Estuaries and Coasts (2020) 43:449–462
https://doi.org/10.1007/s12237-019-00569-3

SPECIAL ISSUE: CLIMATE CHANGE AND ANTHROPOGENIC CHANGE AROUND KOREAN PENINSULA

Influence of Regional Water Temperature Variability on the Flowering Phenology and Sexual Reproduction of the Seagrass *Zostera marina* in Korean Coastal Waters

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Received: 21 April 2018 / Revised: 11 April 2019 / Accepted: 22 April 2019 / Published online: 3 May 2019

Abstract

Increasing sea surface temperature due to global climate change is a major threat to the growth and survival of many temperate seagrasses, while cold-water upwelling can potentially ameliorate high-temperature stress on temperate seagrass meadows during growing seasons. Seagrasses in the coasts of Korea are increasingly influenced by rising water temperatures and water temperature anomalies in recent decades due to climate change, but the impacts of such events on reproductive phenology of seagrasses remain poorly understood. We investigated the reproductive phenology and sexual reproduction of *Zostera marina* in four seagrass meadows along the coasts of Korea. Two study sites were located on the south coast where water temperature shows significant warming trends, while two other study sites were located on the east coast where coastal cold-water upwelling is prevalent. Water temperature exhibited stronger seasonality with cooler winter and warmer summer in the south coast sites than in the east coast sites. Cold-water upwelling events occurred frequently along the east coast of Korea, leading to anomalously cool water temperatures during the growing season. *Z. marina* flowering was prolonged and/or precocious at the east coast sites relative to the south coast sites. The mean flowering period was 5–7.5 months at the east coast sites and 3.5 months at the south coast sites. Moreover, reproductive shoot density and biomass, as well as the corresponding flowering frequency and reproductive efforts were much higher (2–3 times) at the east coast sites than at the south coast sites. Consequently, the potential seed production was higher in the east coast sites than in the south coast sites. Overall, high summer water temperature appeared to reduce sexual reproduction of *Z. marina* in the south coast sites, while regional cold-water upwelling on the east coast changed seasonal temperature patterns and decreased summer temperature highs, consequently provided a relatively long period of optimal water temperature for production of reproductive shoots. Regional water temperature variability has an important role in shifting the flowering responses of seagrass, which could affect the long-term stability and maintenance of seagrass meadows via the regulation of the sexual-asexual reproductive trade-off.

Keywords Climate change · Cold-water upwelling · Flowering phenology · Water temperature · Seagrass · *Zostera marina*

Introduction

Marine ecosystems are dramatically changing as a consequence of global climate change (Doney et al. 2012). Seagrasses are marine angiosperms that form extensive meadows in coastal waters, providing the foundation of ecosystems that are among the most productive on Earth (Duarte and Chiscano 1999). Seagrass meadows provide a wealth of ecologically and economically important ecosystem services (Larkum et al. 2006), but are reportedly declining worldwide (Waycott et al. 2009). Concern is growing over the impacts of ocean warming on seagrasses, particularly in regions where they are already threatened or near their upper thermal tolerance limits (Moore and Jarvis 2008; Marbà and Duarte 2010; Jordà et al. 2012; Thomson et al. 2015). Extensive losses of

Communicated by Richard C. Zimmerman

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seagrass have been reported due to exposure to lethal high water temperatures (e.g., > 30 °C) (Jordà et al. 2012; Moore et al. 2012; Moore et al. 2014; Nowicki et al. 2017; Arias-Ortiz et al. 2018). However, studies of various marine organisms have demonstrated that local or regional cold climatic anomalies such as cold-water upwelling could trigger positive marine ecosystem responses that may potentially offset the adverse impacts associated with gradual warming trends (Curiel et al. 1996; Jupp et al. 1996; Thom et al. 2003; Hessing-Lewis and Hacker 2013).

Plant reproductive phenology is of key importance in controlling the distribution and abundance of plant populations (Silvertown and Charlesworth 2009), and the timing and intensity of plant flowering can be highly responsive to climate change (Post 2003; Diaz-Almela et al. 2007; Inouye 2008). Sea surface temperature is increasing gradually under climate change. The mean global sea surface temperature is projected to rise by 1–3 °C by 2100 (IPCC 2014). The rising water temperature can impact the growth and reproduction of seagrass via alterations of the carbon budget of the plants (Marsh et al. 1986; Zimmerman et al. 1989; Zimmerman et al. 2017). Respiration of seagrass increases at much higher rates than photosynthesis with increasing water temperature, and consequently, seagrass may reduce the C sequestration and storage in plant tissues and drain the C-reserves, leading to a negative carbon budget under high thermal stress (Marsh et al. 1986; Zimmerman et al. 1989; Collier et al. 2011; Staehr and Borum 2011; Eriander 2017; Beca-Carretero et al. 2018; Moreno-Marín et al. 2018). Decreased growth and survival rates of temperate seagrass responding to high-temperature stresses have been reported (Moore et al. 2012; Moore et al. 2014; Nowicki et al. 2017; Arias-Ortiz et al. 2018). High thermal stress during summer could also significantly impact the timing, duration, and intensity of seagrass flowering in the following year due to small overwintering population sizes as well as insufficient amount of carbon in plant tissues available for reproduction (Zimmerman et al. 1989; Collier et al. 2011; Zimmerman et al. 2017; Moreno-Marín et al. 2018).

High water temperature stresses in coastal ecosystems can be mitigated under the conditions such as occurrences of cold-water upwelling or ocean climate transitions from El Niño to La Niña events (Curiel et al. 1996; Jupp et al. 1996; Thom et al. 2003; Hessing-Lewis and Hacker 2013). Anomalous wind-induced upwelling occurs in many coastal areas and can modify coastal environmental conditions via upwelling of cold and nutrient-rich water from the subsurface (Wang et al. 2015). Thus, coastal upwelling events have the potential to affect coastal plant communities, such as macroalgae (Curiel et al. 1996) and seagrass meadows (Jupp et al. 1996; Thom et al. 2003; Hessing-Lewis and Hacker 2013). The episodic upwelling of cool subsurface water can release seagrass from summer thermal stresses (Jupp et al. 1996; Thom et al. 2003). Summertime water temperature reductions resulting from upwelling may enhance seagrass P:R, enabling them to accumulate carbon reserves for use during the subsequent growing season (Zimmerman et al. 1989; Zimmerman et al. 2017). Coastal upwelling events are predicted to intensify under climate change, with strong and consistent changes in timing, intensity, and spatial heterogeneity (Wang et al. 2015). Thus, the effects of coastal upwelling events on seagrass flowering phenology and subsequent seed production should be evaluated.

Variability in the reproductive phenology of seagrasses under various natural and manipulated conditions has been documented (Walker et al. 2001). Temperature is considered a major determinant of the timing of flowering in many seagrass species, but the role of the photoperiod in controlling seagrass flowering phenology is not consistent among species (McMillan 1976; De Cock 1981; Phillips et al. 1981; McMillan 1982; Kaldy and Dunton 2000). Moreover, the flowering phenology of many *Zostera* species is strongly related to latitude, with a delay in the flowering sequence from south to north (Silberhorn et al. 1983; Walker et al. 2001), suggestive of their acclimation and adaptation to regional temperature and light regimes. The sexual reproduction of seagrass can vary significantly across temporal and spatial scales, which suggests that both large-scale and local environmental factors such as temperature, light, and nutrient availability have significant roles in controlling flower induction (van Lent et al. 1995; Diaz-Almela et al. 2006; Potouroglou et al. 2014; Smith et al. 2016; Johnson et al. 2017). However, the effects of these environmental factors on seagrass flowering intensity and seed production remain debated.

