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SPECIAL ISSUE: CLIMATE CHANGE AND ANTHROPOGENIC CHANGE AROUND KOREAN PENINSULA

Influence of Water Temperature Anomalies on the Growth of *Zostera marina* Plants Held Under High and Low Irradiance Levels

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Abstract

Coastal water temperature anomalies are expected to intensify during the current period of global climate change. Sudden water temperature elevation (e.g., heat waves) or decrease (e.g., summer upwelling) can have a far-reaching influence on seagrasses in temperate regions. We examined the influence of anomalously elevated and decreased water temperatures on the growth of *Zostera marina* plants held under two different levels of irradiance. Core samples of wild *Z. marina* shoots were cultured under either suddenly elevated (from the in situ level of 20 to 27 °C during the fall experiment) or decreased (from the in situ level of 27 to 20 °C during the summer experiment) temperature. We included light as an experimental factor because the light requirements of seagrasses increase when plants are under thermal stress. The growth of *Z. marina* shoots under anomalously elevated water temperature conditions, which simulated marine heat waves, was significantly declined, whereas the plant growth under suddenly decreased water temperature conditions, which simulated summer upwelling events, was maintained or slightly increased. In the fall 2014 experimental period, *Z. marina* shoots under the suddenly elevated water temperature condition (27 °C) showed significant decreases in shoot density, biomass, and leaf productivity by ca. 40–80%, whereas plants held under the ambient water temperature condition (20 °C) maintained or slightly increased their growths. In the summer 2015 experimental period, *Z. marina* under the sudden temperature reduction conditions (20 °C) maintained relatively high shoot density and leaf productivity, whereas plants under the in situ high water temperature condition (27 °C) showed significantly reduced growths. The growth of *Z. marina* shoots, which were cultured in the optimal temperature condition (20 °C), was enhanced by increasing underwater irradiance. However, the adverse effects of high water temperature on *Z. marina* growth could not be reversed by increasing irradiance levels at the end of the experiments. According to the results of this study, the intensified sea surface water temperature anomalies induced by global climate change will alter the growth and distribution of temperate seagrasses and, consequently, the structure and function of the coastal seagrass ecosystems in the temperate region.

Keywords Climate change · Growth · Light availability · Seagrass · Water temperature anomalies · *Zostera marina*

Introduction

Seagrasses are highly productive marine angiosperms that form extensive meadows in shallow coastal areas, where they provide diverse ecosystem services, including resources for commercial fisheries, nutrient cycling, sediment stabilization, and globally significant sequestration of carbon (Short and Short 1984; Duarte and Chiscano 1999; Green and Short 2003; Fourqurean et al. 2012). However, seagrasses face increasing threats from both local- and global-scale stresses; loss of seagrass beds has been reported worldwide (Orth et al. 2006; Waycott et al. 2009; Grech et al. 2012). At local scales, declines in seagrass coverage are largely attributable to increased nutrient inputs and coastal transformations resulting in lower water quality and higher turbidity (Short and Wyllie-Echeverria 1996; Orth et al. 2006). Ongoing global climate change, which is increasing sea surface temperature and raising water levels, is considered a global-scale threat to seagrass growth and distribution (Short and Neckles 1999; Hoegh-Guldberg and Bruno 2010).

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Global climate change-related temperature anomalies, such as heat waves and El Niño, can lead to significant changes in coverage, species composition, distributional range, and ecosystem services of seagrass habitats (Franssen et al. 2014; Fraser et al. 2014; Thomson et al. 2015; Hyndes et al. 2016; Reynolds et al. 2016; Nowicki et al. 2017; Arias-Ortiz et al. 2018; Lin et al. 2018). On the other hand, the episodic upwelling of cool and nutrient-rich subsurface water can release seagrass from summer thermal stresses (Thom et al. 2003). Because the frequency and intensity of anomalous temperature events in the marine environment is projected to increase during the current period of ongoing global climate change, more attention should be given to the impacts of the surface water temperature anomalies on seagrass ecosystems (Wang et al. 2015; Frölicher and Laufkötter 2018; Oliver et al. 2018).

High water temperature that exceeds the growth optimal can be a major threat to the growth and survival of temperate seagrasses (Lee et al. 2005; Marbà and Duarte 2010; Jordà et al. 2012; Moore et al. 2012). Numerous previous studies have documented that manipulated exposure to high temperature (e.g., > 25 °C) led to a decrease in the growth, photosynthesis, and survival rate of seagrasses (Touchette et al. 2003; Nejrup and Pedersen 2008; Bergmann et al. 2010; Collier et al. 2011; York et al. 2013; Beca-Carretero et al. 2018; Moreno-Marín et al. 2018). Significant increases in marine heat waves have been detected over the past century, with global average marine heat wave frequency and duration increased by 34 and 17%, respectively, and annual marine heat wave days increased by 54% globally (Oliver et al. 2018). Marine heat waves can cause maximum sea surface temperature anomalies of > 6 °C and last from days to months (Frölicher and Laufkötter 2018). Thus, temperate seagrasses will be increasingly subjected to sudden temperature increases during the growing season; these increase shoot mortality rates (Marbà and Duarte 2010; Jordà et al. 2012; Fraser et al. 2014; Moore et al. 2014; Arias-Ortiz et al. 2018). The mean global sea surface temperature is projected to rise by 1–3 °C by 2100 (IPCC 2014), which, together with the expected longer and more frequent marine heat waves in the future (Oliver et al. 2018), raises concerns over how seagrasses respond to these thermal stresses.

Thermal stress significantly affects the biochemical processes involved in photosynthesis and respiration and the maintenance of carbon balance (Bulthuis 1987; Lee et al. 2007; Collier et al. 2011; Ewers 2013). The respiration rate increases more rapidly than the rate of photosynthesis with increasing temperature, which consequently leads to a negative carbon balance at above threshold temperatures (e.g., 25 °C for *Zostera marina*) (Marsh et al. 1986; Zimmerman et al. 1989; Staehr and Borum 2011; Ewers 2013). Seagrasses usually require increased light levels for survival and growth when water temperatures are elevated (Marsh et al. 1986; Staehr and Borum 2011; Moore et al. 2012; Kim et al. 2015). The adverse interaction effects of low light and high temperature on temperate seagrasses have been well documented (Collier et al. 2011; York et al. 2013; Moreno-Marín et al. 2018). Reduced light availability and exposures to high summer water temperatures usually jointly lead to long-term declines in temperate seagrasses (Fraser et al. 2014; Moore et al. 2014). On the other hand, increased light availability, due to improved water quality, should potentially facilitate the growth and survival of seagrasses in the face of a warming climate (Collier et al. 2011; Zimmerman et al. 2015).

Although the sea surface temperature is increasing gradually under global climate change, some local ecosystems including seagrass meadows may experience sudden water temperature decline due to cold water upwelling or transition from El Niño to La Niña events (Curiel et al. 1996; Thom et al. 2003; Hessing-Lewis and Hacker 2013). Coastal upwelling events in many parts of ocean margins including the east coast of Korea are predicted to intensify under climate change (Park and Kim 2010; Wang et al. 2015). Decreased summer water temperatures and/or shorter high summer water temperature periods induced by cold water upwelling can ameliorate high temperature stress on temperate seagrass meadows over the summer months (Thom et al. 2003). Nutrient-rich upwelling can also cause algal and phytoplankton blooms, which increase turbidity and lower the light availability and, consequently, reduce the growth and survival of seagrasses (McGlathery 2001; Ahn et al. 2006; Hyun et al. 2009; Hessing-Lewis and Hacker 2013; Kim et al. 2014). Thus, light conditions should also be taken into account when examining the effect of water temperature anomalies on seagrasses. There is limited information available regarding the interactive effects of water temperature anomalies (e.g., heat waves and cold water upwelling) and light availability on seagrass growths.

