

Transplantation of corals into a new environment results in substantial skeletal loss in *Acropora tenuis*

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Abstract The degradation of coral reefs, specifically the loss of structural biomass created by coral skeletons, is an important issue in coral reef science. In this study, we give evidence for high skeletal loss in corals transplanted from a high turbidity environment to a low turbidity environment. Specifically, we show that in colonies of *Acropora tenuis*, significantly higher skeletal loss occurred in colonies from Geoffrey Bay (Magnetic Island, Australia, ~8 km offshore) transplanted to Pelorus Island (Palm Islands, Australia, ~16 km offshore), when compared to control colonies and their reciprocally transplanted counterparts. These results may suggest marked intraspecific differences in the physiological condition of coral colonies, possibly causing selective predation by corallivorous organisms, strengthening the need for detailed investigations of the underlying causes as well as the consequences of skeletal loss in an important branching species of coral, *Acropora tenuis*.

Keywords Skeletal loss · Coral physiology · Corallivory

Introduction

Recent declines in coral cover along the Great Barrier Reef (GBR; De'ath et al. 2012) raise the need for further

exploration of causes and consequences of skeletal loss in corals. The biotic interactions between corallivorous fishes and coral species are accepted as a crucial factor demoting growth, survival, and replenishment of coral populations (Neudecker 1979). Along the GBR, the primary continuous consumers of coral biomass are butterflyfishes and the nominally herbivorous parrotfishes, although other corallivorous fish species from different families (e.g. Tetraodontidae, Monacanthidae) and phyla (e.g. *Acanthaster planci*, *Drupella* spp.) are also important (Cole et al. 2008; Bonaldo et al. 2011, 2012). Specifically, butterflyfishes principally feed on coral mucus or single coral polyp tissues (Cole et al. 2008); however, some species (e.g., *Chaetodon unimaculatus*) can remove skeletal material in addition to soft tissue (Motta 1980). Parrotfish species, conversely, remove large portions of coral colonies, which include both tissue and skeletal biomass (Bruckner and Bruckner 1998; Rotjan and Lewis 2008; Bonaldo et al. 2011). Among parrotfishes, scraping species remove only the outer tissue layer and marginal parts of skeletal material, while excavating species remove both tissue and large sections of skeletal material (Bonaldo et al. 2012).

Both coral colony morphology and identity influence the functional type of corallivores targeting the coral colonies; however, the fundamental basis of this selective feeding is largely unknown (Pratchett 2007; Cole et al. 2008). Characteristics that dictate corallivore preferences include, but are not limited to, gross coral morphology (e.g. Hobbs 2013), colony disease/damage (e.g. Hoeksema et al. 2013), symbiont associations and concentrations (e.g. Rotjan et al. 2006), and lipid or energy reserves (e.g. Rotjan and Lewis 2009).

On the GBR, corals in coastal or inner-shelf regions are subject to many adverse influences, including elevated temperatures (Berkelmans 2002), high turbidity (Anthony 2006; Fabricius et al. 2013), enhanced nutrients (De'ath and

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Fabricius 2010), and higher numbers of internal macroborers (Risk et al. 1995; Grand and Fabricius 2010). These conditions have induced a suite of phenotypic (Anthony and Fabricius 2000; Pisapia et al. 2012) and genotypic adaptations (Bay et al. 2009, 2013), leading to intraspecific variation in the physiology of corals with increasing distance from the coast. Thus, the question arises if these physiological differences may affect the interactions between these corals and their environment, such as corallivores. Our study provides a preliminary exploration of intraspecific variation found in skeletal loss of *Acropora tenuis* and strengthens the need for further investigations of the biological attributes of corals from in-shore environments and the consequences of coral predation by corallivorous fishes for coral populations and reef ecosystems.

