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Acclimation and adaptation of scleractinian coral communities along environmental gradients within an Indonesian reef system

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ABSTRACT

In 2007 and 2008, multiple sites were identified in the Wakatobi Marine National Park, South East Sulawesi, Indonesia, which each represented a point along a gradient of light quality, temperature and turbidity. This gradient included 'optimal', intermediate and marginal sites, where conditions were close to the survival threshold limit for corals. Coral communities changed across this gradient from diverse, mixed growth form assemblages to specialised, massive growth form dominated communities. The massive coral *Goniastrea aspera* was the only species identified at the most marginal and optimal sites. Branching species *Acropora formosa* and *Porites cylindrica* were only identified at optimal sites. The *in hospite Symbiodinium* community also changed across the environmental gradient from members of the *Symbiodinium* clade C on optimal reefs (in branching and massive species) to clade D on marginal reefs (in massive species). Substantial variability in respiration and photosynthesis was observed in massive coral species under different environmental conditions, which suggests that all corals cannot be considered equal across environments. Studying present-day marginal environments is crucial to further understanding of future reef bio-diversity, functioning and accretion, and from work presented here, it is likely that as future climate change extends marginal reef range, branching coral diversity may decrease relative to massive, more resilient corals.

1. Introduction

Scleractinian corals are often associated with clear blue water tropical reefs, but can inhabit a wide variety of more 'atypical' environments (Kleypas, 1996; Guinotte et al., 2003; Anthony and Connolly, 2004). Conditions within these atypical environments, such as light availability, sediment loading, inorganic nutrient input, temperature, salinity and aragonite saturation states are often drastically higher or lower than required for optimum growth (Rogers, 1990; Miller and Cruise, 1995; Guinotte et al., 2003). Consequently, scleractinian corals are pushed close to the threshold required for net coral growth. Some of these environmental conditions are associated with high latitude reefs, which have been termed marginal reefs (Celliers and Schleyer, 2002; Perry and Larcombe, 2003; Celliers and Schleyer, 2008). However, the criteria for a reef to be considered marginal (Kleypas et al., 1999) can also be met at low latitudes (Kleypas et al., 1999; Bak and Meesters, 2000; Guinotte et al., 2003), in particular, intertidal, fringing mangroves and terrestrial basin areas (Rogers, 1990; Mitchell and Furnas, 1997; Anthony, 2000). Regardless of the location of these marginal reefs, corals must successfully respond to substantial variations (or gradients) in growth conditions in order to successfully recruit and survive.

Successful colonisation (recruitment and growth) across environmental gradients requires that both the symbiotic microalgae (*Symbiodinium* spp.) and the host coral optimise available resources, while retaining the physiological plasticity needed to survive under different conditions. This trade-off can potentially be achieved through careful interplay between acclimatization and adaptation (Falkowski and LaRoche, 1991; Iglesias-Prieto and Trench, 1994; Hennige et al., 2009). Acclimatization can be achieved through up or down-regulation of key processes used to obtain resources for growth or maintenance. In *Symbiodinium*, this may include photosynthetic reaction centres (Iglesias-Prieto and Trench, 1994; MacIntyre et al., 2002; Hennige et al., 2009), pigment species and organisation (Suggett et al., 2007; Hennige et al., 2009) and Rubisco content per cell (Sukenik et al., 1987; MacIntyre et al., 2002). Host acclimatization may include regulating heterotrophic feeding rates (Anthony, 2000; Anthony and Fabricius, 2000), UV or heat protective compounds (Shick et al., 1996; Dunlap and Shick, 1998; Baird et al., 2009) or respiration rates (Anthony and Hoegh-Guldberg, 2003). Plasticity in coral morphology has also been noted under different

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environmental conditions both at the colony (Anthony and Hoegh-Guldberg, 2003; Anthony et al., 2005) and corallite level (Todd et al., 2004; Crabbe and Smith, 2006).

Given that environmental conditions in marginal systems are less than optimal, it is expected that acclimatization would require considerable resource allocation, which in turn will lower achievable productivity, and ultimately growth (Dubinsky et al., 1984; Miller and Cruise, 1995; Mass et al., 2007). This may be particularly important on marginal reefs, as available resources may not be enough to compensate for the increased demand that marginal environments impose upon many resident corals. Equally, resources may only be obtainable by some coral species e.g. those with the ability to heterotrophically feed on multiple size classes of plankton (Clayton and Lasker, 1982; Houlbreque et al., 2004).

Adaptation is also important and can be a result of host or symbiont competitive fitness, with specific genetic variants within or between species specialising in growth conditions that differ from clear blue waters. Selection for the symbiont is well documented along environmental gradients (LaJeunesse et al., 2004), as are responses to transient stress events (Kinzie et al., 2001; Baker, 2003; Thornhill et al., 2006). Similarly, coral assemblages in terms of species composition may change as environmental conditions become less than optimum. An example is the proliferation of heat tolerant corals in thermally extreme (sometimes intertidal) environments, where environmental history of individual coral species can moderate susceptibility to environmental perturbations (Brown et al., 2000; Brown et al., 2002a; Middlebrook et al., 2008). Additionally, a shift from branching and massive coral communities to massive dominated communities in sub-optimal environments may reflect an apparent greater tolerance of massive corals to withstand environmental stress (West and Salm, 2003; Kenyon et al., 2006).

