



Towards a better understanding of the effects of self-shading on *Fucus serratus* populations

Cédric Hubas based on reviews by *Gwenael Abril, Francesca Rossi and 1 anonymous reviewer*

A recommendation of:

Dynamics of *Fucus serratus* thallus photosynthesis and community primary production during emersion across seasons: canopy dampening and biochemical acclimation

Aline Migné, Gwendoline Duong, Dominique Menu, Dominique Davoult & François Gévaert (2021) hal-03079617, ver. 4 peer-reviewed and recommended by Peer Community in Ecology <https://hal.archives-ouvertes.fr/hal-03079617>

Open Access

Submitted: 05 January 2021, Recommended: 25 June 2021

Published: 02 August 2021

Copyright: This work is licensed under the Creative Commons Attribution-NoDerivatives 4.0 International License. To view a copy of this license, visit <http://creativecommons.org/licenses/by-nd/4.0/>

Cite this recommendation as:

Cédric Hubas (2021) Towards a better understanding of the effects of self-shading on *Fucus serratus* populations. *Peer Community in Ecology*, 100086. [10.24072/pci.ecology.100086](https://doi.org/10.24072/pci.ecology.100086)

Recommendation

The importance of the vertical structure of vegetation cover for the functioning, management and conservation of ecosystems has received particular attention from ecologists in the last decades. Canopy architecture has many implications for light extinction coefficient, temperature variation reduction, self-shading which are all key parameters for the structuring and functioning of different ecosystems such as grasslands [1,2], forests [3,4], phytoplankton communities [5, 6], macroalgal populations [7] and even underwater animal forests such as octocoral communities [8].

This research topic, therefore, benefits from a large body of literature and the facilitative role of self-shadowing is no longer in question. However, it is always puzzling to note that some of the most common ecosystems turn out to be amongst the least known. This is precisely the case of the *Fucus serratus* communities which are widespread in Northeast Atlantic along the Atlantic coast of Europe from Svalbard to Portugal, as well as Northwest Atlantic & Gulf of St. Lawrence, easily accessible at low tide, but which have comparatively received less attention than more emblematic macro-algal communities such as Laminariales.

The lack of attention paid to these most common Fucales is particularly critical as some species such as *F. serratus* are proving to be particularly vulnerable to environmental change, leading to a predicted northward retreat from its current southern boundary [9].

In the present study [10], the authors showed the importance of the vegetation cover in resisting tide-induced environmental stresses. The canopy of *F. serratus* mitigates stress levels experienced in the lower layers during emersion, while various acclimation strategies take over to maintain the photosynthetic apparatus in optimal conditions.

They hereby highlight adaptation mechanisms to the extreme environment represented by the intertidal zone. These adaptation strategies were expected and similar mechanisms had been shown at the cellular level previously [11]. The earliest studies on the subject have shown that the structure of the bottom, the movement of water, and light availability all "*influence the distribution of Fucaceae and disturb the regularity of their fine zonation, which itself is caused by the most important factor, desiccation*", as Zaneveld states in his review [12]. He observed that the causes of the zonal distribution of marine algae are numerous, and identified several points of interest such as the relative period of emersion, the rapidity of desiccation, the loss of water, and the thickness of the cell walls.

The present study thus highlights the existence of facilitative mechanisms associated with *F. serratus* canopy and nicely confirms previous work with *in situ* observations. It also highlights the importance of the vegetative cover in combating desiccation and introduces the dampening effect as a facilitating mechanism.

The effect of the vegetation cover can sometimes even be felt beyond its immediate area of influence. A recent study shows that ground-level ozone is significantly reduced by the combined effects of canopy shading and turbulence [4]. Below the canopy, the light intensity becomes sufficiently low which inhibits ozone formation due to the decrease in the rates of hydroxyl radical formation and the rates of conversion of nitrogen dioxide to nitrogen oxide by photolysis. In addition, reductions in light levels associated with foliage promote ozone-destroying reactions between plant-emitted species, such as nitric oxide and/or alkenes, and ozone itself. The reduction in diffusivity slows the upward transport of surface emitted species, partially decoupling the area under the canopy from the rest of the atmosphere.

By analogy with the work of Makar et al [4], and in the light of the results provided by the authors of this study, one may wonder whether the canopy dampening of *F. serratus* communities (and other common fucoids widely distributed on our coasts) might not also influence atmospheric chemistry, both at the Earth's surface and in the atmospheric boundary layer. The lack of accumulation of reactive oxygen species under the canopy found by the authors is consistent with this hypothesis and suggests that the damping effect of *F. serratus* may well have much wider consequences than expected.

