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Mortality, growth and regeneration following fragmentation of reef-forming corals under thermal stress

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ABSTRACT

Storms inflict damage to corals resulting in fragments that have the potential to regenerate thus contributing to the asexual reproduction of the parental colony. Extreme climatic events like these are predicted to increase in the future due to ocean warming, which is also the primary cause of coral reef bleaching and consequent coral mortality in the tropical and subtropical seas. This way it is urgent to investigate the differential effect of warming over post-fragmentation and regeneration processes among the scleractinian hermatypic coral species. This study investigated the mortality, growth and regeneration capacity of nine reef-forming coral species of the Indo-Pacific. Fragments were exposed to 26 °C, 30 °C, and 32 °C for 60 days. Half of these fragments was inflicted with one injury and the other half was used as control. Mortality, partial mortality, bleaching level, growth and regeneration of artificial injuries were assessed. Mortality increased with temperature, reaching 100% for most species after 60 days, at 32 °C, but *Psammocora contigua* which showed remarkably lower mortality (40%) and all coral fragments of *Turbinaria reniformis* and *Galaxea fascicularis* survived the experiment. Partial mortality was lowest for *P. contigua, T. reniformis*, and *G. fascicularis* even at 32 °C. These three coral species were also the most resistant to bleaching. Growth rates decreased with temperature, with the exception of *G. fascicularis* that maintained similar growth rates at 26 °C and 30 °C. Regeneration rates generally increased with temperature. It was concluded that *P. contigua*, *T. reniformis,* and *G. fascicularis* fragments show higher capacity to withstand higher temperatures.

1. Introduction

Corals are dominant species of tropical coral reef ecosystems and have a unique and complex symbiotic relationship with dinoflagellate microalgae (zooxanthellae), contained within their gastrodermal cells (Hoegh-Guldberg, 1999). The ability of scleractinian corals to deposit calcium carbonate skeletons and to generate the physically complex reef structure is attributed to these dinoflagellates (Meehan & Ostrander, 1997).

Global climate change is leading to both rising sea surface temperatures and ocean acidification, jeopardizing coral reefs survival (Carpenter et al., 2008; Padilla-Gamiño et al., 2013). However, it has been shown by recent studies that the warming of tropical oceans is a much more imminent threat to coral reefs' survival than is ocean acidification (e.g., (Chua et al., 2013; Frieler et al., 2012)). The reef-building corals that undergo bleaching have reduced growth rates and reproductive capacity (Baird & Marshall, 2002; Szmant & Gassman, 1990), impaired healing (Meesters & Bak, 1993), and increased susceptibility to disease (Harvell et al., 1999). Bleaching makes the host organism white due to a loss of symbionts, which allows the underlying skeleton to be visible (Baker et al., 2008). If thermal stress is sustained, this may result in widespread coral mortality (Brown et al., 2002; Szmant & Gassman, 1990). Mass bleaching episodes have the potential to dramatically change coral community structure (Gleason, 1993; Glynn, 1993) and in severe cases cause population collapse and local extinction (Aronson et al., 2000).

An increase in the frequency and intensity of bleaching events is expected (Eakin et al., 2009; Heron et al., 2016), given that sea temperatures surrounding coral reefs are projected to increase by 1–3.7 °C by the year 2100 (IPCC, 2014). Globally, thermally induced bleaching due to climate change was predicted to occur annually in most oceans by 2040 (Crabbe, 2008; Hoegh-Guldberg, 1999; van Hooidonk & Huber, 2009). Associated with ongoing increases of tropical sea surface temperatures (SST) are increases in the frequency and maximum

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intensity of categories 4 and 5 storms (0–25%), and increases in tropical cyclones rainfall rates (5–20%) (Christensen et al., 2013; IPCC, 2014).

Due to wave action (Stimson, 1978), storm surge (Randall & Eldredge, 1977), and touristic activities (e.g. diving, snorkeling, and trampling; (Davenport & Davenport, 2006)) coral fragments may become detached from parent colonies and disperse across the reef (Highsmith, 1982). Increased storminess should favor the ability to propagate effectively by fragmentation (Lasker, 1990). Many branching corals are routinely broken and scattered about during storms (e.g., (Highsmith, 1980; Tunnicliffe, 1981)). Asexual reproduction by fragmentation of plating and massive coral forms has also been noticed (Foster et al., 2007).

Fragmentation of established colonies resulting in the formation of new coral colonies is known as an extremely important asexual mode of reproduction for many of the major reef-building corals (Bruno, 1998; Highsmith, 1982). Fragmentation by corals with high growth rates results in their domination of certain reef zones (Tunnicliffe, 1981), rapid growth of reefs on which these corals are abundant (Glynn et al., 1994), and rapid recovery from disturbances (Glynn & Fong, 2006; Shinn, 1976). Fragmentation may be adaptive (Cook, 1979; Highsmith, 1982; Highsmith et al., 1980), given that a considerable number of the most successful corals have incorporated fragmentation into their life histories. Asexual reproduction is probably the main process involved in the origin of new coral reefs (Glynn, 1993).

There is interspecific variability in reef-building corals' susceptibility to increased temperature (McClanahan et al., 2007; Seveso et al., 2014). Their susceptibility depends on colony morphotype (Brandt, 2009), tissue thickness (Loya et al., 2001), colony size (Shenkar et al., 2005), the capacity to transfer mass and heat (van Woesik & Jordán-Garza, 2011), coral species (Hoegh-Guldberg & Salvat, 1995; Marshall & Baird, 2000), genetic variation between coral populations from widely separated geographic regions (Coles et al., 1976; Glynn et al., 1988; Rowan & Knowlton, 1995), and the genetic constitution of the symbiotic microalgae (*Symbiodinium* spp.) (Rowan et al., 1997).