Eelgrass (*Zostera marina*) is the most widespread seagrass species in the temperate Northern Hemisphere of the Pacific and Atlantic Oceans (Moore and Short 2006), and dominates the coasts of Korea where it is influenced by rising water temperature as well as surface water temperature anomalies caused by regional coastal upwelling events (Lee and Lee 2003; Lee et al. 2005; Park and Kim 2010). Climate change has been increasing sea surface temperature during the past decades on the south coast of Korea (Kim et al. 2009; Kwak et al. 2015). *Z. marina* growth is threatened by increasing summer water temperatures (27–32 °C) because its growth is inhibited at water temperatures exceeding 20 °C (Lee et al. 2005). On the contrary, cold-water upwelling events are common along the east coast of Korea (Park and Kim 2010). The region around 35.5–36.5°N frequently experiences coastal upwelling during summer when southeasterly winds prevail between a low-pressure region over the Asian continent and high-pressure region over the Northwest Pacific (Lee and Na 1985; Park and Kim 2010). Upwelling events in this region occur episodically and drop the high summer water temperature by 5–15 °C for hours to days (Lee and Na 1985; Park and Kim 2010). However, nutrient-rich upwelling can also cause macroalgal and phytoplankton blooms, which may 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). Thus, the upwelling events on the east coast of Korea likely influence the growth and reproductive patterns of *Z. marina* by reducing the sea surface temperature, shortening the duration of high water temperatures, increasing nutrient inputs, as well as decreasing light availability through algal blooms. We investigated the flowering phenology and sexual reproduction of *Z. marina* in four *Z. marina* meadows along the south and east coasts of Korea, which were expected to have different regional water temperature regimes and light and nutrient availabilities. We hypothesized that there were differences in the flowering phenology and sexual reproduction of *Z. marina* across the regions, which might be largely attributed to the regional difference in seasonal water temperature patterns.

Materials and Methods

Study Sites

Four study sites located along a latitudinal gradient along the Korean coast were selected: Duksan Harbor and Bangeojin Harbor on the east coast and Jindong Bay and Koje Bay on the south coast (Fig. 1). *Z. marina* was the dominant seagrass species at all four study sites. In Duksan Harbor and Jindong Bay, *Z. marina* formed monospecific meadows, while *Phyllospadix japonicus* occurred on hard rocky substrata in Bangeojin Harbor, and *Zostera japonica*, *Z. marina*, and *Zostera caespitosa* were distributed sequentially from the intertidal zone to a depth of approximately 5 m relative to the mean lower low water line in Koje Bay. The water temperature regime follows different seasonal patterns among the study sites, mainly due to latitudinal differences and differences in upwelling events (Park and Kim 2010). *Z. marina* was distributed across a wide depth range (0–7 m) at the study sites, specifically at 3–7 m in Duksan Harbor and 0–3 m at the other study sites. All samplings were conducted in carefully selected monospecific *Z. marina* meadows at the study sites (Table 1).

Physical and Chemical Parameters

The water temperature at each study site was monitored every 15 min throughout the experimental period from October 2015 to October 2016 using a HOBO data logger (Onset Computer Corp., Bourne, MA, USA) encased in a waterproof underwater housing. The underwater irradiance at the seagrass canopy level was monitored every 15 min using an Odyssey photosynthetic irradiance recording system (Dataflow Systems Ltd., Christchurch, New Zealand) at each study site. Both the HOBO and Odyssey sensors were placed at the intermediate depth of each study site. Since underwater irradiance is usually measured with a spherical quantum sensor due to the diffuse nature of the light in the field conditions (Kirk 1994; Herzka and Dunton 1997), the logger was pre-calibrated using a LI-1400 data logger and LI-193SA spherical quantum sensor (Li-Cor, Lincoln, NE, USA). The Odyssey recorder and the LI-1400 quantum sensor were placed side-by-side outdoors over 3 days in August 2015. The calibration factor for the Odyssey recorder was then determined as the slope of a simple linear regression fitted to irradiance data of the two sensors. Temperatures were averaged daily, and the daily photosynthetic photon flux density (PPFD; mol photons m^{-2} d^{-1}) was calculated as the sum of the quantum flux over each 24-h period. The duration of PPFDs above light saturation points (H_{sat}) was estimated based on the saturation irradiance of 400 μmol photons m^{-2} s^{-1} required for photosynthesis of intact *Z. marina* plants (Lee et al. 2007). The in situ water depth at each study site was measured using a SCUBA digital bathometer. The water depth relative to the mean lower low water was calibrated by subtracting the tidal height of the given study site based on real-time

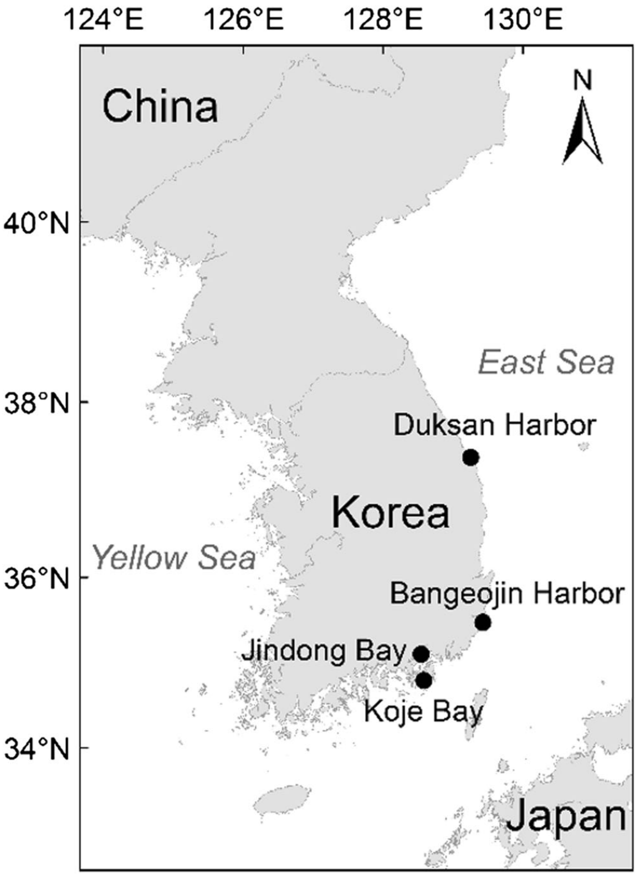

Fig. 1 The four study sites along the east and south coasts of Korea

Table 1 Summary of locations, water depth, water temperature, photosynthetic photon flux density (PPFD), daily light saturation point (H_{sat}), and nutrient concentrations at the four study sites along the east and south coasts of Korea from October 2015 to October 2016. Values are means (ranges). Mean values in the same row with different letters are significantly (Tukey's test, $p < 0.05$) different among the study sites

