



Effects of macroalgae on corals recovering from disturbance

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ABSTRACT

Corals have an ability to recover from disturbance through the regeneration of tissue, but macroalgae are believed to impede this process. In this study, the type of benthic macroalgae deposited on coral skeleton was manipulated experimentally, and the effects on tissue regeneration and skeletal growth of two common coral species *Acropora pulchra* and *Acropora aspera* were observed after disturbance. Macroalgae, common to the study region, but from variable functional groups, were investigated for their influence on coral growth. The green filamentous macroalga *Chlorodesmis fastigiata* significantly reduced tissue recovery in *A. pulchra*, but not in *A. aspera*. It led to the infection of *A. pulchra* with ciliates. The brown seaweed, *Lobophora variegata*, the encrusting coralline alga *Porolithon* (= *Hydrolithon*) *onkodes*, and turf algae, had only minor effects on coral recovery. This suggests that the outcome of the regeneration process is highly variable and dependent upon both, the species of coral and algae involved.

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1. Introduction

Coral reefs are facing threats from ocean acidification, global warming, overfishing, and eutrophication (Hoegh-Guldberg et al., 2007). Overfishing of herbivorous fish and/or diseases of sea urchins has led to significant reductions in rates of grazing (Carpenter, 1985; Coles and Fadlallah, 1991) with consequent increases in the abundance and species composition of macroalgae (Carpenter, 1985). The increased abundance of algae may strengthen the competition with corals, particularly for space and light (Carpenter, 1985; McCook, 2001). These factors, combined with other pulse disturbances that enhance coral mortality, may shift the balance on reefs from coral-dominance to algal-dominance (Bellwood et al., 2004; Diaz-Pulido et al., 2009; Hoegh-Guldberg et al., 2007). The ability of corals to recover from disturbance, in the presence of macroalgae, is therefore a critical aspect of reef resilience and the reversal of degraded reefs to coral dominance (Hughes et al., 2007).

Coral populations can recover from disturbances by two main mechanisms: recruitment and regeneration (Pearson, 1981). Amongst the literature investigating the recovery of corals, only a few studies focus on coral tissue re-growth, and these only partially investigate the potential influence of algae on the process (Bak and Steward-Van Es, 1980; Bak et al., 1977; Diaz-Pulido and McCook, 2002; Fishelson, 1973; Titlyanov et al., 2005; van Woesik, 1998). A few studies showed that lesion healing in massive, non-branching corals was retarded in the presence of colonising macroalgae (Bak and Steward-Van Es,

1980; Bak et al., 1977; Titlyanov et al., 2005; van Woesik, 1998). However, in these studies, algal species were not fully identified and contrary to Diaz-Pulido and McCook (2002), the potential for differing responses to distinct algae was neglected. Critically, they did not isolate and experimentally manipulate the interacting algae, and therefore, the role of specific macroalgae in the hindrance of coral recovery has not been identified. Further, they did not document the potential that variation in the effects on corals can differ amongst seaweeds. The present study aimed to assess the isolated effects of different types of macroalgae on the recovery of coral tissue, after disturbance. Macroalgae, common to the region, and exhibiting a wide range of distinctive morphologies and physiologies, were investigated for their effects on a variety of coral growth parameters.

2. Materials and methods

2.1. General approach, study site and collection of corals and algae

To examine the effects of macroalgae on the regeneration of coral tissue and to observe changes in coral branch thickness, we conducted an experiment where the tissue of two coral species was partially removed and macroalgae placed on the injured area while monitoring coral growth in situ. The branching corals *Acropora pulchra* and *Acropora aspera* were chosen because they are common and abundant in the study area. The macroalgal treatment included four levels, the foliose brown alga *Lobophora variegata* (J.V. Lamouroux) Womersley ex Oliveira, the green alga *Chlorodesmis fastigiata* (C. Agardh) Ducker, the crustose coralline alga (CCA) *Porolithon* (= *Hydrolithon*) *onkodes* (Heydrich) Foslie, and turf algae, mainly the brown *Feldmannia* (= *Hincksia*) *mitchelliae* (Harvey) Kim. The four algae used are common on coral reefs and include

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representatives of different functional form groups (sensu Littler and Littler, 1980). The erect macroalgae were collected from the reef-flat adjacent to the study site and removed together with their rhizoids (if applicable) avoiding damage to the thalli to prevent the potential leakage of chemical compounds.

