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Physiological and Biochemical Responses of *Ulva australis* to Fluctuating Emersion and Submersion

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Abstract

This study investigates the influence of fluctuating emersion and submersion on growth and biochemical composition of *Ulva australis* to elucidate their mechanisms of environmental stress adaptation. Thalli of *U. australis* were grown under laboratory conditions with varying emersion durations i.e. 0.5 h, 1.0 h, 2.0 h, and 5.0 h every 12 h. Biochemical composition was analyzed at final stages of thalli growth focusing on total solute carbohydrate and osmolyte content. The results showed that mild emersions (0.5 h, 1.0 h, and 2.0 h every 12 h) have significantly higher growth rate and total solute carbohydrates contents, compared to thalli without emersion, while during 5.0 h emersion, growth rate was significantly lower than those without emersion. Thalli with 5 h emersion had higher osmolyte content compared to the control ($P<0.05$). Under mild emersion, algae show increased total solute carbohydrate content, indicating enhanced energy storage and maintenance of metabolic processes. While increased osmolyte contents act as osmoprotectant under severe emersion to prevent cellular damage from desiccation. These observed biochemical changes provide insights into the mechanisms of stress adaptation in marine macroalgae, which could have broader implications for understanding and managing coastal ecosystems under changing environmental conditions.

Introduction

Marine algae living in the upper intertidal region face significant stress due to frequent fluctuations in physicochemical environmental conditions, associated with tidal changes. Desiccation, temperature change, exposure to solar radiation and salinity are the major stresses encountered by macroalgae (Contreras- Porcia et al., 2022). Certain intertidal macroalgae, such as green algae (genus *Ulva*) and red algae (genus *Porphyra*) can particularly tolerate the desiccation, just like resurrection plants having desiccation tolerant vegetative tissues (Xie et al., 2013; Guajardo et al., 2016). However, the ability of macroalgae to tolerate the desiccation may differ among the species due to their distinct tidal habitats.

Ulva australis (sea lettuce), widespread green macroalgae species mainly inhabits the shallow marine environments and eutrophic intertidal regions. (Yan et al., 2010). It is characterized by its ability to grow freely, so it can be found both suspended as well as floating on the seawater surface. In coastal areas, intertidal macroalgae experience desiccation due to high temperature and UV radiation exposure during emersion periods. The stress caused by salinity fluctuation and desiccation induces various morphological and physiological changes, including increased production of reactive oxygen species (ROS), which can induce lipid peroxidation, oxidative stress, damage biological molecules like cell membrane, proteins and nucleic acids (Soares et al., 2019). Such prolonged desiccation can also reduce the photosynthetic rate by disrupting the efficiency of photosystems I and II (Flores-Molina et al., 2014). Stress associated with salinity changes and desiccation results in discharge of ions from plasma membrane,

crystallization of solutes, fluctuation in pH, and structural degradation of proteins (Bischof & Rautenberger, 2012). All these stresses may ultimately lead to reduced growth rates under prolonged emersion.

Oceanic tidal cycle is a primary factor in the variability of environmental conditions, causing intertidal species to experience the alternating periods of emersion and submersion. This situation affects the accessibility of oxygen and food to the organisms, as well as induces the risk of desiccation and temperature fluctuation. As a result, these intertidal organisms have adapted themselves to respond oxygen scarcity, significantly reducing their metabolic rate, which may nearly decrease 99% of their aerobic metabolism (Abele et al., 2011; Haider et al., 2020; Steffen et al., 2021). When these organisms are re-submerged, they undergo reoxygenation and sudden intake of oxygen in their body results in increased production of ROS (Kalogeris et al., 2014). Intertidal seaweeds have developed various physiological and biochemical responses to withstand the various challenges posed by emersion. For instance, certain macroalgal species, activate enzymatic and non-enzymatic antioxidative mechanisms during the emersion and submersion periods to prevent cellular damage. Antioxidant enzymes play a very important role in maintaining ROS balance to prevent oxidative damage and support the organism's growth (Gratão et al., 2015; Mittler, 2017). While during prolonged emersion, the contents of antioxidant metabolites like proline, low molecular weight carbohydrates and poly amines increase in response to the stress (Cushman & Oliver, 2011). López‐Cristoffanini et al. (2015) reported that protein profile of the red seaweed *Pyropia orbicularis* changes significantly during low tide. The study revealed an increased emergence of certain proteins, such as chaperones, manganese superoxide dismutase, phycobiliproteins, monodehydroascorbate reductase, peptidylprolyl isomerase and glyoxalase I, which are associated with stress response and antioxidant activity. These findings indicate that during emersion various physiological and biochemical responses associated with desiccation tolerance become activated. These responses include reduced photosynthetic activity, enhanced antioxidant capacity, and the maintenance of the cell physiology during prolonged emersion.