Variables	Duksan Harbor	Bangeojin Harbor	Jindong Bay	Koje Bay
Latitude	37°23′N	35°29′N	35°7′N	34°48′N
Longitude	129°15′E	129°26′E	128°33′E	128°35′E
Water depth (m)	3.4–7.0	0.2–1.9	0.6–2.6	0.1–2.5
Water temperature (°C)	14.9 (5.9–24.9)	17.4 (10.3–29.0)	17.7 (5.3–29.0)	17.3 (4.3–30.4)
PPFD (mol m^{-2} d^{-1})	28.2 (0.2–65.6)	23.8 (0.4–78.0)	22.1 (0.6–60.1)	38.0 (1.6–79.1)
H_{sat} (h)	6.3 (2.7–8.9)	5.2 (2.8–7.1)	5.0 (2.5–7.3)	6.8 (2.8–9.2)
Water column				
NH_4^+ (μM)	1.47 (0.28–3.08)^{a}	1.61 (0.38–5.58)^{a}	4.23 (0.58–10.70)^{c}	2.37 (0.30–8.01)^{b}
$NO_2^- + NO_3^-$ (μM)	2.86 (1.18–7.50)^{b}	4.87 (1.41–10.89)^{c}	2.58 (0.47–10.57)^{a}	2.84 (1.19–5.82)^{b}
PO_4^{3-} (μM)	0.43 (0.18–0.71)^{a}	0.42 (0.21–0.73)^{a}	0.48 (0.13–2.38)^{a}	0.46 (0.23–0.84)^{a}
Sediment pore water				
NH_4^+ (μM)	116.13 (35.82–379.43)^{a}	255.08 (127.53–530.07)^{c}	150.67 (70.31–252.67)^{b}	172.32 (39.85–972.39)^{b}
$NO_2^- + NO_3^-$ (μM)	0.64 (0.01–1.47)^{a}	0.77 (0.09–1.94)^{b}	0.71 (0.01–2.21)^{b}	3.45 (1.46–7.78)^{c}
PO_4^{3-} (μM)	1.79 (0.29–3.65)^{a}	44.23 (2.05–92.95)^{c}	15.97 (4.91–35.47)^{b}	2.19 (0.24–10.22)^{a}

tidal height data along the Korean coastline (Korea Hydrographic and Oceanographic Administration; http://www.khoa.go.kr) from the in situ water depth.

In each sampling month, four water column samples were collected using 50-mL polypropylene bottles in each study site for nutrient concentration analyses. Sediment samples were collected beside a randomly thrown quadrat for *Z. marina* tissue sampling in each study site using a plexiglass corer (5 cm diameter, 10 cm long; $n = 4$) for determining nutrient concentrations in sediment pore water. Sediment pore water was obtained by centrifugation (8000 ×*g* for 20 min). Sediment pore water nutrient concentrations were determined after dilution with low-nutrient seawater (< 0.1 μM). Dissolved inorganic nitrogen (DIN, i.e., NH_4^+ and $NO_3^- + NO_2^-$) and PO_4^{3-} concentrations in both the water column and sediment pore water were measured using standard colorimetric techniques (Parsons et al. 1984). The $NO_3^- + NO_2^-$ concentration was determined after running samples through a column containing copper-coated cadmium, reducing NO_3^- to NO_2^-.

Biological Measurements

Above- and below-ground tissues within four randomly thrown quadrats (30 × 30 cm) were collected to measure shoot density, biomass, and reproductive phenology. *Z. marina* tissues in each quadrat sample were thoroughly cleaned of sediments and separated into vegetative and reproductive shoots. The numbers of vegetative and reproductive shoots were counted to estimate the shoot density (shoots m^{-2}). The flowering frequency was estimated to be the percentage of reproductive shoots to total shoots. The reproductive shoot stages of all reproductive shoots were determined by defining four phenological stages modified from Silberhorn et al. (1983): inflorescence primordia, anthesis, mature seed, and senescence. The site-level phenological stage was determined according to the most developed reproductive shoots at each study site.

To estimate the potential seed production, approximately five reproductive shoots were chosen randomly from each quadrat sample, and the number of spathes per shoot, ovules per spathe, and seeds per spathe were counted for each. The number of seeds per shoot was estimated by multiplying the number of spathes per shoot by the number of seeds per spathe. The potential seed production per unit area was determined by multiplying the seeds per shoot by the maximum reproductive shoot density (Olesen et al. 2017).

All vegetative and reproductive tissues in the quadrat sample were cleaned of epiphytes using a razor blade and oven-dried separately at 60 °C to a constant weight. Biomass was expressed on a per unit area basis (grams dry weight [DW] m^{-2}). The reproductive effort (RE) was estimated to be the percentage of the reproductive shoot biomass to the total biomass.

Statistical Analyses

All data were assessed for normality and homogeneity of variance using box plots and Levene's test. When Levene's test was significant ($p < 0.05$), the variable was either square root–

or logit-transformed to improve the normality and the homogeneity of variance. All nutrient data, number of ovules, and seeds per spathe were square root–transformed, while total shoot density, biomass, and number of spathes per shoot were logit-transformed. Differences in water column and sediment pore water nutrient concentrations, *Z. marina* reproductive and total shoot density and biomass, flowering frequency, RE, and reproductive shoot morphology across the study sites and sampling months were tested using two-way analysis of variance (ANOVA). When significant differences were found among the study sites, post hoc Tukey's test was performed to determine where the differences occurred. All statistical analyses were conducted using R ver. 3.3.1 (R Development Core Team 2016).

Results

Water Temperature, Irradiance, and Nutrient Concentrations

Water temperature exhibited different seasonal patterns at the four study sites (Fig. 2a–d). The study sites on the east coast (Duksan Harbor and Bangeojin Harbor) exhibited weaker seasonal variation in water temperature and had a milder winter and cooler summer than the study sites on the south coast (Jindong Bay and Koje Bay). In Duksan Harbor, Bangeojin Harbor, Jindong Bay, and Koje Bay, the winter minimum temperature was 8.1 °C, 10.3 °C, 5.3 °C, and 4.3 °C, while the mean (range) of the daily water temperature during summer months (June–August) was 19.3 °C (10.5–24.9 °C), 21.8 °C (14.4–29.0 °C), 24.5 °C (18.8–29.0 °C), and 23.6 °C (18.4–30.4 °C), respectively. The number of days when daily water temperature exceeded 25 °C was 0 days, 35 days, 52 days, and 43 days in Duksan Harbor, Bangeojin Harbor, Jindong Bay, and Koje Bay, respectively, throughout the experimental period. The Duksan Harbor site experienced frequent abrupt water temperature drops during March–August 2016, as well as in October 2015, with water temperatures decreasing to 4–10 °C below normal due to cold-water upwelling. Intriguingly, the lowest water temperature in Duksan Harbor throughout the experimental period was recorded in April (5.9 °C), which was lower than the winter minimum temperature (8.1 °C) in February 2016 (Fig. 2a, Table 1). Similarly, the water temperature in Bangeojin Harbor was influenced by cold-water upwelling during June and July 2016, resulting in cold summer temperatures. By contrast, the water temperatures at the Jindong Bay and Koje Bay sites on the south coast showed less fluctuation compared to that in the east coast sites.

Underwater irradiance at the intermediate depth of the seagrass meadow exhibited high temporal fluctuations at all four study sites (Fig. 2e–h). The mean PPFD was relatively constant across the sites (22.1–38.0 mol m^{-2} d^{-1}), and was highest in Koje Bay, followed by Duksan Harbor and Bangeojin Harbor, and lowest in Jindong Bay (Table 1). H_{sat} showed similar temporal patterns to PPFDs (Fig. 2i–l). The means and ranges of H_{sat} were 6.3 h (2.7–8.9 h) in Duksan Harbor, 5.2 h (2.8–7.1 h) in Bangeojin Harbor, 5.0 h (2.5–7.3 h) in Jindong Bay, and 6.8 h (2.8–9.2 h) in Koje Bay (Table 1).

