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Review Paper

Coral-algal relations in reef ecosystems: on the positive roles of algae in reef recovery processes

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Abstract

This paper reviews the possible roles that marine algae may play in the processes of coral reef recovery after disturbance events. Coral reefs suffer from various forms of natural and semi-natural disturbances including storms, tsunamis and extreme fluctuations in seawater levels and temperatures. These disturbances often result in corals and other reef organisms being decimated, leaving the affected substrates devoid of organismal cover and prone to progressive erosion. The present work reviews the processes and mechanisms by which those patches of denuded substrate are recolonized and eventually return to the pre-disturbance state where (most typically) corals regain their dominance, focusing mostly on tropical and subtropical reef ecosystems of the Indo-Pacific. Although newly-opened substrates tend to be initially colonized by marine algae, algal occupation does not totally prevent corals from invading and eventually becoming dominant on those substrates, due to their superior competitive capacity. Observational and experimental studies suggest that corals possess a range of traits that contribute to their successful existence in tropical/subtropical waters. While the relationship between corals and algae in reef recovery processes has traditionally been interpreted in a negative, competitive context, it would be reasonable to suggest that algae do play positive roles including the provision of refugia and appropriate secondary substrates for the settlement and development of coral planulae and young colonies, which in turn help reef recovery processes. Thus we draw attention to the potentially positive roles that algae may play in restoring damaged reefs.

Keywords: marine plants, macroalgae, physical disturbance, coral bleaching, coral reef recovery

Disturbance and recovery of coral reef ecosystems

Reefs under disturbance and their recovery

Tropical and subtropical waters of the world are characterized by the presence of highly productive and species-rich coastal ecosystems including mangrove forests, seagrass meadows and coral reefs. Of these, coral reefs are known to harbour an exceptionally high diversity of marine organisms, due in large part to the presence of structurally complex habitats that are generated through the calcification processes of coralline algae and hermatypic corals (Tokeshi 1999; Dubinsky & Stambler 2011). Coral reef ecosystems are susceptible to natural and semi-natural disturbances which may cause major changes in ecosystem functioning, if the magnitude of disturbance exceeds the threshold of system tolerance/resilience (Steinberg 2012). Throughout the evolutionary history of coral reefs, they have been exposed to various forms of natural catastrophes including super-typhoons, tsunamis, volcanic activities, sea temperature fluctuations and sea level changes that have led to major shifts in reef communities (Pandolfi *et al*. 2011). Severe physical disturbances such as typhoons/hurricanes/cyclones and tsunamis cause extensive damages (e.g., fragmentation and dislodgment) in coral colonies (Woodley *et al*. 1981; Glynn 1990). Death of hard corals leads to the loss of architectural complexity and reef flattening through the collapse of coral skeletons. As such, disturbance is a well-known modifier of reef seascapes. In marine systems, stormy conditions may not only remove or bury subtidal organisms but they may also help form new substrate patches. In the wake of a strong disturbance, newly formed substrates appear as bare rocks and banks formed of sand and coral fragments, with dead/damaged coral colonies providing space for sessile organisms (Massel & Done 1993; Trenberth & Shea 2006; Manzello *et al*. 2007; Rogers *et al*. 2008; Alvarez-Filip *et al*. 2009).

Coral bleaching is often caused by unusually high sea temperatures (>30°C) combined with periods of slack wind, calm seas, high solar radiation, and in some areas, reduced salinity due to flooding and typhoons. Bleaching causes reductions in photosynthesis, tissue growth, regeneration and calcification, subsequently leading to the death of corals (Lesser *et al*. 2007). On some reefs, nearly all corals died within few months after a bleaching event (Baker *et al*. 2008). Elevated seawater temperatures that result in coral bleaching may also negatively affect algae. It is well known that some Corallinaceae species (e.g., *Corallina officinalis*) experience bleaching (Latham 2008), but to date there has been no documented record of mass bleaching of algae or their large-scale decimation due to a bleaching episode.

The speed of recovery often depends on the severity of thermal stress, and on the amount of coral cover remaining after the disturbance (Loch *et al*. 2002; Stobart *et al*. 2005; Guzman & Cortes 2007; Glynn *et al*. 2011). A decline in live coral cover may not follow a single bleaching episode but often depends on accompanying coral diseases, *Acanthaster* predation and the occurrence of repeated bleaching episodes. Eventually, bioerosion and mechanical fragmentation of reef materials generate unstable rubble- and sand-substrates which are unfavorable for coral recruitment (Szmant 2002; Baker *et al*. 2008; Rogers *et al.* 2008). Patterns of loss and recovery in coral cover in some Pacific sites ranged from total elimination to total recovery with periods spanning 10-28 years (Wellington & Glynn 2007; Cabaitan *et al*. 2012). Recovery of non- or lightly-stressed coral reefs was reported to be at 1-10% per annum, while a gradual decline in live coral cover often ensued at sites experiencing severe anthropogenic stresses (Connell 1997; McClanahan *et al*. 2007; Baker *et al*. 2008).

Severe natural catastrophes on coral reefs result in the formation of new substrata, changes in the relative abundances of surviving hermatypic corals and the dominance of non-coral taxa associated with reef assemblages. The fate of a damaged reef depends on factors such as the degree of coral reef damage, the presence of coral and non-coral taxa on the reef and sources of planulae supply for recolonization and restoration of coral populations (Harrison 2011). A damaged coral reef may completely return to its initial state or attain a changed state with the predominance of other species and forms of corals or turn to non-coral taxa reef (Baker *et al*. 2008; Titlyanov & Titlyanova 2012b).

A number of studies reported that severely damaged coral reefs were subsequently transformed into a seaweed-dominant state (coral reef “phase shifts”) (Done 1992; Knowlton 1992; McManus & Polsenberg 2004). Bruno *et al*. (2009), however, indicated that the replacement of corals by algae as dominant benthos was less common and less geographically extensive than assumed, based on a meta-analysis of 3581 quantitative surveys conducted in 1996-2006 involving 1851 reefs around the world. These give credence to the view that such a ‘phase shift’ represents a temporary state of coral reefs on their way to recovery to an initial or changed state (Titlyanov & Titlyanova 2012b).

In the present review, particular attention has been drawn to algal groups involved in coral reef restoration including fast growing, high productive green filamentous algae (mainly ephemeral) which are often the first colonizers of newly formed substrata (Diaz-Pulido & McCook 2002, 2003, 2004; Mumby 2009; Chadwick & Morrow 2011) and crustose calcareous algae that attract coral planulae and promote their metamorphosis (Harrison & Wallace 1990; Harrington *et al*. 2004; Golbuu & Richmond 2007).

Colonization of newly formed substrates

Newly formed substrates (after bleaching events, etc.) made of dead or damaged colonies of hermatypic corals are rapidly colonized by sessile organisms such as sponges, hydroids, gorgonians, coralline algae as well as various algae. As have been shown by field and laboratory studies, microscopic diatoms, fine filamentous blue-green and green algae, tunicates, foraminifers and small-sized polychaetes are the first colonizers on both dead and wounded coral colonies (Diaz-Pulido & McCook 2002, 2003, 2004; Mumby 2009; Chadwick & Morrow 2011).