References

- [1] Jurik TW, Kliebenstein H (2000) Canopy Architecture, Light Extinction and Self-Shading of a Prairie Grass, *Andropogon Gerardii*. *The American Midland Naturalist*, 144, 51–65. <http://www.jstor.org/stable/3083010>
- [2] Mitchley J, Willems JH (1995) Vertical canopy structure of Dutch chalk grasslands in relation to their management. *Vegetatio*, 117, 17–27. <https://doi.org/10.1007/BF00033256>
- [3] Kane VR, Gillespie AR, McGaughey R, Lutz JA, Ceder K, Franklin JF (2008) Interpretation and topographic compensation of conifer canopy self-shadowing. *Remote Sensing of Environment*, 112, 3820–3832. <https://doi.org/10.1016/j.rse.2008.06.001>
- [4] Makar PA, Staebler RM, Akingunola A, Zhang J, McLinden C, Kharol SK, Pabla B, Cheung P, Zheng Q (2017) The effects of forest canopy shading and turbulence on boundary layer ozone. *Nature Communications*, 8, 15243. <https://doi.org/10.1038/ncomms15243>
- [5] Shigesada N, Okubo A (1981) Analysis of the self-shading effect on algal vertical distribution in natural waters. *Journal of Mathematical Biology*, 12, 311–326. <https://doi.org/10.1007/BF00276919>
- [6] Barros MP, Pedersén M, Colepicolo P, Snoeijis P (2003) Self-shading protects phytoplankton communities against H₂O₂-induced oxidative damage. *Aquatic Microbial Ecology*, 30, 275–282. <https://doi.org/10.3354/ame030275>

- [7] Ørberg SB, Krause-Jensen D, Mouritsen KN, Olesen B, Marbà N, Larsen MH, Blicher ME, Sejr MK (2018) Canopy-Forming Macroalgae Facilitate Recolonization of Sub-Arctic Intertidal Fauna and Reduce Temperature Extremes. *Frontiers in Marine Science*, 5. <https://doi.org/10.3389/fmars.2018.00332>
- [8] Nelson H, Bramanti L (2020) From Trees to Octocorals: The Role of Self-Thinning and Shading in Underwater Animal Forests. In: *Perspectives on the Marine Animal Forests of the World* (eds Rossi S, Bramanti L), pp. 401–417. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-030-57054-5_12
- [9] Jueterbock A, Kollias S, Smolina I, Fernandes JMO, Coyer JA, Olsen JL, Hoarau G (2014) Thermal stress resistance of the brown alga *Fucus serratus* along the North-Atlantic coast: Acclimatization potential to climate change. *Marine Genomics*, 13, 27–36. <https://doi.org/10.1016/j.margen.2013.12.008>
- [10] Migné A, Duong G, Menu D, Davoult D, Gévaert F (2021) Dynamics of *Fucus serratus* thallus photosynthesis and community primary production during emersion across seasons: canopy dampening and biochemical acclimation. HAL, hal-03079617, ver. 4 peer-reviewed and recommended by Peer community in Ecology. <https://hal.archives-ouvertes.fr/hal-03079617>
- [11] Lichtenberg M, Kühl M (2015) Pronounced gradients of light, photosynthesis and O₂ consumption in the tissue of the brown alga *Fucus serratus*. *New Phytologist*, 207, 559–569. <https://doi.org/10.1111/nph.13396>
- [12] Zaneveld JS (1937) The Littoral Zonation of Some Fucaceae in Relation to Desiccation. *Journal of Ecology*, 25, 431–468. <https://doi.org/10.2307/2256204>

Reviews

Toggle reviews

Revision round #2

2021-05-19

Author's Reply

[Download author's reply \(PDF file\)](#)[Download tracked changes file](#)

Decision round #2

Dear Aline,

First of all sorry for the late reply.

Your article has been reviewed a second time. Your revised manuscript has been sent to two of the 3 initial referees and your review work has been acknowledged. You will note that a reviewer have suggested few additional minor changes which I would ask you to follow in order to proceed with the recommendation of your article.

I would also like to point out that I did not find any information about the 10 min duration used for dark adaptation of algae (before F_v/F_m measurement) in the references cited. Could you add a reference that specifically addresses the issue of dark adaptation and/or provides some comparison with other studies?

In addition, in the results section, the monthly average inorganic nitrogen concentrations are given but without the standard deviations. Would it be possible to add them?

One of our reviewer appreciated the paragraph added in the intro on the description of the macroalgae. He suggests that you could add a photo of the site/alga/instruments on site.

When submitting your revised manuscript please provide a point by point response to reviewers comments.

I would like to thank you for your work and your confidence, as well as the reviewers for their rigorous and helpful work.

Sincerely,

Cédric Hubas

Preprint DOI: <https://hal.archives-ouvertes.fr/hal-03079617>

Reviewed by anonymous reviewer, 2021-05-11 10:41

The authors revised their manuscript according the reviewer comments and the manuscript is now clearer (especially the different experiments).

