

Responses of algal communities to gradients in herbivore biomass and water quality in Marovo Lagoon, Solomon Islands

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Received: 6 March 2007 / Accepted: 6 August 2007 / Published online: 1 September 2007
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Abstract Settlement tiles were used to characterise and quantify coral reef associated algal communities along water quality and herbivory gradients from terrestrial influenced near shore sites to oceanic passage sites in Marovo Lagoon, the Solomon Islands. After 6 months, settlement tile communities from inshore reefs were dominated by high biomass algal turfs (filamentous algae and cyanobacteria) whereas tiles located on offshore reefs were characterised by a mixed low biomass community of calcareous crustose algae, fleshy crustose algae and bare tile. The exclusion of macrograzers, via caging of tiles, on the outer reef sites resulted in the development of an algal turf community similar to that observed on inshore reefs. Caging on the inshore reef tiles had a limited impact on community composition or biomass. Water quality and herbivorous fish biomass were quantified at each site to elucidate factors that might influence algal community structure across the lagoon. Herbivore biomass was the dominant driver of algal community structure. Algal biomass on the other hand was controlled by both herbivory and water quality (particularly dissolved nutrients). This study demonstrates that algal communities on settlement tiles are an indicator capable of integrating the impacts of water quality and herbivory over a small spatial scale (kilometres) and short temporal scale (months), where other environmental drivers (current, light, regional variability) are constant.

Keywords Algae · Herbivory · Water quality · Coral reefs

Introduction

Reduction in either herbivory, water quality or both have been highlighted as the major localised threats to coral reef health (Littler and Littler 1984; Bryant et al. 1998). Both factors directly influence algal communities and dictate the nature of their equilibrium with hard coral. The trend towards algal dominated reefs has been reported from Hawaii (Hunter and Evans 1995), the Caribbean (Hughes 1994) and the inshore Great Barrier Reef (Done 1992). Algal dominated reefs generally support less productive fisheries and are a step along the “slippery slope to slime” described by Pandolfi et al. (2005).

Numerous studies have explored the relative importance of top down (herbivory) and bottom up (nutrient) pressures on coral reef algal communities. Generally a manipulative approach is employed to test the effects of altered water quality and grazer exclusion in relation to a control. Such studies conducted in Hawaii (Smith et al. 2001) and on the Great Barrier Reef, Australia (McCook 1996) have concluded that herbivore grazing pressure is the major limiting factor for algal growth on coral reefs. However, Lapointe et al. (2004) determined that nutrients limit algal growth on Caribbean reefs. While some researchers have attempted to develop a conclusive paradigm that algal communities are primarily controlled by herbivory (Hughes et al. 1999), it is apparent that the diversity of environments in which coral reefs occur dictates that algal growth may be limited by different factors in different locations.

The diversity of algae that exist on tropical coral reefs have a range of light (Carpenter 1985), nutrient (Bell 1992; Lapointe 1997; Miller et al. 1999), herbivory (Hixon and

Communicated by Environment Editor K. Fabricius.

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Brostoff 1996; McCook 1997), water motion (Glenn and Doty 1992), and substrate (Diaz-Pulido and McCook 2004) requirements. Using the relative dominance model, Littler and Littler (1984) were first to describe the different algal species assemblages and the top-down and bottom up factors that drive them. Steneck and Dethier (1994) refined this system by dividing algae into functional groups; microalgae, filamentous, foliose, corticated, leathery and calcareous crustose algae. However, this can still lead to morphologically different communities being placed in the same functional groups as some algal functional groups (e.g., microalgae) that are morphologically plastic can exist in dense mats up to one metre thick (cyanobacteria) or as encrusting forms.

Observational data from the Great Barrier Reef (GBR) provide evidence of water quality influences on algal community structure. Surveys across a range of reefs in the northern GBR showed that abundance of chlorophytes and rhodophytes were positively correlated with declining water quality (Fabricius et al. 2005). These changes in species assemblages have been clearly demonstrated on degraded reefs where a particular species dominates the degraded environment, e.g., *Sargassum* in the GBR (Done 1992) and the Caribbean (Hughes 1994), and *Dictyosphaeria* in Hawaii (Stimson et al. 2001). Along with changes in community structure, degraded reefs worldwide have undergone a rapid increase in algal biomass over recent decades. Williams and Polunin (2001) documented an inverse linear relationship between percentage algal cover and herbivore biomass across 19 Caribbean reefs. Manipulative studies have shown four fold increases in algal biomass from caging and/or fertilisation experiments (Smith et al. 2001). This physical overgrowth of coral reefs by algae leads to reduced hard coral cover, reduced tourism appeal, increased presence of toxic microalgae and reduced fisheries potential (Done 1992; Wilkinson 1996).

Reefs within the Pacific region remain amongst the most pristine and biologically rich on the planet. Yet many of these reefs are largely unstudied and are under increasing local and global pressures. This study provides an initial insight into the localised threats to coral reefs in Marovo Lagoon in the Western Province of the Solomon Islands.