Studies involving mechanically damaged colonies (with various types of injuries) and dead coral debris (pebbles) of massive and branched corals showed that the injuries and coral pebbles tended to be immediately overgrown by algae and cyanobacteria (Titlyanov *et al*. 2005, 2006, 2008a). After the first month of colonization, algae occupied 1-7% of the lesions and l-4% of the pebbles. Algae settled only on the skeleton surfaces not covered by live coral tissue. The first settlers were microscopic, micro-filamentous, fine filamentous and filamentous-tubular forms (Fig. 1). By the third month, algal cover increased to 30-90% on the injuries and to 25-60% on coral pebbles. The composition of dominant species on the lesions had changed, but ephemeral algae still dominated. During the 6 months of the experimental period, the projected cover of algae amounted to 80% on the lesions and 60-80% on coral pebbles, where an algal turf community with the dominance of ephemeral as well as long-living species was formed (Fig. 2). Algal communities on new substrata lasted from 6-8 months (algal turfs) to some years (Sargassaceae), and subsequently species composition, biomass and density of these communities changed seasonally and depending on

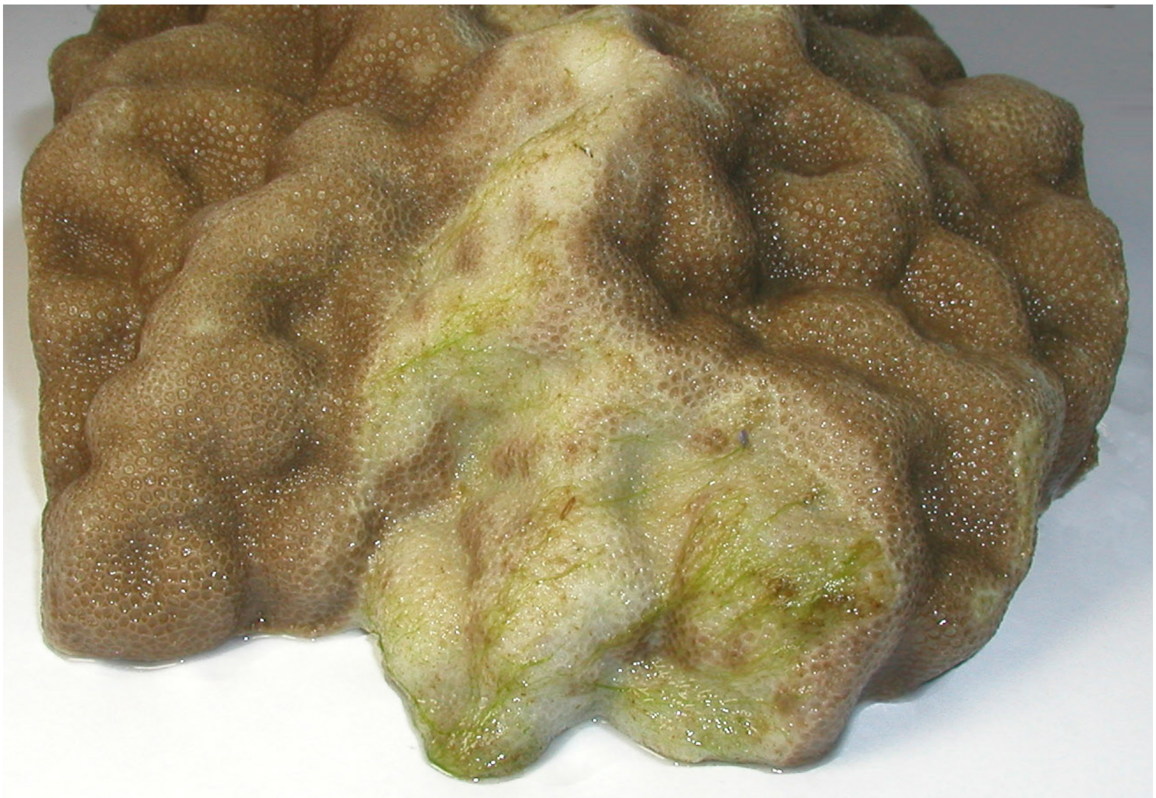

Figure 1: Filamentous and other forms of algae settling on the damaged surface of a massive coral *Porites lutea*.

Figure 2: Algal turf community (upper) abutting a live colony of *Platygyra verweyi*.

competitive abilities of different settlers.

In summary, the speed of coral reef recovery after damages depends on four main factors: (1) degree of coral reef damage; (2) frequency and severity of subsequent disturbances; (3) the presence of reproductively mature parents and propagules of coral species (sexual recruitment and asexual propagation); (4) competitive ability of hermatypic corals and non-coral species under post-disturbance conditions. The first three factors concern the starting conditions of reef recovery and the fourth determines the trend and rate of coral reef recovery and the succession of biological communities. While the importance of the first three factors in coral reef recovery is obvious (Baker *et al*. 2008), that of the fourth is still debatable (Dubinsky & Stambler 2011).

Roles of algae in coral reef ecosystems

On healthy coral reef ecosystems marine plants tend to occupy sites unfavorable for the settlement of hermatypic corals, e.g. sandy and silty substrates in lagoons, in between patch reefs and between separate coral colonies. Algae can even occur in strongly shaded sites such as the base of massive colonies or underneath tabulate and encrusting corals and also at limiting depths of the euphotic zone (Molinier 1960; Lang 1974; Littler *et al*. 1986). They can also survive under high temperatures, dryness and fluctuating salinity, e.g. in splash, upper and mid intertidal zones. Red coralline and brown Sargassaceae algae often occur on wave-exposed reef crests and shallow reef flats, as they can firmly attach to hard substrata and resist strong wave actions (Littler & Littler 1988). Some marine algae also live inside other algae (endophytes) using the “host” cells and tissue as substrata and refugia.

Macroalgal cover in coral reefs of the Indo-Pacific averages 9-12% (Bruno *et al*. 2009), while corals commonly reach 50-90% cover. However, marine algae may sometimes occupy practically all reef substrates, absorbing up to 90% of incident PAR (photosynthetically active radiation) (Zvalinsky *et al*. 1978; Titlyanov 1991; Titlyanov & Titlyanova 2002a, b; Dubinsky & Falkowski 2011).

Thus benthic marine algae (including symbiotic species) play major roles in the functioning and maintenance of coral reef ecosystems. Their varied functions include the following:

(a) Primary production of organic matter

High productivity of coral reefs is associated in part with the efficient light harvesting by reef-associated photosynthetic organisms (marine plants), which in turn reflect their high degree of photo-acclimation to incident light

(Crossland *et al*. 1991; Titlyanov 1991; Titlyanov & Titlyanova 2002b; Dubinsky & Falkowski 2011; Stambler 2011). High primary production in hard corals is due to endosymbiotic zooxanthellae and ectosymbiotic (endolithic) green and blue-green algae (Fine & Loya 2002; Titlyanov & Titlyanova 2002a, 2008; Fong & Paul 2011). It is interesting to note that communities of fine blade-like and fine filiform macroalgae inhabiting the intertidal zone are no less productive than hard corals (Littler & Arnold 1980). In contrast, shaded deep zones of reefs are inhabited mostly by low-productive, long-lived red coralline algae (Fong & Paul 2011).

(b) Building of coral reef base

Crustose calcareous algae of the genera *Porolithon*, *Peyssonnelia*, *Lithothamnion*, *Lithophyllum*, etc. are reef-builders that strengthen the carbonate reef base. They cement together dead colonies' skeletons, coral pebbles and carbonate sand particles, thus protecting the reef from erosion or building a new carbonate layer at the base of a coral reef (Littler & Littler 1988, 1995; Hillis 1997; Chisholm 2003; Diaz-Pulido *et al*. 2007). Communities of large calcified green algae (the genera *Halimeda*, *Udotea*) and red algae (the genera *Amphiroa*, *Galaxaura*) also produce calcium carbonate. Thalli remnants of these algae are transformed into carbonate sand which constitutes important building material of coral reefs (Macintyre *et al*. 1987; Hine *et al*. 1988; Marshall & Davies 1988; Roberts *et al*. 1988; Iryu *et al*. 1995).

