



Adaptive abilities of the Mediterranean red coral *Corallium rubrum* in a heterogeneous and changing environment: from population to functional genetics



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ABSTRACT

Mediterranean benthic ecosystems have been deeply impacted by thermal anomalies during the last decades. Adaptive capacities for marine species facing climate change can include individual acclimatization (during the individual life-span) and genetic selection (considered at the population level). The Mediterranean red coral, *Corallium rubrum*, is well suited to study adaptive evolution in heterogeneous environment. This is a sessile species, which inhabits contrasted environments with a strong genetic structure, and differential responses to thermal stress between populations. This study proposes an integrative study of the adaptive response of *C. rubrum* to thermal stress. To understand the underlying mechanisms of thermal adaptation in this species, we studied three populations of *C. rubrum* from different depths (5 m, 20 m and 40 m depths) and therefore different thermal regimes in the same area. We first surveyed in situ the thermal environment and the corresponding stress levels at the different depths studied here. Then we submitted red coral colonies to different heat shocks in *aquaria* that mimicked in situ stresses (common garden conditions). We measured the expression levels of several candidate genes. Heat shock protein 70 (HSP 70) showed significant differences of expression depending on the depth of origin of the individuals and of their thermal history. Based on a complementary analysis of genetic structure, our study shows the evolution of a differential response at a local scale which might be explained by local adaptation or acclimatization. Our results also underline the trade-off between fitness and potential deleterious consequences linked to heat stress response. It also strongly emphasizes the conservation value of populations living at the edge of the species' range, as they represent an irreplaceable genetic pool for evolutionary rescue.

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1. Introduction

Climate change constitutes a major pressure for many marine ecosystems, including Mediterranean ones (Hughes et al., 2003; Lejeusne et al., 2010; The MerMex Group, 2011). Among other impacts, thermal stress linked to extreme thermal events has been pointed out as a prominent factor in bleaching and mass mortality events on tropical coral reefs (Brown, 1997; Hoegh-Guldberg, 1999; Polato et al., 2010). Temperate and non-symbiotic cnidarians can also be affected by such thermal-linked mortality events as observed in the Mediterranean Sea in 1999 and 2003 (Crisci et al., 2011; Garrabou et al., 2001, 2009). These large-scale mortality events (> 100 km of coastline) affected 30 macro-benthic species including sponges, cnidarians, bivalves, ascidians and bryozoans (Garrabou et al., 2009). Climate change is not linear and

occurs along with an increase in variability of environmental parameters that could lead organisms outside their biological capacity of long-term survival (Hughes et al., 2003; Peck, 2005). Accordingly, estimating the adaptive responses of individuals to thermal stress is a prerequisite for a proper understanding of the evolution of biodiversity. In this context, adaptive capacities can be understood at two different levels. Adaptive capacities at the individual level rely on phenotypic plasticity and define abilities of an organism to deal with narrow or broad ranges among environmental conditions (Gienapp et al., 2008). At the population level, genetically based differences between individuals can provide the basis for a selection driven response. These two levels of biological adaptation can interact through the selection of more or less plastic phenotypes depending on thermal regimes, which can ultimately lead to adaptation to local thermal conditions (i.e. genetically based local adaptation), or enhanced or reduced phenotypic plasticity. Local adaptation should be taken into account for a better understanding of the impact of climate change. High levels of gene flow can prevent the evolution of local adaptation (Lenormand,

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2002). The marine realm generally presents such gene flow. Nevertheless for some marine species characterized by a high genetic structure, cases of local adaptation have now been reported (Sanford and Kelly, 2011). In this context, complementary approaches (as common garden experiments, RNA-seq and RAD-seq) should be used to enhance our knowledge of local adaptation in the sea and more particularly to study the interplay between genetic adaptation and plasticity for different thermal regimes.

Common garden experiments provide an efficient way to test for the local adaptation hypothesis (Kawecki and Ebert, 2004) usually with phenotypic markers as a surrogate for adaptive genetic diversity. However, gene expression levels should be considered as an entire component of the adaptive response (Barshis et al., 2013; Bay et al., 2009; Oleksiak et al., 2002; Ranz and Machado, 2006). Moreover, interpreting this variability of gene expression in light of neutral genetic structure and gene flow should significantly increase our ability to understand adaptive evolution in heterogeneous environment (Alleaume-Benharira et al., 2006).

In this study we propose an integrative study of the adaptive response to thermal stress for the Mediterranean red coral, *Corallium rubrum*. The red coral is a key component of the coralligenous assemblage, one of the richest biodiversity habitats of the Mediterranean Sea (Ballesteros, 2006). It is an asymbiotic octocoral, long-living species (more than 50 years), with low growth and recruitment rates (Marschal et al., 2004; Santangelo et al., 2012). This species is over-harvested for jewelry (Bruckner, 2009) and it possesses all the characteristics of a patrimonial species (Bramanti et al., 2011; Pervanchon et al., 2004). *C. rubrum* has been deeply impacted by mortality events in 1999 and 2003 linked to thermal anomalies, with some sites presenting 80% of affected colonies but with important differences of response between and within populations (Garrabou et al., 2001, 2009). This variability reflects different levels of thermal stress (see Crisci et al., 2011 for another Mediterranean octocoral) but is also probably the consequence of the evolution of different adaptive strategies for this species. Indeed red coral is present from 5 to 800 m depth (Costantini et al., 2011) and is therefore submitted to very contrasted thermal regimes.

