



Symbiont dynamics during thermal acclimation using cnidarian-dinoflagellate model holobionts



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ABSTRACT

Warming oceans menace reef ecosystems by disrupting symbiosis between cnidarians and *Symbiodinium* zooxanthellae, thus triggering bleach episodes. Temperature fluctuations promote adjustments in physiological variables and symbiont composition, which can cause stress responses, but can also yield adaptation if fitter host–symbiont homeostasis are achieved. To understand such processes manipulative studies are required, but many reef-building cnidarians pose limitations to experimental prospects. We exposed *Exaiptasia* anemones to Gradual Thermal Stress (GTS) and Heat Shock (HS) exposures and monitored chlorophyll and symbiont dynamics to test the phenotypic plasticity of these photosynthetic holobionts. GTS enhanced chlorophyll concentrations and decreased *Symbiodinium* proliferation. A recovery period after GTS returned chlorophyll to lower concentrations and symbiont divisions to higher rates. HS triggered a stress response characterized by intense symbiont declines through degradation and expulsion, algal compensatory proliferation, and chlorophyll accumulation. Anemones pre-exposed to GTS displayed more acute signs of symbiont paucity after HS, demonstrating that recurrent stress does not always induce bleaching-resistance. Our study is the first documenting *Symbiodinium* C and D, along with the predominant Clade B1 in *Exaiptasia* anemones. C subclades found in outdoor specimens faded under laboratory exposures. Clade D emerged after HS treatments, and especially after GTS pre-exposure. This highlights the thermotolerance of D subclades found in *E. pallida* and shows that bleaching-recovery can involve shifts of background symbiont phylotypes. This study enlightens the capability of *Exaiptasia* anemones to acclimate to gradually increased temperatures, and explores into how thermal history influences in subsequent stress tolerance in symbiotic cnidarians.

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1. Introduction

The symbioses between cnidarians and dinoflagellates in the genus *Symbiodinium* have key ecological relevance for the sustenance of coral reefs (Dubinsky and Stambler, 2011). These microalgal partners (zooxanthellae) establish intracellularly within their anthozoan hosts, and are able to supply, via autotrophy (photosynthesis) and metabolite exchange (carbon translocation), most of the holobiont's energetic demands (up to >99%) (Muscattine et al., 1981; Steen and Muscattine, 1984; Davy et al., 1996; Davies, 1991;

Verde and McCloskey, 2007; Dubinsky and Stambler, 2011). The genus *Symbiodinium* is divided in nine Clades (A–I) and numerous subclades (Franklin et al., 2012), with a few fully described species (e.g., Lajeunesse et al., 2012; Parkinson et al., 2015). Different genetic types (phylotypes) exhibit diverse efficiency as symbionts (in terms of the efficacy to translocate photosynthates) and diversified host specificity (Lajeunesse, 2002; 2004; Stat et al., 2008). Further, the various phenotypes differ in their light and/or temperature-related sensitivities. Some can withstand higher temperature and or light regimes conferring cnidarian holobionts environmental tolerance to expand their niche to more variable (or extreme) habitats (Goulet et al., 2005; Fitt et al., 2009; Lajeunesse et al., 2009; Oliver, 2009; Keshavmurthy et al., 2014). Direct comparisons among studies at the subcladal levels are complicated though, as there is little consensus on the species classification, coupled with a

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variety of taxonomic markers used (ITS1, ITS2, LSU D1/D2, chloroplast 23 S rDNA and *psbA* minicircle; Rodríguez-Lanetty et al., 2004; Stat et al., 2011; Tonk et al., 2013). At the Clade level thermotolerant *Symbiodinium* have been described within A, B, C, D, E, F, but still there is no clear pattern between physiology and Clade. Some of the most ecologically relevant thermotolerant phylotypes for coral reefs have been designated within D (e.g. D1, D1–4), some C (e.g., C15), and a few A (e.g., A3) for instance (Karako-Lampert et al., 2005; Oliver and Palumbi, 2011; Lajeunesse et al., 2014; Silverstein et al., 2014; Hume et al., 2015; Swain et al., 2017). Cnidarian holobionts harbor dynamic zooxanthellar populations often composed of one or a few dominant *Symbiodinium* Clade (or subclade) accompanied by under-represented background phylotypes—often analytically undetectable—(Lajeunesse, 2002; Baird et al., 2007), which provide phenotypic plasticity for acclimatization processes (Berkelmans and van Oppen, 2006; Silverstein et al., 2014). The combination of holobionts, symbionts and environment is what determines fitness, as proven when different holobionts were infected with different *Symbiodinium* (Fitt, 1985; Perez et al., 2001; Weis et al., 2001; Baker, 2003; Goulet et al., 2005; Seckbach and Grube, 2010; Oliver and Palumbi, 2011; Fabina et al., 2012; Leal et al., 2014; Starzak et al., 2014).