(c) Fixation of atmospheric nitrogen

Blue-green algae of the genera *Lyngbya*, *Oscillatoria*, *Calothrix*, *Anabaena*, *Entophysalis*, *Nodularia*, etc. epiphytically or endolithically inhabiting dead/live corals, seagrasses, hard and soft sediments, engage in the fixation of molecular nitrogen (Bergman *et al*. 1997; Welsh *et al*. 2000; Dong *et al*. 2002a, b, 2006; Lugomela & Bergman 2002; Hamisi *et al*. 2004).

(d) Marine algae as a basal component in the food web of reef ecosystems

Marine macrobenthic and epiphytic algae are the major food for reef-associated fishes and invertebrate grazers (Carpenter 1986; Hay 1997; Burkepile & Hay 2006; Hughes *et al*. 2007). Herbivorous animals could consume nearly 100% of the daily production of macroalgae in one day (Duffy & Hay 1990; Hughes *et al*. 2007). Some fish species selectively graze algal taxa, e.g. green algae of the genera *Cladophora*, *Enteromorpha* and *Ulva*; other fish prefer brown algae of the genera *Sargassum* and *Dictyota* (Duffy & Hay 1990; Hay 1997).

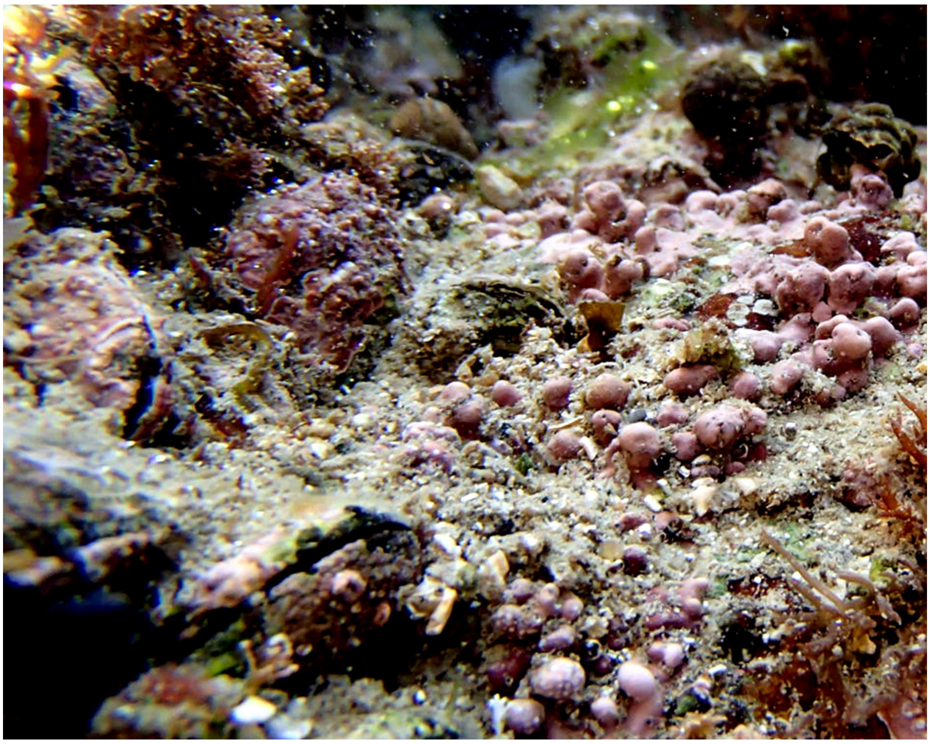

Figure 3: (a) Coralline alga *Lithophyllum okamurae* on exposed surface (Okinawa, Arasaki beach).

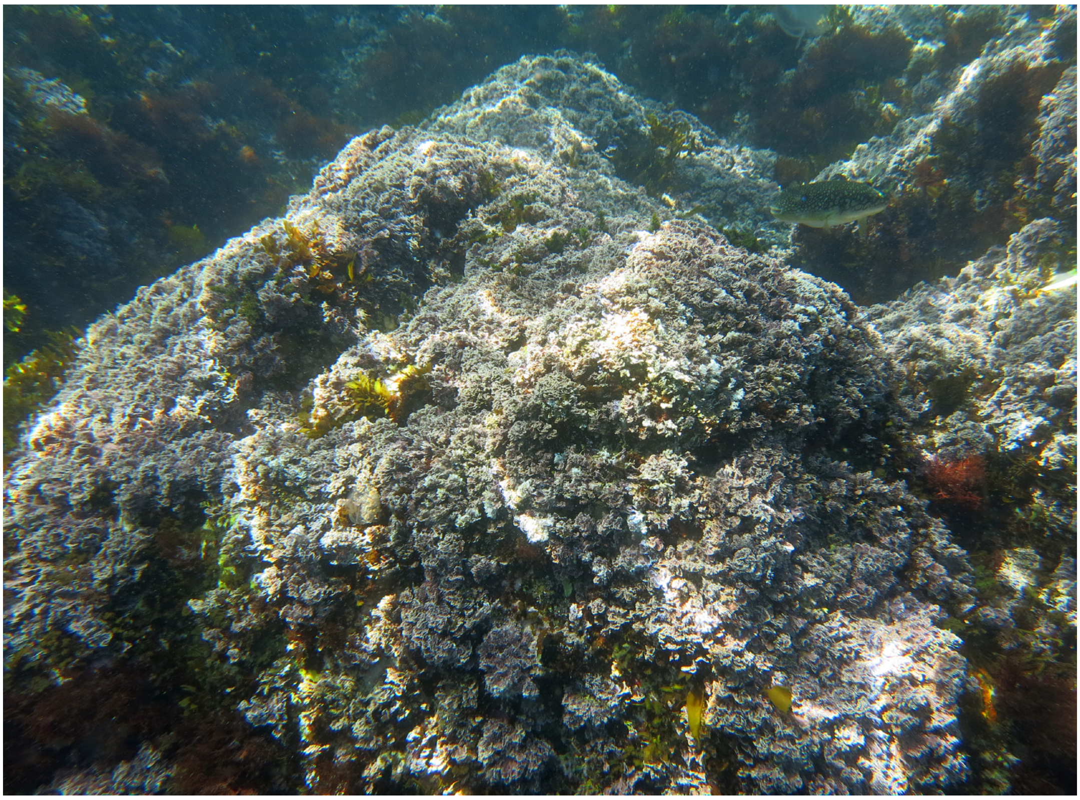

Figure 3: (b) Coralline algae forming a protective crest on exposed rock platform facing the outer sea. Amakusa, Japan (photo: M Tokeshi)

(e) Communities of marine plants provide habitats for animals

Algal turfs, beds of densely-branching Sargassaceae species, articulated coralline algae and seagrasses often serve as refugia for fish, crustaceans and mollusks, particularly their larval stages (Liuzzi & Gappa 2008; Nelson 2009; Fong & Paul 2011). Large macrophytes and calcareous crustose algae are preferred substrates for settlement of many sessile invertebrates such as hydroids, spirorbid polychaetes, bryozoans, and foraminiferans. Old macroalgal thalli and leaves of seagrasses are occupied by numerous epiphytic and, to a lesser extent, endophytic algae. Thus, marine plants provide habitat space for diverse reef-associated taxa.

(f) Protection of reefs from the destructive effects of surfs

Coralline algae are highly resistant to surfs (Fig. 3a, b). Upon settling on reef crests, they develop a strong ridge that functions like a breakwater, protecting delicate forms of algae and animals that inhabit the upper part of the reef slope from damage (Iryu *et al*. 1995; Fong & Paul 2011). Coriaceous and frondose algae of the genera *Turbinaria* and *Sargassum*, which inhabit the lower intertidal zone and the uppermost part of the subtidal zone, play a similar role (Littler & Littler 1988).