To understand the underlying mechanisms of adaptation to thermal stress in this species, we studied three *C. rubrum* populations living in different thermal regimes (5 m, 20 m and 40 m depths) in the same area. This study at short distance, unusual in marine environment, is nevertheless pertinent for this species considering i) the steep environmental gradients observed between depths (see the Results section), ii) the genetic structure observed with microsatellites at short distance and between different depths (Costantini et al., 2011; Ledoux et al., 2010a,b) and iii) the differences of response to thermal stress observed between these depths when considering respiration, growth, calcification and necrosis (Ledoux, 2010; Torrents et al., 2008). Nevertheless the molecular mechanisms underlying the differential responses observed between populations remained to be studied. For this purpose, we first surveyed in situ the thermal environment and the corresponding stress levels for the different depths studied here. Then we submitted sampled individuals to different heat shocks in aquaria (common garden conditions), and we measured the expression levels of several candidate genes.

We thus evaluated the variability of the transcriptional response to stress over different temporal and spatial dimensions and organization scales: between individuals, between populations/depths, between acute or progressive thermal stress and between seasons. We then analyze this variability in regard to the neutral genetic structure of the populations evaluated by using microsatellites. Our results offer convergent hints in favor of genetic or epigenetic basis for variable adaptive capacities of red coral. They also highlight a significantly differentiated molecular response of shallowest individuals facing thermal stress compared to deeper ones, thus emphasize the conservation value of marginal populations.

2. Methods and techniques

2.1. Temperature measurement

Temperatures were recorded at five sites around Marseille (Fig. 1A) by in situ Onset Tidbits autonomous sensors, from June 2010 to January 2012. Sensors were placed at 5, 20 and 40 m, and temperature data were collected every 10 min. To visualize the thermal regime in Marseille's bay, the site of Morgiou and the 4:00 pm data were chosen every day. In order to estimate heat stress in situ at each depth, the numbers of days presenting a value over a given temperature (from 20 °C to 25 °C) were summed over the survey period. In order to measure the magnitude of in situ temperature variation, we calculated the maximum temperature variation rate over 1, 8 and 24 h.

2.2. Sampling for thermal stress experiments

C. rubrum colonies were randomly collected by scuba divers (with authorization for sampling wild marine species), around Riou island at 20 and 40 m depths in March 2011 for short and long heat shock experiments. Samples for “resilience heat shock” experiment were collected in June 2011 at Cap Morgiou for 20 m and 40 m samples, and near Figuier cave for 5 m depth samples, which is the shallowest population near Marseilles and which is near Cap Morgiou (Fig. 1). The distance between Riou and Morgiou-Figuier is about 5700 m. Colonies were quickly transferred to Endoume Marine Station aquaria laboratory. Heat shock experiments were performed after two weeks acclimatization in a semi-closed water circulation system (constant temperature 14–15 °C). Specimens were fed twice a week, alternatively with *Artemia salina* and lyophilized phytoplankton.

2.3. Heat shock experiments

High resolution temperature analysis showed that mortality events in marine Mediterranean communities can be triggered by two main types of positive thermal anomalies: short periods (2 to 5 days) with high mean temperature (27 °C in some regions) and high variability, and much longer periods (1 month) with less warm and more constant temperature (24 °C) (Benssoussan et al., 2010; Crisci et al., 2011).

Considering these data, previous thermotolerance studies (Torrents et al., 2008) and our temperature records in Marseille (see results Section 3.1), we performed three different types of heat shock experiments, to investigate the impact of these different kinds of stress. First, a short heat shock (SHS) was performed in March 2010 with 20 m and 40 m samples from Riou (16 colonies for each depth), with a linear shift from 14 °C to 24 °C in 7 h corresponding to acute stress (Fig. 2). Second, a long heat shock (LHS), was performed in April 2010 with 20 m and 40 m samples from Riou (eight colonies for each depth), with a shift from 15 °C to 25 °C in 30 days, with a 1 °C increase every three days corresponding to progressive stress (Fig. 2).

Third, in order to investigate the impact of previous stress, a “resilient heat shock” (RHS) was performed in June 2011 with 5 m, 20 m and 40 m samples (eight colonies for each depth) (Fig. 2). RHS experiments consisted of a first acute stress (15 °C to 25 °C in 16 h, with 2 h at 25 °C) and a second similar stress (15 °C to 26 °C), separated by a nine day recovery period at 15–16 °C. After first heat shock, the water temperature returned to basal value in 10 h. Such a sequence of thermal events can be observed in natural conditions (see the Results section). The temperatures were continuously recorded by Onset Tidbits autonomous sensors. The choice of a different area (Morgiou-Figuier) was motivated by the will to investigate the response of reiterate stress of the shallowest populations compared to deeper ones.

For all experiments, each colony was divided into two branches for SHS, three for RHS and four for LHS. One branch was kept in the control aquaria, with temperature maintained constant between 14 and 16 °C. The others were submitted to thermal stress (SHS, LHS or RHS protocol).

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