Eelgrass *Zostera marina* is the most abundant seagrass species throughout the coastal waters of Korea, where its growth is influenced by rising water temperatures as well as anomalous temperature decline due to cold water upwelling events (Lee and Na 1985; Lee and Lee 2003; Lee et al. 2005; Park and Kim 2010). In the coastal waters of Korea, *Z. marina* is typically exposed to water temperatures that range from winter minima 5 °C to summer highs near 28 °C (Kim et al. 2016). The growth and abundance of *Z. marina* in this region are threatening by rising summer water temperatures exceeding 20 °C (Lee et al. 2005). On the contrary, in the 35.5–36.5° N latitude band of the eastern coastal waters of Korea, wind-induced cold water upwelling usually drops the sea surface temperatures to < 20 °C during summer, which causes the exposure of *Z. marina* to optimal temperature for growth (Lee and Na 1985; Lee et al. 2005; Park and Kim 2010). In this study, we examined the potential interaction effects of suddenly elevated (simulated heat wave events) or decreased (simulated cold water upwelling events) water temperature and light availability on the growth of *Z. marina*. We hypothesized that (i) sudden water temperature increases will suppress the growth and lower the survival rate of *Z. marina*, (ii) sudden temperature declines during summer periods will enhance seagrass growth, (iii) exposure to the combination of high temperature and low light will result in worst reduction in shoot density and leaf production, and (iv) increased light levels will offset the negative effects of high water temperature to some degree.

Materials and Methods

Sampling Site and Collection of Experimental Plants

The *Z. marina* shoots used for the experiment were collected from Koje Bay (34° 48′ N, 128° 35′ E) off the southern coast of Korea (Fig. 1). The sediment in Koje Bay was composed of approximately 85% sand and 15% silt. The tidal regime is semidiurnal; the tidal amplitude ranges from 2.5 m during spring tides to 1.2 m during neap tides. *Zostera japonica*, *Z. marina*, and *Z. caespitosa* are distributed along a water depth gradient from the intertidal zone to ca. 4 m below the mean lower low water (MLLW) level. Water temperatures ranged from 5 °C in January to 28 °C in August.

Two separate experiments were conducted in fall 2014 and summer 2015 (Fig. 2a). At the beginning of each experimental period, about 20 core samples of *Z. marina* shoots were collected from a monospecific meadow at a water depth of ca. 1 m below MLLW using a cylindrical acrylic plastic core (15 cm diameter, 65 cm long; Fig. 2b). The cylindrical acrylic plastic core was inserted to a sediment depth of ca. 15 cm, and intact eelgrass shoots and sediments within the cylinder were removed from the meadow. The core samples were transported to the laboratory and cultured under ambient water temperature/light conditions (20 °C/250 μmol photons m^{-2} s^{-1} for the fall 2014 experiment and 25 °C/300 μmol photons m^{-2} s^{-1} for the summer 2015 experiment) in a controlled environment room until used in the experiments (1–2 days).

Experimental Design

In each experiment, four to five core samples of *Z. marina* shoots were cultured under each of the four combinations of water temperature (20 and 27 °C) and photon irradiance (150 and 400 μmol photons m^{-2} s^{-1}; Fig. 2a). The experimental water temperature levels were selected according to the seasonal water temperature variation in the sampling site and expected water temperatures during the surface water temperature anomalies, such as heat waves and summer cold water upwelling events. In the fall 2014 experimental period, an ambient temperature condition of 20 °C, which is optimal temperature for *Z. marina* growth in the study area (Lee et al. 2005), was treated as control, while a sudden water temperature increase to 27 °C was considered as a simulated heat wave event treatment (Fig. 2a). The high water temperature of 27 °C was determined according to the maximum sea surface temperature anomalies of > 6 °C caused by marine heat waves (Frölicher and Laufkötter 2018). In the summer 2015 experimental period, an ambient temperature condition of 27 °C at the study site during this period was treated as control, while a sudden water temperature decrease to 20 °C was regarded as a simulated cold water upwelling event treatment. A typical water temperature of < 20 °C was observed during the summer upwelling events on the eastern coastal waters off Korea (Lee and Na 1985; Park and Kim 2010). Overall, the impact of a sudden water temperature increase from 20 to 27 °C (simulated heat waves) on the growth of

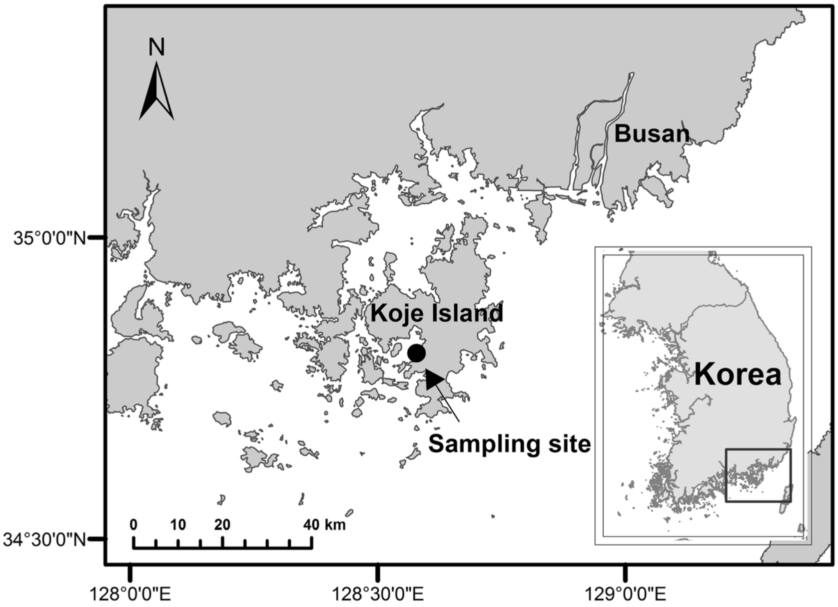

Fig. 1 Map showing the location of the sampling site of *Zostera marina* on the southern coast of Korea

