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Effects of depth and ultraviolet radiation on coral reef turf algae

Anna Fricke [a,b,c,*], Mirta Teichberg [b], Maggy M. Nugues [d,e,f], Svenja Beilfuss [a], Kai Bischof [a]

[a] University of Bremen, Department of Marine Botany, Leobener Str. NW2, 28359 Bremen, Germany
[b] Leibniz Center for Tropical Marine Ecology (ZMT), Fahrenheitstrasse 6, 28359 Bremen, Germany
[c] EA4228 ECOMERS, Université de Nice-Sophia Antipolis (UNS), Faculté des Sciences, Parc Valrose, 06108 Nice cedex 2, France
[d] CRIOBE-USR 3278, CNRS-EPHE-UPVD, 58 avenue Paul Alduy, 66860 Perpignan Cedex, France
[e] Laboratoire d'Excellence 'CORAIL', France
[f] CARMABI Foundation, Piscaderabaai z/n, P.O. Box 2090, Willemstad, Curaçao, Netherlands Antilles

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ABSTRACT

Despite the increasing dominance of turf algae in coral reefs, few studies have investigated their physiological and ecological responses to changes in abiotic factors. We tested the effects of depth and ultraviolet radiation on turf algae at different levels of successional stages using two experiments. Depth-related differences were found for all turf algal communities, characterized by a higher amount of the cyanobacteria taxon *Dichothrix* and the red filamentous genera *Poly-/Herposiphonia* in the shallow and the appearance of oscillating cyanobacteria in deeper waters. In the first experiment, cross-depth transplantation of 153 days old communities influenced percentage cover, biomass and taxa composition. Downward transplantation lowered overall biomass and abundance of the foraminifera *Sorites,* whereas the crustose green alga *Pringsheimiella* and filamentous cyanobacteria colonized the communities. A nearly reverse pattern was observed in upward transplanted communities. Overall we distinguished between sensitive taxa, like *Oscillatoria*, and taxa able to acclimate to alterations in their environment, like *Pringsheimiella*, *Poly/Herposiphonia* and *Dichothrix*. In the second experiment, algae grown for 285 days at 5 m were exposed together with a set of sterile settlement tiles to three UVR regimes at 2 m for 22 days. UVR had no effect on turf algal communities regardless of successional stage. This study highlights the presence of high light and UV tolerant species. The high UV tolerance of turf communities may confer a competitive advantage over other more sensitive coral reef biota, such as corals. This study demonstrates that turf algae are dynamic communities exhibiting species-specific resistance to environmental changes.

1. Introduction

The degradation of coral reefs is commonly associated with a reduction in coral cover and diversity, coupled with an increase in algal biomass and a shift in algal community composition (Diaz-Pulido et al., 2009; McCook, 1999). On pristine healthy reefs, benthic algae are heavily grazed by herbivores and are dominated by crustose coralline algae, as well as diminutive, mixed assemblages of filamentous algae, juvenile macroalgae and cyanobacteria, typically referred to as turf algae (Steneck and Simon, 2001). As reefs degrade, algal biomass increases. Crustose coralline algae are replaced by dense turf algae and large macrophytes (McCook, 1999). Studies on the factors driving algal communities have typically focused on large macroalgal genera like *Sargassum*, *Lobophora*, *Dictyota* or *Halimeda* (Engelen et al., 2005; Mumby, 2009; Mumby et al., 2005; Nugues and Bak, 2008; Teichberg et al., 2013). Turf algae however have become one of the most abundant benthic functional groups on coral reef communities worldwide (Haas and Wild, 2010; Haas et al., 2010; McCook, 2001; Steneck and Simon, 2001). Yet, they have received less attention.

Turf algae play a crucial role in coral reefs (Birrell et al., 2005; Fricke et al., 2011b; Vermeij et al., 2010). They perform multiple functions due to their rapid turnover of organic matter (Carpenter and Williams, 2007; Copertino et al., 2005; Wanders, 1976), their role as microhabitats for certain invertebrates and microorganisms (Barott et al., 2011; Chapman and Waters, 1992; Hacker and Steneck, 1990; Kramer et al., 2012; Olabarria and Chapman, 2001) and their accumulation potential for sediment and detritus (Purcell and Bellwood, 2001; Wiebe et al., 1975; Williams and Carpenter, 1997). Furthermore, due to the opportunistic life histories of many species, they can rapidly colonize dead or

Abbreviations: EC, early community; LC, late community; P, PAR (400–700 nm) treatment; PA, PAR + UV-A (320–700 nm) treatment; PAB, PAR + UVA + UVB (280–700 nm) treatment; PAR, photosynthetically active radiation (400–700 nm); UV-A, ultraviolet-A radiation, considered in the study as (320–400 nm); UV-B, ultraviolet-B radiation, considered in the study as (280–320 nm); UVR, ultraviolet radiation (280–400 nm); 5 m, community grown at 5 m depth; 15 m, community grown at 15 m depth; 5mT, community grown at 15 m and upward transplanted to 5 m depth at T0; 15mT, community grown at 5 m and downward transplanted to 15 m at T0.