The study was conducted in situ on the reef flat (0.5–3.5 m) of Heron Island Reef, GBR (23°26'S 151°52'W), during October 2007 and February 2008. The specific study site comprised an area of 250 m² of a reef dominated by *A. pulchra* and *A. aspera*.

2.2. Preparation of coral branches and macroalgal treatments

In order to simulate disturbance to the coral tissue, a lesion was created at the tip of the coral branches using an air pistol in situ. Healthy coral branches (>12 cm long) attached to their colonies were randomly selected for manipulation and only one branch per colony was used for this purpose. All live coral tissue was removed from the tip of each branch to a point 6 cm below the branch tip. White coral skeleton was exposed after this procedure. The shape and placement of the tissue injuries were sought to imitate partial mortality due to localised disturbances, such as those occurring at the study site when cold weather and rain coincide with low tides (Hoegh-Guldberg et al., 2005).

To determine whether the algae have an effect on the regeneration of injured coral tissue, macroalgae were attached to the exposed skeleton of each coral species, in such a way as to leave a 1 cm space between the attached algae and the live coral tissue on the branch (Fig. 1). This gap was left to allow time for a natural (unforced) encounter of the alga and the coral while allowing time for the coral to recover from the injuries and the alga from the transplant. As a control for coral injury, coral branches of each species were injured (as for the algal treatments), but without algae attached. To minimise colonisation by algae on the controls, injured areas were gently cleaned using a toothbrush once a week, while the edge closest to the growing coral tissue was not cleaned to avoid further injury. There were eight replicate branches per algal treatment and control, and for each coral species.

For the *L. variegata* treatment, four thalli of ca 35 cm² (and 0.8 ± 0.1 g wet weight each) were wrapped around the dead, exposed

coral skeleton using plastic cable ties. In a pilot study, *L. variegata* thalli were readily removed by herbivorous fish. To prevent herbivory, cages were placed around each coral–*L. variegata* pair. These cages were constructed from wide mesh (2.0 × 1.5 cm) and thin wire to minimise impacts on flow and light, and cleaned twice a week. Parallel, unpublished experiments (D. Bender, 2008, MSc Thesis) comparing tissue regrowth in caged vs. uncaged coral branches demonstrated no significant cage effects on airbrushed corals in the absence of algae (one way ANOVA: $P=0.124$ for tissue regeneration and $P=0.181$ for diameter growth). For the *C. fastigiata* treatment, two tufts of 5–7 cm long and a wet weight of 3.3 ± 0.3 g each, were attached to the exposed skeleton using a cable tie. There was no need to use cages for *C. fastigiata* as no herbivory was observed over this alga during the pilot study. Four pieces of the CCA *P. onkodes* (1 × 1 cm) were collected using hammer and chisel, and attached to the dead part of the each coral branch with a non-toxic epoxy resin (“Knead It Aqua”, Selleys®). The epoxy has been successfully used without deleterious effects on reef organisms (Jones et al., 2003). The CCA pieces were monitored for bleaching throughout the study. However, none of them showed signs of bleaching or was overgrown by other organisms. The algal turf treatment consisted of pre-existing algal assemblages naturally established on the branch tips, as the artificial attachment of turf algae proved very difficult. Coral branch tips for this treatment were selected only if the turf algae already occupied ≥2 cm of the branch tip (in all other algal treatments, branches with any turf algal cover were avoided). In this treatment, as the experimental alga was already present – only 1 cm of live tissue was required to be removed to create the gap between the filamentous algae and live coral tissue, consistent with the other algal treatments. Algal quantities were chosen to represent the approximate amount of each type of alga that would normally occur on a standard area of an experimental *Acropora* branch surface, ca 40 cm². The experiment ran for 15 weeks.

2.3. Length and diameter measurements

Measurements were taken at the beginning (23rd October 2007) and at the end of the experiment (5th February 2008). A reference cable tie was placed at a distance of ≥5 cm away from the lesion edge. Tissue accretion/loss was determined by measuring the distance between the cable tie and the tissue lesion border (Fig. 1). The