All nutrient concentrations in the water column (except PO_4^{3-}) and sediment pore water varied significantly (ANOVA, all $p < 0.001$) among the sites and over time, but showed no clear seasonal patterns (Table 1, Fig. 3). Water column PO_4^{3-} levels did not differ significantly ($F_{3,106} = 1.852$, $p = 0.142$) among the study sites. The Bangeojin Harbor site had higher water column $NO_2^- + NO_3^-$ (4.9 μM), sediment pore water NH_4^+ (255.1 μM), and PO_4^{3-} (44.2 μM) concentrations than the other study sites. The Jindong Bay site had higher water column NH_4^+ (4.2 μM) concentrations, whereas the Koje Bay site had higher sediment pore water $NO_2^- + NO_3^-$ (3.5 μM) concentrations (Table 1). The water column and sediment nutrient concentrations at the Duksan Harbor site were relatively low compared to the other study sites (Table 1).

Seagrass Shoot Density and Biomass

The total and reproductive shoot density and biomass varied significantly (ANOVA, all $p < 0.01$) among the study sites and sampling months, and showed clear seasonal patterns, with maxima during April–July and minima during October–January (Fig. 4a–h). Both reproductive and total shoot densities were significantly (Tukey's test, all $p < 0.05$) higher at the sites on the east coast than those on the south coast. The maximum total shoot density reached 414–428 shoots m^{-2} at the east coast sites and 269–289 shoots m^{-2} at the south coast sites, while the maximum reproductive shoot density reached 122–133 shoots m^{-2} at the east coast sites and 25–56 shoots m^{-2} at the south coast sites (Fig. 4a-d). Total biomass was highest in Duksan Harbor, followed by Bangeojin Harbor, and lowest in Jindong Bay and Koje Bay (Tukey's test, all $p < 0.05$). Reproductive shoot biomass was highest at the east coast sites and lowest in Koje Bay (Tukey's test, $p < 0.05$). The maximum total and reproductive shoot biomass were 629–634 g DW m^{-2} and 351–394 g DW m^{-2} at the east coast sites, and 579–621 g DW m^{-2} and 113–121 g DW m^{-2} at the south coast sites, respectively (Fig. 4e–h). Flowering frequency and RE were significantly (Tukey's test, all $p < 0.05$) higher at the east coast sites than the south coast sites (Fig. 4i-l). The maximum RE and flowering frequency were 54.2–57.3% and 34.2–36.5% at the east coast sites and 25.9–27.3% and 12.0–21.9% at the south coast sites, respectively.

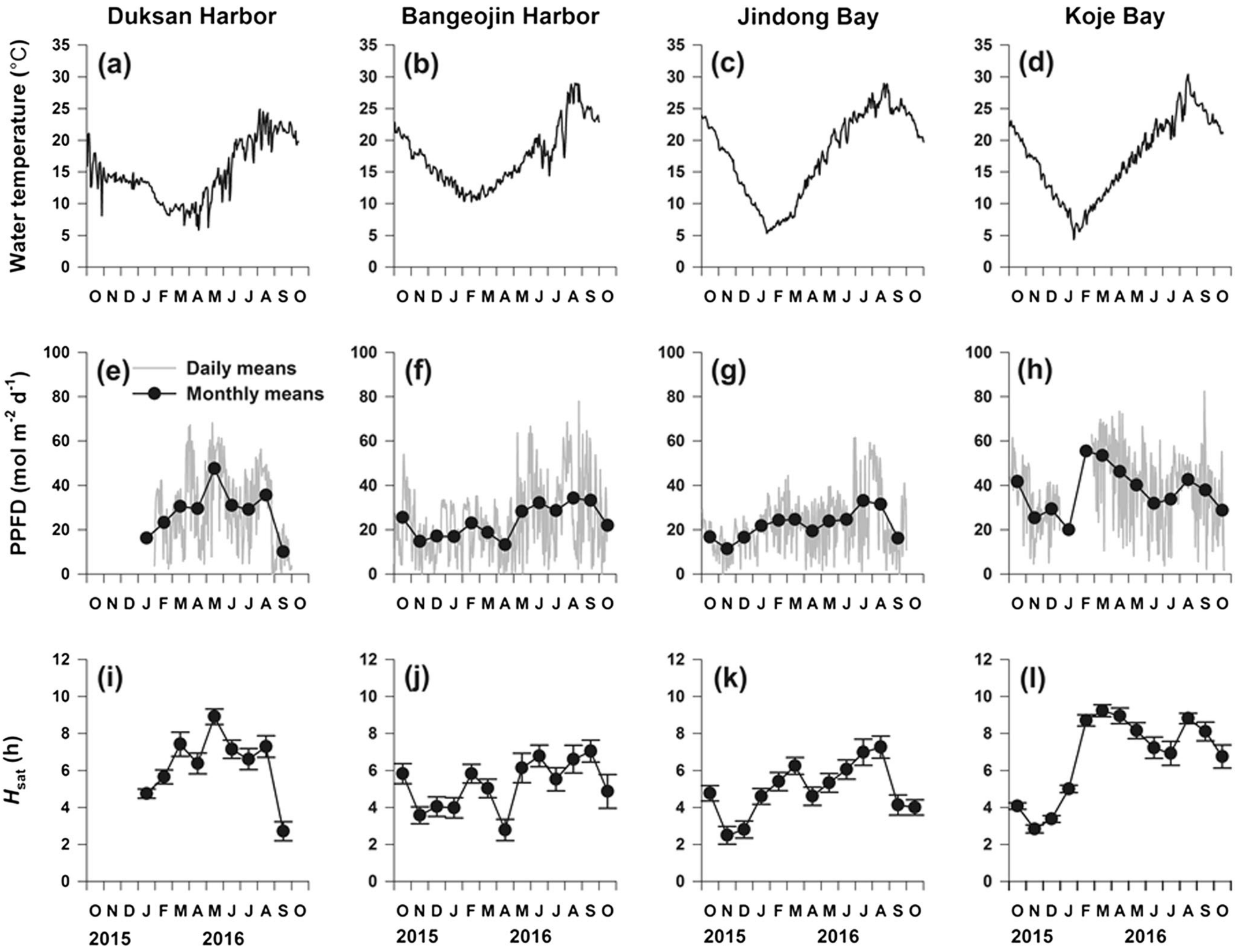

Fig. 2 Seasonal variations in water temperature (**a**–**d**), underwater photosynthetic photon flux density (PPFD; **e**–**h**), and the daily light saturation point (H_{sat}; **i**–**l**) in Duksan Harbor, Bangeojin Harbor, Jindong Bay, and Koje Bay along the east and south coasts of Korea from October 2015 to October 2016

Flowering Phenology and Seed Production

The timing and duration of flowering events were not consistent across the four study sites (Fig. 5). In Duksan Harbor on the east coast, *Z. marina* exhibited a precocious and exceptionally prolonged flowering period starting in late January, before the winter minimum water temperature occurred, and lasting until September in 2016 (Fig. 5a). At the other sites, reproductive shoots were first observed in March, 1 to 2 months after the winter minimum temperature occurred, and lasted until late June (Jindong Bay and Koje Bay; Fig. 5c–d) or August (Bangeojin Harbor; Fig. 5b). Thus, the flowering duration was longer on the east coast (~ 7.5 months in Duksan Harbor and 5 months in Bangeojin Harbor) than on the south coast (~ 3.5 months in Jindong Bay and Koje Bay). The onset of the flowering period occurred under different H_{sat} among study sites, i.e., 5.6 h in Duksan Harbor, 9.2 h in Bangeojin Harbor, 10 h in Jindong Bay, and 11 h in Koje Bay (Fig. 5a–d). The mean H_{sat} during the flowering period was similar among study sites, ranging from 8.8 in Bangeojin Harbor to 11.4 h in Koje Bay. Despite the difference in the timing of flowering events, the flowering period occurred within a relatively consistent water temperature range (9–22 °C) across the four study sites (Fig. 5). Reproductive shoot occurrence was induced under similar ambient water temperatures, ranging from 9 in Jindong Bay to 12 °C in Bangeojin Harbor. In Duksan Harbor on the east coast, anthesis was observed in late February when the water temperature decreased to 9 °C. At the other sites, anthesis was synchronous with the ambient water temperature reaching 15 °C in April. At all four study sites, mature seeds were first observed in May when the water temperature ranged from 13.5 °C in Duksan Harbor to 20.5 °C in Jindong Bay. Reproductive shoot senescence occurred in June at the south coast sites and July at the east coast sites (Fig. 5).