* Corresponding author at: EA4228 ECOMERS, Université de Nice-Sophia Antipolis (UNS), Faculté des Sciences, Parc Valrose, 06108 Nice Cedex 2, France. Tel.: +33 492076846; fax: +33 492076849.
E-mail address: Anna.Fricke@unice.fr (A. Fricke).

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damaged coral colonies and out-compete corals by fast growth rates, potentially reinforcing coral–algal phase shifts (Diaz-Pulido and McCook, 2002, 2004; Titlyanov et al., 2005; Vermeij et al., 2010).

Despite their importance to coral reefs, little is known about the ecology of turf algal communities and their response to changes in abiotic factors. The abundance and distribution of these benthic algae are influenced by a suite of environmental parameters, including light, temperature, nutrients, salinity, sedimentation, depth and wave exposure (Diaz-Pulido et al., 2009; Fricke et al., 2011b, 2011c; Littler et al., 2010; McCook, 1999; Nugues and Roberts, 2003; Vermeij et al., 2010). However, relatively few studies have experimentally tested the direct effect of these physical factors on turf algae (e.g. Copertino et al., 2006; Fricke et al., 2011b; Littler et al., 2010).

As most benthic coral organisms are sessile and photosynthetically active, coral reefs are areas of intense competition for space and light (Benayahu and Loya, 1981; McCook et al., 2001; Titlyanov and Titlyanova, 2008). Light quantity and quality (i.e. spectral composition) are two crucial factors in the usually oligotrophic transparent waters of coral reefs. Short atmospheric path length and the thinness of the stratospheric ozone layer contribute to natural high ultraviolet radiation (UVR) in the tropics (Fleischmann, 1989). As a consequence of climate change, UVR will increase in all latitudes (Karl and Trenberth, 2003; Shindell et al., 1998; Tsay and Stamnes, 1992; Tuck et al., 1992). So far only small changes are reported for tropical latitudes, with an increase of DNA-weighted doses of UVR of 2.8 +/− 2.1% at 15°S and 15°N between 1979 and 1994 (Shick et al., 1996). But even small changes might be significant to tropical marine organisms experiencing the highest irradiances of UVR worldwide (Banaszak and Lesser, 2009).

Light and UVR have important roles in mitigating competition between different reef organisms (Benayahu and Loya, 1981; Jompa and McCook, 2003; Titlyanov et al., 2005). Corals have been shown to be sensitive to intense light and UVR (Gleason et al., 2006; Kuffner, 2001). To date, there are few studies that have investigated UV impacts on tropical turf algal communities (Dobretsov et al., 2005; Wahl et al., 2004), and only one (Santas et al., 1998) dealt with UV effects on Caribbean turf algal communities. This single study showed a decrease in turf algal biomass under artificially enhanced UV-B radiation in a mesocosm experiment in the "Living Coral Reef" mesocosm at the Natural History Museum in Washington. Light effects are often studied over depth gradients. In a recent study, turf algal communities were shown to exhibit large depth related differences in species composition and standing crop, suggesting an important effect of light (Fricke et al., 2011b).

Here we investigated the effect of light quantity related to different water depths and light quality manipulated by different UVR filter treatments on turf algal communities naturally grown in a fringing coral reef at the southwest coast of Curaçao, Caribbean. In a first experiment, turf algae grown over a period of 153 days on ceramic tiles, for examining new recruitment and early succession, at 5 and 15 m depths were cross-depth transplanted (i.e. 5 m tiles were brought to 15 m and vice versa) to test for increasing and decreasing light effects. In a second experiment, turf algal communities grown over a period of 285 days at 5 m depth were exposed together with a set of sterile ceramic tiles to different UVR regimes at 2 m to investigate the effects of increasing light and UVR. The objectives of the study were to determine: 1) whether a change in underwater light regime or UVR can alter the diversity, biomass, and taxa composition of tropical turf algal communities; 2) which taxa were most affected; and 3) whether light and UV effects vary with community age, i.e. successional stage.