Previous studies have provided valuable information on the ability of different marine macrophyte species managing their physiological processes under fluctuating environmental conditions. The studies regarding the photosynthetic capabilities of intertidal algae during emersion under controlled lighting conditions using the measurements of carbon and oxygen flux (Kawamitsu & Boyer, 1999) indicate that the upper species have greater rate of photosynthesis in air. This may be attributed to some kind of relationship between the submerged intertidal alga and its environment. Surif and Raven (1990) demonstrated that upper algae can quickly start photosynthesis in air before desiccation occurs, suggesting that because of desiccation, shorter times for the photosynthesis lead to higher photosynthetic rates when conditions are favorable.

To simulate the natural conditions in the tidal zone, this study has employed a device that allows one side of the *U. australis* thalli to remain in contact with the medium during emersion, to avoid nutritional limitations and salinity stress. This setup mimics the natural environment where many macroalgae rest on the sediment during low tide, with one side of the thalli exposed to air while the other remains in contact with moist sediment. The study aims to investigate the effects of fluctuating emersion and submersion on the growth and biochemical composition of *U. australis* under simulated tidal conditions, an area not extensively explored in previous research. Using a fluctuating emersion and submersion device, we examined how these conditions influenced the growth of macroalgae, focusing on the semi-diurnal tide, a characteristic of Qingdao's intertidal zone. This research provides key insights into the adaptive mechanisms, including biochemical and physiological responses, of *U. australis* to fluctuating emersion and submersion. It will also facilitate in the development of effective management strategies for optimizing the growth conditions of *U. australis* in aquaculture settings and enhancing its resilience to environmental stressors in natural habitats, thereby contributing to sustainable aquaculture practices.

Materials and Methods

Plant Material

U. australis used in this study was the sterile mutant, which was provided by Prof. Akira Taniguchi, Tohuku University, Japan, and was cultured aseptically in f/2 medium (Guillard & Ryther, 1962) at 20℃ and an irradiance of 100 μmol/(m^2.s) (12:12 h light-dark cycle, light period: 06:00 - 18:00) in illuminating incubators.

Natural seawater was subjected to cotton filtration through a 300 mesh gauze filter, and then boiled to minimize bacterial activity. The pH and salinity of the seawater were adjusted to 8.4±0.1 and 30.0±0.1, respectively. These levels were selected based on the results of the annual monitoring of near-shore seawater in Qingdao, ensuring that the experimental conditions closely resemble the natural environment where *U. australis* grows.

Experimental Treatment and Culture Condition

Discs (Ø1.05 cm, thus, 0.87 cm^2) were removed from the marginal region of the thallus with a single genetic individual and transferred to glass cups containing 200 ml f/2 medium. Samples were allowed at least 24 h recuperation period at constant temperature

20℃ before the experiment. A total of 35 rearing units, each unit consisting of a glass cups containing 200 ml f/2 medium and 3 discs, were subjected to seven different treatments: one control treatment without emersion treatment and six emersion treatments with varying emersion durations (0.5 h, 1.0 h 2.0 h 3.0 h 4.0 h and 5.0 h emersion every 12 h). Emersion was done twice in a day, once in light period and second time in dark period. Each treatment was assigned 5 rearing units which were maintained under a light intensity of 100 µmol/ (m^2.s) with a 12:12 h light-dark cycle (light period: 06:00 - 18:00). Growth was monitored over the period of 12 days and medium was renewed daily. The same photoperiod, light intensity, temperature, salinity and frequency of medium renewal were maintained throughout the experiment.

Emersion and Submersion Assays

The emersion and submersion device were placed in the incubator, used for maintaining the cultures (Figure 1).

Growth

The initial fresh weight of each thallus measurements was measured immediately after removal from seawater. Any external water was removed by gently drying the thalli on filter paper. The mean initial weight of the thalli was 25.77±1.16 mg (Mean±SD), and there were no differences in initial weights among treatments (P>0.05). At 3, 6, 9 and 12 days experiment, the fresh weight of all thalli was measured. At the end of 12 day experiment, one half of disc was dried at 60℃ for 24 hours.

The relative growth rate (RGR) in terms of the fresh weight was calculated as the following:

$$RGR\ (\%\ day^{-1}) = 100 \times (\ln W_t - \ln W_0) / T$$

Where, W_t and W_0 are the final and initial fresh weight of the thalli, respectively; T is the duration of the experiment.

Biochemical Composition

All the experimental materials are collected from the same thallus of *Ulva australis*. The preliminary experiment demonstrated consistent biochemical composition across discs derived from this thallus, at the beginning of the experiment, and there was no significant difference between the control and experimental groups. At the end of the experiment, each disc was divided into six parts, for the determination of chlorophyll a, chlorophyll b, protein, total soluble carbohydrate and proline. Surplus samples were stored at -70℃. Chlorophyll a and chlorophyll b concentrations were determined using the method described by Jeffrey and Humphrey (1975). For crude protein content, the method described by Bradford (1976) was used, with bovine serum albumin as the standard. Total soluble carbohydrate was measured by the anthrone reaction with glucose as the standard (Yemm & Willis, 1954). Free proline was estimated by the method of Bates et al. (1973) with L-proline as the standard.

