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Altered seawater salinity levels affected growth and photosynthesis of *Ulva fasciata* (Ulvales, Chlorophyta) germlings

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Abstract

Seawater salinity is greatly influenced by tide, evaporation and rain falls. In this study, we investigated the growth and photosynthetic responses of zygote-derived *Ulva fasciata* Delile germlings to short-term (minutes) and prolonged (days) exposure to different salinity gradients, to evaluate the effect of salinity variation on the early stage of life history in this seaweed. The results showed that, the maximum net photosynthetic rates (NPRm) of *U. fasciata* germlings was observably decreased in desalted (25 and 15) and high (45) salinity seawater in short-term exposure tests (in minutes). However, after 30 min, the photosynthesis activity in medium salinity (25) was maintained at a relative high level (above 70%). After 8 d prolonged culture, the photosynthesis and mean relative growth rate (*RGR*) of germlings were all markedly lowered, whereas the malondialdehyde (MDA) contents increased as the salinity desalted from 34 to 15. The salinity decrease from 34 to 25 had no significant effect on the *RGR*, but obviously influenced the morphology of the germlings. High salinity level (45) significantly depressed the *RGR* and photosynthesis of *U. fasciata* germlings, while it notably increased the MDA contents. The results showed that the salinity elevation had more detrimental effects on *Ulva fasciata* germlings than salinity decrease did. The germlings grown at the salinity seawater levels from 25 to 34, performed preferable photosynthetic acclimation both in temporary and prolonged culture. Broad salinity tolerance from 25 to 34 in *U. fasciata* germlings may have partly evolved as a response to regular diurnal tides.

Key words: salinity stress, *Ulva fasciata*, germlings, photosynthesis, growth, malondialdehyde

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1 Introduction

Ulva fasciata Delile (Ulvales, Chlorophyta) is a potential marine seaweed for commercial aquaculture that distributed widely around the world, occurring from the mid-intertidal to upper subtidal zone, and is cultivated commercially in Japan and other Southeast Asian countries as other *Ulva* species (Ohno, 2006; Hiraoka and Oka, 2008). *U. fasciata* forms a well defined zone of about 5 m touching the mean low tide level on the reef. It is also found to grow in the sides of tide-pools and on the sloping sides of gullies connected to the sea. The algae in this zone have a diurnal and variable daily exposure, and endured long periods of changeable salinity because of evaporative water loss during emersion at low tide (Davison and Pearson, 1996). The tolerance mechanism of macroalgae experiencing variant salinity stress had already been given great interest.

The salinity variability in seawater was well documented (Lee et al., 2003), and the variant salinity greatly influence the marine organisms including many species of macroalgae (Satoh et al., 1983; Lartigue et al., 2003; Yamochi, 2013). For instance, Lartigue et al. (2003) reported that the salinity regime at study site remained mostly between 20 and 30 with changes over 3 occurring rapidly and frequently. However, high temperature enhanced the evaporation capacity from seawater and led to salinity increase, whereas rain falls and overland runoff reduced salinity (Schmitt, 1996). In fact, there was documented temperature increase of 0.74°C in the last century (IPCC, 2007), resulted from continuously elevated CO_2 concentration into atmosphere since the industrial revolution (Florides and Christodoulides, 2009). The global ocean surface salinity changes from 1950 to 2000 was also observed (Durack et al., 2012) and the salinity changes would potentially have persistent effects on macroalgae.

The effects of salinity on *Ulva* species were already studied. Response of *U. fasciata* to salinity and temperature was reported by Mantri et al. (2011), the zoospore induction, regeneration and daily growth rate of the algae were recorded at different optimum salinity levels. Yamochi (2013) studied the effects of desiccation and salinity on the outbreak of a green tide of *Ulva pertusa*, and found that the salinity decreases from 30 to 25 or 20 accompanied with exposure to air, drastically reduced the rate of photosynthesis of *U. pertusa*. Xia et al. (2004) investigated the effects of salinity stress on photosystem II (PS II) performance in *Ulva lactuca*, and found high salinity stress decreased the maximum quantum yield of primary photochemistry and quantum yield of electron transport, and considered the main targets in PSII were

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inactivation of reaction centers and inhibition of the electron transport at the acceptor side of PSII in elevated salinity. Lartigue et al. (2003) investigated the impact of rapid fluctuations in salinity on net oxygen production of *U. lactuca*, and found that changes in salinity resulted in a decline in net oxygen production.

