throughout the Indo-Pacific (Pratchett *et al.* 2008). All corals underlying the survey points were identified to genus. Additionally, all corals were identified to species within a 2 m belt along the same transect. Three replicate transects were deployed within two depth zones, i.e. the reef slope or deep lagoon (8–10 m depth) and reef crest or shallow lagoon (3–5 m depth). Six sites were surveyed around Ashmore Reef, encompassing exposed (South and South-west), sheltered (East and North) and lagoonal (Lagoon and Middle Lagoon) habitats.

Statistical analyses

To test the hypothesis that coral recovery on an isolated coral reef is slow, the variation in average coral cover (both among sites and among years) was analysed using ANOVA following square root–arcsine transformation of proportional cover. The taxonomic composition of coral assemblages was then analysed using multivariate analyses (MANOVA and MDS) to explore changes between the 2005 and 2009 surveys.

We calculated the geometric rate of change (CRg) in coral cover according to Côté *et al.* (2005), using the following formula:

$$CRg = 100 \times (1 - (PCa/PCb)^{1/d}), \qquad (1)$$

where PCa and PCb represent the coral cover at the end and beginning of the study period, respectively, and d is the duration of the study in years.

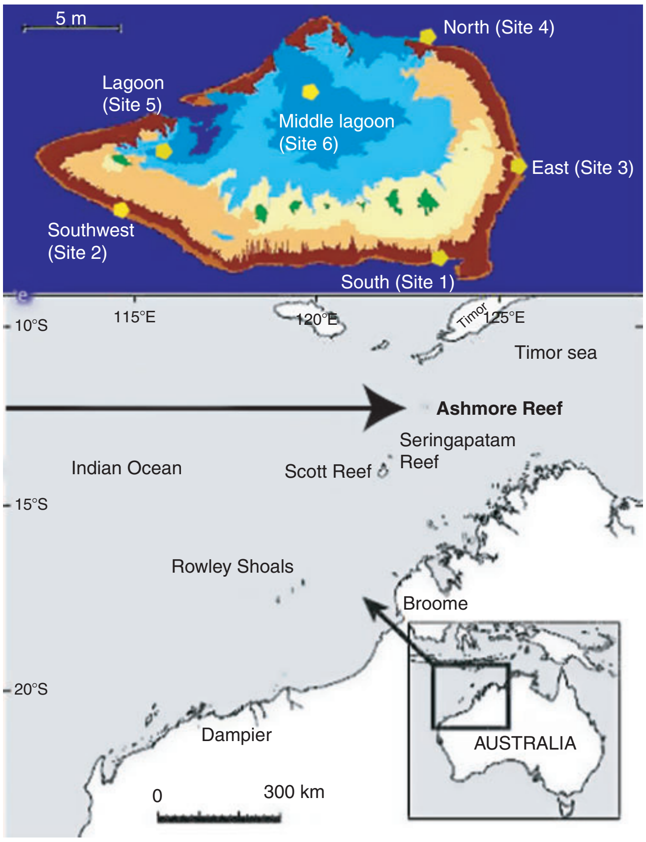

Fig. 1. Map of Ashmore Reef with sites surveyed in 2005 and 2009. Habitats are: dark brown: reef slope; orange: reef flat; yellow: shallow lagoon; green: islands and exposed reef flat; light blue: intermediate lagoon; dark blue: deep lagoon.