Data Treatments and Statistical Analysis

Data set was analyzed using one-way ANOVA, with the fluctuation amplitude treatment as a factor, using SPSS for Windows (Version 11.0). When the significant differences were detected, means were compared using Duncan multicomparative analysis. Differences were considered significant at (P<0.05). In some cases, percentage and ratio data were arcsine transformed, to ensure normality and homoscedasticity.

Results

Growth

The changes in the fresh biomass, daily increments and the relative growth rate (RGR) of *U. australis* thalli under different treatments are shown in Table 1 and Figure 2. Different emersion durations had varying influences on the growth of *U. australis* .On the day 3, RGRs of the thalli experiencing emersion for 0.5 h, 1.0 h, 2.0 h, 3.0 h and 4.0 h every 12 hours were significantly greater than those without emersion (P<0.05). On the days 6 and 9, fresh weight and daily increments of thalli with emersion for 0.5 h, 1.0 h and 2.0 h every 12 h were significantly greater than those without emersion (P<0.05), while thalli with emersion of 3.0 h, 4.0 h and 5.0 h every 12 h showed lower growth rates than those without emersion (P<0.05). On the day 12, RGRs of the thalli with emersion 0.5 h, 1.0 h and 2.0 h, every 12 h were significantly higher than those without emersion (P<0.05), whereas RGRs with emersion of 3.0 h, 4.0 h and 5.0 h in every 12 h were significantly less than without emersion (P<0.05).

Biochemical Composition

The biochemical composition of *U. australis* thalli varied with emersion durations (see Table 1). No statistically significant differences (P>0.05) were found among the final content of chlorophyll a (Chl-a) and chlorophyll b (Chl-b) with 0.0 h, 0.5 h, 1.0 h, 2.0 h, 3.0 h and 4.0 h emersion every 12 h. However, thalli with 5 h emersion every 12 h had significantly lower levels of Chl-a and Chl-b than those without emersion (P<0.05).

The protein content in *U. australis* showed significant fluctuations with different emersion time. The protein contents were significantly lower at emersion time of 0.5 h, 1.0 h, 2.0 h, 3.0 h, and 4.0 h than those without emersion but 5.0 hour emersion group showed a substantial increase in protein content,

reaching 26.72 units, which was significantly higher than the control (Table 1).

Total solute carbohydrate contents decreased with increasing emersion time, except for the 5 h emersion treatment which showed higher total solute carbohydrate contents. Thalli with emersion for 0.5 h, 1.0 h, and 2.0 h every 12 h had significantly higher total solute carbohydrate content than those without emersion, and the content of total solute carbohydrate at emersion 5 h was also significantly higher than that without emersion ($P<0.05$).

The protein to carbohydrate ratio in *U. australis* for 0.5 h, 1.0 h, 2.0 h, 3.0 h and 4.0 h every 12 h was significantly lower than that of without emersion but with emersion of 5.0 h every 12 h this ratio is greater than that without emersion. The free proline contents increased with the increase of emersion time generally. The contents of free proline with emersion time of 2.0 h, 3.0 h, 4.0 h and 5.0 h in every 12 h were higher than that without emersion ($P<0.05$).

Discussion

Due to changing climatic situations, the intertidal community is facing serious challenges. Various researches have been done to understand the effects of vary environmental conditions like salinity, CO_2 and temperature on the behavioral responses and adaptations of intertidal macroalgae (Maharana et al., 2015). Therefore, this study is conducted to evaluate the growth rates and biochemical composition of *U. australis* during different emersion times. Results from this study showed that the growth of *U. australis* can be affected by emersion of different time intervals.

In this study, we observed that short-term desiccation, as evidenced by emersion periods of 0.5 h, 1.0 h and 2.0 h every 12 h on days 6, 9, and 12, induced better growth compared to that of control without emersion. However, emersion periods exceeding 3h every 12 h did not significantly influence the RGR of *U. australis* (Figure 2). These findings align with previous researches indicating that mild desiccation can stimulate the photosynthesis in certain intertidal