Salinity on macroalgae germlings were reported as well. Wong and Phang (2004) found that the most important factor that controlled the biomass production and reproduction for both *Sargassum baccularia* and *Sargassum binderi* at Cape Rachado in Malaysia was rainfall which had direct effect on the seawater salinity. Steen (2004) reported effects of reduced salinity on reproduction and germlings development in *Sargassum muticum* (Phaeophyceae, Fucales), and considered the salinity requirements of the least tolerant initial life stages probably constituted a physiological barrier to the expansion into brackish waters. However, the effects on *U. fasciata* germlings have not been examined over the wide range of salinities found worldwide in estuarine, shelf, and ocean waters.

The goal of this research was to examine how salinity levels in seawater impacted the growth and photosynthesis of *U. fasciata* germlings, which may potentially be utilized in *U. fasciata* abundance control in coast, or in aquaculture wastewater treatment and eutrophication predication. To unravel these effects, we employed zygote-derived *U. fasciata* young germlings to investigate the *in-situ* short-term exposure (in minutes) and prolonged (days) photosynthetic responses to different salinity gradients.

2 Materials and methods

2.1 *Materials collection and culture*

Fertile thalli of *Ulva fasciata* were collected in April 2013 from the middle intertidal zone in Nan'ao Island (23.3°N, 116.6°E) in Shantou, South of China. The specimens were cleaned up with seawater, and transported to the laboratory in an insulated polystyrene cooler (approximately 5°C). Healthy algae were cultured in a glass aquarium containing filtered natural sterilized seawater supplied with 20 μmol/L NO_3^- (KNO_3) and 2 μmol/L PO_4^{3-} (NaH_2PO_4) (salinity was about 33) in CO_2 incubators (GXZ-300D, Jiangnan Instrument Factory, Ningbo, China). The culture medium was aerated vigorously, and was renewed every 3 d, during which the algal samples were wiped with paper towels to remove any visible epibionts if necessary. The pre-culture conditions were maintained at 18°C and about 65 μmol photons m^{-2} s^{-1} (fluorescent illumination) with 14 h: 10 h (light: dark cycle) photoperiod to induce the maturation of sporangia until gametes were released and young germlings appeared.

2.2 *Experimental treatments*

Germlings with approximate 1cm length were employed in present research after the young germlings appeared. The germlings were removed from the beaker and cultured proportionally in CO_2 incubators with aeration. NaCl (AR) and distilled water were used in salinity level manipulation, and the culture mediums were adjusted into four salinity gradients, 15, 25, 34 and 45; all gradients had three replicates.

Approximate 0.2 g fresh weight (Fw) young germlings were cultured in 2 L filtered natural seawater in each treatments, with extra nitrogen and phosphorous (20 μmol/L NO_3^-, 2 μmol/L PO_4^{3-}) in glass aquaria tanks at 20(±1)°C and vigorous aeration. The illumination was controlled at about 70 μmol photons m^{-2} s^{-1} by fluorescent tubes for 12 h: 12 h (light: dark cycle) photoperiod. The culture medium was changed every 2 d. The photosynthetic and morphological traits of the samples were examined after 8 d of laboratory culture.

2.3 *Relative growth rate*

Changes in biomass (fresh weight, Fw) were measured at the end of culture to estimate growth. Mean relative growth rate (*RGR*) was calculated using the formula: RGR (%/d) = ln $(W_t/W_0)/t \times 100$, where W_0 referred to the initial Fw, and W_t referred to the Fw after t days.

2.4 *Photosynthetic oxygen evolution and respiration rate*

The net photosynthetic O_2 evolution rate (NPR) and respiration rate (Rd) of *U. fasciata* young germlings were determined by a Clark-type oxygen electrode (YSI Model 5300, Yellow Springs Instrument Co., OH, USA) with a water jacket connected to a cooling circulator (Cole Parmer, USA) for maintaining the temperature at 20°C. Light intensities were measured with a quantum sensor (SKP 200, ELE International, Leighton Buzzard, UK). Variations of light intensities were attained through changing the distance between photosynthetic chamber and illuminant, which was provided by a halogen lamp. The photosynthesis rates were then obtained. The algal samples were allowed to acclimate to the electrode cuvette environment for a minimum of 10 min before the proceeding of respiration measurement.