2. Materials and methods

2.1. Study location and site

This study was conducted in Curaçao, former Netherlands Antilles (12°01′–12°23′N; 68°44′–69°10′W), an island in the southern Caribbean approximately 70 km north off the coast of Venezuela. The island is bordered by a fringing reef formed by plateaus of Pleistocene coral limestone that form steep cliffs on the seaward site (for further details see Van den Hoek et al., 1972; Wanders, 1976). The experimental site, Buoy 0 (12°07′N, 69°57′), also called Klein Piscadera, is located on the SW coast of the island, 100 m west from the entrance to Piscadera Bay. For a detailed description of the experimental site and of the turf algal communities, see Van den Hoek (1969), Van den Hoek et al. (1972), Van den Hoek et al. (1975) and Van den Hoek et al. (1978).

2.2. Cross-depth transplantation experiment

Twenty-five 9.6 cm × 9.6 cm unglazed ceramic settlement tiles were dispatched at each of two depths (5 and 15 m) in October 2007. The tiles were laid horizontally on oblong grey polyvinyl chloride (PVC) panels (75 × 20 cm) fixed on a frame made of concrete reinforcement bars (100 × 200 cm), anchored on cinder blocks. Each PVC panel carried two- to four-settlement panels fixed by PVC clamps (for further details see Fricke et al., 2011b). In March 2008 (after 153 days of succession), ten tiles from each depth were transplanted either upward to 5 m for the 15 m tiles or downward to 15 m for the 5 m tiles, thus forming four different treatments (Fig. 1**A**): 1) 5 m: community grown at 5 m depth, 2) 15 m: community grown at 15 m depth, 3) *5mT:* community grown at 15 m and upward transplanted to 5 m depth at T0, and 4) *15mT*: community grown at 5 m and downward transplanted to

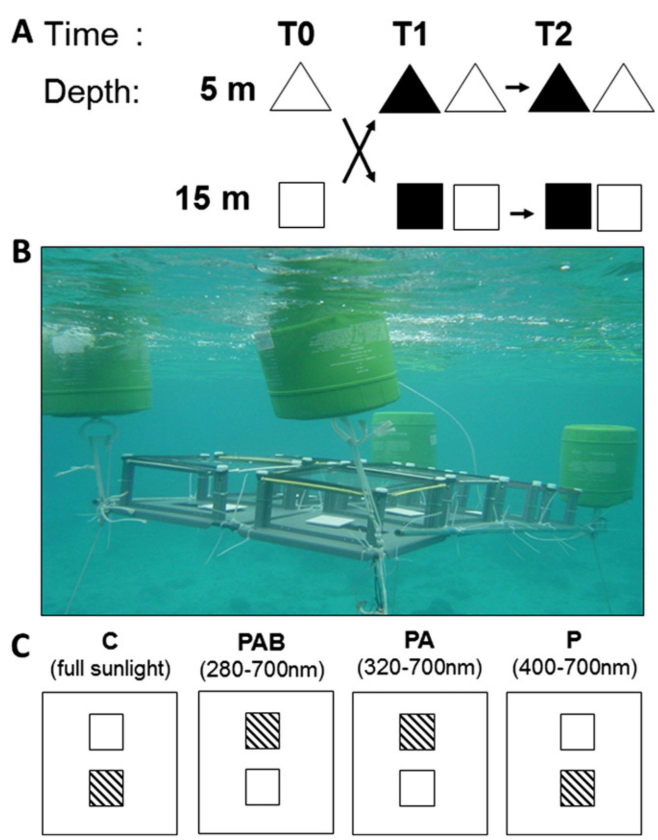

Fig. 1. Experimental setups and designs. A) Cross-transplantation experiment showing the up- or down-transplanted (black-filled) and untransplanted (white-filled) tiles at 5 and 15 m depths at the different times: T0 = experimental start, March 17, 2008, T1 = April 9, 2008, and T2 = May 6, 2008. B) Experimental UV exposure setup at 2 m water depth. C) UV exposure experiment showing the arrangement of experimental units within different treatments of light: C = full sunlight, PAB = PAR + UVA + UVB (280–700 nm), PA = PAR + UVA (320–700 nm) and P = PAR (400–700 nm). The different communities used in the experiment are symbolized by squares: white = early successional community (EC), striped = late successional stages (LC), randomly distributed along the treatments.