Materials and methods

In the course of a large reciprocal transplant study, 20 partial colonies of the coral *Acropora tenuis* ($\sim 10 \text{ cm}^2$) were

collected from Geoffrey Bay (GB; Magnetic Island, Australia, $\sim 8 \text{ km}$ offshore) and 19 partial colonies were collected from the northwest leeward corner of Pelorus Island (PI; Palm Island Group, Australia, $\sim 16 \text{ km}$ offshore) (Fig. 1). All collected colonies were fragmented in half for genetically identical cross (new location) and back (source location) transplantation (cf. Barshis et al. 2010) in February 2013. Cross and back transplantation colonies were taken from 2–4 m depth at both sites, held on board the research vessel to control for transplantation/handling stress, and haphazardly mounted onto a single wire-mesh rack (following Berkelmans and van Oppen 2006), which was placed onto the reef at 2 m depth. Corals from these two sites typically differ in their experienced turbidity levels (Thompson et al. 2011), as GB is closer to the Burdekin River mouth.

All colonies were assessed for partial mortality and stress symptoms (e.g. bleaching) after 2 weeks (mid-February 2013) and 4 months (June 2013) using in situ observations and photographic assessments (Fig. 2). The initial assessment after 2 weeks was performed to ensure that no mortality occurred directly due to transplantation stress. Three GB colonies and

Fig. 1 Map of Australia and the Great Barrier Reef showing cross (new location; *dashed arrows*) and back (source location; *solid arrows*) transplantation. Corals were sourced from Geoffrey Bay ($n=20$) and Pelorus Island ($n=19$), fragmented in half, and used in cross and back transplantations for differential responses from genetically identical individuals

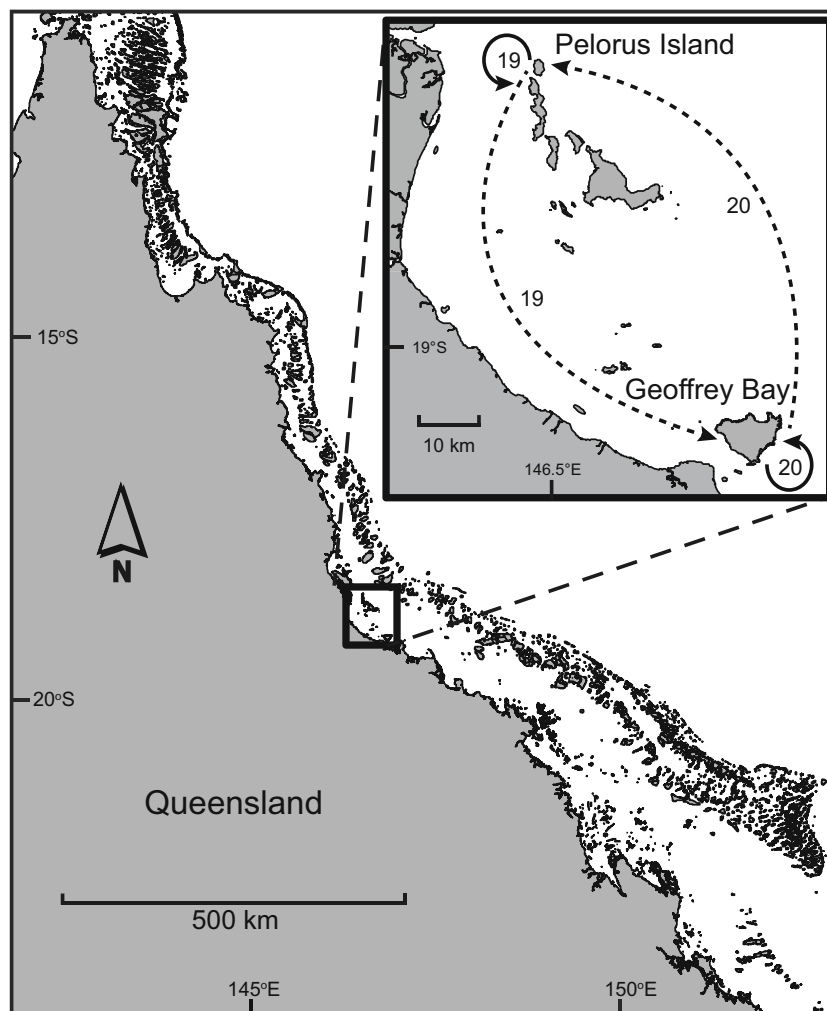
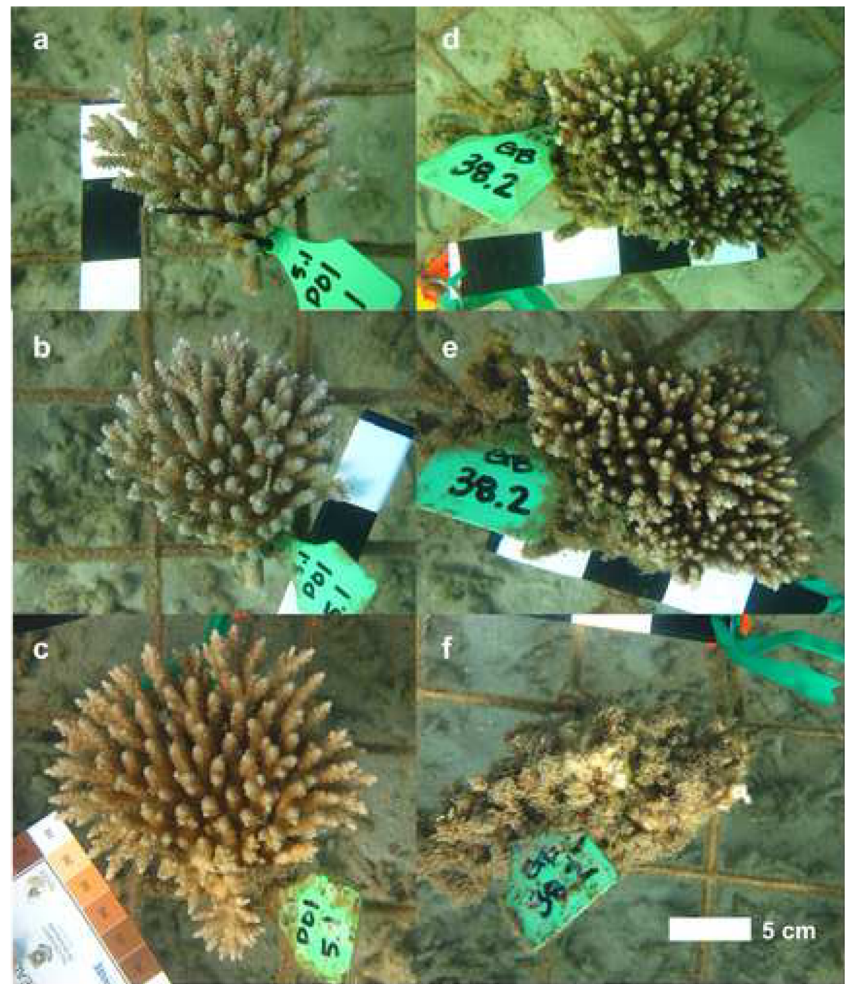


