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Respostas fisiológicas de *Ulva fasciata* Delile (Ulvales, Chlorophyta): comparação de duas populações de locais termicamente distintos do litoral brasileiro.

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ABSTRACT

In a global warming scenario, an increase temperature is expected in addition to the occurrence and intensity of extreme climate events. One example of extreme events is the marine heat waves, which are a major threat to marine macroalgae. *Ulva fasciata* is a cosmopolitan species that occur in the whole Brazilian coast. This study was performed in two regions of Rio de Janeiro State (RJ) coast. Both regions are tropical, however, Arraial do Cabo/RJ is naturally colder than Niterói/RJ due upwelling phenomenon. This study aimed to: (i) confirm that *U. fasciata* individuals from these two Brazilian coast regions are of the same species; and (ii), physiologically analyze individuals of *U. fasciata* in the field and under in-laboratory controlled temperature experiment. We hypothesized that *U. fasciata* populations grown at thermally different locations would present distinct ecophysiological responses. In the field, it was accessed maximum quantum yield (Fv/Fm) and pigment content, and in laboratory, it was also evaluated growth rate. The in-laboratory controlled experiment comprised three phases: (i) a temperature gradient; (ii) a 5-day heat wave (+ 5 °C); and (iii) a 5-day recovery (- 5 °C). The molecular data allow us to state that the two populations belong to the same species. No differences of the fluorescence-derived factors were observed between individuals from both populations in the field, suggesting acclimation. However, differences were detected along all three experimental phases. The analysis of pigment content field data evidenced that individuals from the population of Niterói (warmer site) had higher concentrations of chlorophyll *a* than individuals from Arraial do Cabo (colder site). However, individuals of population from Niterói when cultured at 21 °C showed the lowest values of pigment. The differences observed suggest ecotypes. In conclusion, as the planet becomes warmer and extreme weather events become more frequent, the likelihood that heat wave to occur is higher. Therefore, *U. fasciata* from Arraial do Cabo showed better physiological responses to the effects of heat wave, what could confer them higher competitiveness ability to overcome thermal stress.

KEY WORDS: Chlorophyll, extreme events, fluorescence, Fv/Fm, global warming, heat wave, PAM, pigments, temperature, upwelling.

RESUMO

Num cenário de aquecimento global, um aumento da temperatura é esperado, assim como a ocorrência e intensidade de eventos climáticos extremos. Um exemplo de evento extremo são as ondas de calor marinhas, que são a principal ameaça a macroalgas marinhas. *Ulva fasciata* é uma espécie cosmopolita que ocorre em toda costa brasileira. Esse estudo foi realizado em duas regiões da costa do Estado do Rio de Janeiro (RJ). Ambas regiões são tropicais, mas Arraial do Cabo/RJ é naturalmente mais fria que Niterói/RJ devido ao fenômeno de ressurgência. Esse estudo objetivou: (i), confirmar que os indivíduos de *U. fasciata* dessas duas localidades da costa brasileira são da mesma espécie; e (ii) analisar fisiologicamente indivíduos de *U. fasciata* em campo e em experimentos de temperatura em condições controladas de laboratório. Nossa hipótese era de que populações de *U. fasciata* procedentes de localidades termicamente diferentes iriam apresentar respostas ecofisiológicas distintas . Em campo, foi acessado o rendimento quântico máximo (Fv/Fm) e o conteúdo pigmentar, e em laboratório, foi também avaliada a taxa de crescimento. O experimento em condições controladas de laboratório consistiu de três fases: (i) gradiente de temperatura; (ii) onda de calor (+5 °C) de 5 dias; e (iii) recuperação (- 4 °C) de 5 dias. Os dados moleculares permitiram afirmar que as duas populações pertencem à mesma espécie. Não foram detectadas diferenças nos fatores derivados da fluorescência entre os indivíduos das duas populações avaliadas em campo, sugerindo aclimatação. Contudo, foram detectadas diferenças ao longo das três fases experimentais. A análise do conteúdo pigmentar em campo evidenciou que os indivíduos da população de Niterói (região mais quente) tinham mais clorofila *a* do que os indivíduos de Arraial do Cabo (região mais fria). No entanto, indivíduos da população de Niterói, quando cultivados em 21 °C, mostraram valores menores de pigmentos. As diferenças observadas sugerem ecótipos. Em conclusão, conforme o planeta se torna mais quente e eventos extremos climáticos se tornam mais frequentes, a probabilidade de ocorrência de ondas de calor é maior. Dessa forma, *U. fasciata* de Arraial do Cabo mostro melhor resposta fisiológica aos efeitos da onda de calor, o que lhe pode conferir maior capacidade de competição para superar estresses térmicos.