Identifying patterns and processes of how coral communities respond to environmental conditions has long been a goal in understanding community response to predicted climate change (Hoegh-Guldberg, 1999; Pittock, 1999; Guinotte et al., 2003) and also to anthropogenic stressors such as increased sedimentation and terrestrial runoff (Fabricius, 2005). One study in particular has predicted that marginal reef range will substantially increase as a result of climate change leading to additional areas of ‘borderline’ high temperature regimes (Guinotte et al., 2003), which may even become ‘normality’ as aquatic environments rapidly change (Guinotte et al., 2003); as such, many reef forming coral species will be placed under potentially stressful growth conditions. Examining corals within present-day marginal conditions is thus an important step in determining how coral reef form and function will appear under future climates. At present, such fundamental information is almost entirely lacking. Fortunately, present-day environmental gradients including high and low-latitude marginal systems provide a natural study ground for corals' adaptive (and acclimatory) capacity.

Here, we examined 6 key coral species, *Goniastrea aspera*, *Porites lutea*, *Porites lobata*, *Porites cylindrica*, *Favites abdita* and *Acropora formosa* (see Veron, 2000), across an environmental gradient (five sites) within a reef system in Indonesia. Coral distribution and abundance were measured as well as fundamental properties relating to productivity and metabolism. The identification of *in hospite* symbionts across the gradient was also determined. The results are discussed in the context of (1) which species are better suited to exist in sub-optimal (marginal) environments and what mechanisms may facilitate this, and (2) whether certain holobionts are ‘pre-adapted’ to survive predicted future climate change.

2. Methods

2.1. Sites along an environmental gradient

Five sites within the Wakatobi Marine National Park reef system were selected to provide a range of conditions along an environmental gradient from ‘optimal’ to marginal (Fig. 1, Table 1). Here, ‘optimal’ sites refer to regional sites where coral abundance and diversity is high, and where environmental conditions are close to the expected ‘optimal’ average. The light-temperature environment was characterised in two separate field seasons (July–August 2007; July–August 2008) using HOBO temperature (°C) and light (lux) loggers (Onset, Massachusetts, U.S.A). These loggers were deployed for 1-week periods at similar tidal cycles (where low tide coincided with midday at all sites) to obtain light-temperature minima and maxima. Loggers were de-fouled daily by wiping the bio-film from the upper surface. Lux was used to assess relative diurnal changes in light levels between sites. Since lux is a measure of light weighted to a human perspective, HyperOCR hyperspectral radiometers (Satlantic, Halifax, Canada) were consequently used to assess light quality at all sites in 2007.

A time-synched surface reference radiometer and an underwater radiometer at 1 m (down-welling irradiance), were used to assess wavelength specific light attenuation coefficients, $K_{d(\lambda),}$ according to Beer Lambert's Law from 400 to 700 nm for all sites (Eq. (1)) where E is irradiance. 1 m was the maximum depth at marginal sites so $K_{d(\lambda)}$ was assessed between 0 and 1 m at all sites for consistency. K_d per site was calculated from the average $K_{d(400\text{–}700\,\mathrm{nm})}$ (Eq. (2)), and then used to calculate optical depth, ζ (dimensionless, Eq. (3)), to compare sites of differing turbidity.

$$K_{d(\lambda)} = \left[\ln(E_{1\,\mathrm{m}})(\lambda) - \ln(E_{0.1\,\mathrm{m}})(\lambda)\right] / 0.9\,\mathrm{m} \quad (1)$$

$$K_d(\mathrm{site}) = \left\lfloor \textstyle\sum_{700}^{400} K_d(\lambda) \right\rfloor / 300 \quad (2)$$

$$\zeta = K_d(\mathrm{site}) \cdot depth \quad (3)$$

During 2008 data collection, K_d was assessed using a photosynthetically available radiation (PAR) sensor attached to a pulse amplitude modulated fluorometer (Walz), where E in Eq. (1) represents PAR. The Walz PAR sensor was calibrated against a Li-Cor quantum sensor. This

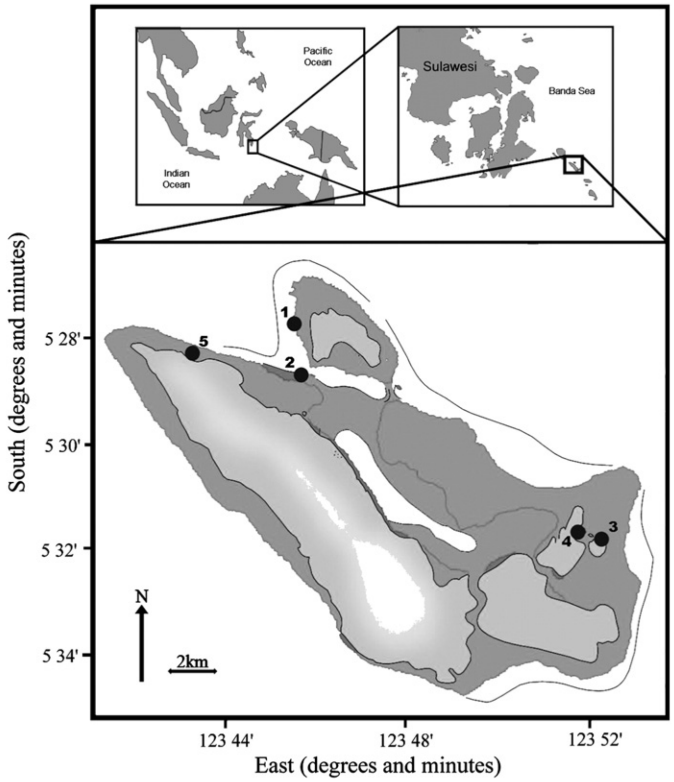

Fig. 1. Map of study sites in the Wakatobi Marine National Park, S.E Sulawesi, Indonesia with latitude and longitude degrees and minutes. Adapted from Hennige et al. (2008a). Sites and numbered 1–5 from optimal to marginal; Site 1—Pak Kasims; 2—Sampela; 3—Loho; 4—Lamohasi; 5—Langeira.