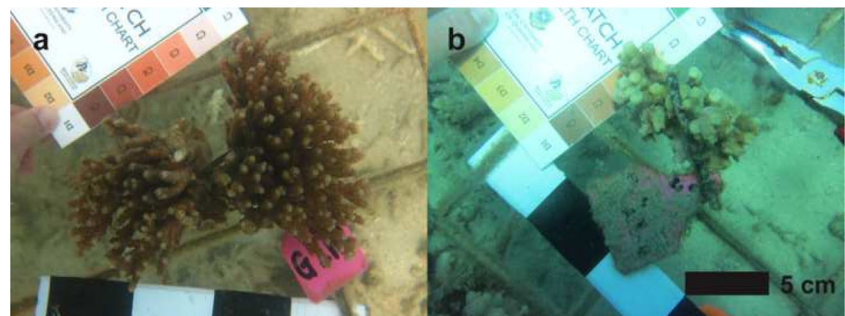
Fig. 2 Time series of *Acropora tenuis* corals sourced from Geoffrey Bay and Pelorus Island from initial deployment at Pelorus Island in the beginning of February 2013 **a, d** to mid-February 2013 **b, e** to June 2013 **c, f**. The Geoffrey Bay colony **f** displays total skeletal loss, compared to the Pelorus Island colony **c** displaying skeletal growth. *Scale bar* is consistent for all photographs



