Tolerance, refuge and recovery of coral communities to thermal bleaching: evidence from reefs of the Seychelles

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Abstract: Long term viability of coral communities is dictated by their ability to withstand environmental change. Three "mechanisms" exist by which reefs may survive stressful conditions: (1) physiological tolerance, (2) via environmental refuge, and (3) repopulation and growth (recovery) once ambient conditions return. During the 1998 El Niño event, sea surface temperatures (SSTs) around the Seychelles persisted above 32°C and more than 75% of all reefs bleached. Since then, SSTs have not exceeded 30-31°C allowing reefs to recover. Analyses of the size frequency distribution of species-specific colonies in the Seychelles indicated that certain species survived the 1998 event (termed type II corals) whilst other species (termed type I corals) did not but have recruited into the systems post 1998. Experiments confirmed type I and II coral species exhibited alternative physiological characteristics that likely determined the post 1998 community. Turbid lagoons containing large colonies of type I species were identified within an oceanic atoll (Desroches) suggesting that these species survived 1998 by recruiting into what have been previously considered sub-optimal habitats and were likely buffered against environmental stress. Consequently, several mechanisms are in active operation that appears to afford Seychelles' reefs some long term resistance to extreme periods of environmental change.

Key words: Seychelles, bleaching, photosynthesis, coral community structure, refuge

Introduction: Aquatic environments are subjected to environmental change, the periodicity of which occurs across a continuum from the short term, (physiological acclimation) to the longer evolutionary term (genetic adaptation). Coral reefs are no exception; in fact the near surface, shallow water, habitat of most reefs accentuates the scale of variability with which corals are exposed to life sustaining resources, primarily light, temperature and nutrition. As such, corals are adapted to living in a highly variable world; however, the Earth is currently experiencing a rate of unprecedented environmental (climate) change that vastly exceeds the rate of evolution and thus places stress on corals' pre-adaptations to environmental variability.

Typically, corals have three "mechanisms" to survive stressful conditions: (1) physiological *tolerance* until conditions return to a nominal 'steady state', which may require resources to be directed from growth and reproduction to cellular repair and maintenance; (2) *refuge* in environments that are not experiencing the same degree of stress; and (3) population *recovery* by new recruitment. Importantly, coral community structure is directly related to the extent of trophic complexity (Graham et al. 2006). Therefore, the relative activity of these mechanisms will determine future coral community composition and productivity and in turn the entire reef ecosystem. The fundamental ecological unit is the species whilst within coral systems reef building corals are the key ecosystems architects; as such, it is crucial that we understand how coral species respond to stress and how linked ecological systems will be affected. As such, it is imperative that we understand the type and extent of "mechanism" selected for in response to environmental variability by key reef building corals.

Coral reefs of the Seychelles are well recognized to have been heavily impacted by the 1998 El Niño event: sea surface temperatures (SSTs) around the Seychelles persisted above 32°C for several weeks and more than 75% (upto 95% in some cases) of all reefs bleached (Goreau et al. 2000, Spencer et al. 2000). Whilst elevated temperature is believed to be the primary factor that induces bleaching, light is also recognized as a factor that can modulate the rate and extent with which the elevated temperature impacts coral functioning (e.g. Smith et al. 2005; Brown & Dunne 2008). Bleaching describes the depigmentation of corals and is thought to occur primarily from loss of, or photosynthetic down-regulation by, the zooxanthellae (Smith et al. 2005). The coral host cannot survive for long periods without a sustained

energetic contribution by the symbiotic algae and the host coral eventually dies. Consequently, bleaching events provide an important indicator of reef response to relatively large, sometimes irregular changes in climate. ENSO events can thus be used as a 'natural' experiment to examine species/community responses to climate driven environmental stress: since 1998 records indicate that SSTs of the Seychelles have not exceeded 30-31°C potentially allowing reefs to recover from repeat exposure (e.g. see NOAA data for Mahé: www.coralreefwatch.noaa.gov/satellite). The limited data for the Seychelles suggests that in the first 5 years following the El Niño event, % live coral cover for Seychelles' islands increased from ca. 3 to 15 % and from ca. 3 to 6% for granitic and calcareous reefs, respectively (Payet, Bijou & Adam in Linden et al. 2005), and so is in an active state of recovery.