Approximate 0.06 g algae (Fw) were introduced into the chamber containing 8 mL of original culture medium that was magnetically stirred. Dark respiration rate (Rd) was obtained by determining dark O_2 consume. The maximum net photosynthetic rates (NPRm) were measured at 400 μmol photons m^{-2} s^{-1}. The gross photosynthetic rates (GPRm) were the sum of NPRm and the respiration consumed O_2 evolution rate. NPRm, Rd and GPRm were all expressed by μmol/(g·h) (calculated by O_2). Photosynthetic parameters were calculated referring to Henley (1993).

2.5 *Short-term exposure tests*

Approximate 1 g (Fw) *U. fasciata* young germlings were employed into four salinity gradients (15, 25, 34 and 45, respectively) in four 1 L flasks to estimate the short-term exposure (in minutes) photosynthetic responses of the germlings to different salinity levels in seawater. The photosynthetic oxygen evolution analysis at 400 μmol photons m^{-2} s^{-1} light intensity was proceeded every other 15 min according to Section 2.4 described as above.

2.6 *Lipid peroxidation determination*

The content of malondialdehyde (MDA) evaluated the level of lipid peroxidation. It was measured by thiobarbituric acid (TBA) reaction method, as described by Heath and Packer (1968). After 8 d indoor culture, approximately 0.2 g (Fw) of algae under each salinity gradients was weighed and homogenized in 5 mL of 0.1% trichloroacetic acid (TCA). The homogenate was centrifuged at 10 000 r/min for 5 min at 4°C. For every l mL of supernatant, 4 mL of 20% TCA containing 0.5% TBA was added. After heating at 95°C for 30 min, the mixture was cooled in an ice-bath and centrifuged at 10 000 r/min for 15 min (4°C). The absorbance of the supernatant at 532 nm was recorded and corrected for unspecific turbidity by subtracting the value at 600 nm. The concentration of MDA was calculated using the extinction coefficient of 155 mmol/(L·cm).

2.7 *Statistics*

Origin 8.0 (Origin Lab Corp., Northampton, MA, USA) was used in data processing and statistical analysis. One-way analysis of variance and the Tukey test were used to analyze differences among treatments Tests for normality and homogeneity of variance were performed to check assumptions of parametric analysis. All the data were expressed as means ± SD ($n \geqslant 3$). A P-value of 0.05 was considered as statistically significant.

3 Results

3.1 *Effect of short-term exposure to different salinity levels on photosynthesis*

The photosynthetic responses of *Ulva fasciata* young germlings in short-term exposure to different seawater salinity levels were displayed in Fig. 1. There was little variation of the maximum net photosynthetic rates (NPRm) in seawater of salinity 34. When the germlings were placed into seawater of salinity 25, the NPRm was decreased within 30 min and then maintained above 70% during the followed procedure. The NPRm of *U. fasciata* germlings in seawater of salinity 15 declined gradually. In seawater of salinity 45, the NPRm was notably decreased and finally became negative after 90 min exposure to this high salinity level.

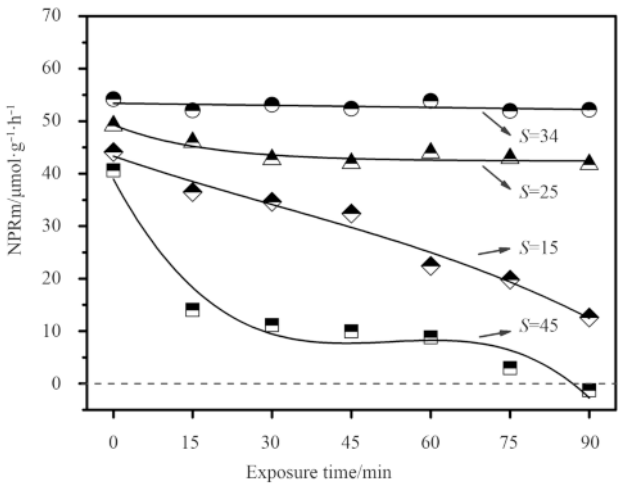

Fig. 1. Photosynthetic responses of *Ulva fasciata* germlings in short-term exposure to different salinity levels in seawater (NPRm: the maximum net photosynthetic rates).

