



Rapid Smothering of Coral Reef Organisms by Muddy Marine Snow

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Estuarine mud, when resuspended in nutrient-rich near-shore water, aggregates to marine snow, and within minutes to hours can exert detrimental or even lethal effects on small coral reef organisms. In a pilot study, estuarine mud was suspended in near-shore and off-shore waters of the Great Barrier Reef to a final concentration of 170 mg l⁻¹. The short-term responses of a coral (*Acropora* sp.) and coral-inhabiting barnacles (subfamily Pyrgomatidae), exposed to either near-shore or off-shore water, were microscopically observed and video recorded. In the off-shore water treatment, flocculation was minor, and aggregate sizes were c. 50 µm. The organisms were able to clean themselves from these small settling aggregates at low siltation (<0.5 mg cm⁻²), and struggled and produced mucus only at high siltation (4–5 mg cm⁻²). In contrast, in near-shore, nutrient-enriched waters, the suspended mud aggregated into large sticky flocs of marine snow (200–2000 µm diameter). The organisms responded to a thin coat of deposited flocs with vigorous cleaning by cirri and tentacle beating. After 5 min struggle, the barnacle stopped moving, calanoid copepods were entangled in the aggregates, and thick layers of mucus were exuded by the coral polyps. Both barnacle and copepods died after <1 h exposure; a short time compared with natural occurrences of marine snow deposition on coral reefs. Enhanced nutrient concentrations are known to contribute to enhance biologically mediated flocculation. This pilot study suggests that the concentration of suspended mud, and extent of stickiness and flocculation, can synergistically affect reef benthos organisms after short exposure. The enclosed macro video recordings clearly visualize these effects, and help convey the important implications for managers: that inshore reefs of the Great Barrier Reef cannot be sustainably managed without managing the adjacent land.

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Introduction

Coral reefs are generally associated with clear and oligotrophic waters, although some shallow coastal reefs on the Great Barrier Reef are exposed to highly turbid waters. The amount of suspended particulate matter around coastal coral reefs is often c. 5 mg l⁻¹, but under high energy conditions may exceed 40 mg l⁻¹ (Larcombe *et al.*, 1995) and can be as high as 200 mg l⁻¹ for mud-polluted coastal reefs (Wolanski & Spagnol, pers. com.). The particulate material consists (in varying proportions) of inorganic particles such as re-suspended clay and calcareous or silicate sand, organic detrital particles and living plankton. Compared with coastal sediment, the riverine and estuarine sediments are muddy and rich in nutrients and detritus (Wolanski, 1994). When river

water enters the sea, the nutrients previously adsorbed to clay become labile, and particles are rapidly colonized by mucopolysaccharide-producing diatoms and microbes. Their mucus increases the stickiness of the particles, resulting in further aggregation and the biologically mediated formation of 'marine snow' (Wolanski & Gibbs, 1995; Ayukai & Wolanski, 1997). At moderate turbulence, such aggregates can exceed 3000 µm diameter (Eisma, 1986). Nutrient-enhanced biological flocculation also occurs as result of ageing of the water, re-suspension, and nutrient regeneration in bottom layers (Kjørboe *et al.*, 1990; Wolanski, 1994; Wolanski *et al.*, 1997; Ayukai & Wolanski, 1997). In areas of high nutrient enrichment, such as the formerly oligotrophic Northern Adriatic Sea, flocs of amorphous aggregates grow to >0.2 m (Herndl & Peduzzi, 1988). The flocs either sink onto the sea floor smothering the benthos like fire blankets, or rise to the water surface by including gas bubbles after a few hours to days of ageing (Stachowitsch *et al.*, 1990).

Full sized figures, tables and animations are stored on the CD-ROM accompanying this article. Use a Web browser to access the start page 'default.htm' and follow the links. The help file 'help.htm' provides answers for some common problems.
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The Great Barrier Reef stretches along 2600 km of the east coast of Australia from 25 to 10°S. River runoff is the largest external source of nutrients to the GBR lagoon (Furnas *et al.*, 1997). The bulk of sediment and nutrient is discharged during flood events, with flood plumes predominantly impinging on the coast and inner lagoon, but occasionally extending into the mid-shelf (Wolanski, 1994). Larger plumes travel many tens of kilometres northward along the coast, and near-shore coral reefs encounter such plumes once every few years. Temporal variability in runoff is great, however the amount of sediments and nutrients imported at each runoff event into the Great Barrier Reef lagoon has increased several-fold due to deforestation, expanding grazing and farming (Walker & O'Donnell, 1981; Wolanski, 1994; Larcombe *et al.*, 1996). The resulting addition of nutrient-rich sediments to the sea is considered by some one of the most severe impacts on coastal reefs on the Great Barrier Reef Marine Park (Bell & Elmetri, 1995).