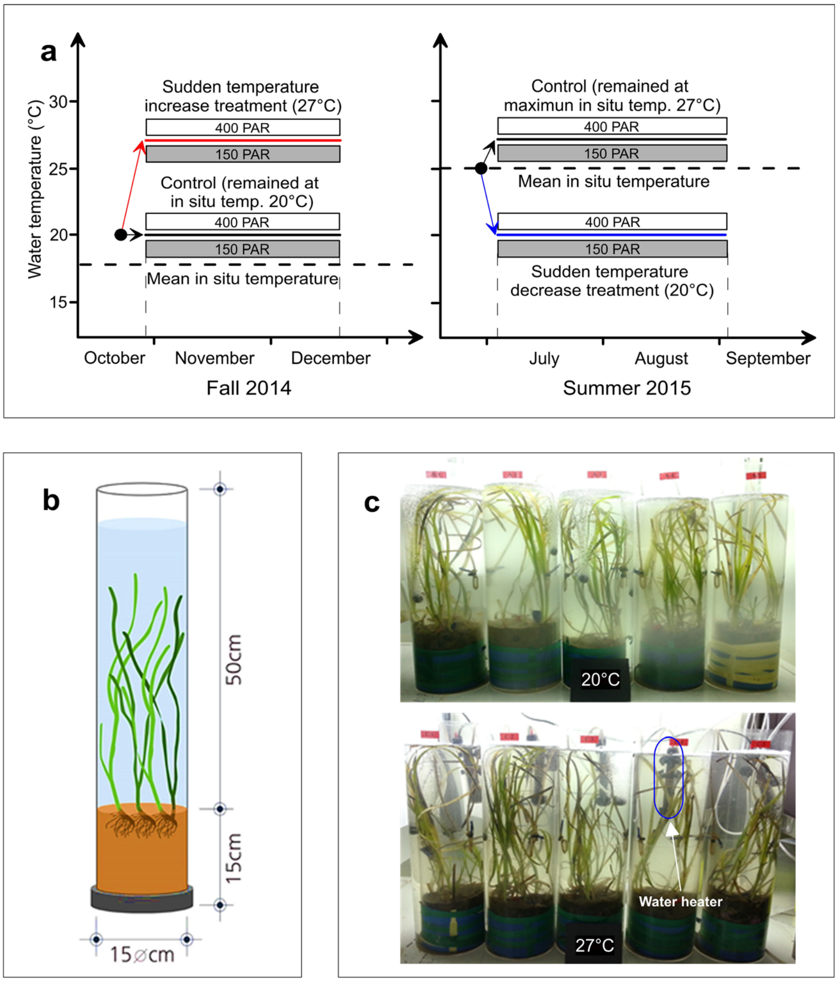

Fig. 2 Schematic diagram of the experimental designs in fall 2014 and summer 2015 (**a**). Diagram of an acrylic plastic incubation chamber (**b**). Photographic images of arrays of incubation chambers (**c**): the upper row of five chambers was maintained under optimal temperature (20 °C); the lower row was maintained under suboptimal temperature (27 °C) using underwater heaters

Z. marina was examined in the fall 2014 experiment, while the influence of a sudden water temperature decrease from 27 to 20 °C (simulated summer cold water upwelling) was examined in the summer 2015 experiment.

The experimental irradiance levels were selected based on the saturating photon irradiance required for *Z. marina* growth in the study site. The saturating photon irradiance measured in the laboratory for photosynthesis of a single *Z. marina* leaf from the study site was ca. 90 μmol photons m^{-2} s^{-1} in summer and 120 μmol photons m^{-2} s^{-1} in fall (Park et al. 2016). The saturation irradiances required for photosynthesis of whole plants in the field condition are typically 3–6 times higher than those required for individual leaves (Herzka and Dunton 1997; Zimmerman 2003; Hu et al. 2012). Thus, we selected two different levels of saturation irradiance: 150 μmol photons m^{-2} s^{-1} as the saturation irradiance for a single leaf and 400 μmol photons m^{-2} s^{-1} as the saturation irradiance for intact shoots.

The experiments were conducted in a controlled environment room with constant temperature (20 °C) throughout the experimental periods. The water temperature of the 27 °C treatment core chamber was increased and maintained at 27 °C using underwater water heaters. The two different levels of irradiance (150 and 400 μmol photons m^{-2} s^{-1}) were provided by LED lights on a 14:10 L:D cycle throughout the experimental period (Fig. 2c). Four to five core samples were randomly assigned to each temperature/photon irradiance treatment combination (i.e., 20 °C/150 PAR, 20 °C/400 PAR, 27 °C/150 PAR, and 27 °C/400 PAR). All the experimental core chambers were cultured for 7–8 weeks, aerated, and regularly cleaned, and the seawater was changed every 2 weeks. The experimental period was decided according to the typical durations of marine heat waves across the Pacific Ocean (1–8 weeks; Oliver et al. 2018) and upwelling events during summer on the coasts of Korea (~ 8 weeks; Lee and Na 1985).

Biological Measurements

Shoot density, morphology, and leaf productivity of *Z. marina* in the culture chambers were assessed every 2 weeks throughout the experimental periods. After counting the number of shoots in each chamber, three were randomly tagged using a modified blade marking technique (Kentula and McIntire

1986); changes in leaf length were measured after 2 weeks. Leaf productivity was estimated using the weight to length ratio (mg cm^{-1}) of the youngest mature leaf, which was usually the third leaf on each shoot (Short and Duarte 2001). The weight to length ratio of in situ *Z. marina* shoots from the donor meadow in Koje Bay was used to estimate the leaf productivity of the experimental *Z. marina* shoots. Approximately 10 shoots were collected from the donor meadow every 2 weeks (corresponding to the schedule of the laboratory experiments); we measured the weight to length ratio of the youngest mature leaves in these collections. A leaf segment 20–30 cm in length was cut from each shoot and oven-dried at 60 °C to constant weight. The weight to length ratio was calculated by dividing the dry weight (DW) by the length of the leaf segment. Leaf productivity was estimated by multiplying the total length of new leaf tissue produced after tagging by the weight to length ratio. The areal leaf productivity (g DW m^{-2} day^{-1}) was calculated by multiplying the leaf productivity per shoot (mg DW shoot^{-1} day^{-1}) by shoot density.

Shoot morphological characteristics were carefully measured in the culture chambers without harvesting *Z. marina* tissues. Specifically, two to three shoots were randomly selected in each chamber every 2 weeks for measurement of sheath length and shoot height. Sheath length was measured from the meristem to the top of the sheath, and shoot height was measured from the meristem to the tip of the longest leaf. At the end of each experimental period, *Z. marina* plants in each chamber were harvested and rinsed in freshwater to remove sediments and epiphytes. For biomass measurement, the tissues were separated into above- (leaf and sheath) and belowground (rhizome and root) portions that were dried at 60 °C to constant weight. Both shoot density and biomass are expressed here on a unit area basis (m^{-2}).

Measurement of the Maximum Quantum Yield

The maximum quantum yield (F_v/F_m) of photosystem II (PSII) was measured with a PAM fluorometer (Diving-PAM; Heinz Walz GmbH, Germany) fitted with an 8-mm fiber optic. Measurements were made at the beginning and end of the summer 2015 experimental period. The measurements were taken in the mid sectors of the youngest mature leaves from 3 to 5 shoots in each chamber. The F_v/F_m was measured after 15-min dark acclimation. The quantum yield was calculated from the following equation: $F_v/F_m = (F_m - F_0) / F_m$, where F_0 is the minimal fluorescence of a dark-acclimated leaf in which all PSII reaction centers are open, and F_m is the corresponding maximum fluorescence measured with all PSII reaction centers closed following a short (0.8 s) burst of saturating light (Van Kooten and Snel 1990; Ralph and Gademann 2005).