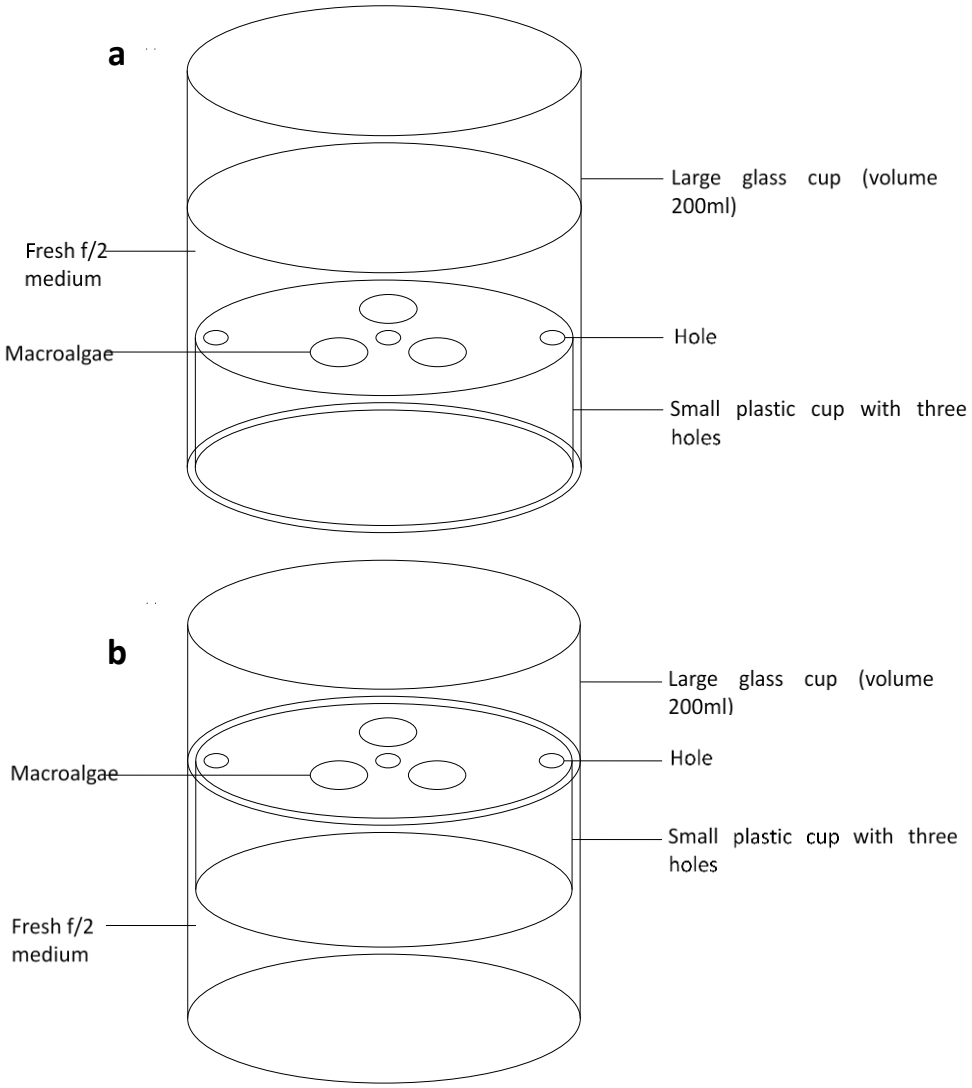

Figure 1. Emersion and submersion assays. The letter "a" and "b" represent submersion procedure and emersion procedure, respectively. There are three holes under the thallus respectively.

Table 1. Effects of different circadian rhythms of emersion time on the proximate biochemical compositions of *U. australis*

Emersion time	Final content (mg/g)																				
	Chl-a			Chl-b			P			C			Pro			Moisture (%)			P/C		
	Mean	SD	SE	Mean	SD	SE	Mean	SD	SE	Mean	SD	SE	Mean	SD	SE	Mean	SD	SE	Mean	SD	SE
0.0h	0.91^{ab}	0.07	0.03	0.49^{a}	0.05	0.02	23.62^{ab}	1.96	1.13	34.28^{b}	1.81	1.05	0.13^{ab}	0.01	0.01	81.10^{a}	0.85	0.38	0.69^{a}	0.06	0.03
0.5h	0.92^{ab}	0.07	0.03	0.44^{a}	0.06	0.03	15.79^{a}	1.24	0.71	44.24^{a}	2.89	1.67	0.08^{a}	0.02	0.02	80.08^{abc}	0.89	0.40	0.36^{a}	0.04	0.03
1.0h	0.98^{b}	0.06	0.03	0.52^{a}	0.07	0.03	19.17^{ab}	2.51	1.45	40.25^{a}	2.44	1.41	0.12^{ab}	0.01	0.01	80.58^{ab}	0.89	0.40	0.48^{a}	0.09	0.05
2.0h	0.89^{b}	0.04	0.02	0.46^{a}	0.02	0.01	17.41^{a}	4.25	2.46	42.72^{a}	1.28	0.90	0.15^{ab}	0.01	0.01	79.83^{abcd}	1.74	0.78	0.39^{a}	0.15	0.10
3.0h	0.85^{b}	0.05	0.03	0.43^{a}	0.10	0.05	16.93^{a}	2.47	1.42	10.78^{c}	0.91	0.52	0.18^{b}	0.01	0.01	78.47^{d}	1.03	0.46	1.59^{b}	0.36	0.21
4.0h	0.84^{b}	0.07	0.03	0.44^{a}	0.08	0.04	20.22^{ab}	5.93	3.42	12.95^{c}	1.05	0.61	0.30^{c}	0.08	0.05	79.36^{bcd}	0.46	0.21	1.56^{b}	0.46	0.27
5.0h	0.64^{c}	0.05	0.02	0.30^{b}	0.07	0.03	26.72^{b}	7.79	4.50	40.84^{a}	5.98	4.23	0.44^{d}	0.05	0.03	78.96^{cd}	0.75	0.38	0.71^{a}	0.12	0.08

Values (n=5) with different letters in the columns were statistically different (P<0.05). Chl-a, chlorophyll a; Chl-b, chlorophyll b; P, protein; C, total soluble carbohydrate; Pro, free proline