Both the immense negative impact of the 1998 El Niño event and subsequent apparent recovery of Seychelles' reefs afford an important natural system to examine how coral reefs respond to environmental change; in particular, how communities recover once growth conditions re-establish towards 'steady state' (Graham et al. 2006). We tested the hypothesis that "species existing as large colonies were least susceptible to stressful environmental conditions" by addressing 3 primary objectives: (1) Examine the size frequency distribution of colonies within a region that was very heavily impacted by the El Niño event and determine which species survived using size as a proxy for age; (2) Identify key physiological characteristics of species deemed to have survived 1998 versus those absent from the system pre 1998 (but present during 2006-7); and (3) Determine if susceptible species survived the 1998 ENSO event through refuge in light-limited environments.

Materials and methods: Coral community structure was examined at two islands in the Seychelles in August 2006 and 2007: (1) the granitic island of Silhouette (off the North East coast of Mahé) and (2) the coral atoll of Desroches (ca. 240 km off the south-west coast of Mahé). 30m continual line intercept transects were used to estimate species specific % cover and 20 m^2 quadrats (at the start of each transect) used to determine the size frequency distribution of hard corals (n = 1800 at all sites and transects). Fragments of key species (*Acropora formosa*, *A. horrida*, *Diploastrea heliopora*, *Favia speciosa*, *Fungia sp.*, *Pocillopora eydouxi*, *P. verrucosa*, *Porites lutea*, and *P. nigrescens*) were taken from 5-8m for physiological measurements in the laboratory; only large (older) colonies were examined.

Respirometry— Each fragment was placed within a custom build respirometer; changes in O_2 were logged continuously using an *Optode* (Aanderaa
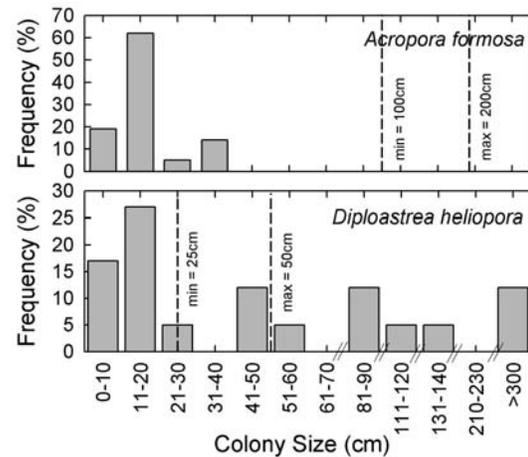

Figure 1. Size (cm)-frequency (%, of all colonies measured) distributions of key coral species from Silhouette high light environment). Examples are shown here for *A. formosa* (type I species n = 45) and *D. heliopora* (type II species, n = 60). Colonies of all other species (n = 32) identified were measured and could be classified as either type I or II corals. Dashed lined indicate size attained by 1998 based on maximum and minimum reported growth rates (see main text).

Inc., Denmark). Temperature was also logged with the *Optode* but did not increase by > 0.25 °C above ambient for any incubation: Initially, O_2 consumption was measured in the dark. A gradient of increasing light between ca. 10 and 1000 µmol photons m^{-2} s^{-1} was subsequently delivered to examine the light response of photosynthesis (P-E). Respiration measurements were again repeated at the end of the P-E run. Each light step (and respiration) was delivered for 15-20 mins. The light intensity was measured within the respirometer upon the surface of the coral using a PAR sensor after each experiment. Daily *in situ* photosynthesis and respiration rates were approximated by applying the P-E characteristics and respiration rates to measurements of the diel light climate from a HOBO (Tempcon Inc., USA) logger at the sampling site. Rates were normalized to coral surface area, as determined using the foil technique.

Thermal tolerance experiments— All fragments were placed in a community tank gradually increased over 3 hours from ambient (ca. 26ºC) to elevated (32ºC) temperature. Photosynthetic physiology was monitored prior to experimentation and then every 12 hours at the elevated temperature using diving PAM fluorometry (following Hennige et al. 2008). Changes of the maximum fluorescence yield (F_m, instrument units) and PSII photochemical efficiency (F_v/F_m, dimensionless) were used as course proxies for symbiont biomass and photosynthetic competency in response to elevated temperature. Both temperature and O_2 saturation were monitored continuously using the *Optode*. Water was changed every ca. 12 hours to minimise the reduction in O_2 saturation (never <

90%), in particular, as corals began to discolor or slough tissue from the host and into the tank.