Just two tiny comments:

- dates at the top of page 4: 26th, 22nd, 27th, 23rd, 4th, 13th, 5th (and superscript format)
- Page 4: "Thalli were selected according to the incident irradiance

Revision round #1

2021-04-01

Author's Reply

[Download author's reply \(PDF file\)](#)[Download tracked changes file](#)

Dear Cédric,

The paper "Dynamics of Fucus serratus thallus photosynthesis and community primary production during emersion across seasons: canopy dampening and biochemical acclimation" has been now revised according to reviewers' comments. A point by point response to reviewers' comments is also provided.

Thanks for considering this second version of our paper.

Yours sincerely,

Aline

Decision round #1

Dear authors,

I now have 3 independent reviews of your paper "Dynamics of Fucus serratus thallus photosynthesis and community primary production during emersion across seasons: canopy dampening and biochemical acclimation". Although this paper has the potential to be recommended by PCI, some important shortcomings have been raised and need to be clarified or corrected before it can be accepted. The reviewers have raised a number of important issues and I agree with their conclusions. Their reports are very constructive and provide a number of recommendations. It appears that the general form can be improved by adding more detail to certain parts. Also, more technical questions were raised concerning the statistical analysis or the analysis of antioxidant properties.

The article is very interesting but authors must bring new elements to their manuscript especially to the material and methods section. They must present their results in a much more readable way.

For all these reasons, I do not consider this preprint suitable for publication in its present form and therefore, I do not recommend it. However, if you are able to amend it in the light of our reviewers' comments, we would be happy to consider it again.

When submitting your revised manuscript please provide a point by point response to reviewers comments.

Yours sincerely,

Cédric Hubas

Preprint DOI: <https://hal.archives-ouvertes.fr/hal-03079617>

Reviewed by *Gwenael Abril*, 2021-03-06 13:33

Review of Migné et al. « Dynamics of *Fucus serratus* thallus photosynthesis and community primary production during emersion across seasons: canopy dampening and biochemical acclimation »

Although I am far from being an expert in all aspects of this study, I found it was well designed and the interpretation of the data are convincing. The paper brings significant information on the links between the C and water cycle in rocky shores, the ecological and physiological adaptation of a macroalgae to strong light, heating and desiccation during the emersion, the period when community primary production is at maximum and when the algae produce most of its biomass.

The study is original as it includes in situ measurements, and sampling for biochemical analysis in the lab. The discussion is convincing, although its reading could be improved. The only critic I can formulate concerns the form of the MS, as this Pre-print version appeared to me like a bit crude.

Here are some suggestions

Provide more precise information on the field experiment, and define better the *Fucus serratus* thallus itself (size height...). This will make the paper more readable for a broader community, because it is a bit difficult to imagine the sampling procedure from the actual text. How are "intermediate", "bottom" layers defined, how many layers in the Thallus, eventually what height? Was the total nb of layers stable seasonally during the experiment?

Maybe organize the discussion in 2-3 sections, last paragraph in page 10 can be a conclusion

Cite more often the figures and tables in the text, and also in the discussion when appropriated.

Figures panels have no A,B,C, although they may be useful, for instance to differentiate "mild conditions" from others. Seasonal nomenclature appeared confusing to me, at least at the first reading.

Fig1&3 present 5 sampling dates and Fig3&4 present 2 sampling dates for the same parameters, which I found a bit disappointing at the beginning of the reading.

Readers also have to refer to Table1 to read Fig.5 nomenclature properly.

Line by line

P4 How were the chambers fixed to the hard substrate?

“The fluorescence signal was always taken from the same place in the middle of the thallus for three individuals, haphazardly selected among thalli from the top of the canopy and three other individuals from the bottom of the canopy or from an intermediate layer of the canopy.” “Three were placed at the bottom of or inside the canopy, and three were placed at the top of the canopy.” And throughout the MS: Some more precise information on the height of the canopy (and/or total nb of superposed thallus within the canopy?) would be very welcome. It is quite difficult to imagine how the “intermediate layer” is defined and what is the distance from the top to the bottom.

P8 Text refers to dates “May”, “August” whereas Fig5 is labelled as M26, M27, A22, etc... The meaning of the nomenclature in Fig. 5 is described only in table 1. One gets lost.

P8 “Our physiological measurements validate intraspecific facilitation as a mechanism regulating the production of intertidal macroalgae stands.” Please be more explicit

P9 “During emersion under mild conditions, photosynthesis, measured as the electron transport rate (rETR), varied in thalli at the top of the canopy in response to changing incident light.” Where and when can we see that? This is not obvious in Fig. 1. What sampling date and hour correspond to “mild” conditions?