Marovo Lagoon supports exceptionally high marine biodiversity (Green et al. 2006) and has World Heritage list potential. The majority of the 12,000 Melanesian people in Marovo occupy small subsistence villages (~200 people) on the mountainous islands of New Georgia, Vangunu and Gatokae. In recent decades Malaysian companies (e.g., Kumpulan Emas) have commercially logged the majority of the Marovo region using unsustainable logging practises that have been described as the most environmentally destructive worldwide (Olsen and Turnbull 1993). Terrestrial ecosystem destruction and lagoon water quality

degradation have been obvious results of these logging operations. The shallow (1–2 m) patch reefs throughout the lagoon offer the most readily accessible areas for subsistence and artisanal fishing. In particular, subsistence fishers target patch reefs close to their villages, which are spread throughout the lagoon. As a consequence of localised logging and fishing pressures, Marovo Lagoon is a unique location to test the influences of herbivory and water quality on algal communities across natural gradients, as it includes numerous small patch reefs within a strong gradient in water quality and herbivory over a small scale (ca. 10 km). Water quality and herbivory pressure were quantified at numerous patch reefs to determine the relative importance of water quality and herbivory pressures. Manipulative caging experiments were combined with the spatial gradients to further explore how herbivory influences algal communities.

Materials and methods

Site

Marovo Lagoon is a large (700 km²) tropical coral reef lagoon enclosed by a unique raised double barrier reef system (Fig. 1). Water quality and herbivory gradients were captured by studying nine separate patch reefs that covered a range in water quality and herbivory. The study reefs were generally located along two transects each extending from the shores of the large volcanic island of Vangunu to the outer barrier reef (Fig. 1). These transects (adjacent to Bili and Chea villages) were chosen based on indigenous marine tenure constraints and were not part of the experimental design, rather the nine individual patch reefs were the experimental unit. At each of the shallow patch reefs, water quality, herbivorous fish biomass and algal biomass, and community structure on settlement tiles were quantified. Sites were chosen to standardise other environmental drivers of algal communities such as current, depth and light.

Algal settlement tiles

Substrate availability is often a major driver of algal community structure (Diaz-Pulido and McCook 2004). Thus, artificial settlement tiles were used as the standard substrates. Six replicate settlement tiles measuring 7 × 7 cm (roughened 3 mm grey PVC) as per Smith et al. (2001) were randomly attached (via concrete blocks) parallel to the substrate at ~1 m below low tide on each of the nine study reefs during January 2005. After five months (June 2005), three of the tiles were caged to provide a simulation of removing all macrograzers from the reefs. Cages

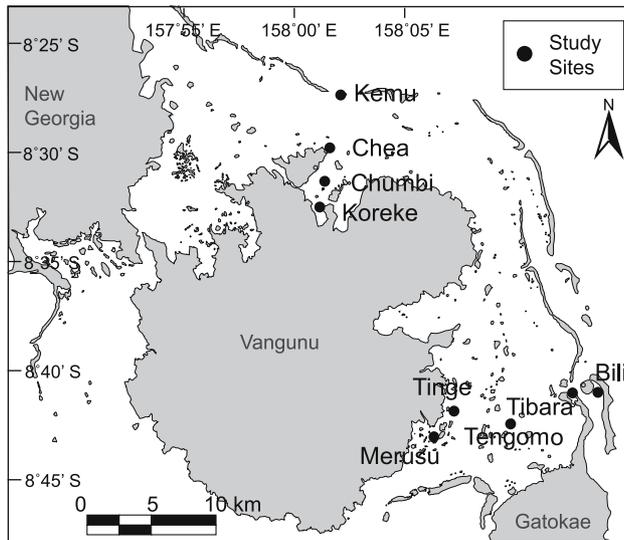


Fig. 1 Location of nine study reefs within Marovo Lagoon

(0.5 m × 0.5 m × 0.5 m aluminium frame covered with 16 mm plastic mesh) were placed around three separate settlement tiles and cleaned every 72 h to prevent algal fouling. Following 28 days of caging, tiles were removed from each of the cages (three replicates per study reef) and the ambient tiles (three replicates per study reef) were also collected. Partial cage controls were not conducted due to evidence from previous similar experiments showing negligible cage effects on light (Stimson et al. 1996) and water motion (Smith et al. 2001). It is not possible to truly control for cage effects in a study of this kind, instead light and water motion were monitored. Incident light (calibrated photosynthetically active radiation sensor on PAM fluorometer—WALZ, Germany) and water motion [clod card (Jokiell and Morrissey 1993)] were quantified inside and outside of three cages at the beginning and end of the experimental period to ensure cages were not influencing these critical parameters.