Statistical Analyses

Significant effects of water temperature and photon irradiance level on shoot density, morphological characteristics, leaf productivity, and F_v/F_m across measurement times were identified by a three-way analysis of variance (ANOVA) model. The differences in eelgrass biomass (at the end of the experimental periods) between water temperature and photon irradiance treatments were analyzed by a two-way ANOVA. When significant differences were detected, a post hoc test was conducted to identify where the significant differences occurred. Before conducting inferential statistical tests, the data were tested for normality and homogeneity of variance. Where necessary, raw variables were log- or square-root-transformed to meet the assumptions of parametric statistics. An alpha level of 0.05 was used in all statistical tests. All statistical analyses were performed with SPSS software (ver. 23.0; IBM Corp., USA).

Results

Shoot Density, Leaf Productivity, and Morphological Characteristics

Shoot density differed significantly ($p < 0.01$) between temperature and light treatment levels in both the fall 2014 and summer 2015 experimental periods (Fig. 3a, b; Tables 1 and 2). At the beginning of each experimental period, the initial shoot densities were not significantly ($p > 0.05$) different among different temperature/light treatment combinations. During the fall 2014 experimental period, shoot density gradually increased by 89.0% under in situ water temperature (20 °C) and high light (400 PAR) treatments and slightly increased by 12.8% under the 20 °C/150 PAR treatment by the end of the experiment. However, shoot density decreased by 72.6–83.2% under elevated high temperature (27 °C/400 PAR and 27 °C/150 PAR) at the end of 7-week experiment. The negative effects of sudden water temperature elevation and low light availability on shoot density were apparent at 2 weeks after the beginning of the experiment and intensified over time (Fig. 3a). In the summer 2015 experiment, shoot density increased by 23.8–47.6% under sudden temperature decrease treatments (20 °C) but decreased by 40.0–67.4% under ambient water temperature condition (27 °C). Significant ($p < 0.05$) water temperature and light effects were detected at 6 weeks after the beginning of the experiment (Fig. 3b). The detrimental effect of high water temperature on *Z. marina* shoot density was exacerbated under low light conditions in both the fall 2014 and summer 2015 experiments (Fig. 3a, b).

Leaf productivity per shoot and areal leaf productivity were significantly ($p < 0.01$) different between water temperature and light availability treatments in both the fall 2014 and summer 2015 experiments (Fig. 3c–f; Tables 1 and 2). During the fall

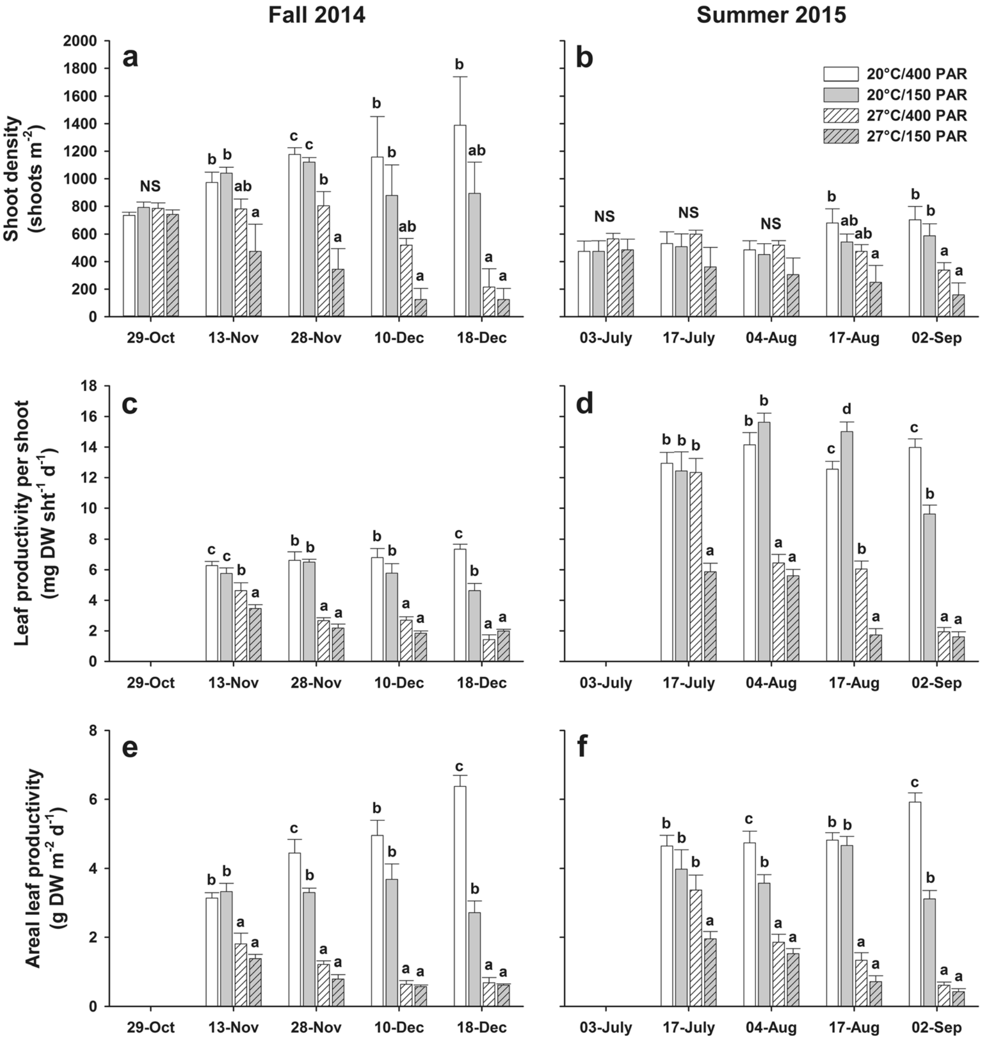

Fig. 3 *Zostera marina*: shoot density (**a**, **b**), leaf productivity per shoot (**c**, **d**), and areal leaf productivity (**e**, **f**) in incubation chambers under different combinations of temperature and light conditions during the experimental periods in fall 2014 and summer 2015. Values are means ± SE ($n = 3$–5). Different letters on the bars indicate significant ($p < 0.05$) differences between treatment means within dates. NS, no significant difference

2014 experimental period, leaf productivity per shoot increased slightly over time under the 20 °C/400 PAR treatment combination but decreased markedly over time under sudden water temperature elevation treatments (i.e., 27 °C/400 PAR and 27 °C/150 PAR; Fig. 3c). During the summer 2015 experimental period, leaf productivity per shoot was relatively consistent over time under the sudden water temperature decrease treatments (20 °C) but decreased markedly under the in situ summer water temperature condition (27 °C) (Fig. 3d). The temporal trends in areal leaf productivity were similar to those of leaf productivity per shoot in both the fall 2014 and summer 2015 experiments (Fig. 3e, f). At the end of the fall 2014 experimental periods, the areal leaf productivity of *Z. marina* under the ambient temperature condition (20 °C) increased by 103.2% in the high irradiance treatment (400 PAR) but slightly decreased by 18.5% in the low irradiance treatment (150 PAR). However, the areal leaf productivity decreased by 55.2–61.9% under the sudden water temperature elevation conditions (27 °C/400 PAR and 27 °C/150 PAR; Fig. 3e). At the end of the summer 2015 experiment, areal leaf productivity increased by 27.3% under the suddenly decreased water temperature and high irradiance condition (20 °C/400 PAR), whereas it decreased by 21.7% under the low water temperature and low light condition (20 °C/150 PAR). However, areal leaf productivity under the ambient high summer temperature conditions (27 °C/400 PAR and 27 °C/150 PAR) decreased by 78.3–81.8% (Fig. 3f).