Results: We will consider each objective in turn from data collected at Silhouette (objective 1 and 2) and Desroches (Objective 3).

Objective 1— Size frequency data were treated so as to estimate whether corals had survived the 1998 bleaching event: coral size expected for the 1998 growth year was estimated from the product of growth rate (cm y^{-1}) and number of years since 1998 (9 for Silhouette). In this way, fast growing species would of course be expected to be much larger than slower growing species assuming that 'cropping', by physical or biological processes are negligible. Growth rates used were the maximum and minimum recorded growth rates for clear waters (see Crabbe & Smith 2005). As such, the predicted sizes for 1998 were highly conservative given known inherent variability of coral growth across species, size class and environment. These predicted sizes (max-min) for 1998 are plotted as the thick vertical broken line in Fig. 2. Size frequency distributions that fall to the left of this line are indicate of colonies that have recruited post 1998; in contrast, those to the right of this line are indicative of colonies that have recruited pre-1998 and so survived the 1998 El Niño bleaching event. Of the key species examined, the acroporid and pocilloporid colonies all appeared to be post 1998 recruits (Fig. 1) whilst some species (*D. heliopora*, *F. speciosa*, *P. lutea*) exhibited colonies that were larger
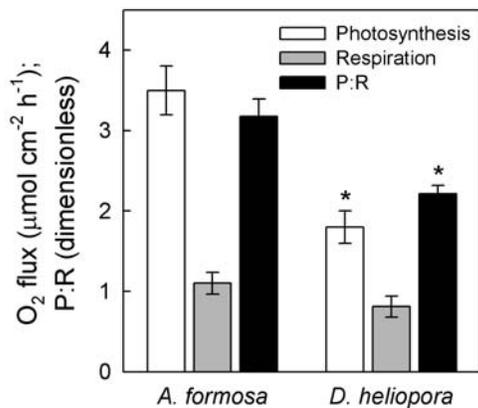
than would be predicted for 1998 (Fig. 1), with some *D. heliopora* and *P. lutea* colonies greater than 5m (data not shown). Corals within these two groups will subsequently be referred to as type I (recruited post 1998) and type II (survived 1998) corals, respectively.
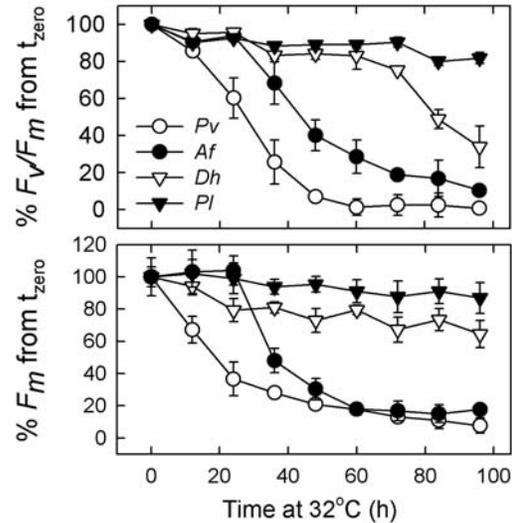

Figure 3. Mean percentage (%) ± standard error (n=3) change in photosynthetic parameters F_v/F_m (the maximum PSII photochemical efficiency) and F_m (the maximum fluorescence yield), measured by PAM fluorometry, with time of exposure of corals to elevated temperature of 32ºC (hours). Percentage change is expressed relative to values at time zero (t_{zero}). Examples are shown here for type I corals *P. verrucosa* and *A. formosa* and type II corals *D. heliopora* and *P. lutea*. All other species followed these type specific patterns (data not shown).

Objective 2— Both respirometry and PAM fluorometry demonstrated that type I and II coral species exhibited very different physiological characteristics. Rates of photosynthesis were higher by a factor of ca. 1.5-2.0 for type I than for type II corals (Fig. 2). Rates of respiration were similar across all species tested. Together these data yield photosynthesis to respiration ratios (P:R) that were highest for the type I corals (Fig. 2). PAM fluorometry was used to test for the response of type I and II corals to thermally induced stress (Fig. 3). The % change in maximum PSII photochemical efficiency (F_v/F_m) relative to time zero was greatest and occurred most rapidly for type I corals. Typically, F_v/F_m decreased by ca. 80-100% of the initial value after 40 to 60 hours at 32ºC (Fig. 3). In contrast, type II corals only exhibited a decrease of F_v/F_m by 40-20% of the initial value after 100 hours at 32ºC. Importantly, these responses by type I and II corals represent very different bleaching processes. For type I corals the decrease in F_v/F_m was the result of tissue sloughing off of the skeleton. The decrease in F_v/F_m