Coral-algal relations

Colonization and competition

As discussed above, algae occupy newly-released substrata within some months and are involved in competitive relationships with survived and newly settled corals and other invertebrates. Successional interactions begin from the first stages of algal community colonization and complete with the transition of a reef into one of the stable states where either hermatypic corals or algae become dominant. With the transition of a damaged reef into a stable state, competitive relationships are generally replaced by symbiotic (mutualistic) relationships that contribute to the maintenance of ecosystem stability or homeostasis.

At early stages of colonization, competition between corals and algae is characterized by overgrowth of competitors and allelopathic influences (McCook *et al*. 2001), where coral polyps that survived a catastrophe tend to be competitively superior (Titlyanov & Titlyanova 2008). In an experiment on the regeneration of adult colonies of *Porites lutea* and *P. cylindrica* from artificially inflicted injuries, coral polyps were able to overgrow more than 100 algal taxa (but not toxic blue-green algae such as *Lyngbya semiplena* and

L. majuscula) (Titlyanov *et al*. 2008a). Injuries up to 20 cm^2 in area healed within 6 months, i.e. the algal-turf community formation was not a serious impediment to the recovery of damaged corals, although the rate of recovery slowed down.

After the formation of algal communities on vacant substrata, competition between coral colonies and algal settlers continue with different modes of competition being involved. These include direct physical interactions such as overgrowing, overtopping, smothering (McCook *et al*. 2001; Box & Mumby 2007; Titlyanov & Titlyanova 2008; Titlyanov *et al*. 2008a) and indirect ones such as environmental modification and space preemption (Dobson & Hudson 1986; Hudson & Greenman 1998), production of allelochemicals (Bak & Borsboom 1984; Paul & Puglisi 2004; Gross 2003; Titlyanov *et al*. 2007) and the stimulation of pathogenic bacteria (Nugues *et al*. 2004; Smith *et al*. 2006). Further, there have been reported cases of macroalgae directly killing and overgrowing neighboring corals (McCook 2001; Jompa & McCook 2003; Nugues *et al*. 2004).

Not all algal species on coral reefs compete with corals for space, e.g. endophytic and epiphytic algae. Corals' main competitors for space include brown algae with large upgrowing thalli (the genera *Sargassum*, *Padina*, *Dictyota*, etc.), dense communities of algal turfs and toxin-producing algae. With the formation of algal communities on a damaged coral reef, the recovery of coral colonies and their expansion over hard substrata may largely be impeded (Titlyanov & Titlyanova 2008), depending on species-specific competitive abilities of algal thalli and coral colonies (Jompa & McCook 2003; Birrell *et al*. 2005) and also on environmental conditions. However, even at this stage of coral/algal competition, adult coral colonies may still remain superior competitors in the absence of strong anthropogenic stresses.

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Algae as competitors

It should be noted that algae can overgrow coral polyps only when they are damaged, weakened or under stressed conditions in general. In an experimental study involving algal species such as *Peyssonnelia conchicola*, *Corallophila kleiwegii*, *Centroceras clavulatam*, *Anotrichium tenue*, *Polysiphonia* spp. (Rh), *Lobophora variegata*, *Sphacelaria novae-hollandiae*, *S. tribuloides* (Ph), *Codium* spp., *Dictyosphaeria* spp. (Ch), these could overgrow colonies of *Porites lutea* only under the light intensity of less than 5% PAR$_0$ (Titlyanov *et al*. 2009a). This is related to the differences in light adaptation between algae and corals. It has been demonstrated that the majority of scleractinian coral species are associated with light levels of 1-80% PAR$_0$ (Titlyanov & Latypov 1991), while red coralline algae can tolerate down to 0.1% PAR$_0$ (Littler & Littler 1988).

Early life stages of many sessile species including hermatypic corals are typically competitively inferior to older and larger individuals (Sebens 1989; Maida *et al*. 2001; Vermeij *et al*. 2009). In similar vein, large-sized, fleshy, coriaceous and foliaceous forms of marine plants as well as algal turfs can limit the success of smaller competitors (e.g., coral planulae, larvae of other sessile organisms, young coral colonies (Grant 1977; Grizzle *et al*. 1996). It has been suggested that the effect of algae on corals is strongest during the coral's earliest benthic stages (Hughes & Jackson 1985; Hughes 1989, 1996; McCook *et al*. 2001; Vermeij & Sandin 2008). Coral recruitment commonly declines when benthic algae become abundant in experimental (Rogers *et al*. 1984; Birrell *et al*. 2005; Hughes *et al*. 2007) and natural settings (Hughes 1989; Birkeland 1996; Edmunds & Carpenter 2001; Vermeij & Sandin 2008). Benthic algal assemblages have direct negative impacts on coral recruitment mainly through the preemption of settlement space (Birrell *et al*. 2005; Vermeij *et al*. 2009; Mumby *et al*. 2007). Additionally, algae can have indirect negative impacts on coral recruits through allelopathy (Gross 2003; Kuffner *et al*. 2006).

Abundance of macroalgae is often attributed to their ability to actively overtake space previously occupied by corals, i.e. their presumed greater competitive capacity than corals, although there is little direct evidence supporting this hypothesis (McCook *et al*. 2001; Fong & Paul 2011). Indeed, we argue that passive colonization of space previously occupied by stony corals that died from causes other than competition with algae (e.g., disease, bleaching) might often have been mistakenly interpreted as evidence of active competition between corals and algae (Vermeij *et al*. 2009). On the other hand, under certain circumstances macroalgae do seem to restrict the growth of coral colonies. In subtropical, high-latitude coral assemblages, polyps on the
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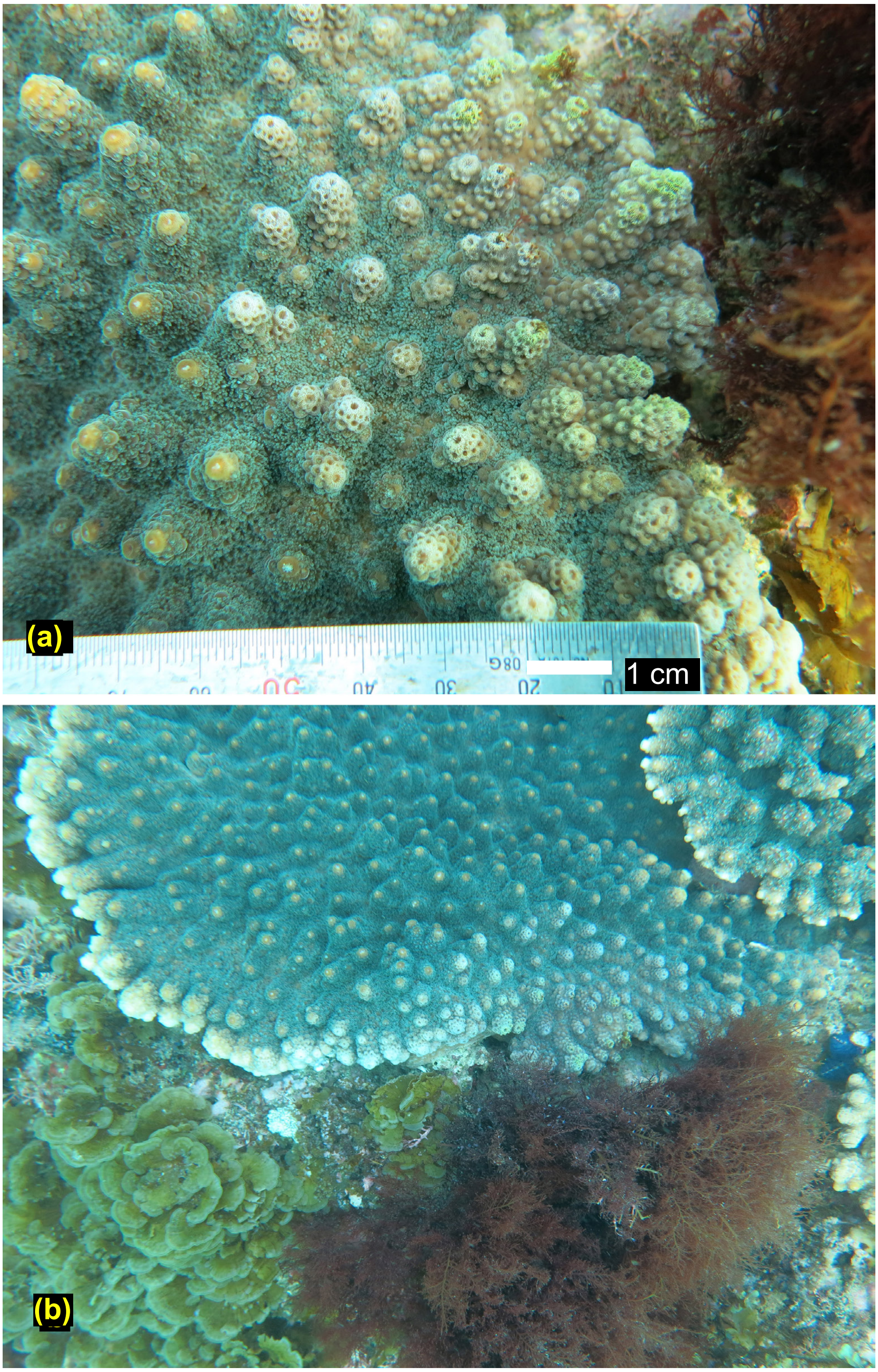