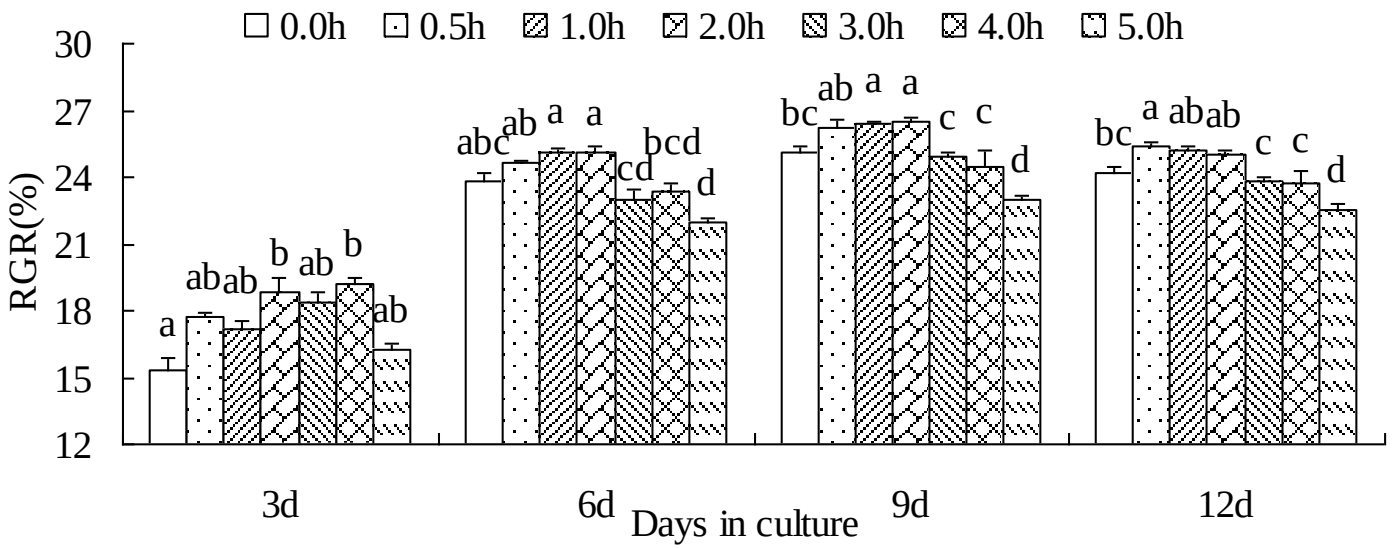

Figure 2. The relative growth rates (RGR) of *U. australis* at different emersion conditions. Means (n=5) with different letters in the same day in culture are significantly different (P<0.05). Error bars represent 1 S.E.

macroalgae, while prolonged desiccation periods inhibit this process. This photosynthetic ability of seaweed is affected due to degradation of proteins and photosynthetic pigments which may be associated with ROS production (Flores-Molina et al., 2014).

Kumar et al. (2011) also observed a similar phenomenon, where short-term desiccation led to a notable increase in the levels of photosynthetic pigments. Furthermore, the increase in carotenoid contents can be linked to their antioxidant properties, which play an important role in neutralizing singlet oxygen ($^1O_2$) by quenching excited chlorophyll or dissipating excess energy via the xanthophyll cycle (Fernández-Marín et al., 2011). Zou et al. (2007) documented an increase in photosynthetic activity during mild emersion in *Ulva lactuca*, which could be due to the reduced aqueous diffusion barrier for CO_2 on the thallus surface, enhancing CO_2 uptake and utilization efficiency.

Migné et al. (2015) further highlighted the mechanism of the carbon flux of marine macroalgae under normal light conditions, suggesting that photosynthetic rate was generally higher underwater, even for non-severely dehydrated species. In *Laminaria digitata*, the respiration rate was more than the photosynthesis during emersion, resulting in net negative productivity. The difference in performance between submerged and aerial conditions was less for upper shore species, like *Fucus spiralis*. In thalli part, electron transport rates were higher underwater for *L. digitata* and *Fucus serratus,* and in air for *F. spiralis* and *Pomacea canaliculata,* these rates were significantly higher, indicating that during emersion, upper shore organisms showed more photosynthesis than the lower organisms.

It can be seen that different emersion time on a 12 h basis had various influences on the chlorophyll a, chlorophyll b, protein and total soluble carbohydrate of *U. australis* (Table 1). The data indicate a significant decline in chlorophyll content level as the duration of emersion increases, suggesting that prolonged exposure to aerial conditions negatively impacts photosynthetic pigments' level in the macroalgae. In the dynamic intertidal zone, macroalgae face significant environmental stress, particularly during prolonged periods of emersion. These conditions lead to substantial water loss and increased production of reactive oxygen species (ROS), which can induce oxidative stress and damage cellular components, including proteins and pigments (Flores- Molina et al., 2014). In our study, we observed a decline in chlorophyll levels under the prolonged emersion, suggesting potential oxidative stress or pigment degradation. Kumar et al., (2011) reported similar findings, where ROS production and lipid peroxidation increased significantly during 3–4 hours of emersion. This was primarily due to increased lipoxygenase (LOX) activity. They observed that initially chlorophyll, phycobiliproteins and carotenoids increased during the first 2 hours of emersion than thaose of control, but these levels subsequently declined with longer exposure times (Kumar et al., 2011). This pattern indicates that while short-term emersion may initially stimulate pigment production, prolonged exposure leads to degradation and oxidative stress.

