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Research Article

The *Ulva* spp. Conundrum: What Does the Ecophysiology of Southern Atlantic Specimens Tell Us?

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Species of the genus *Ulva* are common in anthropogenically disturbed areas and have been reported as the cause of green tides in many areas of the world. In addition, they rank among the main marine groups used in a wide range of commercial applications. By displaying few distinctive morphological characters, some taxonomical identifications are difficult and the genus is under a conundrum. Our aims were to provide ecophysiological information about three *Ulva* species in response to abiotic factors and to evaluate the proposal of ecophysiological information and the chlorophyll-*a* fluorescence technique as auxiliary tool to resolve the long-standing taxonomic confusion. We hypothesize that three cooccurring specimens (*U. fasciata* Delile, *U. lactuca* Linnaeus, and *U. rigida* C. Agardh) have different ecophysiological responses (as measured by the effective quantum yield of photosystem II by pulse amplitude modulated fluorometers) under manipulated conditions of temperature and nutrient concentration. *Ulva lactuca* and *U. rigida* showed different photosynthetic efficiencies related to temperature, whereas no difference was recorded for *U. fasciata* individuals. These results provide a reasonable explanation for the variability in spatial and temporal abundance of these species of *Ulva* on rocky shores. We proposed the use of ecophysiological information by chlorophyll-*a* fluorescence as an auxiliary tool to corroborate the taxonomic distinction of *Ulva* species. We reinforce the statement of *U. fasciata* and *U. lactuca* as distinct valid species.

1. Introduction

The genus *Ulva* (Chlorophyta) comprises cosmopolitan macroalgae that inhabit a gradient from freshwater to fully saline shallow environments [1]. Species of this genus rank among the first species to be established in disturbed environments because of their morpho-physiological features, that allow tolerance to wide range of environmental conditions [2–4]. Some species of *Ulva* have been emphasized due to reports as the cause of green tides in many parts of the world [5]. Additionally, numerous studies have also demonstrated functions in bioremediation of eutrophic environments and uses of their biomass and carbohydrate content in the pharmaceutical, food, and energy chain [6–8].

Ongoing advances in molecular biology have driven taxonomic revisions, and morphological features have lost credibility as the primary species delimitation criterion for many groups (see [9] for algae). *Ulva* is one of the genera involved in a taxonomic conundrum that entangles morphological or molecular data for species identification, mainly involving distinction around *U. lactuca* and *U. fasciata* (see [1, 10–13]). In spite of the undeniable contribution of molecular methods to taxonomy (see [14–17]), there is no easy way to determine the accurate match between the GenBank sequences and the

morphological characterization of most studies, which has led to uncertainty and sometimes to misinterpretation (see [1, 11]).

In the latter context, physiological markers that are associated with the photosynthesis process may be especially helpful. Photosynthetic organisms adjust the operation of their photosynthetic apparatus to optimize or preserve metabolism under stress, which can be detected by chlorophyll-*a* fluorescence variation [18, 19]. In this case, the evaluation of the effective quantum yield of PSII by pulse amplitude modulated (PAM) fluorometers has been proposed as an attractive measure of the ecophysiological condition [20–24]. This technique is notable for performing a nonintrusive real-time analysis under both laboratory and field conditions [25] and has been applied for establishing the differences among morphotypes of macroalgae [26].

Under this background, the aim of this study was to provide comparative ecophysiological information about three cooccurring species of *Ulva* in the Southwestern Atlantic (*Ulva rigida* C. Agardh, *Ulva lactuca* Linnaeus, and *Ulva fasciata* Delile) that were morphologically identified. We assessed the effect of temperature and nutrient variation on the photosynthetic efficiency (by chlorophyll-*a* fluorescence measurements) of the three species. The general tested hypothesis was that species would have different responses to both of the tested factors. We subsequently expect to provide useful information for using PAM fluorometry of *Ulva* as a reliable tool for ecophysiological assessment and for the taxonomic debate about *Ulva*.

2. Material and Methods

2.1. Sampling. The three species of *Ulva* (*U. fasciata*, *U. lactuca*, and *U. rigida*) were collected during summer (January 2010) in the intertidal zone at Prainha Beach (22° 57′S, 042° 01′W), Rio de Janeiro, Brazil. Immediately, the epibionts were removed, and the macroalgae were kept in cool boxes with local seawater (~30 μM NO_3, 3 μM PO_4, 19°C, and 35 PSU) filtered through 10-μm mesh filters.

2.2. The Species. The morphological taxonomy of the three studied species (*U. fasciata*, *U. lactuca*, and *U. rigida*) was based on botanical descriptions and inventories that considered in-depth confrontation among the species descriptions and the Southwestern Atlantic specimens [27–30]. Individuals were prepared as herbarium vouchers and deposited in the herbarium of the Universidade Federal do Rio de Janeiro/UFRJ (under the accession numbers RFA 42441; 42442; 42443).