PALAVRAS-CHAVE: Aquecimento global, clorofila, eventos extremos, fluorescência, Fv/Fm, onda de calor, PAM, pigmentos, ressurgência, temperatura.

Chapter 1

General introduction

Introdução geral

BACKGROUND

Temperature

Anthropogenic climate change is any change in climate caused by the effect of human activity, such as the increase of greenhouse gases in the atmosphere. The magnitude of anthropogenic global climate change is currently considered irreversible at human time scales (Turra et al. 2013). Global warming is one of the major processes resulting from climate change in the marine environment. The warming has been confirmed by ocean temperature data recorded in recent years (Field et al. 2014, Vergés et al. 2014). A rise of 2-4 °C from the average temperature of the planet, including the oceans is speculated to 2100 (Field et al. 2014, Vergés et al. 2014).

Temperature dramatically influences biological processes, acting from molecules to the whole biota (Turra et al. 2013, Ferreira et al. 2014). Thus, global warming is expected to produce major changes in the marine environment, such as changes in the distribution and abundance of species and also changes in the structure of communities, including local extinctions (Harley et al. 2012, Turra et al. 2013, Ferreira et al. 2014). Hereof, recent studies show that climate change is a major threat to marine macroalgae (Wernberg et al. 2011, Harley et al. 2012, Ferreira et al. 2014).

Marine macroalgae are key components of benthic marine ecosystems and their abundance and diversity have fundamental implications for ecosystem services and life in the coastal zone (Dayton and Tegner 1984). Although some macroalgae species have shown high tolerance, or even have benefited from, the global warming increase in temperature tends to bring drastic changes to benthic communities (Mayer-Pinto et al. 2012). Abiotic ecological processes influence marine macroalgae, however, we still lack knowledge on how distinct temperatures promote population structure, geographic differentiation and acclimation/adaptation (Poloczanska et al. 2013).

The effects of temperature on chemical reactions, molecular structures, and physiology of algae are well documented (see Raven and Geider 1988, Davison et al. 1996), although not so well elucidated. The gaps in knowledge are attributed to the difficulty in isolating the factor temperature from other environmental factors (Oliveira et al. 2013). In most cases, due to effects on chemical and molecular levels, macroalgae are physiologically benefited by the increase in temperature (Davison 1991, Wang et al. 2012). The increase in temperature may show no differences on physiology of macroalgae that have their maximum yield close to their physiological limit, which can wrongly suggest toleration of such a situation (Davison 1991, Pearson and Davison 1996, Necchi 2004, Chaloub et al. 2010).

Species naturally exposed to a wider temperature range between summer and winter (temperate species) generally have a higher thermal tolerance when compared to individuals from environments with lower annual thermal amplitude (tropical species) (Padilla-Gamiño and Carpenter 2007). At a smaller scale, marine species that occur in habitats characterized by large temperature variations (*e.g.*, supra and mesolittoral) tend to live closer to their physiological temperature limits, so they may be more vulnerable to global warming than species less tolerant to temperature rising, such as those present on the infra-littoral (Stillman 2003, Ferreira et al. 2014). Under a background of global warming, organisms living close to their physiological limits are likely to be the first to be affected (*i.e.*, tropical species habiting mesolittoral, *e.g.*, species of the genus *Ulva*).