3.2 *Survival and growth*

There were obvious morphological distinctions among the *U. fasciata* young germlings cultured under different salinity levels after 8 d prolonged culture (Fig. 2). Germlings cultured at salinity 15 grew much slower than those at salinity 25 and 34, and their sizes were relatively small. At the salinity levels from 15 to 34, biomass of the germlings increased as the salinity elevated, and the relative growth rates (*RGR*) was notably increased as well ($F_{2,6}$=37.73, P<0.01; Fig. 3), but there was no significant difference between *RGR* of the germlings at salinity 25 and 34 ($F_{1,4}$= 2.74, P=0.17). Growth of germlings was significantly decreased at salinity 45 ($F_{1,4}$=43.53, P<0.01), and the thalli had distinctively dark green color after 8 d culture (Fig. 2). Moreover, approximately (3.4±0.5)% germlings in total were dead when grown at salinity 45 seawater, where the germlings already rotted occupied above half of the thalli was considered as dead.

3.3 *Photosynthetic activity*

Respirations (Rd) of *U. fasciata* young germlings were signi-

Fig. 2. Comparison of morphological responses of *Ulva fasciata* germlings to different salinity (*S*) levels after 8 d culture period. Vertical bars represent the scale 1 cm. a. *S*=15, b. *S*=25, c. *S*=34, and d. *S*=45.

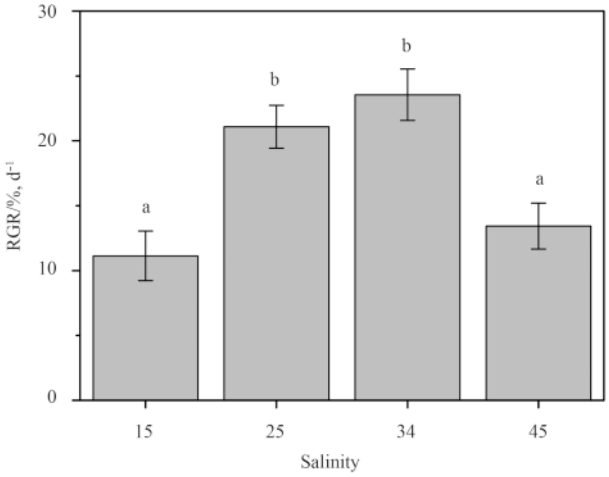

Fig. 3. Relative growth rates (*RGR*) of *Ulva fasciata* germlings grown at different salinity treatments after 8 d culture period. Significant differences among the treatments are indicated by different lowercase letters (the Tukey test, P<0.05). Vertical bars are means ± SD for triplicate samples.

ficantly depressed as the salinity in culture medium declined from 34 to 15 ($F_{2,6}$=20.86, P<0.01; Fig. 4). Likewise, the NPRm ($F_{2,6}$=23.28, P<0.01) and GPRm ($F_{2,6}$=29.52, P<0.01) of the germlings were also decreased. Similarly, the respiration ($F_{1,4}$= 13.83, P<0.05), NPRm ($F_{1,4}$=159.04, P<0.01) and GPRm ($F_{1,4}$= 210.68, P<0.01) of germlings grown at salinity 45 seawater were all notably lower than those in salinity level of 34.