2.3. Experimental Design. All the individuals were maintained in Erlenmeyer flasks in a proportion of 1 g of fresh mass L^{-1} pasteurized oligotrophic ocean water with added trace nutrients (<1 μM NH_4; <1 μM NO_3; <2 μM NO_2; <1 μM PO_4), at 20°C and 200 μmol photons m^{-2} s^{-1} (PAR, photosynthetically active radiation) for 15 days. This phase was established to set all the macroalgae to the same nutritional and physiological state before the manipulative experiment. This PAR was chosen because it is an intermediate value in relation to the saturation parameter that is found in the P-I curves (100–400 photons m^{-2} s^{-1}).

After the nutrient deprivation period, six treatments were applied using combinations of two temperatures and three concentrations of nutrients, with 5 replicates per treatment. The experiment *per se* lasted 10 hours. The factor "Temperature" was represented by 20°C and 30°C, and the factor "Nutrient" was represented by different additions of $NaNO_3^-$ and $Na_2HPO_4.12H_2O$ of Von Stosch's enriched seawater (VSE; 500 μM NO_3^- and 30 μM PO_4^-) [31]. The experimental setup values of temperatures are related to the temperature at the upper intertidal fringe at the sampling site, which ranges between 18°C (high tide) and 32°C (low tide) [29], and the nutrient concentrations were set as 0.1 VSE, 0.2 VSE, and 0.5 VSE. These concentrations refer to a gradient of nutrient concentrations that were recorded in Southwestern Atlantic [32, 33]. The treatment set as 0.1 VSE refers to natural eutrophicated waters (upwelling events at collecting site, Arraial do Cabo, Rio de Janeiro) [32], whereas 0.2 VSE and 0.5 VSE refer to the range of nutrient concentrations that were recorded in the human-disturbed Guanabara Bay, Rio de Janeiro [33].

2.4. Fluorescence Measurements. The photosynthetic efficiency of the three species of *Ulva* in every combination of temperature and nutrient concentration was characterized by chlorophyll-*a* fluorescence measurements using a submersible diving-PAM® fluorometer (Walz, Effeltrich, Germany). The measurements consisted of recording the effective quantum yield of PSII, which was calculated as $Y = (F'_m - F_t)/F'_m$, where F'_m is the maximum fluorescence in the light (obtained by a saturating actinic light pulse – 8900 μmol photons m^{-2} s^{-1}; 0.8 s) and F_t is the steady-state of fluorescence in the light [34, 35]. Considering the possibility of physiological differences along the thallus [36], the fluorescence was measured in a similar region of the thallus in each individual.

2.5. Data Analyses. To determine the effects, if any, of temperature and nutrients on these three species of *Ulva*, based on the Y measurements, a four-way analysis of variance was performed. The analysis included the (i) species (orthogonal, fixed, three levels); (ii) nutrients (orthogonal, fixed, three levels); (iii) temperature (orthogonal, fixed, two levels); and (iv) plot: Erlenmeyer flasks (random and nested in the interaction of factors 1 and 2, two levels). The SNK *post hoc* test was used to examine the nature of the differences that were detected with ANOVA (0.05 significance level). Statistical analyses were performed using GMAV5 for Windows.

3. Results

Differences in the Y were found for the interaction of species and temperature (Table 1). For both *U. lactuca* and *U. rigida*, the individuals that were incubated at 30°C showed a higher photosynthetic efficiency than did those incubated at 20°C, whereas no difference in photosynthetic efficiency was

Table 1: Four-way analyses of variance of the photosynthetic capacities (based on the effective quantum yield of the PSII measurements) of three species of *Ulva* (orthogonal, fixed) that were incubated under different nutrient (orthogonal, fixed, three levels) and temperature (orthogonal, fixed, two levels) conditions. Plot: Erlenmeyer flasks where individuals were incubated (random and nested in the interaction of factors 1 and 2, two levels). SS is sums of squares; DF is degrees freedom; MS is mean of square and P-value *<0.05*.

Source	SS	DF	MS	F	P
Species (Sp)	0.0003	2	0.0001	0.18	0.84
Temperature (Te)	0.0129	1	0.0129	9.40	0.02
Nutrient (Nu)	0.0018	2	0.0009	0.64	0.56
Plot (Te×Nu)	0.0082	6	0.0014	2.29	0.04*
Sp×Te	0.0072	2	0.0036	4.67	0.03*
Sp×Nu	0.0082	4	0.0020	2.64	0.09
Sp×Plot (Te×Nu)	0.0093	12	0.0008	1.29	0.23
Te×Nu	0.0032	2	0.0016	1.15	0.38
Sp×Te×Nu	0.0081	4	0.0020	2.63	0.09
residual	0.0861	144	0.0006		
total	0.1452	179			