During calm periods (currents $< 10 \text{ cm s}^{-1}$), marine snow sinks to the bottom at a rate of $c. 5 \text{ cm min}^{-1}$, the settling speed depending on aggregate quality, density, and size (Eisma, 1986; Alldredge & Gotschalk, 1988; Wolanski *et al.*, 1998). Rates of sedimentation in excess of $200 \text{ mg cm}^{-2} \text{ day}^{-1}$ have been measured on some coastal reefs for periods of days to weeks (Cortés & Risk, 1985; review in Stafford-Smith, 1993). Previous studies on the effect of sediment on corals indicated that corals respond to low concentrations of settling suspended sediment by removing the particles physically or with the aid of mucus excretion, however they die at high rates of sedimentation (Marshall & Orr, 1931). The time (thus energy) required to remove particles increases with particle size, and varies between taxa and colony shapes (Stafford-Smith, 1993). Mucus excretion is not always a successful cleaning mechanism; moreover it can contribute to anoxia and tissue death in corals when sediment adheres to the mucus (Stafford-Smith & Ormond, 1992). Long-term effects of low-level sedimentation include tissue lesions and diseases, decreased calcification, net productivity and growth, and shifts in abundances and species composition (Dodge *et al.*, 1974; Cortés & Risk, 1985; Peters & Pilson, 1985; Rogers, 1990). There have been no studies on whether reef organisms respond similarly to siltation by small aggregates and by marine snow. The short- and long-term effects of marine snow on reef-building corals and filter-feeding benthos of the Great Barrier Reef are thus largely unknown. Here, a pilot study is presented demonstrating rapid detrimental effects on a near-shore coral

and coral-inhabiting barnacles by suspended estuarine sediment added to (a) oligotrophic offshore water, where aggregates were small ($c. 50 \mu\text{m}$), and (b) nutrient-enriched nearshore waters, where the suspended sediment formed large sticky aggregates of marine snow.

Methods

A 15 cm branch of a nearshore coral (*Acropora* sp.) inhabited by coral-dwelling barnacles (family Pyrgomatidae), was collected from a coastal reef near Cairns ($c.$ latitude 17°), and cut into 20 fragments up to 1 cm long, which is the largest size that could be accommodated in the microscope slide. The coral fragments were positioned in groups of four into small dishes (microscope slides with deep wells) submerged in seawater. About 1 h later, two slides each with four fragments were transferred onto the bottom of a 20 l container (0.3 m water column) containing undisturbed coastal waters. Twelve hours later, another two slides with four fragments each were immersed in a similar container with undisturbed surface waters from offshore the Great Barrier Reef in the Coral Sea. A fifth slide with four fragments was kept in the initial container with clean near-shore seawater for reference. The coastal water contained some marine snow, whereas the offshore water was oligotrophic with no marine snow visible under a microscope.

Sediment of terrestrial origin with high mud content was collected from the mouth of a small estuary near Cairns. This mud is naturally resuspended in coastal waters during strong wind. The mud was pre-mixed with in-shore and offshore water, and gently added to the coral-holding containers with inshore and offshore water, respectively. The resulting concentration of suspended particulate matter was 170 mg l^{-1} . Additional microscope slides were immersed in both containers to collect and observe the quantity of settled aggregates. In 30 cm deep quiescent water, the majority of particles and muddy marine snow settled out within 5 min.

Every 5 min, most of the suspended mud had settled and the slides were capped. The corals, barnacles, zooplankton, and aggregates on the slides were observed at a magnification ranging from 6- to 400-fold with both a dissecting and a Olympus inverted microscope, and the images were captured using a Sony CCD video system (Wolanski & Gibbs, 1995). After a few minutes of observation, the slides were returned to the water containers and uncapped, and the mud was re-suspended from the bottom to extend the period of exposure to siltation.