The characteristics of reproductive shoots differed significantly (ANOVA, all $p < 0.01$) among the study sites and sampling months (Table 2). Spathes and ovules developed

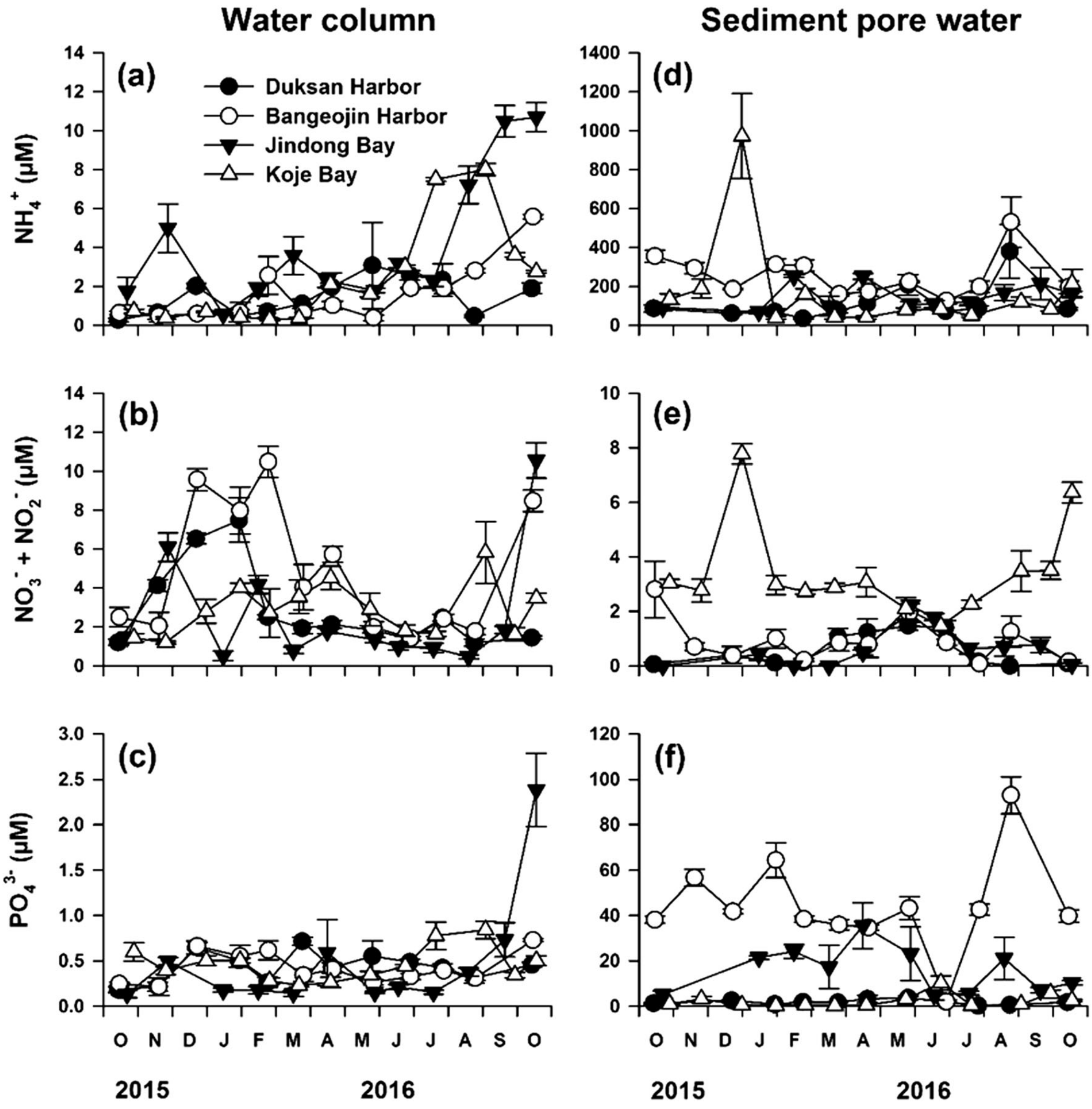

Fig. 3 Seasonal changes in NH_4^+, NO_3^- + NO_2^-, and PO_4^{3-} concentrations of water column (**a**–**c**) and sediment pore water (**d**–**f**) at the four study sites along the east and south coasts of Korea from October 2015 to October 2016. Values are means ± SE ($n = 4$)

asynchronously among study sites, while first mature seeds were observed synchronously in May at all study sites (Table 2). Number of spathes per shoot approached the maximum values after May (south coast sites) or June (east coast sites). The maximum number of ovules per spathe generally occurred in April, while the maximum number of seeds per spathe was observed in May at all study sites except Duksan Harbor where the maximum value occurred in June. The peak number of spathes per reproductive shoot ranged from 27.5 ± 1.9 in Bangeojin Harbor to 29.7 ± 4.0 in Jindong Bay, and the number of ovules per spathe ranged from 9.5 ± 0.4 in Duksan Harbor to 10.8 ± 0.5 in Bangeojin Harbor, while the number of seeds per spathe was lowest in Duksan Harbor (5.0 ± 0.2) and highest in Jindong Bay (7.6 ± 0.7; Table 3). Thus, the estimated number of seeds per shoot was higher in Jindong Bay (226 seeds shoot^{-1}) than the other sites (144–160 seeds shoot^{-1}). The potential seed production was higher in the study sites on the east coast (21,333 seeds m^{-2} in Bangeojin Harbor and 17,600 seeds m^{-2} in Duksan Harbor) than the sites on the south coast (12,556 seeds m^{-2} in Jindong Bay and 3925 seeds m^{-2} in Koje Bay; Table 3).