***Ulva* spp.**

Among marine macroalgae, *Ulva* spp. is probably the most studied genus, due to its cosmopolitan distribution and easy collection (inhabiting the upper mesolittoral) (Joly 1965, Villaça et al. 2010). *Ulva* species have prominent ecological and economic importance such as applications in bioremediation (Neori et al. 1991, Vijayaraghavan and Joshi 2014, Oliveira et al. 2016), production of noxious blooms (Kong et al. 2011, Wang et al. 2011, Guidone and Thornber 2013), study of the bacterial-algae interaction (Provasoli and Pinter 1980), as bioindicators of eutrophication conditions (Kozhenkova et al. 2006), potential source of biofuels (Li et al. 2013), and as a source of food (Mabeau and Fleurence 1993). *Ulva* species also produce bioactive molecules with biomedical applications on cancer and other therapies (Ryu et al. 2013, Wang et al. 2013). Moreover, *Ulva* species are also often used as a model organism in studies of photosystem II fluorescence, photochemistry, algal productivity (Beer et al. 2000, Longstaff et al. 2002, Liu et al. 2012), and temperature (Rautenberger and Bischof 2006, Chaloub et al. 2010, Teichberg et al. 2010).

Temperature is one of the most important factors in the metabolism of *Ulva* spp. (Steffensen 1976), where an increase of 5 °C showed to be harmful and an increase of 10 °C lethal (Steffensen 1976, Fortes and Lüning 1980). Thus, the optimal temperature for *Ulva* growth often coincides with the average temperature of the environment (Steffensen 1976, Fortes and Lüning 1980, Han and Choi 2005). The temperature decrease of 5 °C, albeit harmful, has been shown to stimulate reproduction in *Ulva fasciata* (Mohsen et al. 1972) and *U. pertusa* Kjellman (Han and Choi 2005). No spore release was observed when temperatures dropped by 10 °C (Han and Choi 2005). Mohsen et al. (1972) cultivated individuals of *U. fasciata* from the Mediterranean Sea, in laboratory under a temperature gradient of 15 - 35 °C and observed that: i) maximum growth occurred at 25 °C (same as local average); ii) a temperature drop of 10 °C promoted reduction of mass and total nitrogen; iii) the temperature of 35 °C was harmful; and iv) gamete formation occurred at 15 °C. Another work in which *U. fasciata* from India was cultured on a temperature gradient (15-35 °C), the maximum growth was observed between 25 °C and 30 °C (the local average was 25 °C), and the treatment at 35 °C was harmful (Mantri et al. 2011).

Although widely studied, the genus *Ulva* currently forms a large species complex. Two of the first molecular studies pointed out that Linneaus was right: the genus *Ulva* grouped with the genus *Enteromorpha* (until then distinct), and the two genera were merged (Hayden et al. 2003, Shimada et al. 2003). Shimada et al. (2003) when analyzing specimens from Japan, separated *U. fasciata* and *U. lactuca* Linneaus based on molecular data. Nevertheless, the existence of inconsistencies in the taxonomy of *U. lactuca* around the world was warned: many specimens that were referred to *U. lactuca* were receiving the wrong epithet while specimens belonging to the true *U. lactuca* would be erroneously receiving other epithets (Butler 2007). After this alert, O'Kelly et al. (2010) stated, based on molecular data, that *U. fasciata* from Hawaii (USA) should be referred to as *U. lactuca*. After Butler (2007) and O'Kelly et al. (2010), several articles considered both species (*U. fasciata* and *U. lactuca*) as a single entity (*U. lactuca*). Concomitantly, two papers using on molecular data indicated probable taxonomic errors regarding *U. lactuca* in Australia, (Kraft et al.

2010, Kirkendale et al. 2013). However, in a later review, Comarci et al. (2014) based on Butler (2007) and O'Kelly et al. (2010) suggested that only *U. fasciata* from Hawaii should be referred to *U. lactuca*, and therefore, while new studies are not published, *U. fasciata* and *U. lactuca* should be considered as two distinct and valid species. It is noteworthy that *U. fasciata* and *U. lactuca* can co-occur in the same site in Brazil (Yoneshigue 1985).