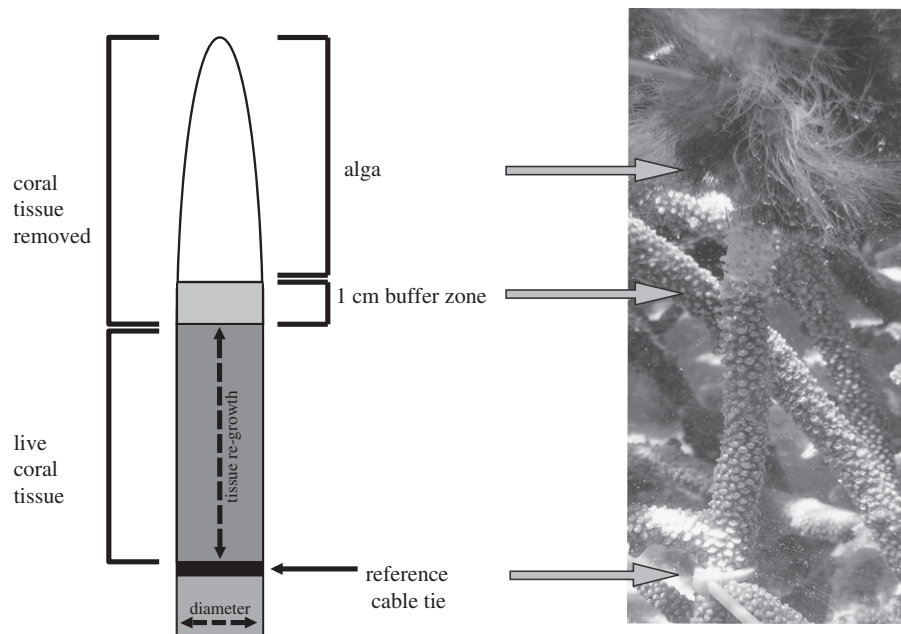


Fig. 1. Preparation of treatments. Coral branches were cleared of 6 cm of tissue at the tip and the algal treatments were attached 1 cm away from the lesion. A reference cable tie was attached at the bottom of the branch (≥5 cm away from the lesion).

branch diameter was measured, between radial corallites, and over live coral tissue, at a fixed distance from the reference cable tie. Both parameters were measured using callipers (Sealey Vernier, 200mm).

2.4. Statistical analysis

The untransformed measurements were analysed using a two-factorial permutational analysis of variance (PERMANOVA) design with coral species and algal treatment as fixed factors and tissue growth/mortality and skeletal diameter accretion as variables. The analysis was based on a Bray–Curtis resemblance matrix and 9999 permutations were performed for each test. Significant statistical interactions were further analysed by pair-wise comparisons. All statistical analysis was done using PERMANOVA+ for PRIMER v6 (PRIMER-E Ltd., Plymouth).

3. Results and discussion

The two coral species showed different responses in the two re-growth parameters, in the vicinity of macroalgae, while recovering from injury. A strong statistical interaction between the coral species and the algal treatment ($P(\text{perm})=0.0001$, Table 1) was found. The response depended on the species of corals and algae involved. *A. pulchra* proved to be negatively affected by *C. fastigiata* in both the rate of encroaching coral tissue over dead skeleton and radial increases in branch diameter (Fig. 2a and b). The recovery of *A. aspera* was less affected by the macroalgal species tested, showing only a significant, but minor reduction in tissue re-growth and branch diameter growth in the presence of *P. onkodes* (Fig. 2a and b). Under the experimental conditions described, most benthic macroalgae had no effect on the rate of either linear expansion of *A. aspera* tissue over dead coral skeleton, or branches thickened. The rate of recovery was equal amongst all algal treatments, but that of *P. onkodes* (Table 1).

3.1. *C. fastigiata*

A comparison between the two experimental coral species showed that *C. fastigiata* had a differential effect on these species ($P(\text{perm})<0.05$, Table 1). While *A. aspera* tissue advanced towards *C. fastigiata* in all instances, the tissue of *A. pulchra* retreated from this alga to the extent that 4 out of the 8 replicate branches lost all coral tissues. The mechanism was most likely allelopathic as the alga and coral were not actually touching. Similarly, Rasher and Hay (2010) reported *C. fastigiata* to cause bleaching in *Porites cylindrica*; and demonstrated that this was based on algal extracts that were found to reduce the effective quantum yield of fluorescence of photosystem II within coral endosymbionts. In the present study, branches of *A. pulchra* that were most severely affected, in addition to other colony branches in close proximity to this alga, developed brown bands. Ciliates were observed, at high densities, in the coral tissues forming these brown bands. An investigation by compound light microscope of more than 12 tufts of *C. fastigiata* was conducted to examine the possibility that *C. fastigiata* was a carrier for ciliates. The examination, however, failed to locate any ciliates, suggesting that it is the interaction between this