Shoot height and sheath length were significantly different ($p < 0.01$) between water temperature and light treatment levels in both the fall 2014 and summer 2015 experiments (with the exceptions of shoot height in fall 2014 and sheath length in summer 2015) (Table 2). Shoot height and sheath length decreased gradually over time under all temperature/light treatment combinations in both the fall 2014 and summer 2015 experiments (Fig. 4). Mean values of shoot height and sheath length were slightly higher under the low water temperature (20 °C) treatment than the high water temperature (27 °C) treatment (Table 1). Trends in the effects of water temperature and light availability on the shoot morphology of *Z. marina* were not consistent across the study periods (Fig. 4).

Table 1 Mean (± SE) values of shoot density, leaf productivity, morphological characteristics, and biomass of *Zostera marina* maintained in experimental chambers under different combinations of water temperature and irradiance during the experimental periods in fall 2014 and summer 2015

Experimental period	Fall (October–December) 2014				Summer (July–September) 2015			
Temperature (°C)	20		27		20		27	
Irradiance (μmol photons m^{-2} s^{-1})	150	400	150	400	150	400	150	400
Density (shoots m^{-2})	946.0 ± 59.3	1086.9 ± 109.9	362.4 ± 116.2	621.4 ± 114.2	514.1 ± 24.2	575.3 ± 48.2	312.5 ± 55.1	500.5 ± 45.4
Leaf productivity per shoot (mg DW $shoot^{-1}$ day^{-1})	5.66 ± 0.39	6.75 ± 0.22	2.37 ± 0.37	2.86 ± 0.31	13.17 ± 1.37	13.40 ± 0.39	3.70 ± 1.17	6.69 ± 2.14
Areal leaf productivity (g DW m^{-2} day^{-1})	3.25 ± 0.20	4.73 ± 0.67	0.84 ± 0.19	1.09 ± 0.15	3.83 ± 0.33	5.03 ± 0.30	1.16 ± 0.35	1.79 ± 0.58
Shoot height (cm)	29.4 ± 1.2	30.0 ± 1.5	29.3 ± 1.7	26.5 ± 0.9	45.3 ± 1.3	43.9 ± 1.6	43.0 ± 1.4	40.1 ± 1.6
Sheath length (mm)	62.0 ± 1.8	65.2 ± 2.2	57.3 ± 2.3	60.0 ± 2.3	91.8 ± 2.5	83.7 ± 2.9	85.5 ± 2.8	82.1 ± 3.6
Aboveground biomass (g DW m^{-2})	69.35 ± 6.05	170.00 ± 44.03	24.55 ± 2.82	42.69 ± 3.31	204.66 ± 30.57	281.80 ± 54.31	78.55 ± 4.39	134.29 ± 25.98
Belowground biomass (g DW m^{-2})	33.54 ± 4.85	159.76 ± 37.11	18.55 ± 5.65	24.23 ± 3.63	252.75 ± 17.55	301.68 ± 32.02	208.11 ± 65.56	94.86 ± 15.38
Total biomass (g DW m^{-2})	102.88 ± 10.69	329.76 ± 81.13	43.10 ± 8.47	66.93 ± 6.94	457.41 ± 46.06	583.48 ± 79.77	286.66 ± 66.27	229.15 ± 41.08
Above-/belowground biomass ratio	2.12 ± 0.18	1.05 ± 0.03	1.41 ± 0.28	1.78 ± 0.13	0.79 ± 0.09	0.92 ± 0.13	0.49 ± 0.19	1.38 ± 0.11

Biomass and Aboveground/Belowground Biomass Ratio

Aboveground, belowground, and total biomass were significantly ($p < 0.05$) different between temperature treatments, but not ($p > 0.05$) between light treatments at the end of the fall 2014 and summer 2015 experiments (with the exception of belowground biomass in fall 2014, which was significantly [$p = 0.035$] different between light treatments) (Fig. 5; Table 3). At the end of the fall 2014 experiment, *Z. marina* shoots in the 20 °C/400 PAR treatment combination had significantly ($p < 0.05$) higher aboveground biomass, belowground biomass, and total biomass than shoots under other conditions (Fig. 5a, c). At the end of the summer 2015 experiment, aboveground and total biomass under the decreased water temperature treatment (20 °C) were generally higher than the values in the high summer water temperature (27 °C; Fig. 5b, d).

The aboveground/belowground biomass ratios did not differ significantly ($p > 0.05$) between the temperature treatments in the fall 2014 and summer 2015 experiments but did differ significantly ($p = 0.001$) between light treatments at the end of the summer 2015 experiment (Fig. 5e, f; Table 3). We detected no consistent patterns in the aboveground/belowground biomass ratios under different temperature/light combinations (Fig. 5e, f).

Maximum Quantum Yield (F_v/F_m)

The F_v/F_m was significantly ($p = 0.001$) different between the temperature treatments and changed significantly ($p < 0.001$) over experimental time; light treatments had no significant ($p = 0.932$) effects on the F_v/F_m (Fig. 6; Table 2). In the first 2 weeks and the seventh week of the experiment, F_v/F_m did not differ significantly ($p > 0.05$) among temperature and light treatments. However, F_v/F_m was significantly ($p < 0.05$) lower under the high water temperature treatment (27 °C) than under the low water temperature treatment (20 °C) at the end of the experiment (Fig. 6).

Discussion

Seagrass Responses to Sudden Water Temperature Elevation and Decrease

The *Z. marina* in the coastal waters of Korea usually shows the highest growth during spring and fall when water temperatures are optimal for its growth (Lee et al. 2005, 2007). In the present study, *Z. marina* shoots cultured under the combination of optimal in situ water temperature and high light conditions (20 °C/400 μmol photons m^{-2} s^{-1}) in the fall 2014 experiment showed > 90% increases in the shoot density and

Table 2 Summary table of three-way ANOVA identifying significant effects of temperature (T), light (L), and measurement time (P) on shoot density, leaf productivity, morphological characteristics, and maximum quantum yield (F_v/F_m) of *Zostera marina* in fall 2014 and summer 2015 experiments. Significant results are indicated in italics ($p < 0.05$)