For each of the tiles collected (three ambient and three caged from each of the nine study reefs), percent cover of each algal functional group on the upper surface of each tile was determined by classifying 24 random points from a

digital image using Coral Point Count V3.2 (NCRI) [based on method for reef transects (Roelfsema et al. 2004)]. Algal functional groups used for this study were; algal turfs (dense turfs of filamentous algae and cyanobacteria); fleshy crustose algae (non-calcareous crusts e.g., *Ulvella* sp., cyanobacteria biofilms); calcareous crustose algae (calcareous encrusting forms of algae) and bare tile (exposed settlement tile void of any algae visible to the naked eye). These functional groups are based largely on (Steneck 1988; Steneck and Dethier 1994), however, it was evident that some microalgae (cyanobacteria) had wide ranging morphologies depending on environmental conditions, so this group was further modified. Tiles with a mixed community of filamentous algae and cyanobacteria growing in dense turfs >3 mm were classified as algal turfs. Cyanobacteria present in biofilms/crusts <3 mm (typically <1 mm) were classified as fleshy crustose algae.

Algal biomass (decalcified dry weight) was quantified for each settlement tile by rinsing the tile in fresh water to remove salts prior to drying for 48 h at 60°C. The algal community was scraped from the tile and soaked in 10% HCl for 24 h, rinsed in distilled water and redried at 60°C for 48 h to a constant weight (± 0.001 g).

Herbivorous fish biomass

Underwater visual censuses of the herbivorous and omnivorous fish species (>~5 cm) and length (L_T) were conducted along four replicate 50 × 4 m belt transects at each of the nine study reefs in September 2005 (using the method based on St John et al. 1990). Herbivorous fish biomass (M) was calculated from this census data and existing published values for the coefficients used in the standard weight–length expression $M = aL_T^b$ (Table 1).

Water quality

All major water quality parameters (total suspended solids, total nitrogen, total phosphorus, sediment nitrogen, sediment phosphorus, dissolved ammonium, dissolved nitrogen oxides, filterable reactive phosphorus) were quantified from single samples at each of the nine study sites when the tiles

Table 1 Constants used to estimate biomass (M) from length (L_T) for major families of grazing fish $M = aL_T^b$

| Family | Species | a | b | Source |
|---------------|------------------------------|--------|-------|--------------------------|
| Acanthuridae | <i>Acanthurus fuscus</i> | 0.0089 | 3.278 | Letourneur 1998 |
| Blenniidae | <i>Blennius ocellaris</i> | 0.0140 | 2.963 | Pereda and Villamor 1991 |
| Pomacanthidae | <i>Centropyge tibicen</i> | 0.0601 | 2.692 | Kulbicki et al. 2005 |
| Pomacentridae | <i>Pomacentrus coelestis</i> | 0.370 | 2.630 | Kochzius 1997 |
| Scaridae | <i>Scarus ghobban</i> | 0.0233 | 2.919 | Murty 2002 |
| Siganidae | <i>Siganus fuscescens</i> | 0.0162 | 3.010 | Letourneur et al. 1998 |

were deployed and another replicate when tiles were collected (January and July 2005, respectively). All samples were collected from 1 m depth (settlement tile depth) by a Niskin bottle as Marovo is often a highly stratified water body, hence surface waters tend not to reflect those experienced by subsurface coral reef community. Total suspended solids were collected by filtering 1 l of seawater through a pre-weighed 0.45 µm polycarbonate membrane filter. Filter papers were rinsed with distilled water and oven dried at 60°C for 48 h to a constant weight (± 0.001 g). Total and dissolved (filtered through 0.45 µm polycarbonate filters) nutrient samples were collected in rinsed polyethylene containers, stored frozen and transported to the laboratory for analysis via inductively coupled plasma atomic emission spectrometry (ICP-AES). Five replicate 25 mm \times 100 mm sediment cores were pooled at each reef to provide a sample for sediment nutrient analysis. Sediment nitrogen and phosphorus were digested and analysed as above.

Statistical analysis

Principal components analysis (PCA) was conducted on normalised water quality values to assess the relationships between the various water quality parameters [Primer v.6 Plymouth Marine Laboratories (Clarke and Warwick 1994)]. The impact of caging on algae biomass and community structure was assessed with a two way ANOVA (site*caging) with site and caging as categorical predictors and dependant algal variables (biomass, % turf, % fleshy, % calcareous, % bare tile). To further explore the hypotheses that water quality and/or herbivory influenced algae community structure and/or biomass a factorial regression model was applied to the dataset of dependant algal variables

(biomass, % turf, % fleshy, % calcareous, % bare tile) and three continuous predictors [herbivore biomass, and the first and second principal component of the water quality data; PC1 and PC2 (Statistica v6.1)]. Light and water motion data from inside and outside the cages was analysed with a one-way ANOVA (Statistica v6.1).

Results

Environmental parameters

Herbivore biomass varied across the nine study reefs from 2.17 ± 0.9 g m⁻² (mean \pm SE) on the inshore Merusu reef to 14.8 ± 3.0 g m⁻² on the offshore Tibara reef (Table 2).