Ulva fasciata Delile has isomorphic diplobiont life history (Figure 1.1) and the phases show similar physiological performance (Beach et al. 1995, Wichard 2015). Diploid sporophytes produce haploid zoospores by meiosis. These zoospores, when under favorable conditions, migrate towards the substrate, where will settle and give rise to gametophytes that produce gametes by mitosis. After the fertilization of gametes and formation of the zygote, the sporophyte will be generated, restarting the historic (Beach et al. 1995, Wichard 2015). *U. fasciata* has simple morphology (two thin layers of cells), abundance and global distribution, including the whole Brazilian coast (Joly 1965, Kraft et al. 2010, Villaça et al. 2010). Because of these characteristics, the species can be used as a model in physiological studies that take into account factors such as temperature.

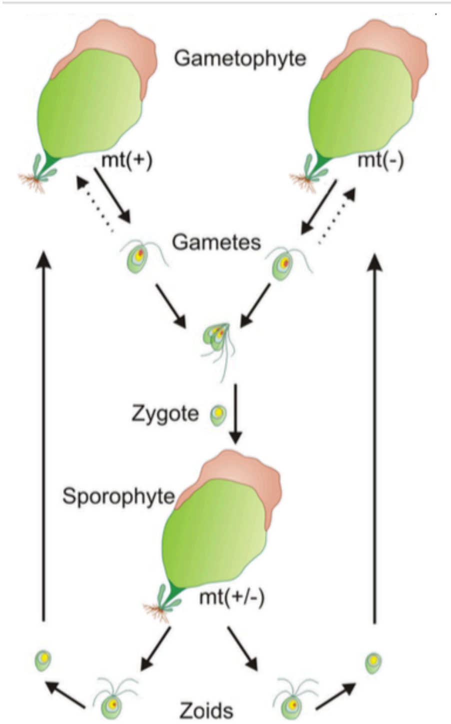

Figure 1.1: The isomorphic diplobiont life history of *Ulva* spp.. The green color of the thalli represents vegetative region; the brownish color represents a fertile region. Dashed arrows indicate rare parthenogenic events. (+) and (−) indicate mating types (mt) (Wichard 2015).

Differences in physiological responses of a species and its populations may result from processes of acclimation or adaptation. However, physiological studies in natural populations alone, do not allow the distinction between these processes, since several environmental variables could mask possible conclusions about the effects of certain abiotic factors (Plastino and Guimarães 2001, Ferreira et al. 2014). Therefore, to study populations in nature together to laboratory-controlled temperature variation is crucial to determine patterns of physiological response by individuals from different populations in response to increase temperature of 4 °C. The data obtained in this study, using *Ulva fasciata* as a model organism, should help better predict the effects of rising temperatures on the future of marine communities under a global warming scenarios.

OBJECTIVES

This study aimed to analyze the effect of temperature on individuals from two tropical populations of *Ulva fasciata* occurring in thermally distinct environments.

Although both regions are located in a tropical environment, one is naturally colder than the other due to a coastal deep-water upwelling phenomenon. By analyzing populations occurring under different thermal conditions, we intend to investigate their local acclimation and adaptation to distinct climate scenarios.

SPECIFIC OBJECTIVES

- Confirm that *Ulva fasciata* individuals from two Brazilian coast regions are the same species;
- Identify *in situ* physiological differences between two populations with different thermal characteristics, based on photosynthetic performance and pigment content;
- Evaluate growth rates, chlorophyll *a* fluorescence and pigment content of specimens of two populations when exposed to a temperature gradient (16 - 31 °C) under laboratorial controlled conditions; and
- Evaluate the effects caused by a sudden temperature increase (simulated heat wave) and the recoverability of specimens from distinct populations, considering growth rates and maximum quantum yield as dependent variables.

HYPOTHESES

- Individuals of *Ulva fasciata* from two populations with distinct thermal characteristics have different photosynthetic performances and pigment content when evaluated in the field;
- Individuals of *Ulva fasciata* from two distinct populations with distinct thermal characteristics respond differently when subjected to the same controlled conditions in the laboratory, characterizing themselves as ecotypes.

