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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.

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%) (Muscatine et al., 1981; Steen and Muscatine, 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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