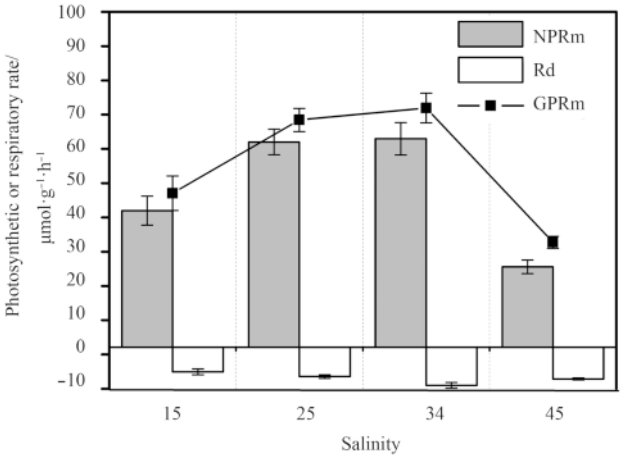

Fig. 4. Variation of photosynthesis rate, respiration and relative growth rate of *Ulva fasciata* Delile germlings cultured under different salinity levels. Vertical bars represent ± standard deviation (SD) of the means (n=3).

3.4 *MDA contents*

The large influence of salinity on *U. fasciata* germlings was readily seen from Fig. 5. As the salinity artificially reduced, the MDA contents increased by 38.95%, 96.07% at salinity 25 ($F_{1,4}$= 6.48, P=0.06) and 15 ($F_{1,4}$=38.25, P<0.01, Fig. 5) compared with salinity 34, respectively. Additionally, the MDA contents increased by 248.34% at elevated salinity seawater (45) compared with ambient salinity seawater (34) ($F_{1,4}$=98.11, P<0.01).

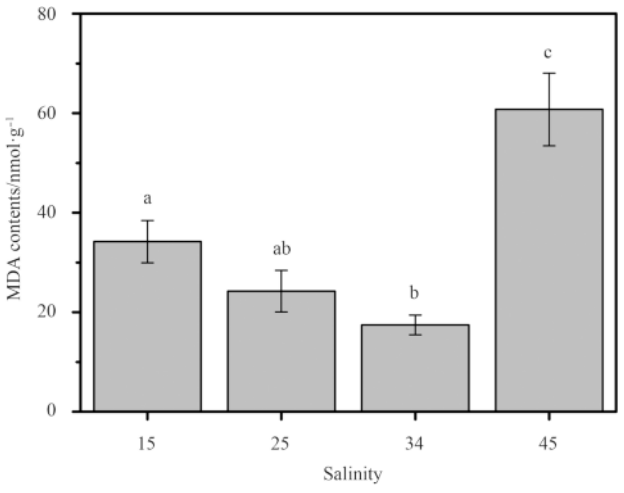

Fig. 5. MDA contents of *Ulva fasciata* germlings cultured under different salinity levels. Significant differences among the treatments are indicated by different lowercase letters (the Tukey test, P<0.05). Vertical bars are means ± SD for triplicate samples.

4 Discussion

4.1 *Growth and morphological responses of Ulva fasciata germlings to different salinity levels*

Present study showed that, the *RGR* was increased as the salinity elevated from 15 to 34, and the germlings in seawater of salinity 15 were relatively small. It might be resulted from the reduced cell viability in *U. fasciata* germlings in response to salinity stress below 15 (Chang et al., 1999). Moreover, there was no significant difference between the *RGR* but obvious morphological distinctions of the germlings in salinity of 25 and 34 levels. The products of photosynthesis were probably not efficient to be utilized in growth of *U. fasciata* germlings, and the consumed products might be used in synthesizing some kind of compounds, to balance the intra/extra-cellular osmotic pressure caused by declined salinity after prolonged culture, as performed in *Griffithsia monilis* (Bisson and Kirst, 1979) and in *Platymonas suecica* (Hellebust, 1976). The salinity 34 in this research was more optimal to the growth of *U. fasciata* germlings.

Growth of *U. fasciata* germlings was significantly depressed in seawater of salinity 45. The considerable *RGR* of the germlings at salinity 45 may be connected with the hyperosmosis and compounds synthesizing for salinity stress resistance; and this need to be further investigated. Additionally, the *U. fasciata* young germlings grown at high seawater salinity level (45) showed dark green color forms after prolonged culture. The Chl *a*, Chl *b* and carotenoids contents in *U. lactuca* exposed to different salinity (48–128) were constant over short periods (12 h) (Xia et al., 2004), but it is worth carrying out further research if these pigments were over charged under high salinity after long-term exposure, which may have influence on the appeared color burn.

