

Short communication

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Shading by invasive seaweeds reduces photosynthesis of maerl from the Ría de Vigo (NW Spain)

<https://doi.org/10.1515/bot-2018-0004>

Received 24 January, 2018; accepted 4 July, 2018

Abstract: The overgrowth and shading of several alien species along the European Atlantic coast are expected to reduce photosynthesis of maerl, decreasing its growth and fitness. In this work, three shade levels (0, 20 and 50%) were set up under laboratory conditions to simulate different competitive scenarios potentially affecting maerl beds. Live individuals of *Sargassum muticum* and *Undaria pinnatifida* were placed over maerl cultures, and the effects of shading were assessed by chlorophyll *a* fluorescence using a pulse-modulated fluorescence monitoring system. Photosystem II efficiency was measured as the ratio of variable to maximal fluorescence (F_v/F_m) as a proxy for the stress experienced by maerl. According to our data, irradiance reduction results in a small, yet significant, impact on the PSII efficiency of maerl, which could have fitness consequences.

Keywords: biological invasion; fluorescence; light stress; maerl beds.

Maerl beds are ecosystems of significant ecological value owing to their high species diversity (Olabarria et al. 1997). Moreover, these beds play a key role in some life cycle stages of certain benthic and pelagic species (Teichert 2014). These valuable ecosystems are now threatened by the introduction of invasive alien seaweed species. Among other hazards, alien seaweeds may limit the available light

reaching the maerl, and therefore reduce photosynthetic activity (Villas-Bôas et al. 2014).

Both the global distribution of maerl beds, ranging from mid to high latitudes, (Peña and Bárbara 2009, Teichert 2014), and their composition, particularly on the European Atlantic coast (e.g. Mitchell and Collins 2004, Peña and Bárbara 2007), have been extensively documented. Maerl is composed mainly of unattached coralline algae, whose species have been defined as ecosystem engineers by several authors because of their ability to modify or maintain habitats (e.g. Yabur-Pacheco and Riosmena-Rodríguez 2007, Teichert 2014). On the Atlantic Iberian coast, they are usually associated with a large number of non-coraline crustose algae such as *Contarinia peyssonneliaeformis* Zanardini, *Hildenbrandia rubra* (Sommerfelt) Meneghini and *Cruoria cruoriaeformis* (Crouan et Crouan) Denizot (Peña and Bárbara 2013). Biodiversity and species richness are higher in maerl beds than in other subtidal communities in the same geographical range (Olabarria et al. 1997).

Many red algae have adapted to low light habitats since their minimum photosynthetic saturation irradiance is lower than that of shallow-living species, making them naturally adapted to subtidal situations (Martin et al. 2005). Because they possess accessory light-harvesting complexes, they can adapt not only to low irradiance but also to the variability in light components at different depths, such as red, far-red, green, blue and ultraviolet radiation, i.e. light quality (Talarico and Maranzana 2000). Nonetheless, the ability of maerl species to perform photosynthesis depends upon a variety of conditions, such as stress induced by abiotic and biotic environmental factors (Riul et al. 2008). Irradiance availability also varies with latitude, so maerl populations are adapted to precise light conditions (Kühl et al. 2001). Consequently, stress symptoms may arise when irradiance or quality changes due to environmental disturbances (Villas-Bôas et al. 2014).

Sargassum muticum (Yendo) Fensholt, *Undaria pinnatifida* (Harvey) Suringar and other introduced algae are spreading quickly along the NW Iberian coast, and causing a decrease in the light reaching maerl beds as a

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result of shading (Peña et al. 2014). Additionally, shading has been proven to cause a negative physiological response in maerl species by imposing stress on the algae (Wilson et al. 2004, Villas-Bôas et al. 2014). Such stress can be measured by means of non-invasive techniques such as the chlorophyll fluorescence approach (Maxwell and Johnson 2000).

The aim of this work is to study the effect of light reduction caused by the overgrowth of invasive macroalgal species on the photosynthetic efficiency of maerl. A mesocosm experiment simulating the natural conditions of maerl beds was set up using alien invaders as screens to produce controlled shading levels.

Maerl samples were collected from the subtidal zone of Cabo de Mar- Bouzas (N42°13'38.6", W8°46'41.6") in the Ría de Vigo, NW Spain at depths of 11 m on 20 May 2016. Samples were obtained using a 0.1-m² Van Veen grab. *Lithothamnion corallioides* (Crouan et Crouan) Crouan et Crouan and *Phymatolithon calcareum* (Pallas) Adey et McKibbin, were the maerl species collected. Live thalli were sorted and kept in tissue culture trays in a tank filled with filtered seawater during the acclimation and experimental period.