Results and discussion

Changes in percent cover

The percent cover of live hard coral at Ashmore Reef tripled, from 10.2% (±1.46 s.e.) in 2005 to 29.4% (±1.83 s.e.) in 2009 (Fig. 2), with a mean annual geometric rate of increase of 30.4%. The percent cover of soft corals doubled, from 4.5% (±0.63 s.e.) in 2005 to 8.3% (±1.4 s.e.) in 2009, with a mean annual geometric rate of increase of 21.6%. Coral cover varied significantly among sites, and was consistently higher in 2009 than 2005 at all sites and depth zones (Fig. 3). In 2009, the mean cover of hard corals at the six sites surveyed at Ashmore Reef ranged from 13.6% (±6 s.e.) at the shallow Middle

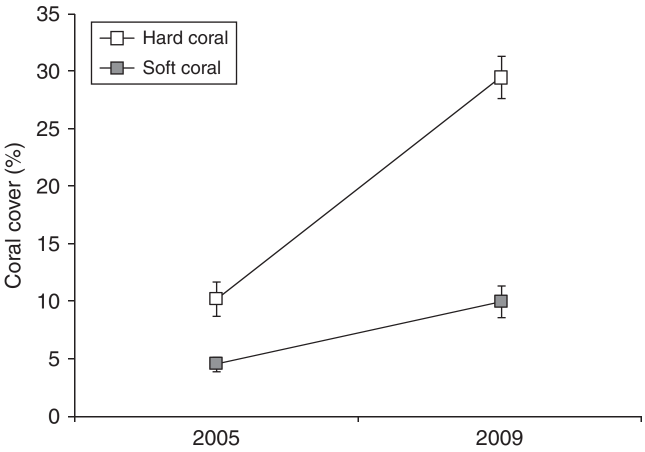

Fig. 2. Change in mean percent cover of live hard and soft coral at Ashmore Reef between 2005 and 2009. Data for 2005 from Kospartov *et al.* (2006). Error bars indicate s.e.

lagoon site to peak at 41% (±1.2 s.e.) at the northern reef slope site.

There are no available estimates of coral cover for Ashmore Reef immediately preceding the 1998 bleaching, but it is likely that there was significant coral loss associated with this event, as was observed at nearby reefs (Smith *et al.* 2008). Coral cover typically takes 5–10 years to recover following major disturbances (e.g. Halford *et al.* 2004), but depends on the local abundance of mature breeding individuals and survivorship of broodstock. In 2005, a general absence of new recruits and large colonies and a high proportion of dead coral were noted at Ashmore Reef (Kospartov *et al.* 2006). By 2009, the establishment of juvenile *Acropora*, *Isopora*, *Fungia* and *Pocillopora* corals was apparent and this is reflected in the change in community composition (Fig. 4). Our findings suggest that it took at least 7 years for the new cohorts of coral to become established following the relatively low cover recorded in 1999 (Skewes *et al.* 1999).