Under the prolonged emersion of 5.0 h every 12 h, the contents of proteins were significantly higher as compared to the control without emersion. This finding is consistent with the observations in resurrection plants, where exposure to dehydration induces a significant increase in the synthesis of heat shock proteins and late embryogenesis abundant proteins (Leprince & Buitink, 2010). Similarly, Gasulla et al. (2013) performed the proteomic analysis on green alga *Asterochloris erici* and highlighted that prolonged emersion led to increase in the abundance of 11–13 proteins which participate in maintaining cellular integrity, regulating glycolytic metabolism and cell cycle. These studies highlight the importance of increased production of proteins during desiccation periods and the adaptive mechanisms employed by intertidal macroalgal species.

It can be seen from Table 1 that the content of total soluble carbohydrate of *U. australis* with emersion time less than and at 2.0 h every 12 h were significantly higher than those without emersion ($P<0.05$). We noticed that carbohydrates contents were lower at 3.0 h and 4.0 h then without emersion but at emersion 5 h every 12 h was again significantly higher than that without emersion. We noticed this fluctuation but could not find out the exact reasons behind this trend therefore further researches are needed to understand the reason of this fluctuation. But during mild desiccation periods, Craige (1969) found that the osmoprotectant sugars within algal cells transition between polymer and monomer forms. This adaptive mechanism ensures that desiccated algal cells accumulate higher concentration of these small molecules to manage osmotic stress. Under the prolonged emersion, when desiccation becomes intense, the proportion of smaller, newly synthesized dissolved organic carbon substances decreases in *U. australis* (Wang et al., 2024).

Furthermore, the content of free proline also increased with increasing of emersion time. Proline is a non-essential amino acid that serves important roles in osmotic regulation and antioxidant defense (Martins et al., 2021). It can both prevent the production of reactive oxygen species (ROS) and scavenge them (Hayat et al., 2012; Signorelli et al., 2014). In the case of extreme dehydration, algae undergo a great loss of water which ultimately increase the salt contents in the cells of organisms resulting in decreased photosynthesis. Due to reduced photosynthesis and salt stress, the uptake of nutrients like nitrogen, growth and development of algae is affected. Soares et al., 2019 conducted a study on *F. serratus* in which they found an increase in proline content during low tide. This increase supported the idea that proline functions as osmoprotectants,

maintaining osmotic balance, suppresses lipid peroxidation, and thereby acts as a membrane stabilizer. Therefore, when algae experience harsh environmental conditions, the contents of proline in the body increases and regulate the metabolic processes in the algal cells, increasing the stability of organisms towards the salt stress (Kumar et al., 2010). So, proline is one of the important compound in algae that help algal species to tolerate salinity stress. The osmolytes accumulated in conjunction with development of stress and tolerance, which indicates that long time of emersion, is an unfavorable condition or circumstance for *U. australis*.

However, physical and chemical factors are multivariate and complexity in the tidal cycles, it is needed to find out the ecophysiological mechanism of emersion and submersion alternation effects on macroalgae in future research.

Conclusion

The biochemical composition and growth of *Ulva australis* highlights its adaptability to changing emersion time. This study has demonstrated the physiological responses of *U. australis,* under fluctuating emersion and submersion conditions. The growth of this intertidal species increases for short emersion periods but longer emersion time does not show any positive influence on its growth. These findings provide valuable insights into the adaptive mechanisms of intertidal macroalgae which can help in devising strategies for optimizing macroalgae cultivation under varying environmental conditions for sustainable aquaculture. Future research should focus on exploring the molecular mechanisms underlying the observed physiological responses. Investigating the long-term effects of fluctuating emersion conditions on macroalgae health and productivity would provide a more comprehensive understanding of their adaptability. Moreover, research on the exploring the potential for genetic improvement to enhance stress tolerance and improve the growth could expand the applications of *U. australis* in pharmaceuticals and food industries.

Ethical Statement

Formal consent is not required for this study.

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Author Contribution

Laiba Saeed: Writing Original Draft – Reviewing and Editing; Qiaohan Wang: Conceptualization, Data Curation; Funding Acquisition, Methodology.

Conflict of Interest

The authors declare no conflict of interest.