Samples were acclimated in nine 6-dish trays for 1 week under natural light with an average irradiance at noon of 17 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$. This value was measured using a Digital Quantum Scalar Laboratory Radiometer (QSL-2100) during the 7 days of the acclimation period. A similar irradiance value was found during daylight hours at the depth from which the maerl sample was extracted (Gil-Moliner 2015). Over the entire experimental period, maerl thalli were held in running seawater at 16°C at the ECIMAT Marine Station (University of Vigo), where the experiment was performed. Seawater was obtained using an intake located in the Ría de Vigo, having a salinity of about 33.

After acclimation, a mesocosm experiment was performed in the same tank during a natural light photoperiod. Three different irradiance treatments were set up to simulate the values reported by Peña and Bárbara (2007) and Stæhr et al. (2000) from maerl beds subjected to a partial light block due to the overgrowth of invasive seaweeds, using 18 sample dishes each. Wire structures (16×12×7 and 16×12×5.5 cm) were used to hold invasive seaweed specimens (*Sargassum muticum* and *Undaria pinnatifida*) over each plate forming a screen to reduce the incoming light. Screen densities for each treatment were set using a QSL-2100, by measuring PAR until the desired light-reduction percentage was obtained: 0, 20 and 50% of the natural light irradiance of 17 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$.

Chlorophyll fluorescence of maerl thalli was measured after 1 week of treatment as a proxy for the stress

response (Villas-Bôas et al. 2014). No other factors or environmental variables that might affect stress were considered since all samples were held under identical experimental conditions.

Chlorophyll fluorescence was measured using a field portable pulse-modulated fluorescence monitoring system (FMS; Hansatech, Norfolk, England). Shading treatments began on 30 May and measurement zero was performed 24 h after acclimation, since maerl's physiological response to experimental conditions has been reported to occur after 12 h (Wilson et al. 2004). The parameters of chlorophyll fluorescence: initial fluorescence (F_0), maximum fluorescence (F_m), variable fluorescence F_v ($F_m - F_0$), were measured. A dark-adaptation period of 30 min was applied before each fluorescence measurement. Our experiment comprised six measurements of algal F_v/F_m values on the following dates: 31 May and 6, 10, 14, 20, 24 June 2016. All samples were kept underwater during measurements to avoid desiccation stress.

Data were compared with a repeated-measures and split-plot design ANOVA. All data are reported as the mean \pm standard deviation (SD) unless otherwise stated, and results with a significance value of $\alpha \leq 0.05$ were considered to be statistically significant. Statistical analyses were carried out using the IBM SPSS Statistics Software v.20.

A total of 324 fluorescence measurements were taken, and F_v/F_m ratio values ranged from a minimum of 0.496 with a 50% shade treatment to a maximum of 0.649 in the Control (0%) treatment. Average F_v/F_m values per group were 0.585 ± 0.017 for the Control treatment, 0.575 ± 0.023 for the 20% shade treatment and 0.565 ± 0.019 for the 50% shade treatment.

There were significant differences in F_v/F_m ratios among light treatments ($F = 27.67$, $p < 0.001$). Tukey's *post-hoc* comparison reported that both 20% and 50% light treatments differed from the Control group ($p = 0.002$ and $p < 0.001$, respectively), as well as from each other ($p = 0.01$).

Time was also found to be a significant factor since the analysis revealed differences between measurement dates ($F = 4.988$, $p < 0.001$). The highest variability was found on 6 June. On 14 June, a drop in F_v/F_m values was recorded in all groups, which matched the lowest irradiance value recorded throughout the experiment (Figure 1). After this low-irradiance episode, fluorescence values rose again, exhibiting values similar to those recorded before the drop. *Post-hoc* testing revealed that only one sampling date (14 June) was significantly different from the others ($p < 0.05$), showing a trend that was similar

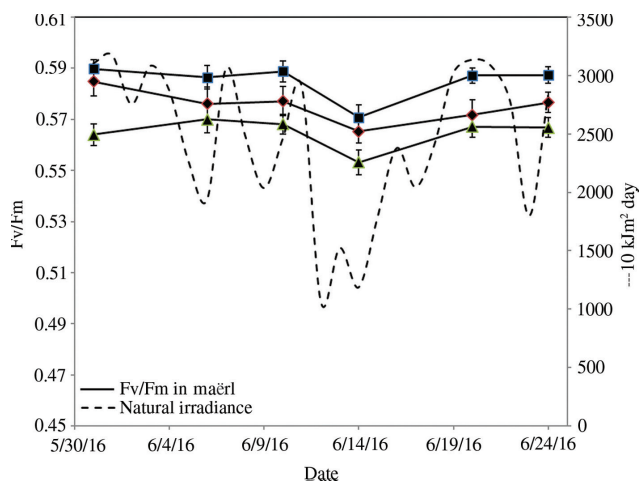


Figure 1: Effect of different irradiance conditions on F_v/F_m in maerl (left axis); symbols represent mean values \pm SE ($n=18$) (squares: control, diamonds: 20% light attenuation, triangles: 50% light attenuation).