one PI colony were lost from the PI site during the experiment (due to abiotic dislodgement or predation) and excluded from subsequent analyses. Skeletal loss of corals was readily identified by removed branches (Fig. 3), and two-dimensional area changes between monitoring periods were measured for each colony by tracing planar outlines of colonies in ImageJ (version 1.46r, National Institutes of Health, USA). In situ visual assessments suggested that little to no skeletal loss occurred from the base of the colonies. Subsequently, area estimates from February and June were regressed against the initial area

measurement (prior to transplantation) to account for colony size. The residuals of the regressions were compared using two-way analyses of variance (ANOVAs) with the different origins (GB or PI) and treatments (transplanted or control) as predictor variables for the February and June measurements. Tukey's HSD was applied post hoc to reveal homogenous groups. All analyses were performed on square root-transformed data to meet assumptions of normality and homoscedasticity of variance. All analyses were performed using the software R 2.15.3 (R Core Team 2013).

Fig. 3 Image of *Acropora tenuis* colony sourced from Geoffrey Bay and deployed at Pelorus Island in **a** February 2013 and **b** June 2013 displaying skeletal loss of colony



Results and discussion

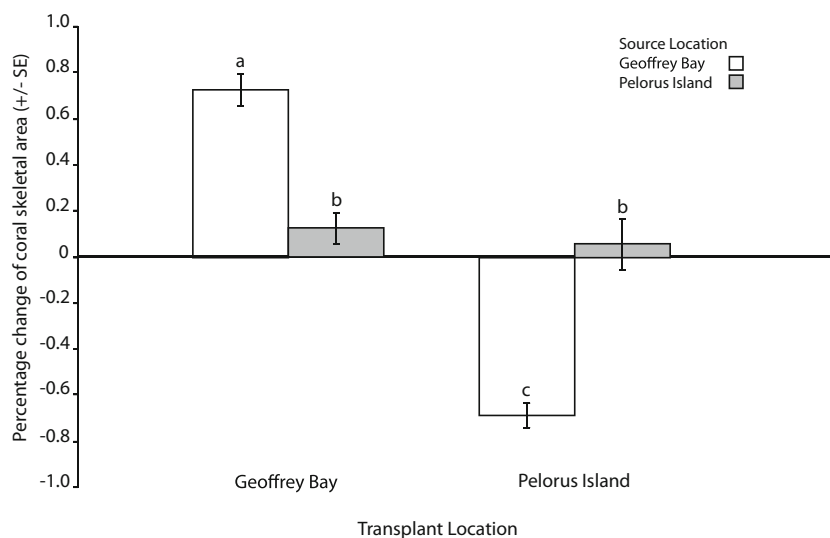
Our study revealed that in June 2013, changes in the total skeletal area of *Acropora tenuis* varied significantly between treatments (Treatment: $F_{1,70}=57.8$, $P<0.001$) and showed a significant interaction effect (Origin \times Treatment: $F_{1,70}=77.0$, $P<0.001$). Origin alone had no significant effect on area changes (Origin: $F_{1,70}=3.1$, $P=0.085$). Tukey's HSD post hoc test revealed that corals transplanted from GB to PI, which were the only colonies to exhibit a negative area change, exhibited significantly greater losses in total skeletal area (-128.73 ± 12.2 cm² mean \pm SE) than all other batches of colonies (Fig. 4). In addition, control corals from GB showed significantly larger increases in total skeletal area than all other colony batches. There were no statistically significant effects in area changes for the measurements taken in February 2013 (Origin: $F_{1,70}=0.2$, $P=0.631$; Treatment: $F_{1,70}=2.4$, $P=0.120$; Origin \times Treatment: $F_{1,70}=0.6$, $P=0.434$). These results suggest that the transplantation of colonies from GB to PI triggered a significant loss in total skeletal area, as all other batches of colonies exhibited positive area changes (with the highest increase in control corals from GB). Given that no changes occurred within the first 2 weeks after transplantation, initial stress does not appear to be responsible for the observed pattern. Instead, the results point towards extrinsic factors at PI driving skeletal loss in corals transplanted from GB.