Principal components analysis of water quality data (Fig. 2) revealed two major groups of water quality parameters. The dissolved and sediment nutrients were co-correlated along the PC1 axis whilst the total nutrients and suspended solids were co-correlated along both PC1 and PC2 (Fig. 2). PC1 and PC2 represented 60 and 20% of variability, respectively, and hence a study reefs position on these two axes provided a useful index of water quality status. Negative scores for PC1 and PC2 represent sites with high dissolved and total nutrients, respectively. It should be noted this is a unitless relative scale for the sites within this study area only. Merusu reef had the lowest PC1 score indicating high inputs of dissolved nutrients, whilst Tengomo reef had the lowest PC2 score indicating high total nutrients and suspended sediments. The three offshore reefs (Kemu, Bili, Tibara) had highest values of both PC1 and PC2 indicating low sediments and nutrients (Table 2).

Table 2 Water quality (mean of two sampling times) and herbivore biomass for each of the study reefs

| | Merusu | Koreke | Chea | Tengomo | Tinge | Chumbi | Bili | Kemu | Tibara |
|-----------------------------------|------------|------------|------------|------------|------------|------------|------------|-------------|------------|
| TSS (mg l ⁻¹) | 2.30 | 2.23 | 1.99 | 2.09 | 1.45 | 1.4 | 1.1 | 0.6 | 0.9 |
| NH ₄ (µM) | 1.562 | 0.497 | 0.355 | 0.426 | 0.497 | 0.923 | 0.213 | 0.355 | 0.213 |
| NO _x (µM) | 1.136 | BDL | BDL | 0.142 | 0.284 | 0.781 | BDL | BDL | BDL |
| FRP (µM) | 0.064 | BDL | BDL |
| TP (µM) | 0.256 | 0.192 | 0.128 | 0.288 | 0.128 | 0.192 | 0.096 | 0.128 | 0.128 |
| TN (µM) | 8.165 | 7.455 | 7.81 | 14.91 | 6.035 | 4.97 | 4.26 | 3.905 | 4.615 |
| Sed P (mg kg ⁻¹) | 320 | 270 | 270 | 190 | 220 | 190 | 210 | 220 | 170 |
| Sed N (mg kg ⁻¹) | 460 | 240 | 260 | 250 | 290 | 290 | 320 | 270 | 240 |
| Herb. Fish g m ⁻² (SE) | 2.17 (0.9) | 2.25 (0.8) | 2.80 (0.3) | 8.71 (1.9) | 4.77 (1.4) | 8.42 (3.9) | 6.36 (1.0) | 13.29 (3.2) | 14.8 (3.0) |
| Water Quality PC1 | -5.38 | -0.11 | 0.33 | -0.32 | 0.65 | -0.33 | 1.48 | 1.66 | 2.04 |
| Water Quality PC2 | 0.99 | -1.15 | -0.62 | -3.01 | 0.43 | 0.68 | 1.11 | 1.13 | 0.43 |

Total suspended solids (TSS), dissolved ammonium (NH₄), dissolved nitrogen oxides (NO_x), filterable reactive phosphorus (FRP), total phosphorus (TP), total nitrogen (TN), sediment phosphorus (Sed P), sediment nitrogen (Sed N), herbivorous fish biomass (Herb. Fish), water quality principle component scores for PC1 and PC2

BDL below detection limit (0.06 µM FRP, 0.14 µM NO_x/NH₄)

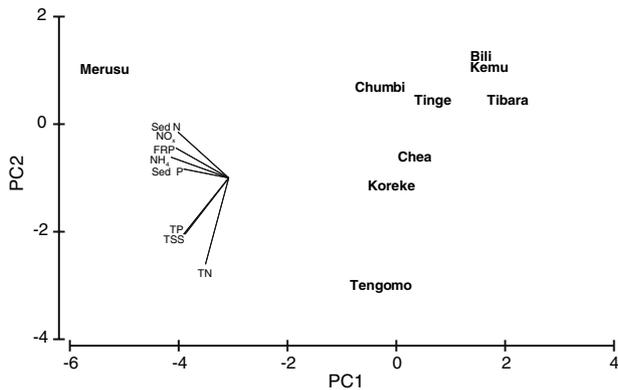


Fig. 2 Principal components analysis of water quality parameters across the nine study reefs in Marovo. Vectors of the water quality variables (see Table 2 for abbreviations) have been overlaid. PC1 = 60.6%, PC2 = 20.3%

Algal community composition

After 6 months, the algal settlement tiles across the nine study reefs had developed a range of algal communities. Distinct differences could be observed visually between the inshore and offshore tiles and the ambient and caged tiles (Fig. 3). Inshore reefs were generally dominated by algal turf (filamentous algae and cyanobacteria). Offshore reefs were generally characterised by a mixed community of calcareous crustose algae (~40%), fleshy crustose algae (~30%) and bare tile (~30%) (Fig. 4a). These site variations were evident from a significant site effect in the