Figure 4. Acroporan coral polyps suffering from abrasion by macroalgae: (a) Polyps of *Acropora japonica* are partially bleached and killed by the repeated abrasive movements of the thalli of *Gelidium elegans* (to the right of the photo); (b) partially damaged colony of *Acropora japonica* due to the abrasive movements of neighboring *Gelidium elegans* (photos taken in Amakusa, Japan, by M Tokeshi).

edges of acroporan colonies are often injured and killed by whipping, abrasive movements of neighboring macroalgae such as *Gelidium elegans* (Fig. 4).

Corals as superior competitors in coral reef recovery

Recovery rates of damaged coral colonies may vary greatly, as demonstrated by experimental ecophysiological studies on healthy and damaged coral colonies (Titlyanov *et al*. 1998, 1999, 2000a, 2001a, b, c, d, 2005, 2006, 2007, 2008a, 2009a; Titlyanov & Titlyanova 2002a, b, 2008, 2009, 2012a, b) and by the monitoring of coral reefs after natural catastrophes in different regions of the world (Loch *et al*. 2002; Stobart *et al*. 2005; Guzman & Cortes 2007; Wellington & Glynn 2007; Baker *et al*. 2008; Rogers *et al*. 2008). During coral reef recovery, hermatypic corals are often superior competitors to macrophytes and cyanobacteria which do not impede coral recruitment. High competitive abilities of hermatypic corals are related to various morphological and physiological aspects:

(1) Long-term (tens to hundreds of years) presence and growth of certain coral colonies (Veron 1986), while marine plants exist from days to a few years at most (Loban & Harrison 1994). Corals are permanent (long-living) settlers on hard substrata and gradually overgrow other non-toxin producing organisms. At the same time, algae (toxic or large forms) constitute only a temporary impediment to corals as they may be replaced by other, non-toxic forms which cannot impede coral settlement and recovery (Titlyanov & Titlyanova 2008). This replacement may occur during seasonal changes in species composition of algal assemblages or under stressful conditions (disturbances by storms, grazing by animals, etc.). After disappearance of harmful algae, bleached polyps (which were under direct contact with toxic or large algae) could recover in 2-4 weeks and continue to occupy the substrate (Titlyanov & Titlyanova 2008).

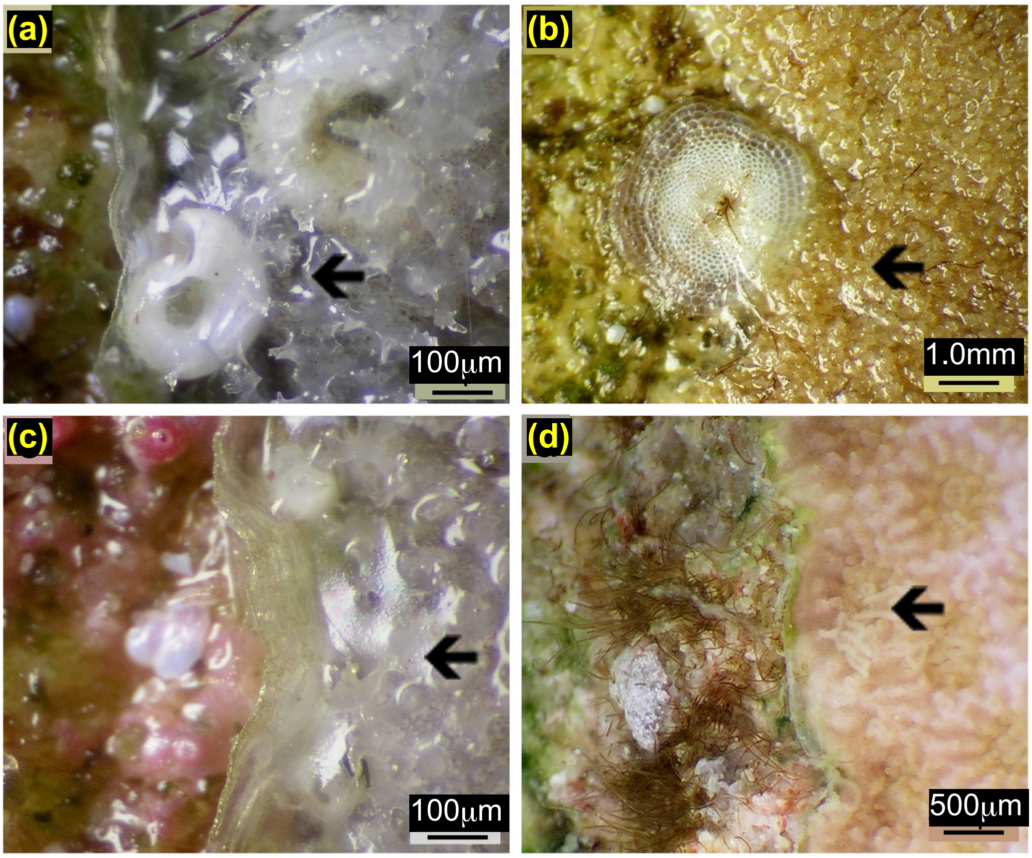

Figure 5: Newly formed tissue of *Porites lutea* overgrowing other colonizers on the substrate: (a) *Spirorbis* sp.; (b) bryozoan; (c) Corallinaceae red algae; (d) algal turf.

(2) High regenerative capacity of corals. Newly-formed live tissues of corals can gradually overgrow the dead parts colonized by algae. Corals' ability to recover from damages, depending on the position, size, shape and type of the damage, has been well documented (Bak & Steward-van Es 1980; Bak 1983; Wahle 1983; Rinkevich & Loya 1989; Meesters *et al*. 1993, 1994; Meesters & Bak 1995; Hall 1997, 2001; Oren *et al*. 1997; Marshall 2000). For example, the newly-formed tissues of the corals *Porites* spp. and *Montipora grisea* tightly adjoined to the substrate with the exception of the front line (Titlyanov *et al*. 2005). This portion of the live tissue edge (probably not calcified or slightly calcified) had no zooxanthellae and appeared as a transparent extension that grew over other colonizers on the substrate (Fig. 5). The width of the tissue stripe depended on coral species, e.g. 100-300 µm wide in *Porites lutea*, 50-100

Figure 6: Growing coral polyps going round an impediment, a green alga *Parvocaulis parvulus*.