This raises two important questions: 1) what are the underlying causes driving the skeletal loss of colonies from GB at PI, and 2) what are the possible consequences for coral populations, given predicted environmental changes in the future? There are several possible explanations for the skeletal loss in corals from GB at PI. Skeletal loss could be due to transplant effect; however, since measures were taken to monitor and account for the stress associated with transplantation, and no skeletal loss occurred within the first 2 weeks, this is unlikely.

Human-induced damage (Hawkins and Roberts 1992) is another possible cause of skeletal loss, yet this is doubtful as human destruction is usually indiscriminant, whilst the observed patterns of skeletal loss appear to be selective to GB corals transplanted to PI. Coral disease, specifically skeletal eroding band (SEB), could be a potential cause for skeletal loss as it can colonise exposed coral skeleton; however, this disease is not sufficient on its own to cause tissue mortality followed by substantial skeletal loss (Page and Willis 2008). Macroborers are also an unlikely cause of skeletal loss, as the quantity of skeletal loss and short duration of experiment do not conform with previous studies (e.g., Risk et al. 1995; Tribollet et al. 2002). Similarly, corallivorous invertebrates, including the crown-of-thorns seastar and *Drupella* spp., target coral tissue, leaving the skeletal structure largely intact (Cumming and McCorry 1988; Pratchett 2007). Thus, the most parsimonious explanation for the skeletal loss observed in this study is probably selective predation by corallivorous fishes (Neudecker 1977, 1979). Among fish, it is unlikely that butterflyfishes inflicted the observed damage, as these species usually cause little or no skeletal loss. Instead, the extent of skeletal loss suggests that larger piscine corallivores, specifically parrotfishes or tetraodontiform species from PI may be responsible for the observed pattern in selectively targeting transplanted corals from GB.

Factors underpinning positive selection of corals by large corallivorous fishes have been studied in the Caribbean, where overall nutritional content, reproductive structures, symbiont type and densities, high abundance of macroborers, and skeletal hardness may underlie parrotfish foraging patterns (Littler et al. 1989; Rotjan and Lewis 2005, 2009; Rotjan et al. 2006). Higher nutritional gain may be a reason for the clear preference for corals from GB. On the GBR, lipid stores within corals have been found to be two-fold higher in *Acropora* corals on inshore reefs compared to offshore reefs (Anthony

Fig. 4 Mean change in coral skeletal area (percentage of initial area \pm SE) for colonies fragmented and reciprocally transplanted between Pelorus Island and Geoffrey Bay after 4 months. Letters indicate homogenous groups identified by Tukey's HSD



2006). While this gradient is likely to decrease between inshore locations, it appears possible that lipid stores in colonies from GB are higher, making these colonies a more lucrative food source. Higher symbiont densities or different symbiont types may fortify this effect, as darker coloring of corals from GB suggests higher densities of zooxanthellae and GB corals are known to harbor different symbiont types than PI corals (Abrego et al. 2009). In addition, the abundance of macroborers, which is known to be higher in turbid, inshore environments (Risk et al. 1995), may influence the nutritional content of GB colonies. Thus, if large corallivorous fishes caused the skeletal loss, these fishes may have selected corals from GB due to fundamental physiological differences, suggesting high intraspecific variation between colonies from coastal environments.

The removal of dead and live coral is considered to be a key functional process on coral reefs. Our study reveals striking intraspecific differences in skeletal loss in *Acropora tenuis* following transplantation of colonies to a new environment. The extent and selectiveness of the damage suggest that corallivorous fishes may have driven the pattern by preferring *A. tenuis* colonies from a specific location. Thus, intraspecific variation and physiological adaptations may be crucial to coral populations and corals exposed to a new environment, possibly including a different suite of predators, may be heavily targeted and subsequently experience significant reductions in their reproductive output or suffer complete mortality.

It is not yet known how projected changes in environmental conditions will affect the physiology of scleractinian corals or the behaviour of coral-associated fauna. Presumably, all coral species at different sites (e.g. longitudinally and latitudinally) will undergo physiological changes, yet inshore corals may be most affected and required to adapt at a faster pace. Our findings may provide evidence for this trend and emphasise the need for detailed assessments of physiological adaptations of corals and the ecological consequences arising from such adaptations.

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