GENERAL APPROACHES

Specimens

Ulva fasciata was collected on the upper mesolittoral zone, at two thermally distinct sites on the Rio de Janeiro State (RJ) coast, Brazil (Niterói and Arraial do Cabo). Five transects, three meter long each, were placed perpendicularly to the coastline, three meters away from each other and over the target population. On each transect one healthy individual was collected from four randomly selected points totaling 20 specimens per population. After macroscopic epibionts were removed, thalli were transported to the laboratory in seawater soaked paper inside a thermal box. Voucher specimens from Niterói and Arraial do Cabo populations were deposited in the herbarium of the Institute of Bioscience, University of São Paulo (SPF-57878 and SPF-57877, respectively).

Niterói site (NI)

The NI population refers to the Itacoatiara beach (22°58' S and 43°02' W) and was sampled on 5th February 2015 and then on 8th February 2016. Samples from 2015 were used in laboratory experiments while samples collected in 2016 were sued to obtain field data. Itacoatiara beach has very low anthropogenic impact including the absence of any nearby sewage influence (Carneiro et al. 1987, Teixeira et al. 1987, Catanzaro et al. 2004). However, small levels of localized impact by sunbathers are occasionally observed, mainly during the summer. The sea surface temperature ranges from 21 to 28 °C along the year, averaging 24 °C (Marazzo and Nogueira 1996, Catanzaro et al. 2004). This site is characterized as a non-upwelling region.

Arraial do Cabo site (AC)

The AC population refers to Prainha beach (22°58' S and 42°02' W) and was sampled on 4th February 2015 and on 7th February 2016. Samples collected in 2015 were used in laboratory experiments while collections from 2016 were used to obtain field data. The region is characterized by the occurrence of the southeastern Brazil coastal upwelling phenomenon (Valentin et al. 1987). This upwelling is a result of the combination of northeast winds, the proximity of the continental shelf break, an abrupt change in coastline, and also the Earth rotation itself (Valentin et al. 1987). Low temperatures and high amounts of nutrients characterize the upwelled waters. When the upwelling phenomenon is on its maximum (January-March) sea surface temperatures reach values as low as 15 °C. The maximum sea surface temperature in the AC site is 28 °C and the annual average is 20 °C (Guimaraens and Coutinho 1996, 2000). The algal collection in this site occurred during the austral summer when upwelling is the strongest (Valentin et al. 1987).

Chapter 4

Final considerations

Considerações finais

The main aim of this study was to analyze the effect of temperature on physiological processes of individuals from two tropical populations of *Ulva fasciata* occurring in thermally distinct environments using both field and laboratory controlled experiments. Molecular data confirmed that the two populations belong to the same species, with low genetic differentiation between them. In the laboratory, specimens were cultured under a temperature gradient (16 °C, 21 °C, 26 °C and 31 °C) followed by a heat wave (+ 4 °C) and recovery period (- 4 °C). We analyzed growth rates, fluorescence and pigment content. In the field, we analyzed fluorescence and pigment content from both populations within a 24-hour time difference between assessments. By comparing populations occurring under different thermal conditions, we intended to discuss and generate knowledge about thermal acclimation or adaptation of this species under warming scenarios. Novel data on how different organisms respond to distinct thermal conditions, such as those presented in this study, have received renewed interested due to our need to better understand the relationship among population dynamics, the effect of local (e.g., the upwelling phenomenon) and global processes (*e.g.*, global warming) and also to calibrate ecological models (Guimaraens et al. 2005, Cheung et al. 2009, Harley et al. 2012).

The analysis of field data evidenced more chl *a* in individuals of *U. fasciata* from Niterói (warmer site) than individuals from Arraial do Cabo (colder site), although no differences in fluorescence parameters could be detected between both populations. The differences in chl *a* concentration might be due to differences in turbidity between sites. The upwelled waters have less turbidity (Valentin et al. 1987), and then, there is more solar irradiance available for benthic organisms, when they are submerged, and an inverse correlation between pigment content and irradiance has been observed (Ramus et al. 1976a, 1976b, 1977). However, the water temperature could also be affecting the chl *a* concentration, since low temperature can be damage to *Ulva* species, promoting a reduction on pigment content (Mohsen et al. 1972, Mantri et al. 2011).