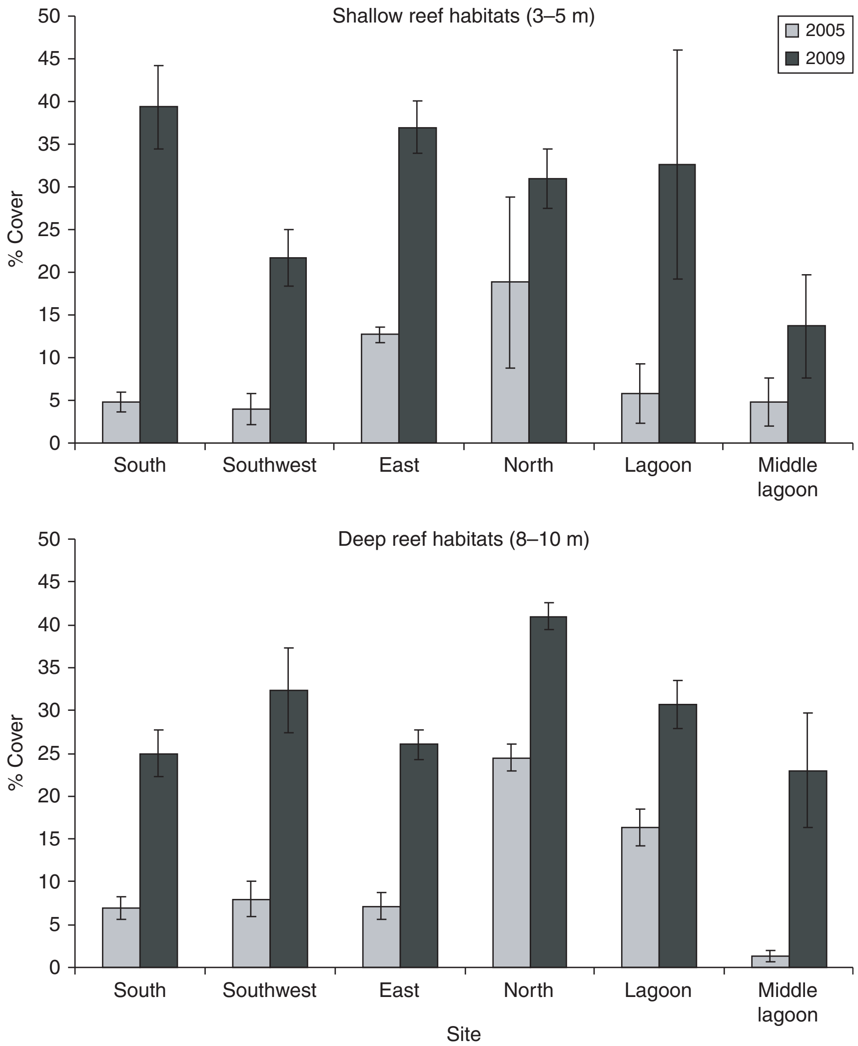

Fig. 3. Temporal comparison of hard coral cover for the reef crest and shallow lagoon (3–5 m) and reef slope and deep lagoon (8–10 m) comparing coral cover in 2005 (Kospartov *et al.* 2006) to comparable data from surveys at the same sites in 2009. Error bars indicate s.e.

Generally, isolation contributes to local population instability and increased risk of extinction by decreasing individual reproductive success or by increasing reproductive variance (Robertson and Butler 2009), which both undermine long-term species persistence (Worm *et al.* 2007). At Ashmore Reef, recovery in coral cover recorded from 2005–09 was rapid (e.g. compared with Graham *et al.* 2011), but overall recovery was severely delayed. It appears likely that recent recovery was driven by gradual accumulation of new recruits during the 7 years from 1998 to 2005, which have only recently begun to contribute to local population replenishment; reef-building corals such as *Acropora* are not sexually mature until ~5 years of age. Further unimpeded recovery is needed before the effective size of the population will increase (i.e. number of breeding individuals, for further discussion of effective population size see Frankham *et al.* 2002).

However, recovery has been recorded in similar areas; the recorded geometric rate of recovery at Scott Reef (~220 km to the south-west of Ashmore Reef) was 10.5% over 6 years (Smith *et al.* 2008). A study on coral reef recovery after an outbreak of *Acanthaster planci*, the corallivorous starfish, reported an overall annual rate of increase of 0.8–4% for multiple reefs of the Great Barrier Reef (Lourey *et al.* 2000). In Moorea, coral cover increased ~5.8% per year despite repeated disturbances (Adjeroud *et al.* 2009). In the Chagos Archipelago, Indian Ocean, there was evidence of rapid recovery (based on high levels of coral recruitment) in the aftermath of the 1998 bleaching (Sheppard *et al.* 2002). The reporting of coral recovery