	Fall 2014					Summer 2015			
	Source	*df*	MS	*F*	*p*	*df*	MS	*F*	*p*
Shoot density	T	1	6,878,249	63.192	*< 0.001*	1	477,155	13.482	*< 0.001*
	L	1	999,813	9.186	*0.003*	1	387,905	10.960	*0.001*
	P	4	162,074	1.489	0.213	4	16,911	0.478	0.752
	T × L	1	87,242	0.802	0.373	1	100,535	2.841	0.096
	T × P	4	660,349	6.067	*< 0.001*	4	163,866	4.630	*0.002*
	L × P	4	100,376	0.922	0.455	4	13,705	0.387	0.817
	T × L × P	4	130,832	1.202	0.317	4	5562	0.157	0.959
Leaf productivity per shoot	T	1	315.758	187.751	*< 0.001*	1	2712.723	419.055	*< 0.001*
	L	1	15.239	9.061	*0.003*	1	107.510	16.608	*< 0.001*
	P	3	7.421	4.413	*0.005*	3	126.236	19.501	*< 0.001*
	T × L	1	2.206	1.312	0.245	1	78.649	12.150	*0.001*
	T × P	3	12.071	7.178	*< 0.001*	3	119.190	18.412	*< 0.001*
	L × P	3	0.811	0.482	0.695	3	34.131	5.272	*0.002*
	T × L × P	3	4.466	2.655	0.051	3	51.864	8.012	*< 0.001*
Areal leaf productivity	T	1	224.042	289.560	*< 0.001*	1	362.746	288.882	*< 0.001*
	L	1	18.085	23.374	*< 0.001*	1	34.963	27.844	*< 0.001*
	P	3	0.157	0.203	0.894	3	7.050	5.615	*0.001*
	T × L	1	9.202	11.893	*0.001*	1	3.304	2.631	0.107
	T × P	3	8.592	11.105	*< 0.001*	3	13.507	10.757	*< 0.001*
	L × P	3	3.503	4.527	*0.005*	3	2.041	1.625	0.185
	T × L × P	3	5.114	6.609	*< 0.001*	3	5.256	4.186	*0.007*
Shoot height	T	1	82.568	14.514	*< 0.001*	1	138.828	19.463	*< 0.001*
	L	1	1.497	0.263	0.611	1	67.214	9.423	*0.004*
	P	4	42.963	75.520	*< 0.001*	4	2317.614	324.916	*< 0.001*
	T × L	1	11.436	2.010	0.164	1	8.613	1.207	0.278
	T × P	4	11.933	2.098	0.100	4	16.138	2.262	0.079
	L × P	4	7.643	1.343	0.272	4	6.497	0.911	0.467
	T × L × P	3	13.337	2.351	0.088	4	6.501	0.911	0.467
Sheath length	T	1	513.590	33.943	*< 0.001*	1	233.817	8.382	*0.006*
	L	1	237.753	15.713	*< 0.001*	1	494.166	17.714	*< 0.001*
	P	4	1024.080	67.681	*< 0.001*	4	13,257.921	475.260	*< 0.001*
	T × L	1	22.093	1.460	0.234	1	81.629	2.926	0.095
	T × P	4	29.725	1.964	0.120	4	500.948	17.958	*< 0.001*
	L × P	4	34.450	2.277	0.079	4	67.335	2.414	0.065
	T × L × P	3	84.684	5.597	*0.003*	4	102.333	3.668	*0.012*
F_v/F_m	T					1	0.082	12.120	*0.001*
	L					1	0.000	0.007	0.932
	P					3	0.111	16.476	*< 0.001*
	T × L					1	0.005	0.694	0.410
	T × P					3	0.037	5.425	*0.003*
	L × P					3	0.007	0.991	0.406
	T × L × P					3	0.003	0.414	0.744

Fig. 4 *Zostera marina*: shoot height (**a**, **b**) and sheath length (**c**, **d**) in incubation chambers under different combinations of temperature and light conditions during the experimental periods in fall 2014 and summer 2015. Values are means ± SE ($n = 5$–10). Different letters on the bars indicate significant ($p < 0.05$) differences between treatment means within dates. NS, no significant difference

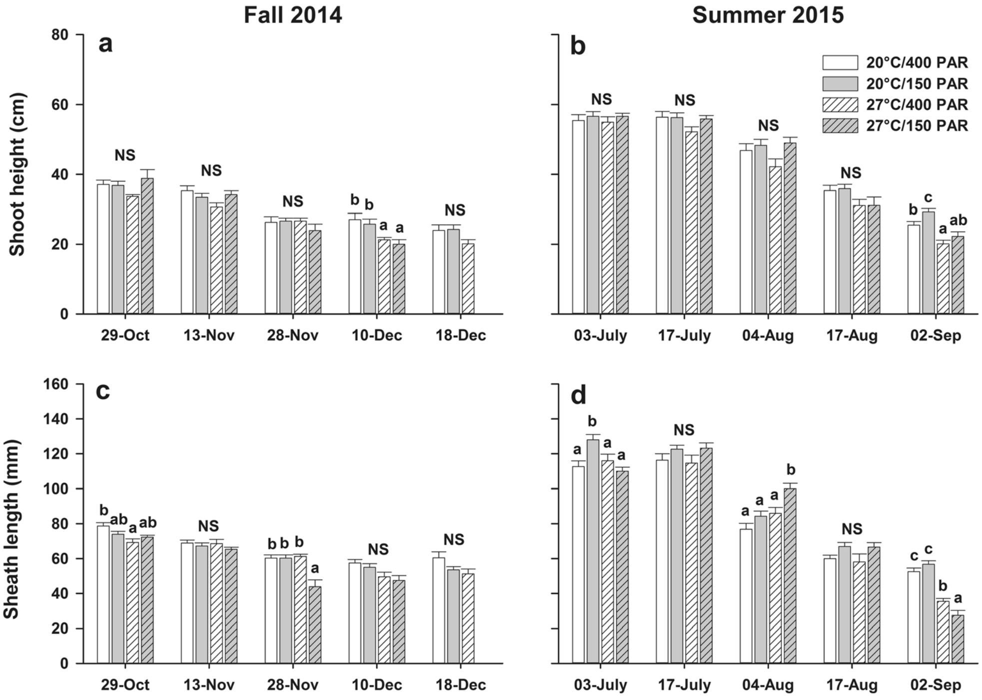

Fig. 5 *Zostera marina*: above- and belowground biomass (**a**, **b**), total biomass (**c**, **d**), and above- to belowground biomass ratio (**e**, **f**) in incubation chambers at the end of the experimental periods in fall 2014 and summer 2015. Values are means ± SE ($n = 3$–5). Different letters on the bars indicate significant ($p < 0.05$) differences between treatment means within dates