Results and discussion

In the clean off-shore seawater samples exposed to mud, the mud flocs were small, with a mean floc size averaging 50 μm . These flocs settled individually on the animals, and were mechanically pushed away one at a time, both by barnacles and coral. After 5 min of exposure to settling particulate matter, the amount deposited was 0.5 mg dry weight cm^{-2} . The coral polyps were extended, and only small amounts of particles and mucus adhered to the surface. As typical for balanoid barnacles, the cirri were extended, but flicked occasionally (Animation 1) in a cleaning beat (Anderson & Southward, 1987). Both coral and barnacle showed no apparent sign of stress. The groove around the barnacle was kept clean of particles, and only a few small mud flocs adhered to the cirri. Thus the animal seemed able to cope with small quantities of small flocs.

After *c.* 30 min of exposure, the amount of mud deposited was 4 mg cm^{-2} . The barnacles beat their cirri vigorously and tried to push away the mud, however the mud began to clog up the cirri (Animation 2). After 50 min of exposure (5 mg cm^{-2}), the barnacle cirri were heavily laden with mud flocs and moved only slowly (Animation 3). The mud around the barnacles was too thick to be pushed away, thus the particles slid back into the groove which filled with mud [Figure 1(a)]. The coral polyps were buried and contracted. Soon after, they exuded large amounts of mucus [Figure 1(b)], possibly in an effort to remove the mud (Rogers, 1990). However, in the absence of currents, this mucus could not dislodge the mud already sticking to the surface of the organisms.

In nutrient-enriched inshore waters, muddy marine snow was present and formed large flocs (typically 200 to 2000 μm in diameter), probably due to the presence of organic detritus and mucus as coagulant agent [Figure 1(c)]. The material appeared extremely sticky, with large amounts of detrital material attached to the organic matrix (Animation 4). Live copepods which got in contact with the sticky flocs got entangled and were unable to free themselves (Animation 5). After 5 min of exposure to this muddy marine snow, large (up to several mm) patches covered the slides and organisms, however the amount deposited was only 0.5 mg dry weight cm^{-2} . Where these patches occurred, the small animals were completely buried. The barnacles initially exhibited vigorous movement, but were unable to mechanically free themselves by pushing away the sediment, seemingly because the flocs were sticky and too big (Animation 6). The coral-inhabiting worm attempted in vain to push away individual mud particles (Animations 7 and 8). The

energy expenditure to remove the sediment appeared significant, and movement of both coral-inhabiting worm and barnacles slowed. Thus the animals were completely smothered after 5 min by muddy marine snow, while this stage took about 1 h to reach for mud settling in oligotrophic water. After <2 h, the small filter feeders (barnacles and copepods) were dead (Animation 9), and the corals were covered by a thick mucus layer. Two days later, much of the settled muddy marine snow was still present.

On coral reefs, relatively slow current speeds (<3 cm s^{-1}) are often sufficient to remove the small aggregates from the tops and flanks of mound-shaped and branching corals (Rogers, 1990), however it is not known whether sticky marine snow is also readily removed. Faster and turbulent flow is required to remove small aggregates from plate and encrusting corals with high surface roughness. Organisms sitting in the numerous depressions, grooves, and ditches on the complex reef structure are exposed for even longer periods to deep mud deposits, removed by currents only during high energy conditions. Our observations support previous suggestions that the latter micro-habitat is likely to be uninhabitable for many small sessile organisms (including coral recruits) on reefs exposed to muddy sediment deposits (Sato, 1985; Babcock & Davies, 1991).

A large proportion of reef-inhabiting sessile organisms, or modules of organisms such as coral polyps, are in the size range of millimetres to centimetres. This component of the reef community is commonly overlooked, and its role in the ecosystem is little understood. However, due to their small size, these organisms may be particularly vulnerable to terrestrial runoff and muddy marine snow. Indeed, reefs close to river mouths are often dominated by few, but very large, individual coral colonies (many m^2 in area) belonging to only a few species, and small colonies are greatly under-represented in comparison with clear-water reefs (Costa Rica: Cortés & Risk, 1985, Great Barrier Reef: K. Fabricius, pers. obs.). This indicates firstly, that only a small proportion of species tolerate muddy environments, and secondly, that survival of small colonies appears to be lower in mud-exposed reefs compared to clear-water environments (Cortés & Risk, 1985). There are many explanations for low survival of small colonies, however failure to settle or smothering of recruits by sediment may be among the most significant ones (Sato, 1985). The size of coral recruits remains *c.* 5 mm for up to a year, i.e. periods of calm conditions, leading to prolonged (days) deposition of suspended particles, are likely to occur while they are small and unable to remove layers of sticky marine snow from their surfaces.