One immediate concern among coral reef biologists is the frequency and severity of bleaching episodes, causing paling, starvation and eventual death of photosynthetic cnidarians due to the loss of their microalgal partners and/or their pigments (Glynn, 1996; Lesser and Farrell, 2004; Venn et al., 2006; Hughes et al., 2017). In this sense, the capabilities of different holobiont systems to respond to maximum environmental limits either adapting, acclimating or both will determine the survival of reefs in the wake of future impacts (Coles and Brown, 2003; Weis et al., 2008; Weis and Allemand, 2009; Davy et al., 2012; Graham et al., 2015). After a bleaching episode, low-abundance *Symbiodinium* living within the host or in the surrounding seawater can play a major role in the recovery and acclimatization of the holobiont (e.g., Lajeunesse et al., 2004; Coffroth and Santos, 2005; Stat et al., 2011). This is because perturbations alter the relative composition of *Symbiodinium* communities by favoring the proliferation of opportunistic phylotypes with stress tolerance (Berkelmans and van Oppen, 2006). These emerging stress-resistant symbionts can derive from background populations already in the host (i.e. symbiont ‘shuffling’), or from free-living *Symbiodinium* in the water column that infect the host (i.e. symbiont ‘switching’). In either case, these phylotypes may proliferate and assist the cnidarian holobiont to survive during the perturbation, and even to forthcoming impacts (Schoenberg and Trench, 1980; Baker, 2003; Fautin and Buddemeier, 2004; Lewis and Coffroth, 2004; Jones et al., 2008; Silverstein et al., 2014). There is some evidence of thermotolerant *Symbiodinium* D and A phylotypes becoming predominant after a bleaching event, and replacing the original zooxanthellae in populations of corals and anemones (Lajeunesse et al., 2004; Coffroth and Santos, 2005; Goulet et al., 2005; Berkelmans and van Oppen, 2006; Cunning et al., 2015). Besides symbiont genotypic rearrangements, physiological responsive adjustments in photosynthetic pigments concentrations and in *Symbiodinium* population dynamics—via mitotic proliferation, degradation/autophagy/symbiophagy and cellular extrusion—take place during thermal stress (Downs et al., 2009; Seckbach and Grube, 2010; Dubinsky and Stambler, 2011; Hoegh-Guldberg, 2012; Hanes and Kempf, 2013). Bleaching resistance and/or reversibility to bleach and recover are key processes assisting corals in the face of warming oceans (Baker et al., 2004; Castillo and Helmuth, 2005; Grottoli et al., 2006, 2014; Oliver and Palumbi, 2011; Wang et al., 2012; Mayfield et al., 2013).

Model organisms suitable to elaborate stressor-response

predictions of cnidarian-dinoflagellate symbiosis are challenging to find, because of the extreme diversity of holobiont combinations (host and symbiont phylotypes) and habitats, and because many reef-building corals pose limitations to experimental prospects. The zooxanthellate sea anemones in the genus *Aiptasia* (recently renamed as *Exaiptasia*; Grajales and Rodríguez, 2014; Grajales et al., 2016) have been used to study photobiology because of their manipulability under laboratory conditions, and ability to live aposymbiotically (algae free). Such traits turn them into promising species to explore disruption and restoration of cnidarian symbioses under extreme conditions (e.g., Schoenberg and Trench, 1980; Steen, 1986; Weis et al., 2008; Lehnert et al., 2012; Starzak et al., 2014; Krediet et al., 2015; Oakley et al., 2017). Worldwide, the prevailing *Symbiodinium* phylotype associated with *Exaiptasia* spp. has been described to be *S. minutum* ITS2 type B1_{Aiptasia}. However, populations from Florida possess a dominant thermo-tolerant subclade A4, plus one minor lineage of C (Goulet et al., 2005; Xiang, 2009; Pochon et al., 2010; Thornhill et al., 2013). Little is known about background phylotype shifts in these anemones (Grajales et al., 2016).

In this study we used *Exaiptasia pallida* (= *Aiptasia pallida*) as a cnidarian-dinoflagellate symbiotic system to address the following points: (1) to monitor symbiont variables (zooxanthellae population and chlorophyll dynamics) in holobiont acclimation towards gradual thermal manipulation versus un-manipulated individuals in the laboratory; (2) to examine the recovery of symbiotic homeostasis in anemones pre-exposed to high temperature treatments, and evaluate if thermal pre-exposures confer bleaching resistance to a subsequent drastic heat shock; and (3) to characterize via Next Generation Sequencing (NGS) background *Symbiodinium* Clade shifts of retained versus released algal material under different thermal scenarios.

2. Materials and methods

2.1. Sampling of organisms and pre-experimental settings

Specimens of the sea anemone *Exaiptasia pallida* (oral disc diameter 5 mm) were collected in November 2013 from outdoor running-seawater tables at the Hawai’i Institute of Marine Biology (HIMB), Kane’ohe Bay (Oahu, Hawai’i, U.S.A.), using spatulas to release the foot from the substrate and minimize trauma. Temperature and light irradiance at the shaded tanks housing the anemones were measured every two hours for one week, yielding an average irradiance of 20 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (Photometer LI-COR LI-1400 data logger connected to a Cosine collector), and an average water temperature of 25 °C. This expressed as Daily Light Integral (DLI = Average irradiance in $\mu\text{mol m}^{-2} \text{s}^{-1} \times 0.0432$ [or $\times 3600 \text{ s} \times 12 \text{ h photoperiod}/1,000,000 \mu\text{mol per mol}$]) revealed a DLI of 0.864 $\text{mol photons m}^{-2} \text{d}^{-1}$.

2.2. Experimental setup

The anemones were brought into the laboratory and were placed in independent 15 mL chambers with filtered seawater (FSW, 0.7 μm) that was changed daily. In total we had 50 chambers with a single anemone counting for the 30 experimental animals (six replicates for each of the five treatments), plus 20 back up specimens accordingly distributed by treatments to cover for eventual mortality. The control incubation conditions were 25 °C with a light regime photoperiod of 100 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, 12-h light/12-h dark (DLI of 4.32 $\text{mol photons m}^{-2} \text{d}^{-1}$). Anemones were fed twice a week with freshly hatched brine shrimp, *Artemia* sp. *nauplii* (San Francisco Bay Brand®). Specifically 1 mL solution of concentrated living brine shrimp culture was injected nearby the

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