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References

Abele, D., Vázquez-Medina, J. P. & Zenteno-Savín, T. (2011). *Oxidative Stress in Aquatic Ecosystems*. Wiley-Blackwell. https://doi.org/10.1002/9781444345988

Bates, L. S., Waldren, R. P. & Teare, I. D. (1973). Rapid determination of free proline for water-stress studies. *Plant Soil,* 39, 205-207. https://doi.org//10.1007/BF00018060

Bischof, K., & Rautenberger, R. (2012). Seaweed responses to environmental stress: reactive oxygen and antioxidative strategies. In C. Wiencke & K. Bischof (Eds.), *Seaweed biology: Novel insights into ecophysiology, ecology and utilization* (pp. 109-132). Springer Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-28451-9_6

Bradford, M. M. (1976). A rapid and sensitive method for the quantization of microgram quantities of protein utilizing the principles of protein-dye binding. *Analytical Biochemistry,* 72, 248-254. https://doi.org/10.1016/0003-2697(76)90527-3

Contreras-Porcia, L., Meynard, A., Piña, F., Kumar, M., Lovazzano, C., Núñez, A., & Flores-Molina, M. R. (2022). Desiccation stress tolerance in *Porphyra* and *Pyropia* species: a latitudinal analysis along the Chilean coast. *Plants,* 12(1), 12. https://doi.org/10.3390/plants12010012

Craigie, J. S. (1969). Some salinity-induced changes in growth, pigments, and cyclohexanetetrol content of *Monochrysis lutheri. Journal of the Fisheries Board of Canada*, 26(11), 2959-2967. https://doi.org/10.1139/F69-282

Cushman, J. C., & Oliver, M. J. (2011). Understanding vegetative desiccation tolerance using integrated functional genomics approaches within a comparative evolutionary framework. In *Plant desiccation tolerance* (pp. 307-338). Springer Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-19106-0_15

Fernández-Marín, B. Míguez, F. Becerril, J. M. & García-Plazaola, J. I. (2011). Activation of violaxanthin cycle in darkness is a common response to different abiotic stresses: A case study in *Pelvetia canaliculata*. *BMC Plant Biol*ogy, 11, 181.

Flores-Molina, M. R., Thomas, D., Lovazzano, C., Núñez, A., Zapata, J., Kumar, M., Correa, J. A. & Contreras-Porcia, L. (2014). Desiccation stress in intertidal seaweeds: Effects on morphology, antioxidant responses and photosynthetic performance. *Aquatic Botany,* 113, 90-99. https://doi.org/10.1016/j.aquabot.2013.11.004

Guajardo, E., Correa, J. A., & Contreras-Porcia, L. (2016). Role of abscisic acid (ABA) in activating antioxidant tolerance responses to desiccation stress in intertidal seaweed species. *Planta*, 243, 767-781. https://doi.org/10.1007/s00425-015-2438-6

Gasulla, F., Jain, R., Barreno, E., Guéra, A., Balbuena, T. S., Thelen, J. J., & Oliver, M. J. (2013). The response of

Asterochloris erici (Ahmadjian) Skaloud et Peksa to desiccation: a proteomic approach. *Plant, Cell & Environment*, 36 7, 1363-78. https://doi.org/10.1111/pce.12065

Gratão, P. L., Monteiro, C. C., Tezotto, T., Carvalho, R. F., Alves, L. R., Peters, L. P., & Azevedo, R. A. (2015). Cadmium stress antioxidant responses and root-to-shoot communication in grafted tomato plants. *Biometals*, 28(5), 803-816. https://doi.org/10.1007/s10534-015-9867-3

Guillard R. R. & Ryther J. H. (1962). Studies of marine planktonic diatoms: I. *Cyclotella nana Hustedt,* and *Detonula confervaceae* (Cleve). *Canadian Journal of Microbiology,* 8, 229-239. https://doi.org/10.1139/m62-029

Haider, F., Falfushynska, H. I., Timm, S. & Sokolova, I. M. (2020). Effects of hypoxia and reoxygenation on intermediary metabolite homeostasis of marine bivalves *Mytilus edulis* and *Crassostrea gigas*. *Comparative Biochemistry and Physiology A- Molecular and Integrative Physiology,* 242, 110657. https://doi.org/10.1016/j.cbpa.2020.110657

Hayat, S., Hayat, Q., Alyemeni, M. N., Wani, A. S., Pichtel, J., & Ahmad, A. (2012). Role of proline under changing environments: a review. *Plant signaling & behavior*, 7(11), 1456-1466.

Jeffrey, S. W., & Humphrey, G. F. (1975). New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton. *Biochemie und physiologie der pflanzen,* 167, 191-194. https://doi.org/10.1016/S0015-3796(17)30778-3

Kalogeris, T., Bao, Y. & Korthuis, R. J. (2014). Mitochondrial reactive oxygen species: a double edged sword in ischemia/reperfusion vs preconditioning. *Redox Biology,* 2, 702–714. https://doi.org/10.1016/j.redox.2014.05.006

Kawamitsu, Y., & Boyer, J. S. (1999). Photosynthesis and carbon storage between tides in a brown alga, *Fucus vesiculosus*. *Marine Biology,* 133, 361-369. https://doi.org/10.1007/s002270050475

Kumar, M., Gupta, V., Trivedi, N., Kumari, P., Bijo, A. J., Reddy, C. R. K., Jha, B. (2011). Desiccation induced oxidative stress and its biochemical responses in intertidal red alga *Gracilaria corticata* (Gracilariales, Rhodophyta). *Environmental and Experimental Botany*, 72, 194–201. https://doi.org/10.1016/j.envexpbot.2011.03.007