There was death occurred in *U. fasciata* germlings when cultured under seawater salinity of 45 after prolonged culture. Although the high external osmotic pressure would be resisted via increasing in organic solute levels without a lag (Ahmad and Hellebust, 1988) at high salinity stress, hyperosmosis in seawater caused by exorbitant salinity level was higher than that in macroalgae cells in long-term, which resulted in water-loss in protoplasts and alteration of enzymatic reaction mediums, and then the enzymatic activities changed. More or less, redundant salinity would permeate into protoplasts through the cell-wall and cell membrane, and aggravated the protoplasts damage (Dickson et al., 1980). Moreover, stress tolerances caused ATP consumptions, and when the stress causes too much ATP consumptions, the plant suffers severe and permanent damages that lead to the cell death (Ying et al., 2005; Huang and Shen, 2009). Death in *U. fasciata* germlings after prolonged culture in high salinity levels was probably caused by hyperosmosis in seawater, which mainly resulted in water-loss in protoplasts and denature in enzymatic activities, and exorbitant energy consumptions.

4.2 *Photosynthetic responses of U. fasciata germlings to desalted salinity levels*

NPRm of *U. fasciata* germlings was observably decreased in seawater of salinity 25 in short-term exposure tests. However, after 30 min desalting culture, the photosynthesis activity was maintained at a relatively higher value (above 70%). Yet the respiration was notably depressed. Hellebust (1976) also found that high-salinity-adapted *P. suecica* cells suffered a temporary loss of their photosynthetic capacity when transferred into low salinities, and believed that this temporary loss of photosynthetic capacity in response to osmotic shock, was due to a non-specific re-

lease of soluble cell constituents to regain the normal permeability properties and readjustment of cellular composition to the new osmotic environment. Gessner and Schramm (1971) considered the temporary loss was mainly connected with affected carbon supply in desalted seawater. Due to regain of normal permeability properties and readjustment of cellular composition after prolonged culture, young germlings of *U. fasciata* performed considerable desalting photosynthetic resistance at salinity level of 25.

Nevertheless, lowered salinity level at 15 significantly depressed the photosynthesis of *U. fasciata* germlings. This depression of photosynthesis might be owing to the detrimental effects of reduced salinity on germling cells viability, which was documented by Chang et al. (1999). On the contrast, the salinity of 15 at 25°C was considered as the optimum salinity for zoospores induction of *U. fasciata*, while the optimum regeneration of the quadriflagellate zoospores was at salinity 30 and 25°C at 15 μmol photons m^{-2} s^{-1}, and higher daily growth rate of them was recorded at salinity 30 to 25 and 25°C (Mantri et al., 2011). The salinity requirements of *U. fasciata* in different stages (i.e., zoospores, germlings) might be variable, and it was worth further investigation.

Many macroalgae have adaptive salinity range for their growth. *Hypnea musciformis* collected from a mangrove estuary exposed coast had broad photosynthetic tolerances to salinity with maxima at 20 in winter and 36 in summer (Dawes, 1998). Liu et al. (2001) found that there were also broad salinity tolerances from 15 to 30 for *Gracilaria tenuistipitata* var. *liui*, 15–40 for *U. pertusa*, and 25–35 for *G. filicina*. It was also reported that, photosynthesis of *U. pertusa* was higher than 2.5 mg/(g·h) (calculated by O_2) at a salinity range of 15–29 but decreased below 1.6 mg/(g·h) at salinity 5 and 10 (Yamochi, 2013). In present study, *U. fasciata* germlings grown at the salinity seawater levels from 25 to 34, performed preferable photosynthetic acclimation both in temporary and prolonged culture. Broad salinity tolerance in *U. fasciata* germlings may have partly evolved as a response to regular diurnal tides.