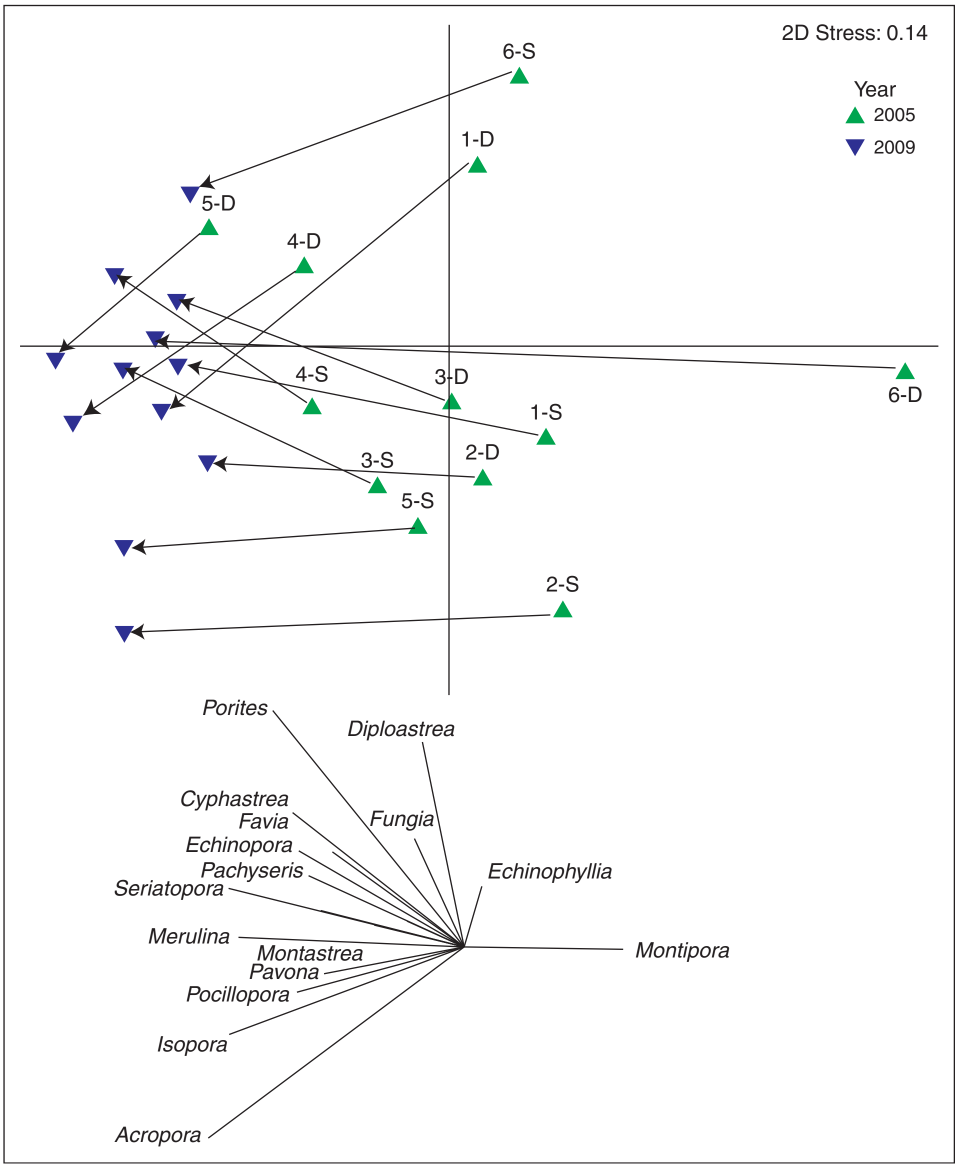

Fig. 4. Non-metric multidimensional scaling (MDS) of community changes in hard corals between 2005 and 2009 at Ashmore Reef. Arrows show the magnitude and trajectory of change at each site (S: 3–5 m; D: 8–10 m). Vectors show the genera most influential in driving the changes (correlation of 0.4 and above).