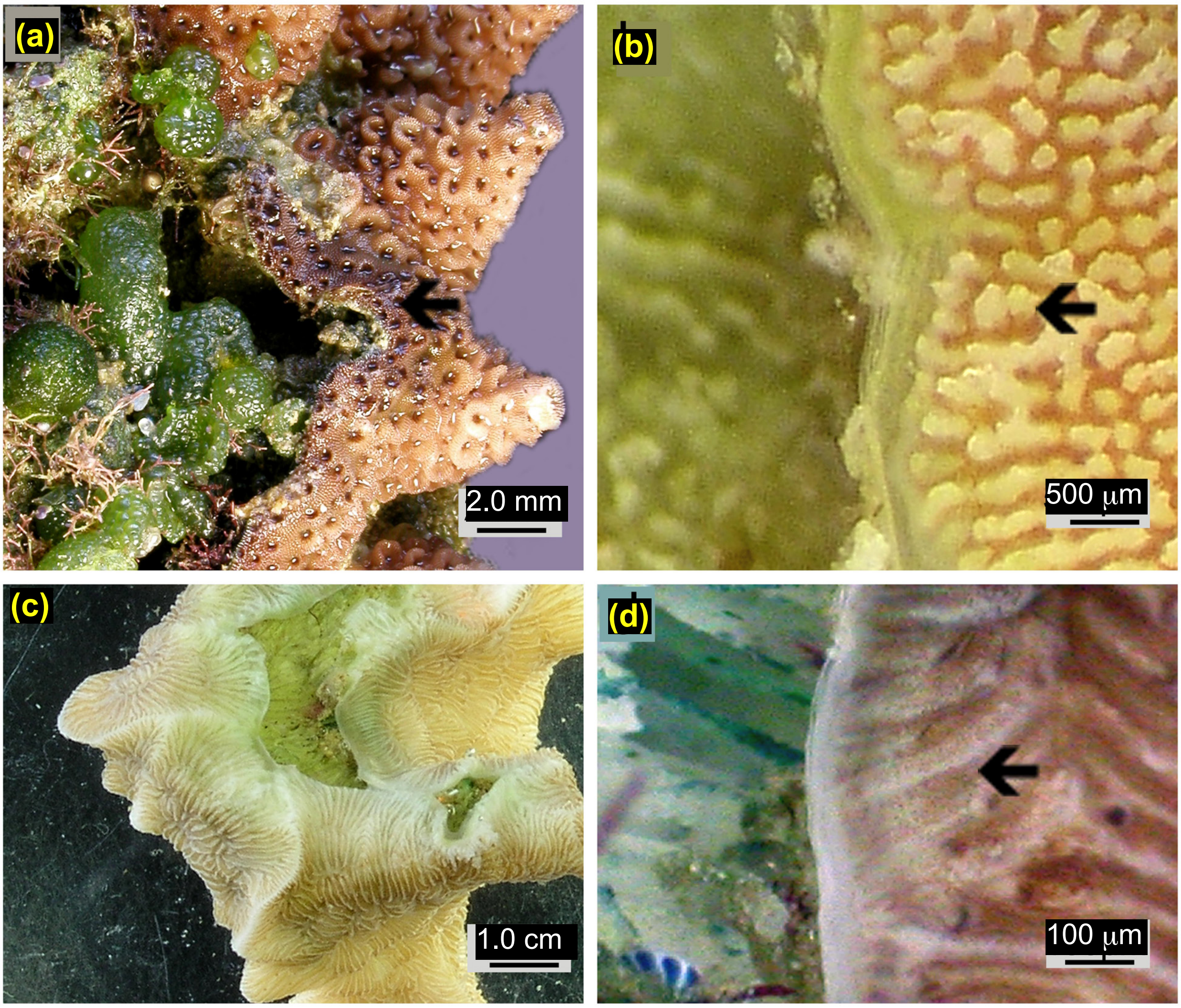

Figure 7: Characteristics of lesion healing in a branched coral *Acropora* sp. and a foliaceous coral *Pavona divaricata*: (a) *Acropora* sp. overgrowing the green alga *Dictyosphaeria cavernosa*; (b) Overgrowth of the lesion by a thin blade-like tissue formation in *Acropora* sp.; (c) and (d) lesions healing (newly formed tissue) in *P. divaricata*.

µm in *P. cylindrica* and 50-200 µm in *P. rus*. The newly-formed coral tissue was able to go round impediments (Fig. 6) or rise above the impediments to overgrow. In the latter case, the impediment (live or lifeless object) was entombed into the coral skeleton.

A branched coral *Acropora* sp. and a foliaceous coral *Pavona divaricata* demonstrated different processes of lesion healing. After fast recovery (4-6 days) of damaged tissues, polyps began to occupy dead areas of the lesion by spreading and overgrowing with a thin blade-like formation consisting of soft tissue and hard skeleton (Fig. 7). Sharp crystals (like spines or teeth), sometimes covered by live tissue (bearing zooxanthellae), projected along the front line of the "blade". The blade did not adjoin firmly to the substratum and could rise above the lesion at a distance of 1 mm or more. As the blade expanded over the substratum, its back portion fixed newly formed skeleton to the lesion, entombing all sessile organisms into the skeleton. Our research to date suggests that this mechanism of substrate colonization is characteristic of many encrusting coral species and widely observed on coral reefs.

Expansion of massive corals may be temporarily hampered by obstacles such as tall and dense algal turfs, large fleshy algal thalli or large sessile animals. In such cases, new polyps may form "bolsters" in front of and above the impediment (Titlyanov & Titlyanova 2008) and these may eventually close up, entombing algae into the coral skeleton (Fig. 8).

On damaged reefs, coral polyps coming into direct contact with algae tend to become bleached by allelopathic substances, abrasion, smothering or shading (Fig. 9). However, bleached polyps may remain alive for a long time and recover after cessation of negative algal influences. For instance, experiments on the physical contact of *Porites lutea* colony fragments with a mat of the blue-green alga *Lyngbya bouillonii* demonstrated that the contact during one month inhibited growth and photosynthesis of the coral and bleached its polyps, due to a significant decline in zooxanthellae density and their total chlorophyll content (Titlyanov *et al*. 2007). These bleached fragments completely recovered in the absence of *L. bouillonii* under the light intensity of 30% PAR$_0$ for two months (Fig. 10).

Figure 8: Final stage of regeneration of massive colonies of hermatypic corals: (a) damaged (2-3 years ago) colony of the coral *P. lutea*; (b) - (d) regeneration of massive colonies of the coral *Platygyra verweyi*.