4.3 *Photosynthetic responses of U. fasciata germlings to high salinity levels*

Significant inhibition of *U. fasciata* germlings photosynthesis by high salinity (45) in this study seemed to be associated with the decreases of PSII complex activity as in *Spirulina platensis* (Lu and Vonshak, 2002), or with the inhibition of quantum yield of PSII electron transport at the quinone pool level as in *Euglena* stressed by salinity (González-Moreno et al., 1997). Xia et al. (2004) found that high salinity (48–128) significantly decreased the photosynthetic O_2 evolution in *U. lactuca*, and similar results were observed in *Spirulina platensis* (Lu and Vonshak, 2002). It was considered that PSII was highly susceptible to salinity stress (Corney et al., 2003; Xia et al., 2004). The photosynthesis activity of the germlings in the present study was depressed regardless in short-term exposure or prolonged culture. This significant decrease in photosynthetic O_2 evolution induced by high salinity stress might indicate that the main targets in PSII might be the inactivation of reaction centers, and inhibition of the electron transport at the acceptor side of PSII (Xia et al., 2004), and as a consequence of prolonged stress, the enzyme catalysis activity was affected directly (i.e., considerable degradation of D1-protein in PSII-reaction, Richter et al., 1990). Moreover, osmotic pressure in marine macroalgae that was determined by salinity in seawater, mainly impacted the intra/extra-cellular moisture distribution and photosynthesis in algae. Active oxygen-containing species and hydroxyl radicals caused by high salinity stress were highly reactive, denatured essential components of cells including proteins, membrane lipids and nucleic acids were formed in both respiration and photosynthesis (Bowler et al., 1992). Thus, it was not excluded that the direct damages in germling cells caused by high salinity stress, such as inner organelle membrane damages included in MDA contents, would depress the membranes resistance and mobility transcellular pathway, and finally resulted in structures and physical integrity damages on cell/organelle membranes.

5 Conclusions

The detrimental effects of elevated salinity level were generally greater than these of desalted seawater. *U. fasciata* germlings grown at the salinity levels from 25 to 34, performed preferable photosynthetic acclimation both in temporary and prolonged culture. Broad salinity tolerance from 25 to 34 in *U. fasciata* germlings may have partly evolved as a response to regular diurnal tides. We proposed that the enhanced evaporation capacity and local rain falls gave rise to extreme salinity variation (for instance, high/low salinity levels), which would greatly impact the early growth of *U. fasciata* germlings.

References

Ahmad I, Hellebust J A. 1988. The relationship between inorganic nitrogen metabolism and proline accumulation in osmoregulatory responses of two euryhaline microalgae. Plant Physiology, 88(2): 348–354

Bisson M A, Kirst G O. 1979. Osmotic adaption in the marine alga *Griffithsia monilis* (Rhodophyceae): the role of ions and organic compounds. Australian Journal of Plant Physiology, 6(4): 523–538

Bowler C, van Montagu M, Inze D. 1992. Superoxide dismutase and stress tolerance. Annual Review of Plant Physiology and Plant Molecular Biology, 43: 83–116

Chang W-C, Chen M-H, Lee T-M. 1999. 2, 3, 5 triphenyltetrazolium chloride reduction in the viability assay of *Ulva fasciata* (Chlorophyta) in response to salinity stress. Botanical Bulletin Academia Sinica, 40: 207–212

Corney H J, Sasse J M, Ades P K. 2003. Assessment of salt tolerance in eucalypts using chlorophyll fluorescence attributes. New Forests, 26(3): 233–246

Davison I R, Pearson G A. 1996. Stress tolerance in intertidal seaweeds. Journal of Phycology, 32(2): 197–211

Dawes C J. 1998. Marine Botany. 2nd ed. New York: John Wiley & Sons, Inc, 82–85

Dickson D M, Wyn Jones R G, Davenport J. 1980. Steady state osmotic adaptation in *Ulva lactuca*. Planta, 150(2): 158–165

Durack P J, Wijffels S E, Matear R J. 2012. Ocean salinities reveal strong global water cycle intensification during 1950 to 2000. Science, 336(6080): 455–458

Florides G A, Christodoulides P. 2009. Global warming and carbon dioxide through sciences. Environment International, 35(2): 390–401

Gessner E, Schramm W. 1971. Salinity: plants. In: Kinne O, ed. Marine Ecology. Volume 1. London: Wiley-Interscience, 705–720

González-Moreno S, Gómez-Barrera J, Perales H, et al. 1997. Multiple effects of salinity on photosynthesis of the protist *Euglena gracilis*. Physiologia Plantarum, 101(4): 777–786