Kumar, M., Kumari, P., Gupta, V., Reddy, C. R. K., & Jha, B. (2010). Biochemical responses of red alga *Gracilaria corticata* (Gracilariales, Rhodophyta) to salinity induced oxidative stress. *Journal of Experimental Marine Biology and Ecology,* 391(1-2), 27-34. https://doi.org/10.1016/j.jembe.2010.06.001

Leprince, O., & Buitink, J. (2010). Desiccation tolerance: From genomics to the field. *Plant Science*, 179, 554-564. https://doi.org/10.1016/j.plantsci.2010.02.011

López‐Cristoffanini, C., Zapata, J., Gaillard, F., Potin, P., Correa, J. A., & Contreras‐Porcia, L. (2015). Identification of proteins involved in desiccation tolerance in the red seaweed *Pyropia orbicularis* (Rhodophyta, Bangiales). *Proteomics*, 15(23-24), 3954-3968. https://doi.org/10.1002/pmic.201400625

Maharana, D., Das, P. B., Verlecar, X. N., Pise, N. M., & Gauns, M. (2015). Oxidative stress tolerance in intertidal red seaweed *Hypnea musciformis* (Wulfen) in relation to environmental components. *Environmental Science Pollution Research,* 22, 18741-18749. https://doi.org/10.1007/s11356-015-4985-6

Martins, M., Soares, C., Figueiredo, I., Sousa, B., Torres, A. C., Sousa-Pinto, I., Veiga, P., Rubal, M., & Fidalgo, F. (2021). Fucoid Macroalgae Have Distinct Physiological Mechanisms to Face Emersion and Submersion Periods in Their Southern Limit of Distribution. *Plants*, 10(9), 1892. https://doi.org/10.3390/plants10091892

Migné, A., Delebecq, G., Davoult, D., Spilmont, N., Menu, D., & Gévaert, F. (2015). Photosynthetic activity and productivity of intertidal macroalgae: In situ measurements, from thallus to community scale. *Aquatic Botany,* 123, 6-12. https://doi.org/10.1016/j.aquabot.2015.01.005

Mittler, R. (2017). Ros are good. *Trends in plant science*, *22*(1), 11-19. https://doi.org/10.1016/j.tplants.2016.08.002

Signorelli, S., Coitiño, E. L., Borsani, O., & Monza, J. (2014). Molecular mechanisms for the reaction between• OH radicals and proline: insights on the role as reactive oxygen species scavenger in plant stress. *The Journal of Physical Chemistry B*, 118(1), 37-47.

Soares, C., Carvalho, M. E., Azevedo, R. A., & Fidalgo, F. (2019). Plants facing oxidative challenges—A little help from the antioxidant networks. *Environmental and Experimental Botany*, 161, 4-25. https://doi.org/10.1016/j.envexpbot.2018.12.009

Steffen, J. B. M., Haider, F., Sokolov, E. P., Bock, C. & Sokolova, I. M. (2021). Mitochondrial capacity and reactive oxygen species production during hypoxia and reoxygenation in the ocean quahog, *Arctica islandica*. *Journal of Experimental Biology,* 224, 1–13. https://doi.org/10.1242/jeb.243082

Surif, M. B., and Raven, J. A. (1990). Photosynthetic gas exchange under emersed conditions in eulittoral and normally submersed members of the Fucales and the Laminariales: interpretation in relation to C isotope ratio and N and water use efficiency. *Oecologia*, 82, 68-80. https://doi.org/10.1007/BF00318535

Wang, L., Peng, C., Liu, Z., Zhang, X., Xu, Z., Liu, Z., Hu, J., Qin, S., & Zhong, Z. (2024). Regulation of desiccation-immersion cycle on the rate and fate of dissolved organic carbon release by *Ulva pertusa. Marine environmental research*, 204, 106943. https://doi.org/10.1016/j.marenvres.2024.106943

Xie, X., Gao, S., Gu, W., Pan, G., & Wang, G. (2013). Desiccation induces accumulations of antheraxanthin and zeaxanthin in intertidal macro-alga *Ulva pertusa* (Chlorophyta). *PLoS One*, 8(9), e72929. https://doi.org/10.1371/journal.pone.0072929

Yan, L., Tao, L., Dan, Y., Jing, Z., Xu-Min, W., & Qing-Li, G. (2010). Biological characteristics and molecular systematics studies on common green algae of Ulvaceae. *Periodical of Ocean University of China*, 40(12), 71-80

Yemm E. W. & Willis A. J. (1954). The estimation of carbohydrates in plant extracts by anthrone. *Biochemical Journal,* 57, 508-514. https://doi.org/10.1042/bj0570508

Zou, D., Gao, K. & Ruan, Z. (2007). Daily timing of emersion and elevated atmospheric CO_2 concentration affect photosynthetic performance of the intertidal macroalga *Ulva lactuca* (Chlorophyta) in sunlight. *Botanica Marina*, 50(5-6), 275-279. https://doi.org/10.1515/BOT.2007.031