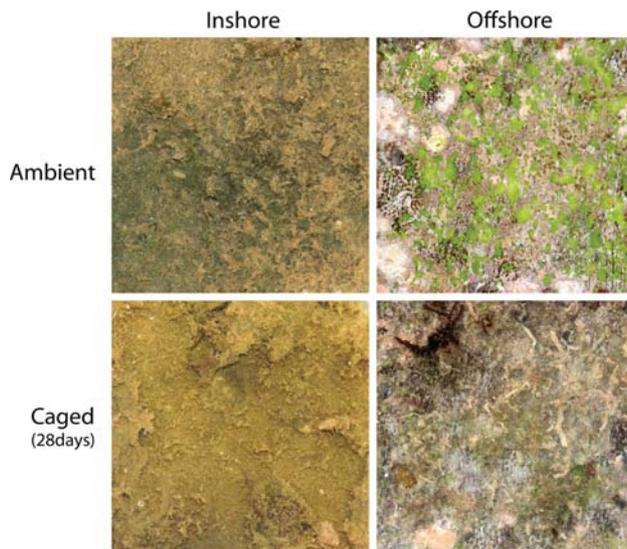


Fig. 3 Representative algal settlement tiles from inshore and offshore reefs exposed to ambient and caged conditions. Both ambient and caged inshore tiles are dominated by dense algal turfs. Ambient offshore tiles had a diverse community of fleshy and calcareous crustose algae. The offshore caged tiles had a sparse algal turf in addition to fleshy and calcareous crustose algae

ANOVA across all algal types (Table 3). Caging (for 28 days) had a significant effect on community structure (Table 3), resulting in a shift to algal turf dominated tiles on all study reefs (Fig. 4b). However, the significant interaction term (Table 3) in the ANOVA indicated this change in algal communities after caging was manifested differently depending on site. The factorial linear regression revealed significant positive relationships between herbivore biomass and cover of calcareous ($F_{1,10} = 40.9$, $P < 0.001$) and fleshy crustose ($F_{1,10} = 9.4$, $P < 0.05$) algae on settlement tiles. Conversely, algal turf cover on settlement tiles was negatively related to herbivore biomass ($F_{1,10} = 23.8$, $P < 0.001$) (Fig. 5; Table 4). There was no relationship between the cover of any of the algal categories and either water quality PC1 or PC2 axis.

Algal biomass

Algal biomass on the ambient tiles varied significantly ($F_{8,36} = 12.18$, $P < 0.001$) across the nine study reefs, with higher biomass at sites with low herbivory/water quality (Fig. 4a). Settlement tiles on the degraded inshore Merusu reef had the highest algal biomass with ambient tiles $7.23 \pm 1.95 \text{ mg cm}^{-2}$ and caged tiles $7.35 \pm 1.37 \text{ mg cm}^{-2}$ (mean \pm SE). Offshore reefs had lower biomass communities of $1\text{--}2 \text{ mg cm}^{-2}$, that increased following caging to $3\text{--}4 \text{ mg cm}^{-2}$ (Fig. 4). The significant ($F_{8,36} = 2.47$, $P = 0.03$) cage*site interaction term in the ANOVA indicates caging (for 28 days) was having a differential effect on algal biomass across the nine sites. Caging resulted in a significantly ($P < 0.05$) higher algal biomass on tiles from all reefs except the two inshore reefs (Merusu, Koreke), which already had a high biomass on ambient tiles (Fig. 4; Table 3). The factorial regression analysis revealed water quality PC1 and herbivore biomass were interacting ($F_{1,10} = 7.7$, $P < 0.05$) to determine the algal biomass on the settlement tiles. Algal biomass was negatively related to water quality PC1 ($F_{1,10} = 18.1$, $P < 0.01$) and herbivore biomass ($F_{1,10} = 22.2$, $P < 0.001$), indicating algal biomass increases as grazing decreases and sediments and nutrients are increased (Fig. 5; Table 4). Both caged and ambient tiles were used for this analysis, with caged tiles assigned the same water quality PC1 and PC2 values as their respective ambient tile and a herbivorous fish biomass of zero. There was no co-correlation between the predictors [herbivore biomass and water quality PC1 ($F_{1,16} = 1.29$, $P = 0.27$) or PC2 ($F_{1,16} = 0.08$, $P = 0.78$) or between water quality PC1 and PC2 ($F_{1,16} = 0.00$, $P = 0.99$)]. The cages used did not significantly alter light (ambient: $904 \pm 5.5 \mu\text{mol m}^{-2}\text{s}^{-1}$ and cage: $871 \pm 14.5 \mu\text{mol m}^{-2}\text{s}^{-1}$, $F_{1,4} = 4.65$, $P > 0.05$), or water motion (measured as clod card loss, ambient: $11.04 \pm 0.53 \text{ g day}^{-1}$ and cage: $10.45 \pm 0.27 \text{ g day}^{-1}$, $F_{1,4} = 0.99$, $P > 0.05$).