Heath R L, Packer L. 1968. Photoperoxidation in isolated chloroplasts: I. Kinetics and stoichiometry of fatty acid peroxidation. Archives of Biochemistry and Biophysics, 125(1): 189–198

Hellebust J A. 1976. Effect of salinity on photosynthesis and mannitol synthesis in the green flagellate *Platymonas suecica*. Canadian Journal of Botany, 54(15): 1735–1741

Henley W J. 1993. Measurement and interpretation of photosynthetic

light-response curves in algae in the context of photoinhibition and diel changes. Journal of Phycology, 29(6): 729–739

Hiraoka M, Oka N. 2008. Tank cultivation of *Ulva prolifera* in deep seawater using a new "germling cluster" method. Journal of Applied Phycology, 20(1): 97–102

Huang Qing, Shen Hanming. 2009. To die or to live: the dual role of poly (ADP-ribose) polymerase-1 in autophagy and necrosis under oxidative stress and DNA damage. Autophagy, 5(2): 273–276

IPCC (Intergovernmental Panel on Climate Change). 2007. Climate Change 2007: Synthesis Report. Cambridge, UK: Cambridge University Press

Lartigue J, Neill A, Hayden B L, et al. 2003. The impact of salinity fluctuations on net oxygen production and inorganic nitrogen uptake by *Ulva lactuca* (Chlorophyceae). Aquatic Botany, 75 (4): 339–350

Lee Y-H, Kim D-J, Kim H-K. 2003. Characteristics of the seawater quality variation on the South Coastal Area of Korea. KSCE Journal of Civil Engineering, 7(2): 123–130

Liu Jingwen, Dong Shuangxiu, Ma Shen. 2001. Effects of temperature and salinity on growth of *G. tenuistipitata* var. *liui*, *U. pertusa*, *G. filicina* and NH_4-N uptake of *G. tenuistipitata* var. *liui*. Haiyang Xuebao (in Chinese), 23(2): 109–116

Lu Congming, Vonshak A. 2002. Effects of salinity stress on photosystem II function in cyanobacterial *Spirulina platensis* cells. Physiologia Plantarum, 114(3): 405–413

Mantri V A, Singh R P, Bijo A J, et al. 2011. Differential response of varying salinity and temperature on zoospore induction, regeneration and daily growth rate in *Ulva fasciata* (Chlorophyta, Ulvales). Journal of Applied Phycology, 23(2): 243–250

Ohno M. 2006. Recent developments in the seaweed cultivation and industry in Japan. In: Phang S M, Critchley A T, Ang P O, et al., eds. Advances in Seaweed Cultivation and Utilisation in Asia. Kuala Lumpur: University of Malaya Maritime Research Center, 1–20

Richter M, Rühle W, Wild A. 1990. Studies on the mechanism of photosystem II photoinhibition I. A two-step degradation of D1-protein. Photosynthesis Research, 24(3): 229–235

Satoh K, Smith C M, Fork D C. 1983. Effects of salinity on primary processes of photosynthesis in the red alga *Porphyra perforata*. Plant Physiology, 73(3): 643–647

Schmitt R W. 1996. If rain falls on the ocean-does it make a sound? Fresh water's effect on ocean phenomena. Oceanus, 39(2): 4–8

Steen H. 2004. Effects of reduced salinity on reproduction and germling development in *Sargassum muticum* (Phaeophyceae, Fucales). European Journal of Phycology, 39(3): 293–299

Wong C-L, Phang S-M. 2004. Biomass production of two *Sargassum* species at Cape Rachado, Malaysia. Hydrobiologia, 512(1–3): 79–88

Xia Jianrong, Li Yongjun, Zou Dinghui. 2004. Effects of salinity stress on PSII in *Ulva lactuca* as probed by chlorophyll fluorescence measurements. Aquatic Botany, 80(2): 129–137

Yamochi S. 2013. Effects of desiccation and salinity on the outbreak of a green tide of *Ulva pertusa* in a created salt marsh along the coast of Osaka Bay, Japan. Estuarine, Coastal and Shelf Science, 116: 21–28

Ying Weihai, Alano C C, Garnier P, et al. 2005. NAD^+ as a metabolic link between DNA damage and cell death. Journal of Neuroscience Research, 79(1–2): 216–223