P9 1/3 > “appears to suggest” change to “suggests”

P9 “Photosynthesis was limited in the lowest layer of thalli due to self-shading which prevented light from reaching them, but was effective in the intermediate layers under relatively low local irradiance.” What is the difference between “intermediate layers” and “lowest layers”? how many layers in total? Does the number of layers vary seasonally?

More detailed information on the number of layers present at the different sampling dates and sites would be very helpful to readers.

P9 “beneath the canopy” does this correspond to “lowest layers”, “bottom”, “intermediate”, bottom and intermediate?

The discussion is sometimes hard to follow because it never refers to figures. Example: “The optimal photosynthetic quantum yield (F_v/F_m) also dramatically decreased during emersion periods of spring and summer in thalli at the top of the canopy, but not in thalli beneath the canopy.” Cite appropriate figure

“The same thalli are, however, unlikely to be at the top of the canopy in consecutive low tides and inhibition can be reversed by self-shading.” Why? How many thalli per sampling point or per m²? It would really be interesting for reader from a broader community to have more basic information on *Fucus serratus* as “studied object”: size of thalli, height of mats, etc. Was the biomass per m² the same for all the sampling periods?

P10 “Because the xanthophyll cycle is the principal non- photochemical quenching mechanism in brown algae,” any reference for that?

Table 1: date are probably much more convenient in the text than M26, A22, D4...

Fig. 5 could be more readable

end of review

Reviewed by *Francesca Rossi*, 2021-02-23 09:35

I find the paper of a great interest to understand *Fucus* physiological adaptations to environmental changes. The measurements done on the algae are of great value and interest. I, however, find that the large effort taken to do all these measurements is not enough valued using well sounded statistical approaches that can assist in testing the hypotheses declared in the aims of the paper at the end of the introduction. As far as I

could understand the hypotheses was that *tFucus thallis* change their strategy from photoprotection to scavenging following changes in environmental conditions, considered as a proxy for climate change and that this mechanisms occur more in the apical than distal part. Therefore, I would design a statistical model that takes into account all these variables and not use merely the sampling dates as explanatory variable. I also wonder if an assessment for colinearity was done for the PCA. It seems from the figure that all variables had a similar importance in structuring points across the first 2 axes of PCA

Reviewed by anonymous reviewer, 2021-04-01 12:42

The manuscript submitted by Migné et al. focused on the brown macroalga *Fucus serratus* and on the evolution of the primary production of *F. serratus* community, the algal photosynthesis and metabolites involved in photoprotection or exhibiting antioxidant activities, during emersion periods at different times of the year. They also compared seaweeds above the canopy to those living underneath or at the bottom of the canopy. The results are very interesting and highlights the small scale variation within the same *F. serratus* population and also according the time of the year. This study also shows the dampening canopy effect during emersion period especially in summer on understory *F. serratus* but also probably on other algal and animal species living underneath.

I still have some comments on the manuscript:

First, in the introduction, the authors said that “*Fucus serratus* is the lowermost zone-forming furoid”. I do not agree with that as on Brittany shores, you can find either *Himantalia elongata* and/or *Bifurcaria bifurcata*, which are also furoids, at the lowermost zone on the shore, just below the *F. serratus* zone and above the *Laminariales* zone.

In the M&M section, I am surprised that the authors used gallic acid as the standard to assay phenolic compounds of *Fucus serratus*: this phenolic acid is not present in brown seaweeds as opposed to phloroglucinol, which is the monomer of phlorotannins (= phenolic compounds of brown seaweeds). As the standard curve for both phenolic acids are different, the levels of phenolic compounds in *F. serratus* could then be a little different than those presented actually.

Although the M&M section is quite developed, I think that the method to assay chlorophyll a is missing or the authors used the same method as for xanthophyll pigments (although this method is optimised for those pigments and not for chlorophyll a)?

I did not find the Supplementary material of the manuscript but did the authors present only hydrogen peroxide, ascorbate and glutathione levels? or also the different correlation plots (TBI vs. air temperature, Fv/Fm vs. RWC, DR values vs. PAR just before emersion). If only the levels, the authors could probably add those correlations plots as well.

To explain the fact that Fv/Fm of seaweeds above the canopy reached 0 on the 13th August 2018, the authors hypothesize the impact of harsh conditions on those seaweeds, conditions that occurred the previous days of the measurements. This assumption may be correct. However, looking at the environmental data (Table 1), it seems that the same conditions were observed on the 22nd August 2017 but Fv/Fm did not reach 0 on that day. Do the authors have another explanation for the difference between these two days?

In the conclusion of the manuscript, the authors are talking about the foundation role of this brown macroalga but I think that they should emphasize on the impact that its disappearance will have on the community of alga and fauna living underneath if *F. serratus* could not adapt to thermal extremes predicted in the near future.