Fig. 4 Patterns in algal biomass and community structure on (a) ambient tiles and (b) caged tiles

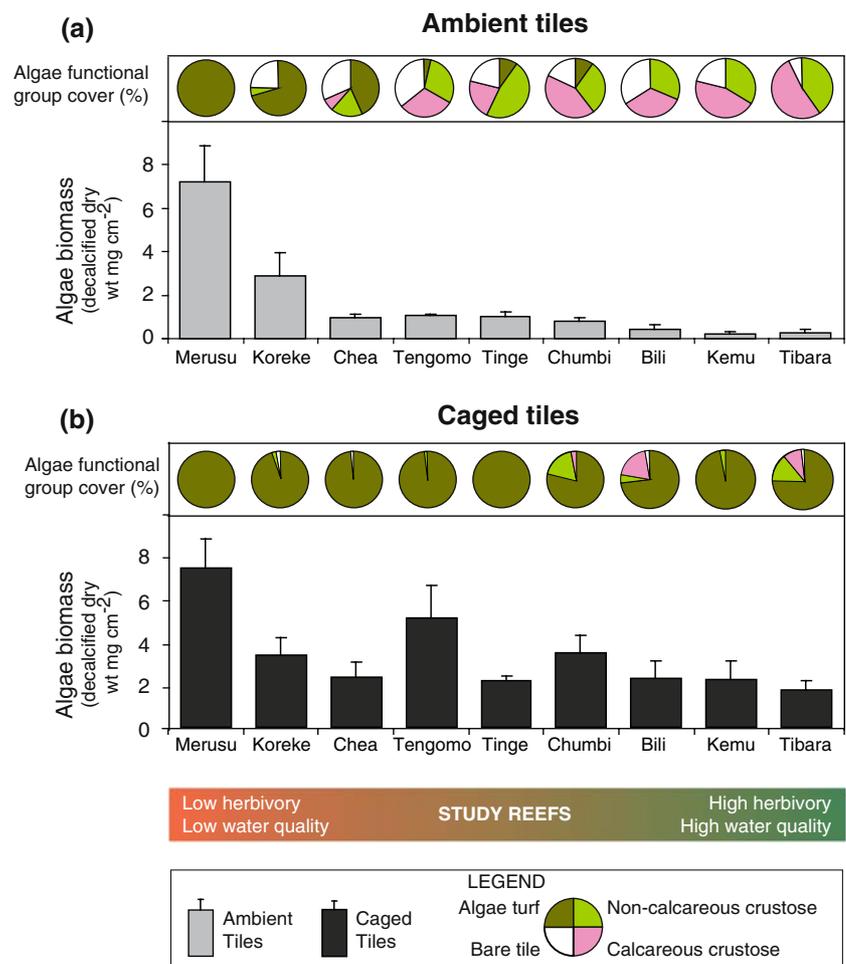


Table 3 *F* and *P* values from two-way (site*cage) ANOVA of algal type (algae turf, calcareous crustose, bare tile and fleshy crustose) and biomass

| | Site <i>df</i> = 8,36 | | Cage <i>df</i> = 1,36 | | Site*Cage <i>df</i> = 8,36 | |
|---------------------|-----------------------|----------|-----------------------|----------|----------------------------|----------|
| | <i>F</i> | <i>P</i> | <i>F</i> | <i>P</i> | <i>F</i> | <i>P</i> |
| Algae Turf | 55.98 | <0.001 | 1088.44 | <0.001 | 47.32 | <0.001 |
| Calcareous Crustose | 37.01 | <0.001 | 239.58 | <0.001 | 14.99 | <0.001 |
| Bare Tile | 6.47 | <0.001 | 197.86 | <0.001 | 5.27 | <0.001 |
| Fleshy Crustose | 5.2 | <0.001 | 62.46 | <0.001 | 4.12 | 0.001 |
| Biomass | 12.18 | <0.001 | 38.85 | <0.001 | 2.47 | 0.03 |

Discussion

Reef algal communities exist along a continuum of top down control to bottom up control depending on specific biological and environmental (e.g., herbivory and water quality) parameters at that site. Knowledge of where a particular reef is on the continuum is critical to coral reef managers who wish to mitigate the threat of an algal phase shift. Anthropogenic changes to herbivory and water quality have been implicated in shifting the equilibrium between algae and coral, leading to algal dominated degraded reef environments (Hughes 1994; McCook 1996, 1999; Szmant

2002; Lapointe et al. 2004). The impact that these top down (herbivory) and bottom up (water quality) factors have on algae depends upon the magnitude of the treatment and background conditions at the study site. In reality both water quality and herbivores are important in structuring benthic reef communities and their relative importance is likely to vary across reefs in space and time. Results from the current study are unique as they have used empirical data to elucidate the relative importance of water quality and herbivory on algal community structure and biomass across nine study reefs. This interaction between herbivory and water quality determined the biomass of algae present

