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Effect of tidal environment on the trophic balance of mixotrophic hexacorals using biochemical profile and photochemical performance as indicators

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ABSTRACT

Fluctuations of environmental factors in intertidal habitats can disrupt the trophic balance of mixotrophic cnidarians. We investigated the effect of tidal environments (subtidal, tidal pools and emerged areas) on fatty acid (FA) content of *Zoanthus sociatus* and *Siderastrea stellata*. Effect on photophysiology was also accessed as an autotrophy proxy. There was a general tendency of a lower percentage of zooplankton-associated FAs in colonies from emerged areas or tidal pools when compared with colonies from the subtidal environment. Moreover, tidal environment significantly affected the photophysiology of both species. Colonies from the subtidal generally showed lower values of α, ETR_{max} and E_k when compared with their conspecifics from tidal pools or emerged areas. However, the absence of consistent patterns in F_v/F_m and in dinoflagellate-associated FAs, suggest that these corals are well adapted to intertidal conditions. This suggests that intertidal pressures may disturb the trophic balance, mainly by affecting heterotrophy of these species.

1. Introduction

Intertidal environments are among the most demanding habitats for marine organisms due to considerable fluctuations in environmental parameters, including changes in temperature, salinity, solar radiation and dissolved oxygen (Helmuth et al., 2006; Thompson et al., 2002). These pressures may affect intertidal biota by exposing them to abiotic extremes such as desiccation, osmotic stress and aerial exposure, as well as limitation in food availability either considering short-term or long-term time scales (e.g. Freites et al., 2002; Romaine et al., 1997; Teixeira et al., 2013). Symbiotic cnidarians are particularly vulnerable to environmental changes such as elevated temperature and intense light irradiation (Weis, 2008). Indeed, these stressors may led to a decrease in the photosynthetic pigments of the dinoflagellates of genus *Symbiodinium* with whom the host establishes the symbiosis and/or the expulsion of the dinoflagellates by the host, leading to a phenomenon known as bleaching (Brown et al., 1995).

The symbiosis between cnidarians and *Symbiodinium* is mainly based on nutritional changes in which the host provides the symbiont with inorganic nitrogen, phosphorus and carbon whereas the dinoflagellate supply the host with the majority of its photosynthetically fixed carbon (Sutton and Hoegh-Guldberg, 1990; Weis, 2008). An alternative source of carbon for the host is by plankton ingestion, particularly during bleaching events or when light is limited (Houlbrèque and Ferrier-Pagès, 2009). The photosynthetically fixed carbon and the heterotrophically derived carbon are the main constituents of lipids, essential in several important biochemical and physiological processes (Hulbert, 2003; Rodrigues et al., 2008; Ward, 1995). However, it seems that, in cnidarians, they are incorporated through different mechanisms resulting in different functions. More specifically, photosynthetically fixed carbon seems to be primarily used for instant energetic processes such as respiration, while the carbon obtained heterotrophically is used as structural lipids (e.g. phospholipids) that are crucial for membranes' formation (Bachar et al., 2007). Moreover, while lipids obtained from autotrophic carbon are mainly constituted by saturated (SFA) and monounsaturated (MUFA) fatty acids (FA), lipids obtained from the

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heterotrophic carbon are mainly composed by polyunsaturated fatty acids (PUFA) (Yamashiro et al., 1999). In this way, the physiology of symbiotic cnidarians is largely related with the origin of their FAs which, in turn, may be strongly influenced by environmental changes (Leal et al., 2013; Papina et al., 2007; Tolosa et al., 2011).

High light exposure and temperature as well as food limitation are common in tropical intertidal habitats and have been proven to influence the FA content of cnidarians (e.g. Almoghrabi et al., 1995; Leal et al., 2013; Papina et al., 2007; Tolosa et al., 2011) and their symbionts (e.g. Diaz-Almeyda et al., 2011; Kneeland et al., 2013; Zhukova, 2007; Zhukova and Titlyanov, 2006). However, these studies have used manipulative approaches and might not properly reflect the complexity of stressors that organisms find in the wild.

Photochemical parameters are good indicator of health and adaptation capacity of mixotrophic organisms, particularly when considering autotrophy. For example, a reduction in the maximum quantum yield of photosystem II (PSII), F_v/F_m, is strongly related to photosynthesis impairment due to photoinhibition and/or photodamage (Maxwell and Johnson, 2000). On the other hand, light-response curve parameters α (initial slope), maximum electron transport rate (ETR_{max}) and E_k (light-saturation coefficient) express the ability of the endosymbiont to adapt and tolerate short-term changes in light (Ralph and Gademann, 2005).

The present study aims to explore the effect of different tidal environments (subtidal areas, tidal pools and emerged intertidal areas exposed to air during low tide) on the FA content of mixotrophic hexacorals, namely the zoanthid *Zoanthus sociatus* and the scleractinian coral *Siderastrea stellata*. Photophysiological parameters were also used as indicators of endosymbiont photobiological performance, which contribute for the autotrophy of these organisms. Both species are often abundant in intertidal West Atlantic tropical environments (Correia, 2011; Rabelo et al., 2015), being therefore exposed to forceful fluctuations driven by tidal regimes. This way, the present work will be a major contribution to the knowledge on the ecology of mixotrophic hexacorals, namely when facing stressful conditions as the ones found in intertidal environments.