alga and this species of coral (*A. pulchra*) that led to the infestation by ciliates. A potential mechanism for the observed outcome may incorporate an algal driven impairment of the coral's immune systems, with the coral then becoming susceptible to a ciliate invasion. Potentially, poisonous algal secondary metabolites extruded from the alga may weaken the coral's immune system (Rasher et al., 2011). There are however, many alternative potential drivers (e.g. algal photosynthates increasing microbial activity that cause hypoxia and coral mortality (Smith et al., 2006; Barott et al., 2012)) and the exact mechanisms require further investigation. The high density of ciliates was found on no other coral–algal treatment, nor in control branches. The branches showing brown bands did not recover during the course of this study. The disparate response of *A. aspera* to that of *A. pulchra* in the presence of *C. fastigiata*, together with the negative effects of this alga that have been reported elsewhere (Rasher and Hay, 2010), raises some interesting questions regarding the properties of *A. aspera*.

In contrast to the effect of *C. fastigiata* on *A. pulchra*, no other algae led to coral tissue receding away from attached algae. Both coral species examined exhibited positive tissue growth towards all other types of algae investigated (Fig. 2a).

3.2. *L. variegata*

Interestingly, the *L. variegata* treatments only had a minor influence on the recovery of the two coral species compared to the effects of *C. fastigiata*. The linear tissue expansion of *A. pulchra* did not seem to be affected, yet the thickening of the branch, interpreted as skeletal diameter accretion, was reduced. Comparable observations were made by Titlyanov et al. (2005), who report that *L. variegata*, amongst other macroalgae, did not prevent the closure of lesions and was overgrown by massive *Porites* spp. Similarly, but on a reef scale, Diaz-Pulido et al. (2009) showed that inshore reefs dominated by acroporid corals were able to outcompete this alga and return from an *L. variegata* dominated to a coral dominated state within an annual cycle following a large scale coral mortality event. In much of the literature, *L. variegata* has been reported to have detrimental effects on coral reef ecosystems as it caused coral mortality when in competition with *Porites* and other massive coral species (Jompa and McCook, 2002; McCook et al., 2001; Nugues and Bak, 2006). The discrepancy between this study and most of the current literature might arise from the fact that the majority of studies focused on massive coral species. Alternatively, the distance between macroalgae and coral tissue may vary between studies and impact significantly on the results; or water chemistry differences between different sites may enhance the competitive abilities of this alga over corals (Diaz-Pulido et al., 2011).

3.3. *Feldmannia mitchelliae* and *P. onkodes*

Turf algae (mainly *F. mitchelliae*) did not have a significant effect on the re-growth of coral tissue, or changes to branch thickening, in either of the corals studied (Table 1). These findings are in accordance with other studies that show no effects of turf algae on coral physiology (e.g. McCook, 2001). In our study, however, the CCA *P. onkodes*

Table 1

Statistical analysis. PERMANOVA to test for the effects of algal treatment and coral species on coral tissue re-growth and skeletal diameter. Conclusions of the pair-wise comparisons are also included. A = algae, C = coral, Cfas = *Chlorodesmis fastigiata*, Lvar = *Lobophora variegata*, and CCA = *Porolithon onkodes*.

Source of variation	df	Sum of squares	Mean square	Pseudo-F	P(perm)	Conclusions/pair-wise test
C	1	433.8	433.8	1.2102	0.3203	ns
A	4	4271.7	1067.9	2.9792	0.0003*	
A×C	4	6513.5	1628.4	4.5427	0.0001*	<i>A. pulchra</i> : Cfas<all other treatments, control>Lvar=CCA; <i>A. aspera</i> : CCA<control; Cfas <i>A. pulchra</i> ≠Cfas <i>A. aspera</i>
Res	59	21,149	358.46			
Total	68	32,368				

* = Significant, $P(\text{perm})<0.05$; ns = not significant, $P(\text{perm})>0.05$.