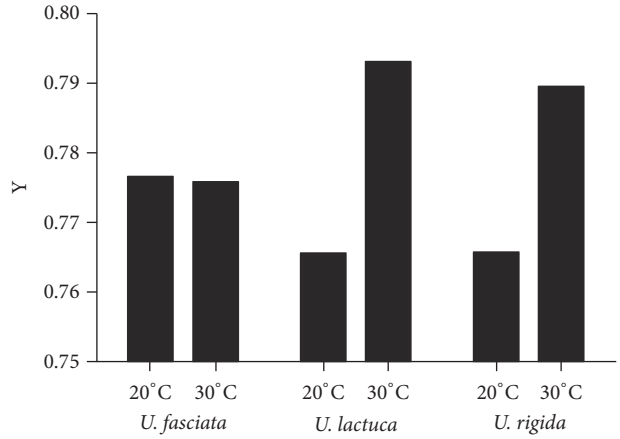

Figure 1: Photosynthetic capacities of the three species of *Ulva* under two temperature conditions (based on the effective quantum yield of PSII measurements). Data from different nutrient conditions and plots (Erlenmeyer flasks where individuals were incubated) were pooled. n=30. Standard deviation values are not shown because of scale-bar limitation (left to right: 0.021, 0.023, 0.032, 0.019, 0.026, and 0.035).

recorded for *U. fasciata* individuals (Figure 1). Even when an ANOVA was performed for only *U. fasciata*, no difference in photosynthetic efficiency was found.

4. Discussion

There are currently 403 species of *Ulva* in the literature, of which 131 have been flagged as accepted [37]. Even with the development of new tools for taxonomic precision, the identification in the practice may differ from author to author. In this sense, fast and real-time physiological assessment can be helpful to distinguish species and morphotypes of macroalgae.

In this study, two of the three species of *Ulva* (*U. lactuca* and *U. rigida*) showed differences in the Y as related to temperature. Although these species present large morphological distinctions, both showed a higher photosynthetic efficiency at the highest experimental temperature (30°C), denoting the sensitivity of these species to this temperature value. The physiological differences can be linked to the hydrodynamic environment, once they are under submergence for long periods of time. In this case, this effect of temperature on photosynthetic metabolism is well known for macroalgae [38, 39], and several positive effects on chemical reactions and molecular structures have been reported due to the changes in protein compounds and enzymatic activities [40, 41].

In contrast, *Ulva fasciata* did not show differences in the photosynthetic efficiency related to the temperature variation. Specifically, this is the most abundant of the three species in the sampling place, dominant at the upper limit of the intertidal zone, as also reported by Guimarães and Coutinho [42]. Its photosynthetic apparatus tolerates changes of at least 10°C with no loss of efficiency, as corroborated by our study, which can confer an ecological advantage and seems to support its relative spatial and temporal dominance on rocky shores [38, 43].

Despite their unequal abundances, the three species are usually recorded throughout the year, although this cooccurrence is most evident during the summer [29]. The summer period is characterized by high irradiance (i.e., high temperatures on rocky shores), cold waters, and a high input of nutrients from the upwelling and rainfall runoff [44, 45]. Taken together, these results suggest that the ecophysiological differences that were pointed in this study provide a reasonable explanation for the variability in the spatial and temporal abundance of these species of *Ulva* on rocky shores.

It is important to highlight that despite the absence of nutrient effects on the photosynthetic response of *Ulva* species in our study, we are not fully disregarding the importance of this factor as a driver of the spatial and temporal variability of *Ulva* species on rocky shores. Nutrient enrichment favors ephemeral foliose macroalgae (see [3]) by increasing the photosynthetic response [46]. In fact, the

genus *Ulva* is recognized by the affinity for nitrogen [47–49], and differences in photosynthetic efficiency have been predicted (if not among species, at least among nutrient concentrations), in contrast to the present results. Considering the proper experimental design and applied manipulative measurements, we attribute these findings to a saturated rate of nutrient availability: light supply in our experiment.

One of the most vexing taxonomic concerns refers to the *U. fasciata* and *U. lactuca* species, which cooccur with *U. rigida*. Regarding *U. fasciata* and *U. lactuca*, there is a long-standing taxonomic debate (see [1, 10–13, 50, 51]). Meanwhile, several studies confirm *U. rigida* as a consistent valid species [52–54]. We corroborate the previous claim of Hiraoka et al. [10], Shimada et al. [50], and Kirkendale et al. [1]. Our study considered ecophysiological and morphological (based on [28–30]) data for specimens from Southwestern Atlantic. Therefore, we propose the use of ecophysiology as a complementary tool for taxonomic distinction among macroalgae based on chlorophyll-*a* fluorescence to enlighten this debate with additional taxonomic evidence. Similar morphophysiological studies, based on classic morphometry and photosynthetic responses (maximum electron transport rates, ETRmax), suggested different species of *Durvillaea* (Phaeophyceae) for two morphotypes cooccurring in southern Chile [26].

However, how this ecophysiology method would respond on other marine macroalgal taxa remains to be tested. We understand that it is hard to apply the methodology to identification of freshly collected specimens or species in the field without further investigation, either by morphology or molecular methods. We also recognize the undeniable contribution of morphology and molecular methods to taxonomy, and our proposal aims to enlighten the debate with additional evidence.

Data Availability

The data used to support the findings of this study are available from the corresponding author upon request.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

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