Figure 2. Rates of O$_2$ production (photosynthesis, P) and consumption (respiration, R), mmol O$_2$ cm^{-2} h^{-1}), and rates of P expressed relative to R (P:R, dimensionless). Examples are shown here for *A. formosa* and *D. heliopora* (mean ± SE, n = 3). All other species examined followed patterns the same as for *A. Formosa* (*A. horrida*, *P. eydouxi*, *P. verrucosa*, referred to as 'type I' corals) or *D. heliopora* (*F. speciosa*, *P. lutea*, referred to as 'type II' corals) (data not shown). Daily rates have been adjusted to hourly rates here. Asterisks represent significant differences between the two species for a t-test performed for each variable (i.e. P, R or P:R).
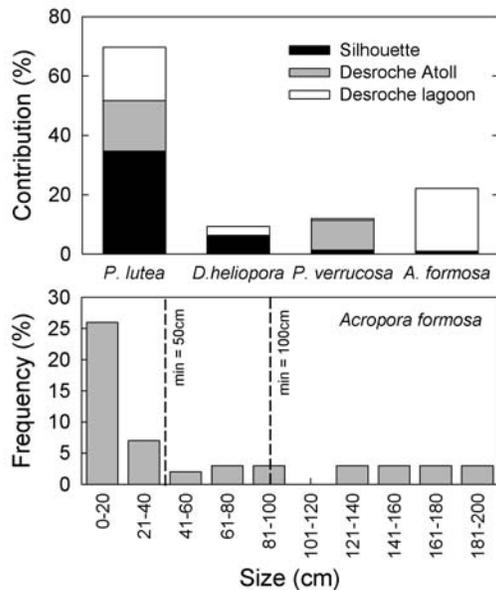
Figure 4. Relative contribution (%) of the four key coral species to the hard live coral community at each site: Silhouette (n=15), Desroches atoll (n=15) and lagoon (n=25). Lower panel is size frequency of *A. Formosa* colonies measured in the turbid lagoon (n = 53).

actually represents an increase in contamination to the minimum fluorescence yield from the skeleton (not shown) and so is not a physiological response from the zooxanthellae *per se*. This is representative of an *acute* bleaching response that appears to primarily target the host. Thus, the decline in symbiont biomass (i.e. the maximum fluorescence yield, F_m) is directly from a loss of coral host tissue containing the symbiont and occurs as abruptly as the change in F_v/F_m. In contrast, type II corals exhibited a gradual decline in F_m where the symbionts downregulated photosynthetic activity (Fig. 3). Here, host tissue remains in tact on the host skeleton and represents a *chronic* symbiont-targeted bleaching response.

Objective 3— Live coral cover estimated from all transect surveys at Silhouette and Desroches (outer high-light atoll and inner low-light lagoon) was 18.1 ± 1.1, 16.3 ± 0.8 and 7.0 ± 0.46 (mean % ± standard error), respectively. Of this cover, the relative contribution of key type I and II coral species was highly site specific. Coral abundance at Silhouette's granitic reef was dominated by *P. lutea* and *D. heliopora* but at the carbonaceous reefs of Desroches atoll by *P. lutea*; however, pocilloporids were also abundant. Importantly, the turbid waters of Desroches lagoon within the atoll were dominated by large colony sizes of the type I coral *A. formosa* and to a much lesser extent *P. lutea* (Fig. 4). Size frequency distribution of the *A. formosa* demonstrated that these lagoons contained colonies that certainly survived the 1998 El niño event. Growth rates used here were the

maximum and minimum recorded growth rates for turbid waters (Crabbe & Smith 2005).

Discussion: Different species of coral appear to fall into groups that have either been susceptible to the 1998 bleaching event and only recently recruited (termed here as type I corals) or survived the 1998 bleaching event (termed type II corals). Combined with specific type I and II physiological responses, the community data provide clear evidence that several mechanisms shape the response of coral reefs to environmental variability.