Discussion

Flowering Phenology Under Different Regional Water Temperature Regimes

In the present study, the timing and duration of flowering periods in *Z. marina* meadows differed significantly across

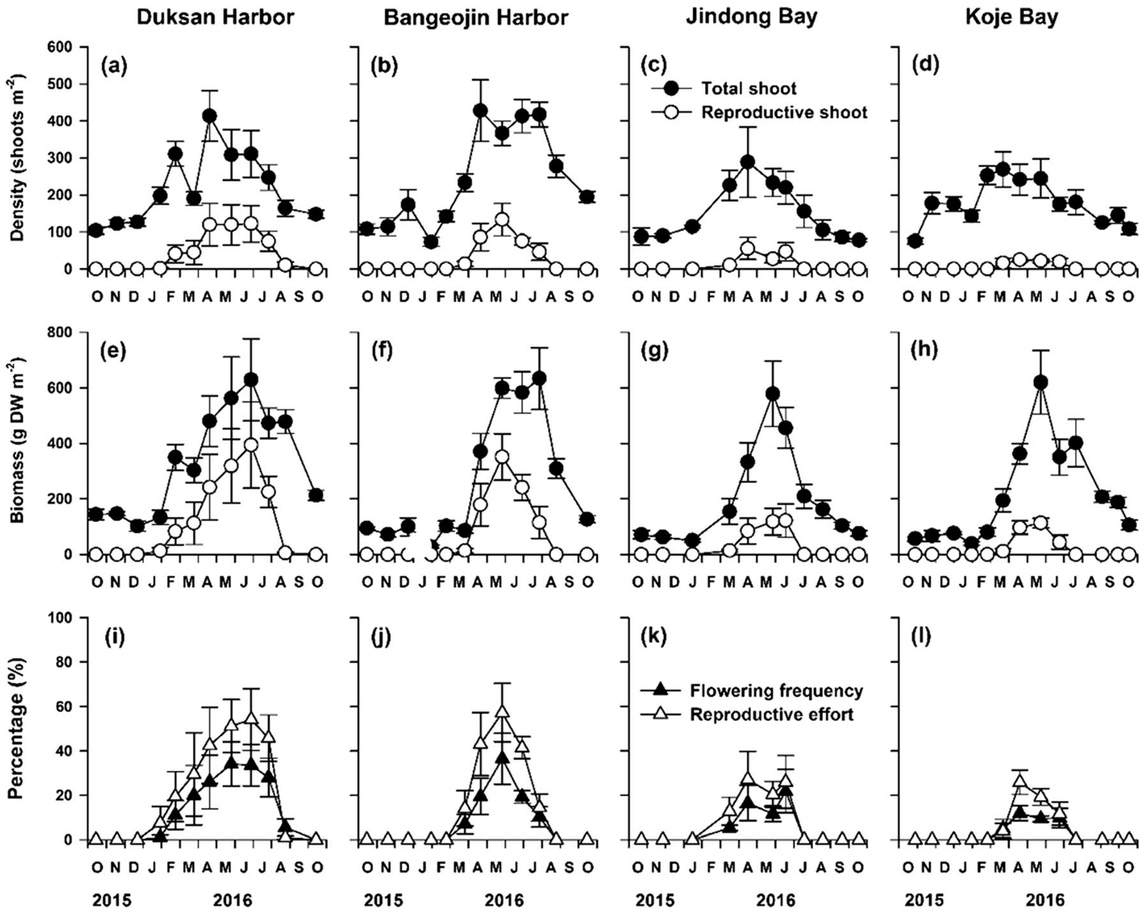

Fig. 4 *Zostera marina*. Seasonal variations in total and reproductive shoot density (**a**–**d**), biomass (**e**–**h**), and flowering frequency and reproductive effort (**i**–**l**) in Duksan Harbor, Bangeojin Harbor, Jindong Bay, and Koje Bay along the east and south coasts of Korea from October 2015 to October 2016. Values are means ± SE ($n = 4$)

the east and south coasts of Korea. Temperature and photoperiod have been found to be determining factors triggering the initiation of flower primordia (Bernier et al. 1993). In natural seagrass meadows, flowering occurs primarily within a certain range of day length and temperature increases following the winter minimum (McMillan 1980; Phillips et al. 1981). It is well documented that the flowering sequence of *Z. marina* is usually delayed with increasing latitude (Jacobs and Pierson 1981; Silberhorn et al. 1983; Walker et al. 2001), suggesting the important role of latitudinal differences in temperature progression for flower development. However, the reproductive phenology of *Z. marina* at the present study sites did not follow this typical trend. Reproductive primordia and anthesis were first observed at the northernmost site on the east coast (Duksan Harbor), which appeared approximately 2 months later at the south coast sites (Fig. 4). This is most likely attributable to the influence of milder winter water temperature on flowering induction on the east coast. Water temperature exhibited different seasonal patterns at the four study sites in the east and south coasts. The east coast sites (Duksan Harbor and Bangeojin Harbor) had a milder winter and cooler summer than the study sites on the south coast (Jindong Bay and Koje Bay; Fig. 2a–d). In January 2016, water temperature at the east coast sites was ca. 13 °C, which is optimal temperature for flowering (Setchell 1929; Silberhorn et al. 1983), whereas water temperature at the south coast sites was much lower and continuously decreased to the winter minima of 4–5 °C. Early flowering inductions due to warm winter temperature have been reported in both marine and terrestrial plants (Phillips et al. 1981; Abu-Asab et al. 2001). Phillips et al. (1981) reported that a simulated mild winter caused early flowering in *Thalassia testudinum*, whereas a simulated cold winter delayed the initiation of flowering by approximately a month. Thus, the early flowering observed at the east coast sites was probably due to the warmer winter water temperature in this region.

Precocious flowering shoots in Duksan Harbor required more time for seed maturation than the other three sites, probably due to low water temperatures during spring (February–April), and mature seeds were observed synchronously in May across the four study sites. Thus, early flowering of *Z. marina* did not lead to early seed maturation at the study sites. The flowering phenology at all study sites except Duksan Harbor was very similar to that described in previous