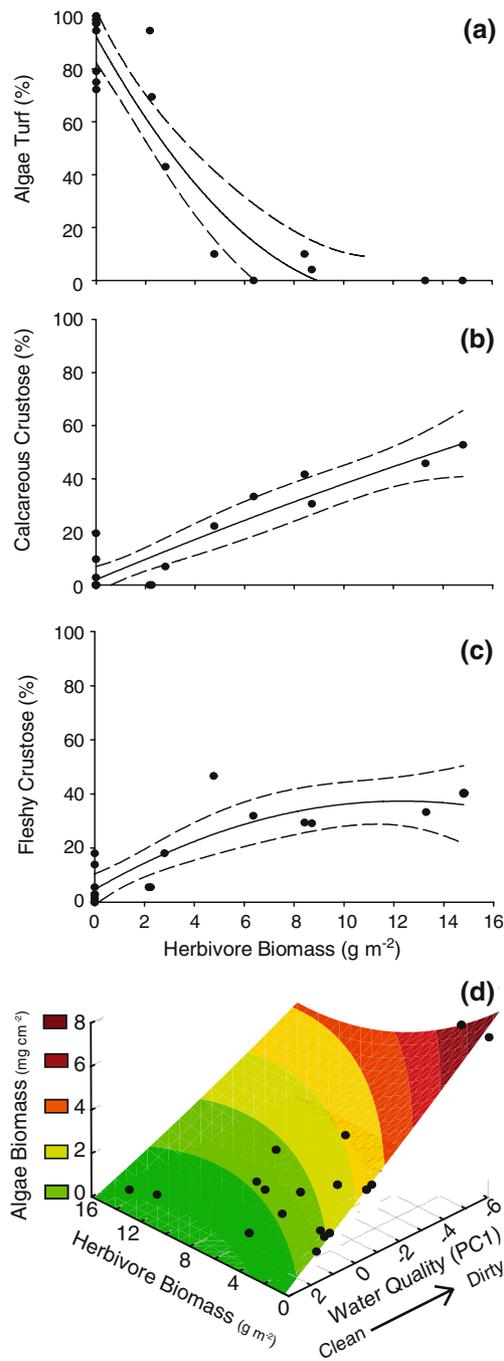


Fig. 5 Statistically significant relationships between herbivore biomass and % cover of **a** algae turf, **b** calcareous crustose and **c** fleshy crustose algae on settlement tiles. Logarithmic regressions and 95% confidence bands have been fitted to the data. The interaction between water quality PC1 and herbivore biomass in determining algae biomass is presented in three dimensions, with colours representing algae biomass (**d**)

on settlement tiles (Fig. 5). Higher concentrations of bioavailable dissolved nutrients (PC1) increased the biomass of algae present on the low herbivore biomass reefs.

The functional forms of algae present on settlement tiles across Marovo Lagoon was determined by herbivore biomass and not by either of the water quality principal components. Tiles on reefs with a high biomass of herbivorous fish were represented by grazing resistant calcareous and fleshy crustose algae. Following caging these communities were rapidly (28 days) overgrown by a dense turf of cyanobacteria and filamentous algal species that are typical of the low herbivory inshore reefs. This rapid shift shows the vulnerability of coral reefs to changes in key processes such as herbivory. The herbivore biomass across the study reefs in Marovo is relatively low ($2.2\text{--}14.8\text{ g m}^{-2}$) compared with reefs worldwide; $7.5\text{--}44\text{ g m}^{-2}$ in the Great Barrier Reef (Russ 2003), $2.7\text{--}15.4\text{ g m}^{-2}$ in the Caribbean (Williams and Polunin 2001), $25\text{--}160\text{ g m}^{-2}$ in Hawaii (Friedlander and DeMartini 2002).

Despite this limited herbivory, the low nutrient status of Marovo has prevented rapid overgrowth of the reefs by large frondose, leathery or corticated groups observed in the Caribbean (Hughes 1994), Hawaii (Hunter and Evans 1995), and Great Barrier Reef (Done 1992). The removal of grazers on some reefs in Marovo has caused a shift to algal turfs, which are able to flourish in low nutrient environments via nitrogen fixation (Larkum et al. 1988). Based on the correlations between herbivore biomass and macroalgal cover developed by Williams and Polunin (2001) for Caribbean reefs, reefs in Marovo would have 20–70% macroalgae cover. However, the oligotrophic status of Marovo has limited the growth of macroalgae to <5% and hence reefs are still in a low algal/high coral state (Green et al. 2006). Many reefs in the Pacific are currently in this low nutrient/low herbivory situation as herbivorous fish are targeted by local subsistence and artisanal fishing communities. The targeting of herbivorous fish through night spearfishing is an increasingly popular means of fishing in Melanesia, particularly as depleted fish stocks make traditional forms of fishing less productive. This makes these reefs particularly susceptible to rapid algal phase shifts in the event of low levels of nutrient enrichment of the system through catchment disturbance or sewage runoff. These interactive effects of herbivory and water quality on algae biomass in Marovo are explained by the factorial regression model (Fig. 5d).