In many coral bleaching reports, there is noticeable variation in the extent of bleaching, as some colonies remain pigmented but adjacent ones of the same or different species undergo bleaching (Baker et al., 2008; Montano et al., 2010; Rowan et al., 1997). These different susceptibilities lead to major structural shifts in coral communities (Aronson et al., 2004; Ostrander et al., 2000), where hardier corals (i.e. massive and encrusting thick-tissued species) will eventually replace less resilient corals (i.e. branched and thin-tissued species) (Kayanne et al., 1999; van Woesik et al., 2011).

The aim of this work was to evaluate how elevated temperatures will affect the mortality, growth and regeneration after fragmentation of an important number of reef-building corals of the Indo-Pacific oceans. Such an evaluation is crucial to understand the differential vulnerability of reef-forming coral species to global climate change.

2. Material and methods

2.1. Study species

This study evaluated nine Indo-specific coral species with contrasting morphologies: four branching species (*Acropora tenuis, Pocillopora damicornis, Stylophora pistillata,* and *Psammocora contigua)*, three plating species, (*Montipora capricornis* brown morphotype (BM), *Turbinaria reniformis,* and *Echinopora lamellosa)*, one encrusting species (*Montipora capricornis* green morphotype (GM)), and one massive species (*Galaxea fascicularis)*. All coral colonies used in this study have been kept in captivity at Oceanário de Lisboa (Portugal) for several years, which gave us knowledge on their thermal history.

These coral species were chosen in order to use the largest number of species available at Oceanário de Lisboa with different levels of bleaching susceptibility: severe (*A. tenuis, P. damicornis,* and *S. pistillata*), high (*M. capricornis*), moderate (*E. lamellosa*), and low (*T. reniformis, G. fascicularis,* and *P. contigua*) (Marshall & Baird, 2000), and different colony morphology, a characteristic that has been proven to have influence in coral species susceptibility to thermal stress (Loya et al., 2001). Coral species identification was made according to Veron (Veron, 2000).

2.2. Acclimation conditions and experimental setup

The experiments were conducted at Oceanário de Lisboa, Portugal (www.oceanario.pt).

Twenty replicate fragments were cut from each coral colony using a pincer or a pair of pliers. For the branching coral colonies the fragments were cut approximately 20–40 mm in length and the fragments for the plate, encrusting and massive corals were obtained by cutting approximately 30 mm sided squares. A single colony per coral species was targeted in order to eliminate sources of variation from other factors that affect thermal susceptibility (Desalvo et al., 2008) such as tissue thickness (Loya et al., 2001), genetic constitution of the symbiotic microalgae (*Symbiodinium* spp.) (Rowan et al., 1997), metabolic rates (Gates & Edmunds, 1999), mucus production rates (Fitt et al., 2009), tissue concentration of fluorescent pigments (Salih et al., 1998), and thermal history (Brown et al., 2002). All fragments were placed over egg crate panels in the coral stock aquarium until acclimation to the experimental aquarium.

The live wet mass of each coral fragment was obtained by blotting it with a paper towel to remove excess seawater, then weighing it in air on an electronic balance to the nearest 0.01 g (Titlyanov et al., 2005). Each fragment was glued with epoxy putty to the top of a pre-weighed and numbered nylon expansion anchor. Placement of the fragment varied by morphology with the branching fragments in vertical position and the plating, encrusting and massive fragments placed in horizontal positions. Then, the set (coral fragment + anchor) was weighed to remove the epoxy putty weight off the calculations and placed back over egg crate panels in the coral stock aquarium.

After one day in the coral stock aquarium, the sets were acclimated 1 °C per hour above the temperature of the coral stock aquarium (25.1 ± 0.4). Coral reef-flat communities can experience temperature changes of 1 °C hour^{-1} during spring tides (Berkelmans & Willis, 1999), and most of the coral species in this study colonize the reef-flat zone (Brown & Suharsono, 1990), so we used this heating rate to be similar to the conditions that most of these corals would experience in their natural environment. In order to standardize, this heating rate was applied for all the coral species. The coral fragments were placed 2 cm apart from one another and arranged by coral species. Fragments were exposed to three temperature treatments: control 26 °C (26.1 ± 0.2 SD), 30 °C (30.2 ± 0.5 SD) and 32 °C (32.2 ± 0.5 SD) seawater temperatures during sixty days, with the duration of one, five and seven hours of acclimation, respectively.

Ten coral fragments of each species were used as controls (undamaged) and the other ten fragments were inflicted with circular injuries designed to simulate damage by predators, after being acclimated to the experimental aquarium. These artificial injuries were 3 mm in diameter and were done using a Dremel rotatory tool with a cutting disk. Only one injury was inflicted to each coral fragment in their middle section to avoid edge effects (Supplementary material – Image 1). After these procedures, all fragments were placed over two 40 × 40 cm egg crate panels suspended 15 cm below the water surface of the experimental aquarium.

The experimental aquarium (400 L) was fitted with a sump (280 L) filled with bioballs for biological filtration in which two Fluval M300 heaters, as well as a Hailea 500 chiller controlled water temperature. For water circulation purposes, an AquaMedic OceanRunner 3500 pump provided a turnover rate of 5 times per hour. An AquaMedic Turboflotor 5000 Shorty protein skimmer helped keeping nutrient concentrations low and increased surface water motion in the aquarium was accomplished by using an AquaClear 110 powerhead. Lighting