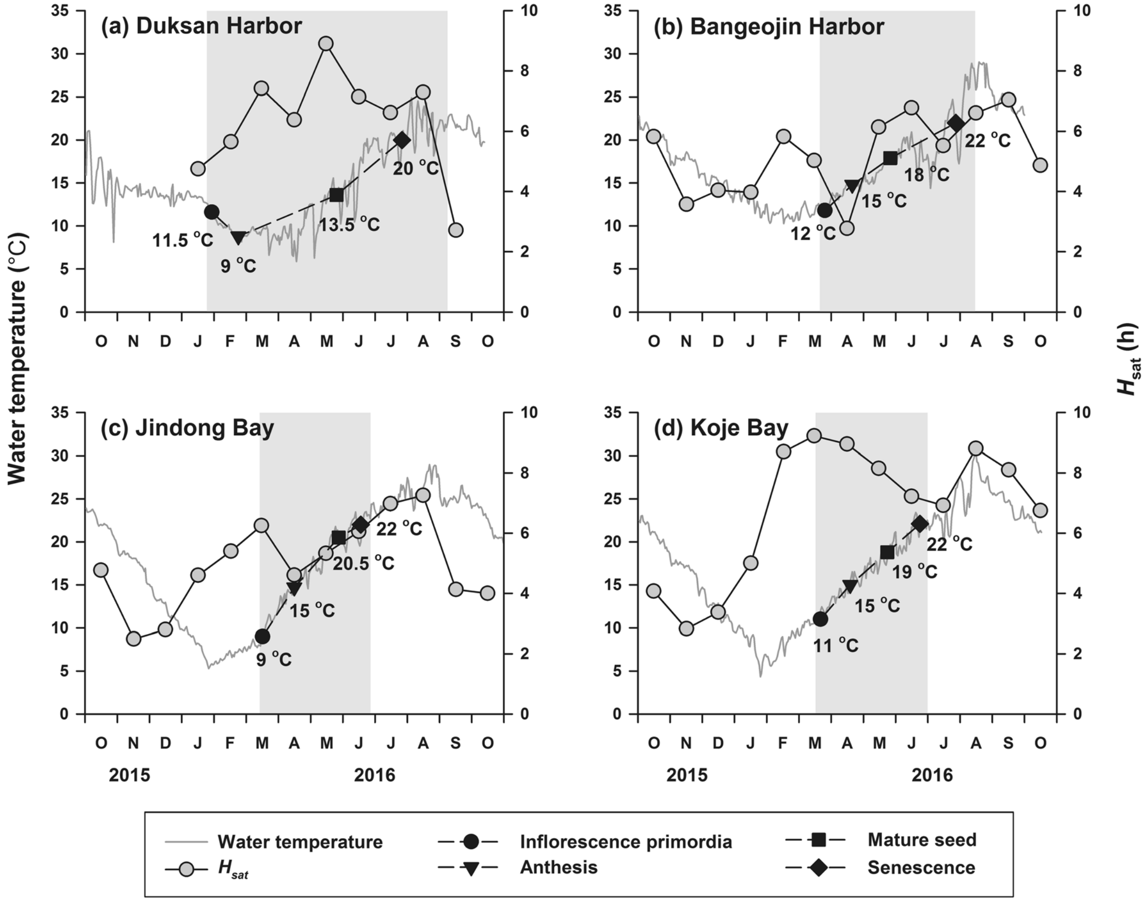

Fig. 5 Timing and duration of flowering events of *Zostera marina* along the seasonal water temperature and the daily light saturation point (H_{sat}) changes in Duksan Harbor (**a**), Bangeojin Harbor (**b**), Jindong Bay (**c**), and Koje Bay (**d**) on the east and south coasts of Korea from October 2015 to October 2016. Gray areas indicate flowering periods. The timing of each flowering event represents the timing of the first record of the event at each study site

studies. For example, anthesis and mature seeds in *Z. marina* was observed at water temperatures of around 15 °C and 20 °C, respectively, in Bangeojin Harbor, Jindong Bay, and Koje Bay, in agreement with temperatures reported at various locations along the east coast of the USA (Churchill and Riner 1978; Silberhorn et al. 1983). Flowering of *Z. marina* under

Table 2 *Zostera marina*. Characteristics of reproductive shoots in the four study sites along the east and south coasts of Korea from January to August 2016. Values are means ± SE

Variables	Site	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
No. of spathes per shoot	Duksan Harbor	5	6.8 ± 1.0	11.2 ± 1.5	12.6 ± 1.0	15.8 ± 1.9	28.3 ± 2.7	28.6 ± 1.8	28.8 ± 2.8
	Bangeojin Harbor				6.4 ± 0.8	18.1 ± 1.6	25.5 ± 1.8	27.5 ± 1.9	
	Jindong Bay				5.7 ± 0.7	26.4 ± 1.7	29.7 ± 4.0		
	Koje Bay				11.6 ± 1.1	26.8 ± 3.3	29.0 ± 2.5		
No. of ovules per spathe	Duksan Harbor	11.7 ± 0.9	10.8 ± 1.4	11.0 ± 0.4	11.2 ± 0.3	11.3 ± 0.5	8.2 ± 0.7	4.9 ± 0.8	8.3 ± 0.6
	Bangeojin Harbor				12.8 ± 0.4	12.2 ± 0.9	7.6 ± 0.4	6.0 ± 1.0	
	Jindong Bay				10.1 ± 0.5	7.2 ± 0.9			
	Koje Bay				11.9 ± 0.4	7.8 ± 0.8			
No. of seeds per spathe	Duksan Harbor					4.0 ± 0.2	5.6 ± 0.3	4.7 ± 0.4	5.5 ± 0.8
	Bangeojin Harbor					7.2 ± 0.7	6.7 ± 0.8	2.1 ± 0.5	
	Jindong Bay					10.0 ± 0.6	5.4 ± 0.6		
	Koje Bay					7.0 ± 0.6	3.4 ± 0.4		

Table 3 *Zostera marina*. Potential seed production calculated from reproductive shoot density, the number of spathes per shoot, and the number of seeds per spathe in the four study sites along the east and south coasts of Korea in 2016. Values are means ± SE. Values of the same variable with different letters are significantly (Tukey's test, $p < 0.05$) different among the study sites

Site	Maximum reproductive shoot density (shoots m^{-2})	Maximum spathes per shoot	Number of ovules per spathe	Number of seeds per spathe	Potential seed production (seeds m^{-2})
Duksan Harbor	122 ± 49	28.8 ± 2.8	9.5 ± 0.4^{a}	5.0 ± 0.2^{a}	17,600
Bangeojin Harbor	133 ± 43	27.5 ± 1.9	10.8 ± 0.5^{b}	5.8 ± 0.5^{a}	21,333
Jindong Bay	56 ± 30	29.7 ± 4.0	9.9 ± 0.6^{a}	7.6 ± 0.7^{b}	12,556
Koje Bay	25 ± 5	29.0 ± 2.5	10.3 ± 0.7^{a}	5.4 ± 0.6^{a}	3925

low water temperatures (8–9 °C), as observed at the Duksan Harbor site, has been also reported in other studies (Phillips 1972; Harrison and Mann 1975). Moreover, the senescence of reproductive shoots was delayed by a month and the flowering period was prolonged at the study sites on the east coast (5–7.5 months) compared to the south coast (3.5 months) because of a longer period under the temperature conditions suitable for *Z. marina* flowering (15–20 °C; Setchell 1929). The lower summer water temperature conditions in the east coast sites compared to the south coast sites was largely attributable to the episodic upwelling events in the east coast. Our water temperature data revealed the occurrence of upwelling events in the study sites on the east coast, which is consistent with the results of many previous studies that focused on upwelling events in the same region (Lee and Na 1985; Park and Kim 2010; Han et al. 2016). Daily water temperature did not exceed 25 °C throughout the summer months in Duksan Harbor due to, at least partially, the occurrence of cold-water upwelling. Several upwelling events occurred during June–August and decreased the summer water temperature to as low as 15–20 °C at the Bangeojin Harbor site. Thus, coastal cold-water upwelling events on the east coast of Korea significantly changed the seasonal pattern of water temperature, compared to that on the south coast, which affected the flowering phenology of *Z. marina*. This variability in flowering phenology could represent a valuable indicator of changes in the water temperature environment.

Environmental Factors Influencing Sexual Reproduction

Z. marina at the study sites on the east coast showed much higher density and biomass of reproductive shoot and seed production than those at the study sites on the south coast of Korea. These results suggest that regional water temperature variability may have the potential to alter the reproductive strategy of seagrass. High water temperatures or heat waves generally lead to low survival of reproductive shoots (Thom et al. 2003) and seed abortion (Thomson et al. 2015), but the opposite effects have also been reported (Diaz-Almela et al. 2007; Potouroglou et al. 2014). The flowering response of seagrasses to water temperature variability may vary among species and spatial locations (McMillan 1980; Phillips et al. 1981). Milder winter and cooler summer water temperatures induced by coastal cold-water upwelling and climate change (e.g., El Niño and La Niña) led to an increased flowering intensity of *Z. marina* at the east coast sites and Pacific Northwest eelgrass systems (Thom et al. 2003). By contrast, Potouroglou et al. (2014) reported that sea surface temperature was positively correlated with the flower density of *Z. marina* around the Isles of Scilly, UK, where summer water temperatures (16–18 °C) were much lower than at the sites in this study. A positive relationship between the prevalence and intensity of flowering and annual maximum sea surface temperature has been reported in *Posidonia oceanica* meadows throughout the Mediterranean (Diaz-Almela et al. 2007). However, the Mediterranean seagrass *Ruppia drepanensis* showed maximum sexual reproduction at 20 °C under laboratory culture conditions, while lower (14 °C) and higher (30 °C) temperatures inhibited flower induction (Santamaría and Hootsmans 1998). The variability in flowering responses to water temperature is possibly attributable to species-specific optimal growth temperatures and the extent to which they have accumulated carbon reserves to support flowering initiation (Lee et al. 2007; Zimmerman et al. 2017). Thus, any definite conclusion of the effects of temperature on seagrass flowering should be avoided without considering the thermal tolerance and ambient temperature regimes of seagrasses within their distribution range.