Our studies are preliminary, and need to be extended to many species of reef organisms and a wide range of levels of turbulence, nutrient enrichment and siltation. Nevertheless, there is an apparent contrast between the ability of the small filter feeding organisms to sustain settlement of small flocs of marine snow in off-shore waters, yet their inability to cope with the large flocs formed in near-shore waters. In oligotrophic waters, the organisms can remove small mud flocs one by one, and may cope in the short-term with exposure to $c. 5 \text{ mg mud cm}^{-2}$. In more eutrophic coastal waters, they were unable to mechanically remove the settling large muddy marine snow flocs, and animals were swamped by sticky marine snow after short exposure to low concentrations of mud. Our visualization suggests that low to moderate concentrations of large aggregates formed in coastal areas exposed to terrestrial mud runoff can be detrimental, or even lethal, for small benthos organisms within only a few hours of exposure. These observations may have important management implications. Indeed they suggest that inshore reefs of the Great Barrier Reef cannot be sustainably managed without managing the adjacent land.

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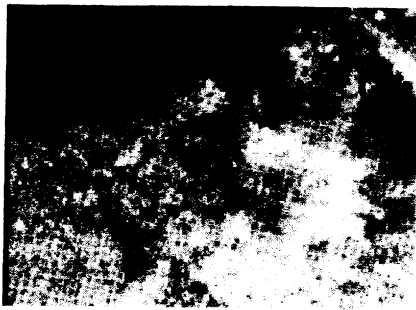
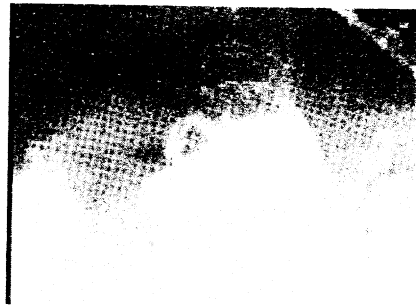


FIGURE 1(a). The cirri of Pyrgomatid barnacles clog up by adhering particles, and the grooves around the animals fill with mud at high rates of sedimentation of suspended estuarine mud ($c. 4 \text{ mg dry weight cm}^{-2}$).



ANIMATION 1. The barnacle remains in feeding posture, interrupted only by short cleaning beats, when exposed to low amounts of settling estuarine mud suspended in oligotrophic off-shore waters. Floc sizes in the suspension are small ($c. 50 \mu\text{m}$).



FIGURE 1(b). The tip of a coral branch (*Acropora* sp.) exuding copious amounts of mucus in response to sedimentation. The coral begins to shed the mucus, forming inflated pockets.



ANIMATION 2. The barnacle exhibits vigorous cleaning beats at higher rates of mud deposition ($c. 4 \text{ mg cm}^{-2}$) in oligotrophic water, however the particles start clogging up the cirri.



FIGURE 1(c). Typical ambient muddy marine snow (at $<5 \text{ ppm}$ of mud) in inshore waters of the Great Barrier Reef (December 1998), showing a Copepod entangled in an aggregate of marine snow.



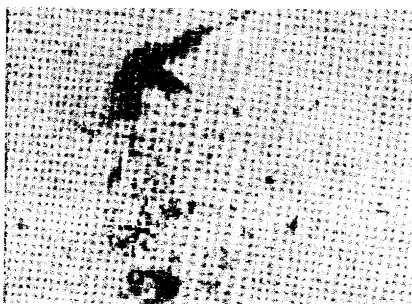
ANIMATION 3. In oligotrophic water, particles remain unaggregated even in thick deposits of mud. The barnacle tries to push away the mud, however the deposits are too thick, thus the mud starts filling the groove around the animal and the barnacle is unable to clean itself.



ANIMATION 4. Estuarine mud aggregates consisting of detrital material and phytoplankton embedded in a mucus matrix. Note the microzooplankton circling around the flocs.



ANIMATION 7. A large floc of muddy marine snow which incorporates particulate organic matter covers the coral nearly completely. A coral-inhabiting worm attempts unsuccessfully to push away the debris.



ANIMATION 5. A copepod is entangled in a 500 μm wide aggregate. The copepod is unable to free itself.



ANIMATION 8. The coral is completely covered and only tips of the tentacles protrude from the mud. The polyps stopped moving and retracted after an initial effort to free themselves.



ANIMATION 6. The estuarine mud is highly aggregated and settles on and around the barnacle as an elastic and sticky layer. The barnacle tries hard to clean itself, however is unable to remove the deposits.



ANIMATION 9. After <1 h of exposure to sticky marine snow, the barnacle is dead.