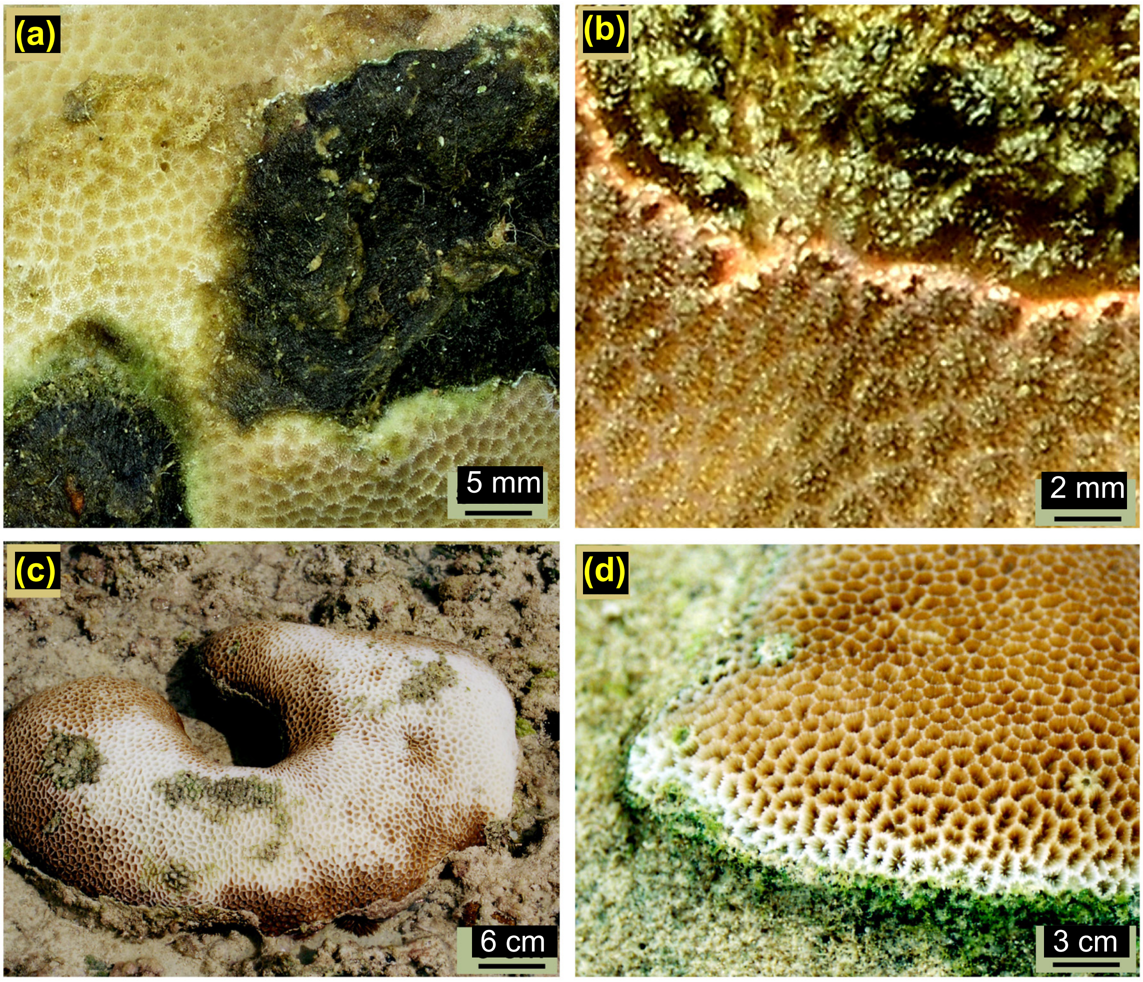

Figure 9: Bleaching of hermatypic coral polyps under allelopathic and direct physical influence: (a) bleaching and growth inhibition of the polyps of *P. lutea* under allelopathic contact with the blue-green alga *Lyngbya majuscula*; (b) *P. lutea* under allelopathic contact with *Lyngbya semiplena* (coral changing growth form in upright direction); (c) and (d) bleaching of the coral *P. verweyi* polyps under direct physical influence of macroalgae.

Similarly, our observations in Amakusa, Japan, showed that a colony of encrusting *Acanthastrea* sp. was observed to recover after having been covered by algae for several months and suffering from partial discoloration.

(3) Advantage of size. In tropical and subtropical waters, healthy adult coral colonies of all growth forms except encrusting ones do not generally compete with algae because of their large sizes (height) surpassing algal assemblages, conceding only to Sargassaceae species on rare occasions. Coral colonies shade the bottom space immediately underneath and deprive fast-growing algae of necessary light. On shaded substrates under coral colonies, mainly slow-growing coralline algae settle which in turn promote the attachment of hermatypic corals' planulae (Fong & Paul 2011).

(4) Different ways of feeding in corals, including photosynthesis of zooxanthellae, predation, consumption of particles of organic (animal) origin and digestion of own zooxanthellae (Titlyanov *et al*. 1996; Titlyanov & Titlyanova 2002a). These allow corals to survive under unfavourable conditions such as low light conditions and waters poor in nutrients. For instance, *Stylophora pistillata* was shown to survive and acclimate under a wide range of light intensities from 0.8 to 95% PAR_0. Acclimation to low light conditions (8 and 30% PAR_0) involved maximizing the light harvesting capacity by increasing photosynthetic pigment concentration in zooxanthellae and zooxanthellae population density in coral branches. Under the extremely low light level (0.8% PAR_0), the coral lost zooxanthellae by digestion but retained high concentrations of chlorophyll. The photo-acclimation process is dynamic and immediate. Changes in pigment

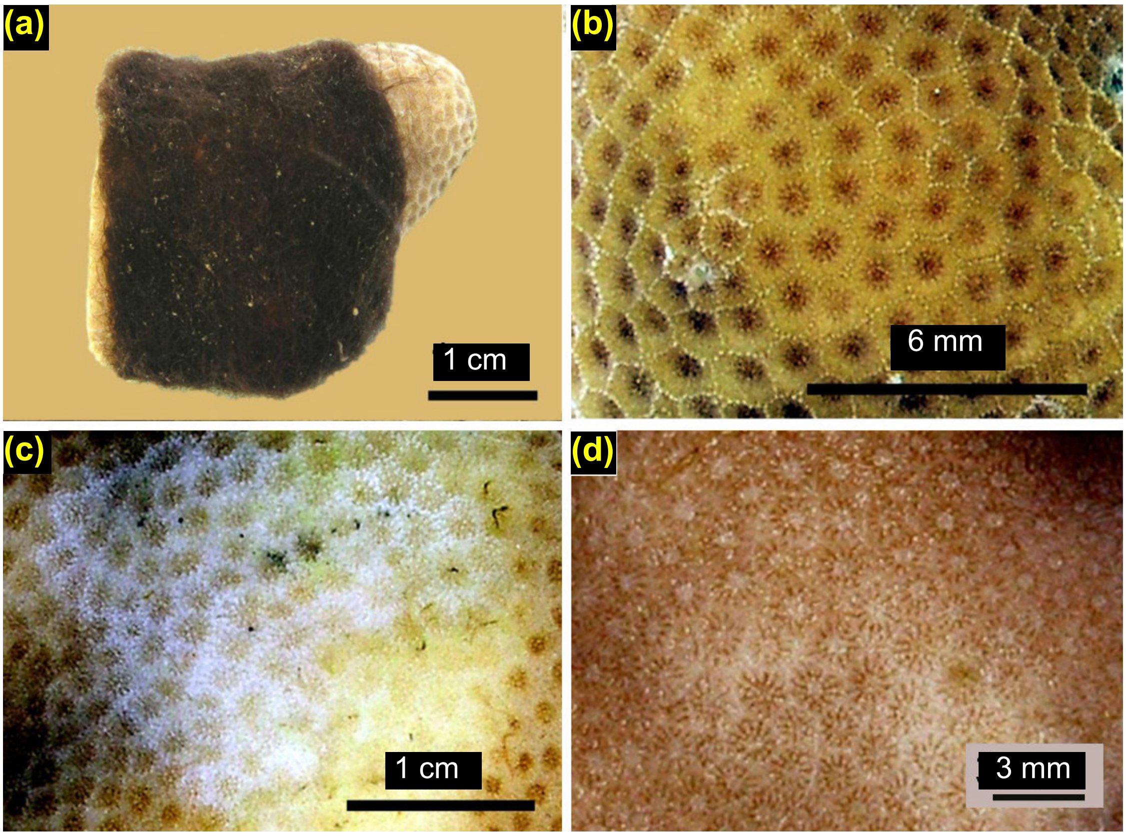

Figure 10: Bleached polyps of the coral *P. lutea* after direct (30 days) contact with the blue-green alga *Lyngbya bouillonii* and their recovery during 60 days (adapted from Titlyanov *et al*. 2007): (a) colony fragment of the coral *P. lutea* in direct contact with the blue-green alga *L. bouillonii* under experiment; (b) polyps of the coral *P. lutea* before the experiment; (c) the same bleached polyps after maintenance under direct contact with *L. bouillonii*; (d) the same recovered polyps after the experiment.

concentration in zooxanthellae occurred within 2-4 days and changes in zooxanthellae population density within 40 days. Zooxanthellae population densities were regulated by changes in the rates of division and degradation (digestion) of symbiotic cells (Titlyanov *et al*. 2001c).