Table 1. ANOVA for community structure of total hard coral cover, testing for differences between 2005 and 2009 among sites and depth at Ashmore Reef

Proportional cover of corals was arcsine (square-root (*x*)) transformed to improve normality and homoscedasticity

	df	*F*-value	*P*-value
Year	1	60.52	<0.001
Site	3	6.80	<0.001
Depth	1	0.63	0.432
Year × site	3	0.86	0.466
Year × depth	1	0.06	0.802
Site × depth	3	1.42	0.246
Year × site × depth	3	0.22	0.879
Error	56	–	–

Table 2. MANOVA for community structure of hard corals (based on 32 genera), testing for differences between sites and depth at Ashmore Reef between 2005 and 2009

Proportional cover of corals was arcsine (square-root (*x*)) transformed to improve normality

	Pillai's Trace	*F*-value	Effect df	Error df	*P*-value
Year	0.95	12.72	33	24	<0.001
Site	2.41	3.24	99	78	<0.001
Depth	0.85	4.03	33	24	<0.001
Year × site	2.17	2.05	99	78	<0.001
Year × depth	0.70	1.74	33	24	0.081
Site × depth	2.07	1.76	99	78	0.005
Year × site × depth	2.09	1.80	99	78	0.004

trajectories is rare, but previous records of rates of coral cover increase suggest that an increase of 30.4% per year is unusually rapid.

Changes in community composition

Long-term records of changes in composition are rare, and most document coral decline in the decade following disturbance. On the Great Barrier Reef, for example, a general lack of recovery has been reported for some reefs (Cheal *et al.* 2010) and disturbances are causing increasing shifts in community structure (Wakeford *et al.* 2008). At Ashmore Reef, changes in community structure have also accompanied the increase of coral cover between 2005 and 2009 (Tables 1, 2; Fig. 4). There was a significant decline in *Montipora* spp., but a relative increase in several important reef-building genera such *Acropora*, *Isopora* and *Pocillopora* at shallow sites and *Porites* and *Favites* at deeper sites. The largest increases in cover occurred in those genera that were already relatively common in 2005 (Fig. 5), suggesting that recovery is primarily driven by self-recruitment and regrowth of fragments or colonies that suffered only partial mortality (see also Smith *et al.* 2008).

There are inherent differences in the susceptibility or resilience of corals to climatic disturbances, such that coral species may become locally and globally extinct at different times (Burt *et al.* 2008; Riegl and Purkis 2009). Previous studies describing coral community disturbance and subsequent recovery have found that the genera *Acropora* and *Pocillopora* are highly susceptible to storm damage, bleaching and corallivore outbreaks, but these are also often the taxa that rapidly recolonise bare substrates (Burt *et al.* 2008). In contrast, it is common for massive coral taxa such as *Porites* spp. and Faviidae to suffer only partial mortality, and for colonies to begin the recovery