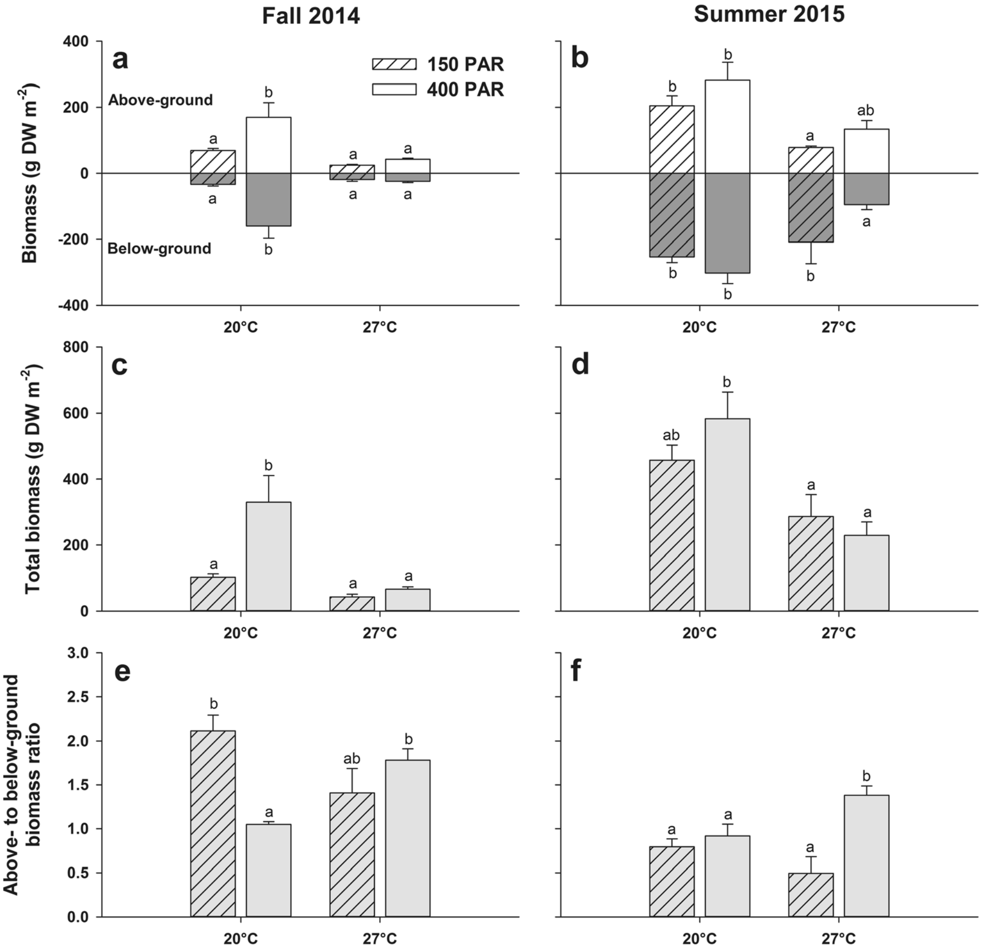

Table 3 Summary table of two-way ANOVA identifying significant effects of temperature (T) and light (L) on aboveground biomass, belowground biomass, total biomass, and the aboveground/belowground biomass ratio of *Zostera marina* at the end of the experimental periods in fall 2014 and summer 2015. Significant results are indicated in italics ($p < 0.05$)

	Fall 2014					Summer 2015			
	Source	*df*	MS	*F*	*p*	*df*	MS	*F*	*p*
Aboveground biomass	T	1	17,771.490	8.970	*0.024*	1	80,221.543	12.301	*0.003*
	L	1	8467.807	4.274	0.084	1	18,918.199	2.901	0.111
	T × L	1	4084.223	2.061	0.201	1	490.295	0.075	0.788
Belowground biomass	T	1	13,593.511	9.604	*0.021*	1	67,745.249	16.588	*0.001*
	L	1	10,440.667	7.376	*0.035*	1	4431.727	1.085	0.315
	T × L	1	8718.511	6.160	*0.048*	1	28,181.245	6.900	*0.020*
Total biomass	T	1	62,450.493	9.270	*0.023*	1	295,406.657	17.997	*0.001*
	L	1	37,713.746	5.598	0.056	1	5037.057	0.307	0.588
	T × L	1	24,737.279	3.672	0.104	1	36,105.819	2.200	0.160
Above- to belowground biomass ratio	T	1	< 0.001	0.006	0.943	1	0.028	0.406	0.534
	L	1	0.287	4.446	0.080	1	1.091	15.919	*0.001*
	T × L	1	1.243	19.222	*0.005*	1	0.622	9.073	*0.009*

areal leaf productivity. On the contrary, the growth of *Z. marina* shoots was negatively affected by a sudden temperature elevation from 20 to 27 °C during the fall experiment, which was a simulated heat wave event. The shoot density and areal leaf productivity were significantly reduced after 1 week culture under the elevated water temperature of 27 °C, which consequently led to the significantly low biomass in the conditions. Touchette et al. (2003) reported that *Z. marina* that were cultured at elevated temperatures (3–4 °C above ambient water temperature) for 14 weeks decreased its shoot density and weight by 40–50%. Nejrup and Pedersen (2008) also reported overall negative effects of extremely high water temperatures (25–30 °C) on *Z. marina* growth, in which both the photosynthetic rate and leaf productivity decreased by 50–75% and shoot mortality increased 12-fold after 6 weeks of the high water temperature treatment. Similar negative effects of manipulated high water temperatures (25–28 °C) on the growth of *Z. marina* were found in temperate and subarctic populations (Bergmann et al. 2010; Beca-Carretero et al. 2018; Moreno-Marín et al. 2018). Marked reductions in growth and large-scale losses of seagrass have also been reported in natural seagrass meadows when plants experienced lethal high water temperatures (e.g., > 30 °C) (Jordà et al. 2012; Moore et al. 2012, 2014; Nowicki et al. 2017; Arias-Ortiz et al. 2018). High water temperature that exceeds the optimum temperature threshold for seagrass growth usually results in critical metabolic imbalances with severe reductions in photosynthesis and increases in respiration and, consequently, a negative carbon balance; this may cause low growth and high mortality rates (Zimmerman et al. 1989; Collier et al. 2011; Moreno-Marín et al. 2018). Thus, the sudden water temperature elevation induced by marine heat waves will probably lead to continual and severe declines in shoot density, biomass, and leaf productivity, with consequent irreversible degradation of *Z. marina* meadows. Global climate change has elevated sea surface temperatures (IPCC 2014) and increased the frequency and intensity of extreme thermal events such as heat waves (Oliver et al. 2018). Temperate seagrasses, especially those near their southern distributional limits, are at risk of local extinction due to the intensified thermal stresses induced by climate change (Short and Neckles 1999; Waycott et al. 2009).

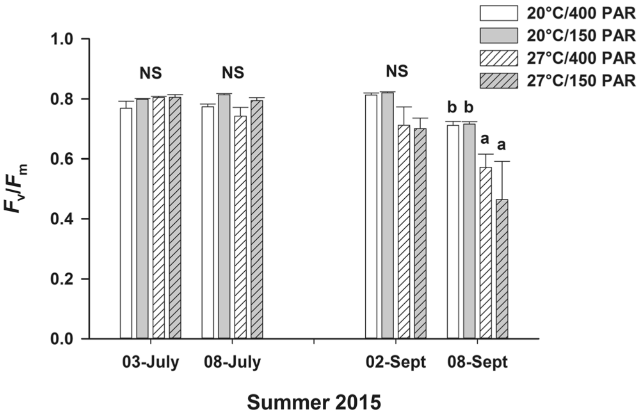

Fig. 6 *Zostera marina*: maximum quantum yield (F_v/F_m) in incubation chambers under different combinations of temperature and light conditions at the beginning and end of the experimental periods in summer 2015. Values are means ± SE ($n = 3$–5). Different letters on the bars indicate significant ($p < 0.05$) differences between treatment means within dates. NS, no significant difference