Resilience— Of the key coral species tested here, acroporids and pocilloporids (our type I corals) are most susceptible to catastrophic *acute* thermal bleaching, a finding supported by other observations from the western Indian Ocean (McClanahan et al. 2007). Type I species are fast growing with large and successful reproductive output as opposed type II corals, which appear to reach large sizes despite slower growth rates: a clear sign that these species are resilient to periodic large changes in growth environment. Type I corals also appear to be more reliant on autotrophy as opposed to heterotrophy to sustain their metabolic needs for growth and cellular maintenance. Whilst this is obviously beneficial under 'optimal' reef building high-light environments this strategy is at a cost during extreme changes in temperature. Firstly, potential symbiont (autotrophic)-based mechanisms associated with bleaching, such as reactive oxygen production (Smith et al. 2005) will be greater where autotrophy per unit biomass of coral tissue is highest. Secondly, lower heterotrophy yields less potential to sustain metabolic demands for tissue re-growth and repair once autotrophy becomes compromised (Grottoli et al. 2006).

Alternative patterns of photosynthetic response from the elevated temperature experiment were observed for type I and II corals (Fig. 3) implying that at least two different forms of bleaching are evident. Likely, the two phenomena observed here both represent a complex composite of processes, which together can be used to describe discoloration of corals. Presumably, these phenomena may also operate in concert. Whether these phenomena are mutually exclusive in nature is debatable, in particular since our experiments here are obviously acute temperature exposure treatments, which are not necessarily representative of elevated temperature trends associated with El Niño warm water events; however, the alternative response to elevated temperature by the two coral types is consistent with the community data suggesting that the different 'bleaching' responses may inevitably prescribe the relative sensitivity to environmental change.

Refuge— Acroporids were highly sensitive to elevated temperatures yet remained the dominant coral genus in the turbid lagoons of Desroches. Here colonies were relatively large despite the lower growth rates that would be expected for the relatively low light environment (see Crabbe & Smith 2005). Temperature induced bleaching is moderated by light availability and so the observation would imply that these turbid waters offer refuge. Analogous findings have been reported for Alphonse Atoll (Iluz et al. 2008) where seagrass-based DOM release has reduced UV penetration and enabled 'type I' species to flourish. However, understanding the dominance by *Acropora* at Desroches is not so clear. It is possible that *Acropora* may have substantial potential to upregulate heterotrophy; however, this suggestion would assume that the elevated turbidity is from particulates that offer some organic enrichment to justify the energy invested in turning to heterotrophy. Alternatively, the low light environment may select against species with a lower P:R, i.e. those that are more heterotrophic, if the organic quality of particulates in the atoll was low. Unfortunately, the answer is not clear from the data available. In particular, the confounding nature of the type II coral *P. lutea* within the lagoon and of the type I coral *P. verrucosa* within the atoll cannot be explained.

Recovery— Our data suggest that Seychelles' reefs are in a stage of recovery. Percentage cover data are higher than those reported for 2004 (Linden et al. 2005). Such recovery is driven by physiological investment in growth and recruitment post 1998. Long term persistence of type I corals is driven by investment in high growth and fecundity; in contrast type II corals persist through investing into processes that regulate maintenance and physiological recovery (*tolerance*). Recruitment is a function of connectivity between reef units that act as refuge zones versus impacted zones. Whilst it is difficult to prescribe the relative contribution of recruitment of type I versus II corals, the small colony size of the fast growing acroporids and pocilloporids under 'optimal' growth conditions indicates that substantial recruitment must be accounted for by these less resilient species; furthermore, that some source for recruits must exist and be connected to the islands studied here. High recruitment was previously reported for the relatively remote Seychelles island of Aldabra (Stobart et al. 2005) suggesting that connectivity may not necessarily be a function of closely spaced reef units.

In summary, we have observed that Seychelles reefs are clearly susceptible to environmental stress beyond the thresholds for optimal growth but possess species that confer some level of tolerance. These reefs are still undergoing a phase of recovery towards pre-1998 conditions, as indicated by the relatively recent recruitment of type I corals (Fig. 1). Whether a 'true' pre-1998 community structure can ever return will of course depend on the subsequent frequency with which extreme environmental perturbations further act to 'crop' the more susceptible species and whether apparent refuges remain connected to other suitable growth environments. These refuges are often deemed to be sub-optimal growth environment for corals; however, our results demonstrate that these environments must have high conservation value.

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