Predation may be interpreted as adaptation to low light levels. Under the illumination of 2% PAR_0, capture and ingestion of *Artemia salina* nauplii by the coral *S. pistillata* were stimulated, with increasing ratios of ingested to killed nauplii; i.e., prey ingestion was more efficient at 2% PAR_0 than at 20 or 90% PAR_0. It has been mentioned that under high/moderate light, corals most actively hunt in early morning hours, whereas under conditions of shading, they hunt throughout the day. When light is deficient, predation appears to be the major source of obtaining food in corals (Titlyanov *et al*. 2000 b, c). A decrease in photosynthesis of *S. pistillata* under light limitation also induced an increase in both chlorophyll concentration and zooxanthellae population density. Both responses require nitrogen that is generally insufficient in seawaters above coral reefs. For maintaining these responses the coral is capable of using nitrogenous compounds derived from captured zooplankton prey (Titlyanov *et al*. 2000c).

(5) Corals' capacity to clean off organic and inorganic sediments from colony surfaces. Corals exhibit both active and passive removal of sediment particles (Lasker 1980). They have a variety of mechanisms for coping with sediments including the use of their tentacles and cilia, stomodeal distension through water uptake, and entanglement of particles in mucus which later sloughs off the colony surface (Hubbard & Pocock 1972). Where currents are strong, water movement will help keep sediment particles from settling on colony surfaces, and corals will have to spend less energy in sediment rejection. Species differ in their ability to reject sediments, colony and polyp morphology playing an important role (Hubbard & Pocock 1972). The amount and type of sediment will influence the ability of a coral to maintain its surfaces free of sediments (Rogers 1990).

Colonies of some genera of hermatypic corals exhibit changes in orientation and morphology, which appear to occur in response to sediment stress (Bak & Elgershuizen 1976). This would reduce the possibility of settlement of spores and planulae on colony surfaces and help corals survive under conditions of high sedimentation. Macroalgae under such conditions become covered with sediments that limit their production and absorption of nutrients (Titlyanov *et al*. 2011a, b). Only crustose calcareous algae have a mechanism of surface cells' sloughing (Keats *et al*. 1994).

(6) The ability of coral planulae to attach to and grow on the thalli of competitors. Calcareous algae are considered the preferred substrate for attachment and development of coral planulae. When planulae receive certain chemical triggers secreted by crustose coralline algae, they stop swimming, attach to the substrate and develop into the primary polyps (Harrison & Wallace 1990; Harrington *et al*. 2004; Golbuu & Richmond 2007). It was shown that this induction effect of settlement is species-specific (Heyward & Negri 1999; Golbuu & Richmond 2007). Microbes living on algae may also induce/stimulate planulae settlement and metamorphosis (Neumann 1979; Richmond 1987; Morse *et al*. 1988; Zaslow & Benayahu 1996; Leitz 1997; Heyward & Negri 1999). Moreover, settlement and survival of coral planulae may be influenced by independent as well as synergistic effects of macroalgae and microbes (Vermeij *et al*. 2009).

These suggest that not only red calcareous algae but also other representatives of algal turfs may serve as substrata for planula settlement. When 11 macroalgal species were tested on their effects on the swimming and settlement of *Platygyra daedalea* larvae, algal turfs and crustose calcareous algal groups had minor effects on coral settlement, while upright calcareous and fleshy macroalgae inhibited settlement (Diaz-Pulido *et al*. 2010).

(7) Coral fragments' capacity to attach to and grow on hard substrata and also the possibility of their non-attached existence. This feature is considered of importance in coral reef restoration after strong typhoon/tsunami damages. Coral fragments or even colonies could be dislodged, transported by water movements and relocated in new habitats. Under certain conditions, coral fragments may successfully attach to hard substrata or grow together with live colonies. Unattached fragments may survive for a long time on soft substrates, often acquiring a spherical form due to rolling (Veron 1986; our own observations). In contrast, algae detached from the substrate are most likely to perish.

(8) Mobility of corals. Some coral species, most notably of the Family Fungiidae, are capable of actively moving over hard and soft substrata (Veron 1986), which allows them to aggregate in favourable microhabitats where competition with algae may be reduced.

Thus, hermatypic corals tend to be competitively superior to macroalgae under natural/semi-natural conditions of reef ecosystems. While the competitive capacity of some macroalgae is enhanced under the advanced states of seawater contamination (Rosenberg 1985; Doering *et al*. 1995; Harlin 1995; Fletcher 1996; Raffaelli *et al*. 1998; Taylor *et al*. 1999; Nixon & Buckley 2002; Thornber *et al*. 2008), the combination of traits described here gives credence to the view that in the majority of cases corals outcompete algae on coral reefs damaged by natural catastrophes.

* * *

Concluding remarks: positive roles of marine algae in coral reef recovery

In conclusion, we draw attention to the positive roles of algae in first colonizing newly-formed substrata after disturbance events and in contributing to the restoration of coral-dominant states typical of undamaged reefs.

It may be argued that damaged coral reef ecosystems can return to a homeostatic state that has been lost during a natural catastrophe. We suggest that this is mainly achieved through the colonization of newly-formed substrates by marine algae, with the following characteristics:

1. Maintenance of ecosystem productivity through the settlement of highly productive morpho-functional forms such as fine-filamentous, filamentous and lamellar Chlorophyta and Rhodophyta (Sergeeva *et al*. 2007). While in healthy coral reefs symbiotic microalgae including zooxanthellae are the main primary producers, multi-cellular algae and cyanobacteria may often become the main primary producers that occupy denuded substrata after a catastrophe. Photosynthetic rates (per unit area of substrate) of algal communities may be equal to or greater than that of zooxanthellae in hermatypic corals (Littler & Littler 1988; Littler *et al*. 1991; Titlyanov *et al*. 2007). Algal communities temporarily become the main supplier of organic matter and energy in a damaged reef ecosystem.

2. Protection of coral reef base and newly-formed carbonate substrata (dead coral colonies) from erosion and continuation of carbonate reef base building. Calcareous algae (Littler & Littler 1988) help cement dead colonies and their debris into the carbonate reef base.

3. Colonization of vacant substrates by algae enhances the biodiversity of an entire reef assemblage (Sergeeva *et al*. 2007; Baker *et al*. 2008; Fong & Paul 2011).

4. Symbiotic relations between algae and corals also promote homeostasis and coral reef recovery in damaged reef systems through transport of assimilates from endolithic symbiotic algae (e.g., *Ostreobium quekettii*) to coral tissue (Fine & Loya 2002; Titlyanov *et al*. 2008b, 2009b), which intensifies during a bleaching episode (Fine & Loya 2002), or by coral digestion of own zooxanthellae that intensifies under extreme conditions (low light, starving, osmotic shock) (Titlyanov *et al*. 1996).

5. Release of secondary chemicals by encrusting calcareous algae (or their bacterial biofilm) promotes planula settlement and growth on their surfaces (Hadfield & Paul 2001; Negri *et al*. 2001; Vermeij *et al*. 2009; Ritson-Williams *et al*. 2010).

6. Planulae and young colonies attached to calcareous algae at the base of algal turf are protected from predatory/grazing organisms and from desiccation and bleaching in the intertidal. Coral growth is enhanced by the accumulation of zooplankton and other organisms in algal turfs (Sorokin 1990).

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