Summer cold water upwelling will cause a sudden decrease of surface water temperature, and the decreased water temperature may alter the responses of marine foundation species, thereby offsetting changes associated with gradual warming trends (Curiel et al. 1996; Thom et al. 2003; Hessing-Lewis and Hacker 2013). In the summer 2015 experiment, *Z. marina* shoots held under ambient water temperature of 27 °C decreased the F_v/F_m by 35% and the shoot density and leaf productivities by ca. 40–85% by the end of the experimental period. By contrast, the growth of *Z. marina* shoots was enhanced when the plants were exposed to the sudden temperature reduction from 27 to 20 °C. The optimal growth temperature for eelgrass *Z. marina* in the study area is in the range 15–20 °C, and the growth is inhibited by water temperatures > 20 °C (Lee et al. 2005). The sudden water temperature decrease treatment in the summer 2015 experiment increased the growth rate of *Z. marina* shoots, resulting in increases in the shoot density and areal leaf productivity by ca. 30–50% under high light condition. This is in line with the results of numerous laboratory studies that *Z. marina* cultured at optimal temperature of 20 °C showed much higher leaf production and survival rate than those cultured at higher temperatures (e.g., > 25 °C) (Nejrup and Pedersen 2008; Salo and Pedersen 2014; Beca-Carretero et al. 2018). Thom et al. (2003) documented that *Z. marina* in a bay system increased the density and biomass substantially in response to consecutive warm winters and cool summers, which was associated with coastal cold water upwelling and a climate change event such as the transition from El Niño to La Niña. Reduced exposure of *Z. marina* to high summer water temperature could occur in some areas such as the eastern coast of Korea where strong upwelling events are prevalent during the summer months (Son et al. 2006; Park and Kim 2010). The frequency of these upwelling events has become increasingly anomalous due to stronger and more persistent southerly winds, such as typhoons, blowing off the coasts of the Korean peninsula (Son et al. 2006; Park and Kim 2010). Summer surface water temperature decrease induced by climate change may play an increasingly important role in the maintenance and stability of *Z. marina* populations in the upwelling regions.

Interaction Effects of Light Availability and Anomalously Elevated and Decreased Water Temperature

In the present study, *Z. marina* shoots cultured under high water temperature with lower underwater irradiance (27 °C/150 PAR) exhibited the lowest values in shoot density, leaf productivity, and aboveground biomass, although the values of these parameters were not statistically significantly lower than those under the 27 °C/400 PAR condition. Negative effects of high water temperature and low underwater irradiance on the temperate seagrass growths have been reported (Collier et al. 2011; Moreno-Marín et al. 2018). Beca-Carretero et al. (2018) reported that light-limited *Z. marina* could be more sensitive to warming because light limitation would reduce the optimum temperature for growth and photosynthesis by 5 to 10 °C. Bulthuis (1987) also documented similar patterns for many seagrass species that the optimum temperature for photosynthesis decreased from 25 to 35 °C at saturating light to as low as 5 °C when irradiance was much lower. Thus, plants that grow at light-limited conditions may be highly vulnerable to extreme temperatures. The effects of exposure to high temperature or low light or to both are largely related to alterations in the carbon budget of the plants (Moreno-Marín et al. 2018). The stressors usually reduced the sequestration and storage of C in plant tissue, drained the C reserves, and led to a negative carbon budget; this could finally result in higher shoot mortality and decline of population size (Collier et al. 2011; Ewers 2013; York et al. 2013; Eriander 2017; Beca-Carretero et al. 2018; Moreno-Marín et al. 2018). The more often and intensive heat waves and gradually increasing summer sea water temperature due to global climate change, combined with severe light reduction events caused by various anthropogenic activities, may become serious problems for the temperate seagrass, which exists near its upper thermal limits (Marbà and Duarte 2010; Collier et al. 2011; Jordà et al. 2012; Moore et al. 2012; Thomson et al. 2015). These combined effects of high water temperature and low irradiance may lead to losses of indigenous seagrass population and/or replacement by other algae and seagrass species and ultimately result in the transformation of structure and ecosystem services of seagrass meadows (Collier et al. 2011; Franssen et al. 2014; Thomson et al. 2015; Hyndes et al. 2016; Arias-Ortiz et al. 2018).

Higher irradiance of 400 μmol photons m^{-2} s^{-1} had an overall positive effect on the shoot density, leaf productivity, and biomass of *Z. marina* in both the fall 2014 and summer 2015 experiments. However, the enhancement effect of increased light availability on *Z. marina* growth was varied according to the condition of water temperature. The high irradiance treatment did not significantly enhance the growth of *Z. marina* when the plants were cultured in high temperature conditions (27 °C) for 7–8 weeks. Collier et al. (2011) found similar patterns in a temperate seagrass species *Zostera muelleri*. The growth and photosynthesis of *Z. muelleri* could not benefit from the high irradiance treatment (400 μmol photons m^{-2} s^{-1}) after culturing at a high temperature of 33 °C, which is 6 °C higher than the optimal growth temperature (Collier et al. 2011; York et al. 2013). Because the irradiance threshold generally increases with increasing temperature, seagrass requires higher light availability for growth and survival under high temperature stress conditions (Marsh et al. 1986; Staehr and Borum 2011; Moore et al. 2012; Ewers 2013; Kim et al. 2015). However, plants could not utilize light for photosynthesis under lethal temperature conditions due to the damage of photosynthetic apparatus although there is enough light (Collier et al. 2011; York et al. 2013). Thus, increased light availability to a saturating level for whole plants (400 μmol photons m^{-2} s^{-1}) could not alleviate the negative effects of the high water temperature (27 °C) on *Z. marina* growth at the end of this experiment.

By contrast, the growth of *Z. marina* at the optimal growth temperature of 20 °C was significantly enhanced under the increased underwater irradiance (400 μmol photons m^{-2} s^{-1}) compared to that under lower light condition (150 μmol photons m^{-2} s^{-1}). This result suggests that an increase of light availability plays a critical role on enhancing *Z. marina* growth under the optimal temperature condition. On the east coast of Korea, the cold water upwelling event in summer can drop the water temperatures from 27–28 to < 20 °C, which were optimal for *Z. marina* growth (Lee et al. 2005; Nejrup and Pedersen 2008; Park and Kim 2010). It can be suggested that growth of *Z. marina* will be more significantly affected by increased light availability due to improved water quality when the water temperature was decreased by the summer cold water upwelling.

In conclusion, the growth of *Z. marina* was dramatically reduced by the sudden elevation of water temperature from the ambient water temperature of 20 to 27 °C during the fall 2014 experiment, which simulated the water temperature condition in marine heat waves. By contrast, the growth of *Z. marina* was significantly enhanced by the sudden decrease of water temperature from the summer high water temperature of 27 to 20 °C, an optimal growth temperature for *Z. marina*, during the summer 2015 experimental period, which simulated the temperature condition during summer cold water upwelling events. Increase of underwater light availability (400 μmol photons m^{-2} s^{-1}) benefited the growth of *Z. marina* when the plants were cultured under optimal growth temperature (20 °C). However, high irradiance level could not alleviate the detrimental effects of the extremely high water temperature (27 °C) on the growth of *Z. marina* at the end of the experiments. Global climate change generally induces increasing sea surface temperatures and the frequency and intensity of sea surface water temperature anomalies including heat waves and coastal cold water upwelling (IPCC 2014; Wang et al. 2015; Oliver et al. 2018). The increased incidence of high thermal stresses will drive dramatic declines in *Z. marina* growth, with consequent irretrievable degradation of *Z. marina* habitats. By contrast, summer cold water upwelling may alleviate the negative effects of heat stress especially in areas with high light availability. The results of the present study provide invaluable information that will be useful for predicting the fate of temperate seagrasses under the intensified surface water temperature anomalies induced by global climate change.

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