Natural irradiance (right axis) recorded during the experimental period is shown as a dashed line. X-axis shows the dates over which the experiment was conducted.

to the marked decrease in natural irradiance at the time (Figure 1) due to overcast conditions, according to Meteogalicia (www.meteogalicia.es), the official Galician Meteorological Service.

Between-factor interaction (“shade-level” \times “time”) was not significant ($F=0.451$, $p=0.920$) implying that all light treatments had a similar effect at different times.

According to our results, the photosynthetic efficiency (F_v/F_m) of maerl decreased concomitantly with the increase in the degree of shading for all the experimental treatments. In their studies on other maerl species, Villas-Bôas et al. (2014) concluded that stress conditions are met when F_v/F_m values are below 0.5 and that coral-line algae are healthy when this value is above 0.5. Wilson et al. (2004) stated that variability among F_v/F_m values increases with stress. Our results did not show any significant differences between the variability of the different light treatments. This apparent inconsistency may be attributed to the fact that their F_v/F_m values of around 0.4 were consistently lower than ours due to the much harsher conditions (i.e. complete darkness) imposed on the algae before measurement.

However, although the values obtained in the present study were never low enough to be considered a stress condition according to the criterion of Villas-Bôas et al. (2014), our results on maerl in NW Iberia showed a significant decline in the photosynthetic efficiency of the algae in response to shading. As for the variation with time, the low results on 14 June were in response to the lowest

natural irradiance recorded during the experiment. Irradiance values on 20 June returned to normal, and the F_v/F_m values recovered accordingly. This ability to recover from light disturbances is consistent with the resilience and stability of maerl (de Ruiter et al. 1995).

The literature suggests that red algae are both “light-intensity and light-quality adapters” (*sensu* Talarico and Maranzana 2000). These authors emphasise the fact that genes encoding phycobilisome subunits and their assembly are dependent on green and red light pulses. In particular, the modulation of the ratios between spectral components would seem to act as photomorphogenetic “signals” regulating algal metabolism and growth. Therefore, if low radiation conditions caused by extreme overgrowth of invasive macroalgae are imposed over long time periods, the metabolism and growth of maerl may be jeopardized. In fact, a single day (14 June) of extremely low radiation caused a sharp decrease in the photosynthetic efficiency values (F_v/F_m) of maerl under all of the shading conditions. Thus, light competition and continuous shading caused by the overgrowth of invasive algae could also affect maerl pigment composition and subsequently, the photosynthetic efficiency of photosystem II. This study shows that shading may have small but significant impacts on the photosynthetic efficiency of maerl beds. Our results point to a decrease in photosynthesis in response to a 20% or 50% light reduction as compared with that of the control group. It is possible that shading levels higher than 50%, however slight, may have a harmful effect on the organisms, or that maerl may be able to endure stress levels close to full shade, but these are questions that must be addressed in future research. Further experiments including a wider set of long duration light treatments are needed to determine the minimum light requirements of maerl. Also, the precise light interception caused by algal invaders on maerl beds in Northwest Spain is yet to be determined, as are the long term effects of the overgrowth of these species under natural conditions.

Acknowledgements: This research has been developed in the frame of the Agri-Food Research and Transfer Centre of the Water Campus (CITACA) at the University of Vigo (Spain), supported by the Galician Government. The authors thank Carlos Villaverde for statistical assistance. We also thank the Biological Oceanography group at the University of Vigo (ECIMAT), particularly Antonio Fuentes, for their logistic support and C. Teed for her English improvements of the text. We appreciate the valuable review of the manuscript by two anonymous reviewers and

by the editor, Prof. Matthew J. Dring, which has helped to substantially improve the final version.

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Bionotes



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Graphical abstract

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<https://doi.org/10.1515/bot-2018-0004>
Botanica Marina 2018; x(x): xxx–xxx

Short communication: The
photosynthetic efficiency
(F_v/F_m) of maerl decreased
concomitantly with the
decrease in natural irradiance
and with the increase of
shading level imposed by
invasive algal species.

Keywords: biological invasion;
fluorescence; light stress; maerl
beds.