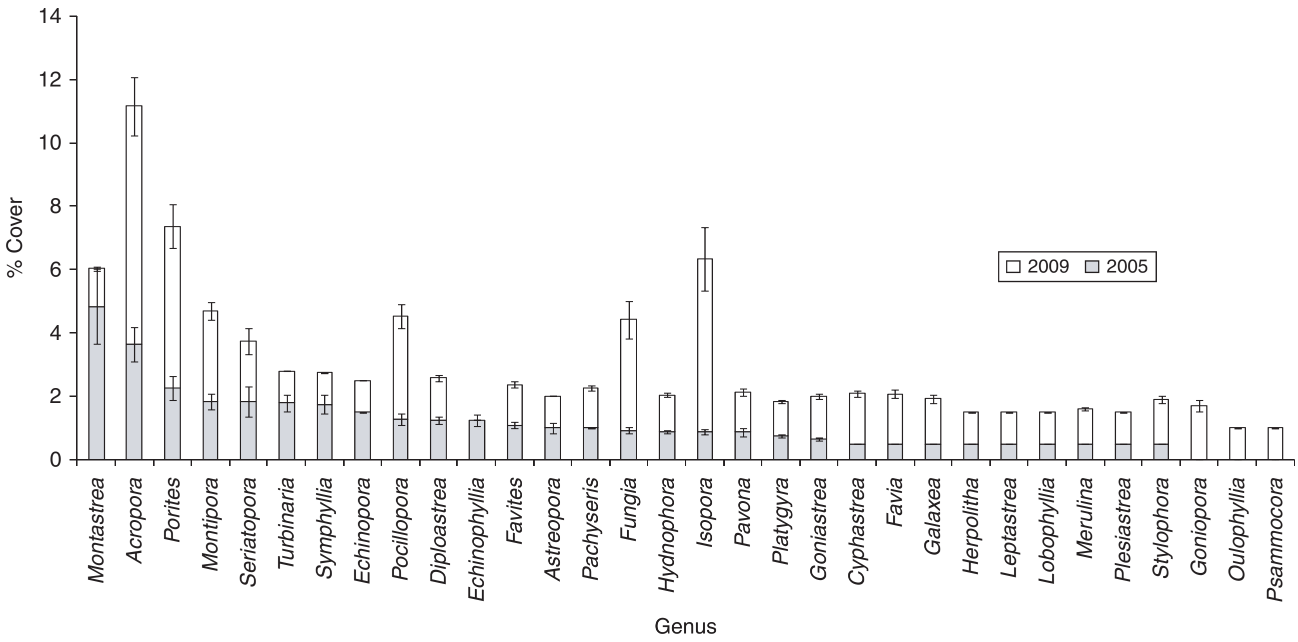

Fig. 5. Changes in the percentage cover of all coral genera between 2005 and 2009 at Ashmore Reef. Error bars indicate s.e.

process almost immediately after a disturbance (Brown and Suharsono 1990).

There is a shortage of quantitative baseline data about coral biodiversity at Ashmore Reef. We documented 186 species of scleractinian coral (zooxanthellate hermatypic hard coral) from 14 families and 51 genera in 2009, which brings the overall reef-building coral species inventory for Ashmore Reef to 275 species. Within a regional context, this places Ashmore Reef among the reefs with the highest coral diversity. To detect changes, depletions or extinctions in the biodiversity of corals at Ashmore Reef in the future, there is a need to not only maintain the current levels of reserve management, but to maintain quantitative species-level coral biodiversity monitoring in the standard survey protocol.

The results of the present study have important implications for the future of wider coral reef biodiversity on Ashmore Reef. For example, losses in live coral cover and structural complexity associated with coral degradation or shifts in community structure have been shown to cause losses in fish diversity and abundance (Jones *et al.* 2004; Graham *et al.* 2006). In particular, changes in the community composition of species that specialise on corals for food and shelter are likely to occur (Pratchett *et al.* 2008), leading to possible local extinctions (Pratchett *et al.* 2004). Specialist corallivores are intimately linked to the corals on which they feed and should these species decline in abundance, primary production by zooxanthellate corals will effectively be lost from coral food webs (Glynn 2004).

Conclusions: coral reef resilience

Many reef systems appear to be experiencing systematic declines in live coral cover (Bellwood *et al.* 2004; Gardner *et al.* 2005) reflecting widespread ecosystem degradation and unprecedented rates of biodiversity loss (Pimm 2009), but this study has revealed sustained increases in the status of coral communities at Ashmore Reef. The resilience of coral communities at Ashmore Reef is likely to have been enhanced by its isolation and protection from anthropogenic disturbances. The consequences of shifts in coral community composition for other reef organisms depend on the resulting changes in structural complexity and spatial heterogeneity (Nyström *et al.* 2008; Graham *et al.* 2011). Those genera that are observed to have increased their representation at Ashmore Reef include branching corals, which add substantially to the complexity and heterogeneity of a reef, suggesting positive flow-on effects to the coral-associated biodiversity in future.

Isolated reefs are not immune from the increasing effects of global climate change (Sheppard 2009; Graham *et al.* 2011) and the long-term fate of isolated reefs such as Ashmore Reef will depend on the recurrence and severity of major disturbances relative to expected rates of recovery. Although isolation may lead to delays in coral recruitment, our study suggests that reducing the severity and geographic extent of anthropogenic disturbances will make a significant contribution to increasing the rate of coral community recovery from extreme climate events.

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