2. Materials and methods

2.1. Study area

The study area is located in the Arembepe village, Camaçari Municipality, Bahia, Brazil (12°46′49.65″S, 38°10′58.90″O) (Fig. 1a). In this area there are three strands of beachrock parallel to the shore that mark ancient shorelines with two of them being exposed during low tide. The tidal extremes in the region range from −0.1–2.7 m and during low tide, these beachrocks rise to almost 2 m of the waterline, forming a perennial lagoon between them. As a result, tidal pools are formed over these beachrocks together with large areas that are completely exposed to air. This study was developed between the two strands of beachrocks closer to shore, which are those exposed at low tide (Fig. 1b). Samples were collected in October 2012 during the beginning of the warm dry season in tidal pools with approximately 0.25–0.50 m^3.

2.2. Sampling

Samples were collected during low tide (0.1 m) with a hammer and a chisel. Submerged colonies of *Z. sociatus* and *S. stellata*, were sampled from subtidal areas and tidal pools (n = 5 per species per habitat, samples with approximately 35 and 70 cm^2, respectively). Moreover, colonies of *Z. sociatus* that were exposed to air during low tides were also sampled (n = 5, samples with approximately 35 cm^2). Depending on the tidal range, *Z. sociatus* colonies can remain emerged during 3–5 h in each tidal cycle. No colonies of *S. stellata* were found exposed to air during low tide. Sampled colonies of each were separated from each other by a minimum distance of 15 m. Samples were dark adapted for pulse amplitude modulation (PAM) fluorometry (see section 2.3) and after individually packed in plastic bags, and transported in isothermal boxes, to the laboratory in Universidade Federal da Bahia.

Afterwards, coral samples were stocked for 1 week in a recirculating aquarium system with controlled water temperature (26 ± 1 °C), salinity (35 ppt) and pH (8.0–8.2 units) illuminated from above with full spectra T5 fluorescent lamps (4 × 80 W, 10 000 K) emitting a Photosynthetic Active Radiation (PAR) of 160 ± 20 µmol Quanta.m^{-2}.s^{-1}. This was done to allow the excretion of ingested plankton or particulate matter that can bias the FA quantification. The aquarium system (please refer to Rocha et al. (2015) for more detailed information) operated with synthetic salt water prepared by mixing Red Sea Salt (Red Sea Aquatics Ltd, Israel) with freshwater purified by reverse osmosis (Aqua-win RO-6080, Thailand). During this period a partial water change of 10% of system volume was performed every day with synthetic salt water. After this period *Z. sociatus* polyps were detached from the rock substrate with a scalpel, whereas *S. stellata* polyp tissue was removed with an air pick. After, samples were flash-frozen in liquid nitrogen and lyophilized until FA analyses.

2.3. In vivo Chl fluorescence

Photosynthetic activity of the polyps was monitored by measuring non-intrusively variable chlorophyll fluorescence through PAM fluorometry (Schreiber et al., 1986), using a DIVING-PAM (Walz, Effeltrich, Germany) fluorometer with a DIVING-F fiberoptics (active diameter 5.5 mm, outer diameter 8 mm; length 1.5 m; blue LED 470 nm, DIVING-PAM/B). The fiberoptics was positioned perpendicularly to the surface of the polyps, and all measurements were made at a fixed distance of 1 mm.

Colonies were dark-adapted for 20 min, after which one saturation pulse (0.8 s) was applied to determine the minimum- or dark-level fluorescence (F_o) a parameter expected to correlate with the chlorophyll *a* (Chl *a*) content (Serôdio et al., 2001) and the maximum fluorescence (F_m). F_o and F_m were used to determine the maximum quantum yield of PSII (Schreiber et al., 1986):

$$F_v/F_m = \left(\frac{F_m - F_0}{F_m}\right) \quad (1)$$

The photosynthetic activity of coral samples was assessed by generating rapid light-response curves (RLCs) of relative electron transport rate on PSII (ETR). For this, colonies were exposed to eight incremental 10 s steps of irradiance ranging from 1 to 1149 µmol quanta $m^{-2}s^{-1}$. The protocol for the construction of RLCs was set to match the most commonly used procedures for cnidarians (Ralph et al., 2002). ETR was calculated as:

$$ETR = E\left(\frac{F'_m - F_s}{F'_m}\right) \quad (2)$$

where F_s and F'_m are steady-state and maximum fluorescence emitted by a light-adapted sample (arbitrary units), respectively. RLCs were characterized by fitting the model of Platt et al. (1980), estimating the parameters α (initial slope), ETR_{max} (maximum ETR) and E_k (light-saturation coefficient) as described by Cruz and Serôdio (2008).

2.4. Fatty acids analyses

The determination of the FA profile was based on the experimental procedure already described by Rosa et al. (2007) and Lopes et al. (2016). Each replicate sample (300–330 mg of dry mass) was dissolved in 5 mL of acetyl chloride/methanol (1:19 v/v; Merck), shaken, and heated (80 °C; 1 h). After cooling, 1 mL of Milli-Q distilled water and 2 mL of n-heptane pro analysis (Merck) were added, and samples were shaken and centrifuged (2300 g, 5 min) until phase separation. The

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