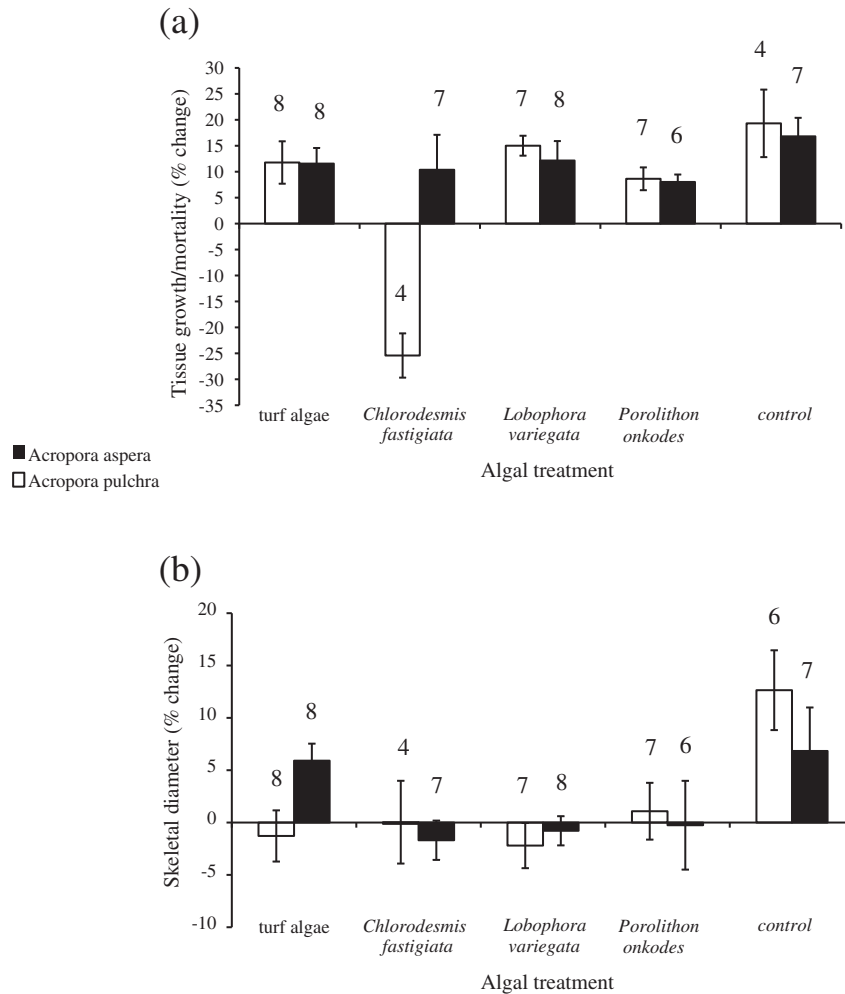


Fig. 2. (a) Percent change of tissue growth/mortality (mean \pm SE) in the presence of different macroalgae (algal treatments) measured between the reference cable tie and the lesion edge. (b) Percent change (mean \pm SE) of the two coral species' diameter measured just below the reference cable tie at the base of the coral branch in the presence of the different algal treatments. n = numbers on top of columns, where an n<8 for all but *C. fastigiata* is due to the loss of the entire branch. In the case of *C. fastigiata* it is due to tissue mortality.

significantly slowed coral tissue re-growth, in addition to branch thickening, in both coral species although its effects were far less detrimental than the observed effects of *C. fastigiata* on *A. pulchra*.

This study demonstrates that the interaction of corals and benthic algae is species specific. Under the experimental conditions applied in this study, *C. fastigiata* was the most aggressive species in the competition with corals. The alga hindered the recovery of *A. pulchra* as shown by tissue expansion measurements where tissue die-back as opposed to growth was observed. This macroalga also hindered branch diameter expansion in both coral species. We showed, however, that, under the applied field conditions, half of the benthic macroalgae studied, do not significantly affect coral recovery after disturbances. Corals weakened by inflicted injuries, were usually able to recover: grow towards macroalgae that had been placed at a distance in the presence of *L. variegata*, *P. onkodes* and *F. mitchelliae*. Undoubtedly, there are several very aggressive algal species whose competitive abilities have been described in the literature. This study included some of these algae and their effect on coral recovery was found to be specific to the coral species they interacted with. The results showed that algal inhibition of coral recovery is not a necessary outcome, even in circumstances in which large herbivores are excluded. Expected human-induced changes to reef ecosystems are predicted to alter the specifics of this outcome because further reductions in seawater pH and water quality, rising temperatures, and unabated overfishing are equally as likely to change the physiology of algae, as they do coral. Generally, it is assumed that

non-calcareous macroalgae will thrive under these conditions (Hughes et al., 2007), however the existence of nutrient dependent trade-offs between growth and secondary metabolite formation (Jormalainen et al., 2003), differential CO₂ uptake mechanisms and temperature impacts on carbon fixation (Giordano et al., 2005), encourage a more open attitude and suggest that the response is likely to be highly species specific.

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