Although not as visually dramatic as the *Sargassum* overgrowth of coral reefs in other parts of the world, low biomass algal turfs covering bare substrate can have significant influence on coral recruitment success as well as other aspects of coral ecology. Coral larvae have specific requirements for the physical and chemical state of substrate. The calcareous crustose algal communities found on tiles in high herbivore biomass sites are the preferred surface for coral larvae recruitment and metamorphosis (Morse et al. 1988; Heyward and Negri 1999; Webster et al. 2004), whereas the dense algal turfs found in the low herbivory/

Table 4 Beta [normalised regression co-efficient (slope)], *F* and *P* values from factorial regression of algal community composition (% algae turf, % calcareous crustose, % bare tile and % fleshy crustose)

| | Herbivore biomass <i>df</i> = 1,10 | | | Water quality PC1 <i>df</i> = 1,10 | | | Herbivore * WQ PC1 <i>df</i> = 1,10 | | |
|---------------------|---------------------------------------|--------------|--------------|---------------------------------------|--------------|--------------|--|-------------|--------------|
| | Beta | <i>F</i> | <i>P</i> | Beta | <i>F</i> | <i>P</i> | Beta | <i>F</i> | <i>P</i> |
| Algae Turf | −1.02 | 25.61 | 0.000 | −0.38 | 0.37 | 0.556 | 0.46 | 1.59 | 0.237 |
| Calcareous Crustose | 0.96 | 40.81 | 0.000 | −0.11 | 0.06 | 0.810 | −0.05 | 0.04 | 0.854 |
| Bare Tile | 0.76 | 4.78 | 0.054 | 0.75 | 0.49 | 0.501 | −1.06 | 2.88 | 0.121 |
| Fleshy Crustose | 0.94 | 11.06 | 0.008 | 0.50 | 0.34 | 0.574 | −0.23 | 0.21 | 0.658 |
| Biomass | −0.59 | 22.20 | 0.001 | −1.63 | 18.20 | 0.002 | 0.62 | 7.73 | 0.019 |

WQ PC2 results have not been included, as they were not significant

Bold values are significant ($P < 0.05$)

poor water quality sites can inhibit coral recruitment (Birrell et al. 2005; Kuffner et al. 2006). The pressures of degraded water quality and depleted stocks of herbivores may yield their greatest impacts on coral reefs in post disturbance (bleaching, storms) scenarios where successful coral recruitment onto bare or calcareous algal substrates is critical (Diaz-Pulido and McCook 2002). The settlement tile methodology used in the current study provides a simulation of algal communities following such a disturbance and is a potential monitoring tool to identify reefs at most risk from a phase shift. Due to the resilience of coral reefs to change (Nystrom et al. 2000), the impacts of water quality and herbivory degradation (or improvement through management) is often not manifested in the reef community until a dramatic phase shift takes place. The ability of algal settlement tiles to provide a rapid, temporally integrated indicator of water quality and herbivory (independent of current reef condition) makes them particularly useful for assessment of management success. In Roviana Lagoon (100 km NW of Marovo in the Solomons), algal assemblages on settlement tiles inside community managed marine reserves were typical of high grazing reefs (low biomass, crustose algae) compared to the adjacent control reef (high biomass turf algae) (Aswani et al. 2007).

The use of algal communities on settlement tiles as an indicator of water quality and herbivory pressures to coral reefs is promising. However, the relationships between algae and water quality and herbivory observed in this paper are not general principles to be applied to all reefs. They apply across the range of water quality and herbivory quantified on these reefs, which is a small subset of the magnitude of conditions that threaten reefs worldwide. These algal settlement tiles provide a standardised measure of water quality and herbivory status by visually comparing tiles from various reefs. This visual tool has proved useful for the communication of these results to indigenous resource owners/managers in Marovo and Roviana (Aswani et al. 2007). The detailed community composition and biomass information outlined in this

and biomass against herbivore biomass and water quality principal components 1 and 2 (WQ PC1, WQ PC2)

paper provides more specific information on the relative importance of water quality and herbivory at a particular reef.

The algal communities in Marovo Lagoon are primarily controlled by the biomass of herbivorous fish and to a lesser extent water quality. Healthy diverse communities of calcareous and fleshy crustose algae recruited onto settlement tiles on mid and outer lagoon reefs. Inshore reefs with low herbivorous fish abundance were colonised by dense cyanobacteria and filamentous algal turfs. The biomass of these various algal communities was determined by both water quality and herbivory. The majority of the reefs studied in Marovo can be considered to have algal communities typical of a healthy reef system (Steneck and Dethier 1994). Algae considered typical of degraded reefs were present on inshore reefs depleted of herbivores and exposed to sediments and nutrients from large scale logging in the catchments. The inshore reefs of Merusu and Koreke are most at risk from an algal phase shift as they had the lowest herbivore biomass and high dissolved nutrient concentrations (negative PC1). The fast response (increase in turf algae) of tiles on the outer reefs to herbivore exclusion (caging) shows the susceptibility of reefs in “pristine” water quality conditions to over harvesting of herbivores.

Acknowledgments This study would not have been possible without the assistance from many Marovo people, in particular Chea and Bili communities, Morgan Jimuru and Terrence Siloko. The logistic support from Corey and Waelinah Howell and Grant and Jill Kelly made working in such a remote location possible. The field and academic assistance from Joelle Prange, Norm Duke, Ove Hoegh-Guldberg, Alistair Grinham and Guy Marion is much appreciated. We also thank the three reviewers of this manuscript whose comments and advice improved the presentation of this work. This study is part of a wider initiative to conserve the marine biodiversity of Marovo Lagoon funded by the John D. and Catherine T. MacArthur Foundation (grant 80152).

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