The similar values of fluorescence-derived parameters contents suggest that these two populations were well acclimated to field conditions at the moment of measurements. We speculate that both populations being located at similar latitude, thus, under similar solar irradiance, could explain this pattern. In macroalgae exposed to extreme abiotic fluctuations and conditions, especially those occurring in mesolittoral in tropical areas, the photoperiod is determinant to photosynthesis performance (Henley and Ramus 1989, Plastino and Oliveira 2002). The comparison between our data to the literature suggests that the putative differences between both collecting sites are not enough to create detect disparity in photosynthetic performances. *Ulva* spp. was described to adjust its chlorophyll content to irradiance variations linked to location and time of the year (Merceron et al. 2007). Although we have examined only once, our collection occurred when the upwelling phenomenon is described to be on its maximum (January – March) (Valentin et al. 1987). Because of that, we expected physiological differences to be more pronounced between populations.

Although no differences could be detected for fluorescence field data, there were differences on maximum quantum yield between individuals from NI and AC populations of *U. fasciata* considering specimens in all three laboratorial experimental phases: the temperature gradient, the heat wave simulation, and the recovery period. The fluorescence data for laboratory experiments were opposite to what we expected for heat wave and recovery results. Results strongly suggested that individuals from AC have higher competitive ability to overcome thermal stress (warming) than individuals from NI, which can have implications for the distribution and conservation of different genetic stocks in a warmer future. Furthermore, we expected that individuals from NI would obtain higher photosynthetic performance at higher temperatures, considering that the NI population experiences higher temperatures along the year due to the absence of the upwelling phenomenon and, also because the optimal temperature of *Ulva* often coincides with the environment average (Steffensen 1976, Fortes and Lüning 1980, Han and Choi 2005). Indeed, maximum growth rates for individuals from Niterói were observed at 26 °C (2 °C higher than the 24 °C annual average), however, for individuals from AC, the maximum growth rates occurred at 26 °C and 31 °C (6 °C and 11 °C higher than the 20°C annual average, respectively).

During heat wave, however, maximum growth rates of *U. fasciata* were observed for individuals from AC (at 30 °C), while the temperature of 35 °C did not promote growth in both populations. In addition, the maximum quantum yield data revealed negative physiological effects on *U. fasciata* during the heat wave simulation being more pronounced during the night than during the day. The period of the night promoted a sharp drop in Fv/Fm values, which was not recovered when returned to light. This pattern was even more pronounced in individuals previously acclimated to higher temperatures. Similar results have been previously observed for terrestrial alpine shrubs (Buchner et al. 2013), therefore, the ameliorating effects to heat stress could be phylogenetically widespread within the autotrophs. However, due to the lack of studies supporting this affirmation, generalizations should be considered with care.

Decrease in temperature induced *U. fasciata* gametes production in both NI and AC populations in laboratory experiments. We suppose all the individuals used in experiments were gametophytes due to the swimming orientation of the propagules and the lack of plantlets growing in vials' walls. Lower temperature is considered an environmental stress for tropical species, thus formation of spores and gamete release can be considered an adaptation to avoid unfavorable environmental conditions such as the decrease in temperature for tropical species, in other words, an escape strategy.

In conclusion, we could not detect drastic physiological differences when characterizing individuals of *U. fasciata* from two thermally distinct populations of Rio de Janeiro State coast. However, when individuals from these two populations were brought to laboratory and cultivated under similar conditions, physiological differences could be detected. As the planet becomes warmer and extreme weather events become more frequent (Field et al. 2014) the likelihood that 1 - 4 °C warmer sites will experience 4 - 5 °C heat waves are more likely (Smale and Wernberg 2013, Field et al. 2014, Hobday et al. 2016a). *U. fasciata* from AC showed better physiological responses to the effects of heat wave. In a global warming scenario, gradual changes in the spatial distribution of ecotypes of *U. fasciata* along the two collecting sites is likely to occur due to the observed differences in thermal responses between the two populations. Further studies should help better understand phenotypic and genotypic components of these responses of *U. fasciata* and also improve our knowledge on physiological ecology of organisms inhabiting regions impacted by upwelling waters.

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