The reproductive processes of flowering plants are often highly sensitive to high-temperature stress, where even a single-day exposure to extreme temperatures can lead to reproductive failure (Zinn et al. 2010). Reduced fruit and seed production have been widely reported for numerous terrestrial plant species in response to high-temperature stress (Hedhly 2011). The seagrass *Z. marina* at our study sites was probably threatened by high-temperature stress because summer water temperatures in this region are considerably higher than the optimal temperature (20 °C) for *Z. marina* growth (Lee et al. 2007). At our study sites, the summer maximum water temperatures (24.9–30.4 °C) were all far above the optimal temperature for *Z. marina* growth in this region, which indicates that high summer water temperature is a threat to these *Z. marina* populations (Lee et al. 2005). However, the extent to which the *Z. marina* meadows had been subjected to high water temperature stresses varied across the study sites on the east and south coasts. *Z. marina* was exposed to high water temperatures of > 25 °C for 43–52 days in the south coast sites, but for 0–35 days in the east coast sites throughout the experimental period. Long-term exposure to high water temperature (> 25 °C) may lower carbon assimilation and storage and drain the carbon reserves in plant tissues, resulting in decreases in the growth and survival rates of *Z. marina* (Marsh et al. 1986; Zimmerman et al. 1989; Collier et al. 2011; Staehr and Borum 2011; Eriander 2017; Zimmerman et al. 2017; Beca-Carretero et al. 2018; Moreno-Marín et al. 2018). Under high temperature conditions, such as the warm summer in the south coast sites of the present study, plants might divert resources to withstand heat stress, thereby limiting the amount of carbon available for reproductive development during the following growing season (Zimmerman et al. 1989; Wahid et al. 2007; Zimmerman et al. 2017). Assuming that the observed seasonal temperature pattern is typical at the south coast sites, this may explain the observation of reductions in sexual reproduction at *Z. marina* meadows in the south coast sites where summer temperatures were close to an upper lethal level of ca. 30 °C for the species (Greve et al. 2003). Sea surface temperature was increasing at a rate of 0.01–0.03 °C $yr.^{-1}$ during the past decades on the south coast of Korea (Kim et al. 2009; Kwak et al. 2015), indicating that global warming will continually threaten the growth and reproduction of *Z. marina* in the regions. On the contrary, at the study sites on the east coast, the summer water temperature highs were reduced due to cold-water upwelling, leading to cooler summer water temperatures than the south coast sites. The monthly mean water temperature did not exceed 20 °C until August 2016 at the east coast sites, while the mean water temperature reached 21–25 °C in June–July at the south coast sites. Lower summer water temperature at the east coast sites could be favorable to the induction and development of *Z. marina* reproductive shoots (Setchell 1929). This is consistent with the results from Willapa Bay, WA, USA where warm summer reduced the flowering intensity of *Z. marina*, while cool summer water temperatures induced by coastal cold-water upwelling and climate change enhanced the sexual reproduction (Thom et al. 2003). Given the frequency and intensity of the upwelling events have 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 upwelling may play an important role in controlling the reproductive strategy of *Z. marina* in the regions.

Insufficient irradiance has been found to restrict reproductive shoot induction in many seagrass species including *Z. marina* (McMillan 1976; van Lent et al. 1995; Johnson et al. 2017; Olesen et al. 2017). Olesen et al. (2017) reported that the investment for sexual reproduction of *Z. marina* tended to decrease under low light conditions, resulting in reduced reproductive shoot density and seed production. In the present study, the light availabilities in the *Z. marina* meadows were similar at all the study sites on the east and south coasts (23.8–28.2 mol m^{-2} d^{-1} in the east coast sites and 22.1–38.0 mol m^{-2} d^{-1} in the south coast sites). Additionally, values of H_{sat} (5.0–6.8 h) in the all present study sites were higher than that required for the maintenance of whole plant carbon balance and growth for *Z. marina* (3–5 h; Zimmerman et al. 1991). However, much higher reproductive efforts were observed at the east coast sites than the south coast sites. These results suggest that the light condition has only a minor role in determining the intensity of sexual reproduction of *Z. marina* in this study region.

Nutrient availability can influence the formation and development of reproductive shoots in *Z. marina* (Jackson et al. 2017; Johnson et al. 2017). Although nutrient availability in shallow waters on the east coast of Korea is increased by intensive upwelling of nutrient-rich subsurface waters, the nutrients in surface water can be depleted by fast-growing macroalgae and phytoplankton, which have higher nutrient requirements than seagrasses (Duarte 1995; Hyun et al. 2009; Kim et al. 2011). For example, after Typhoon Megi, cold and nutrient-rich waters entrained into the surface layer led to an increase in phytoplankton growth in the East Sea, while NO_3^- and PO_4^{3-} concentrations remained relatively low, at 1.51 and 0.27 μM, respectively (Son et al. 2006). Similarly, rapid removal of water column nutrients from upwelled water due to phytoplankton blooms has been reported on the east coast of Korea (Hyun et al. 2009). Because phytoplankton and submerged macrophytes can rapidly take up nutrients from the water column, increased nutrient availability by coastal upwelling was not detected by direct measurement of water column nutrient concentrations in the present study. The water column nutrient concentrations in our study sites on both the east and south coasts were consistently above those required for *Z. marina* growth (Zimmerman et al. 1987). Pore water NH_4^+ levels in all our study sites were also much higher than the threshold concentration of nitrogen limitation (100 μM) for *Z. marina* growth (Dennison et al. 1987; Zimmerman et al. 1987; Lee et al. 2007). Thus, the water column and pore water nutrient availability probably did not significantly affect reproductive efforts of *Z. marina* in these study sites. Although light reduction by algal blooms was rarely detected in the present study sites during the experimental period, additional nutrient input by upwelling of nutrient-rich water may act as a potential stressor that stimulates macroalgae and phytoplankton growth that compete with *Z. marina* for light (McGlathery 2001; Ahn et al. 2006; Hyun et al. 2009; Hessing-Lewis and Hacker 2013; Kim et al. 2014).

In conclusion, sexual reproduction of *Z. marina* at the south coast sites appeared to be reduced significantly by high summer water temperature, whereas *Z. marina* at the east coast sites prolonged the flowering period and enhanced sexual reproduction in response to warm winter and cool summer water temperatures, which was due to, at least partially, cold-water upwelling events on the east coast. The results of the present study suggest that *Z. marina* can respond to different regional patterns of seasonal water temperature by altering its flowering phenology and reproductive strategies. Because the sea surface temperature and the intensity and frequency of temperature anomalies such as heatwaves and cold-water upwelling are predicted to increase under climate change (Park and Kim 2010; IPCC 2014; Wang et al. 2015; Oliver et al. 2018), there should be greater efforts to clarify the long-term impacts of the regional surface water temperature shifts on coastal seagrass ecosystems.

Acknowledgements We thank MJ Kim, ES Kim, SJ Na, G Lee, and YJ Hyun for their many hours of field and laboratory assistance. This research was supported by the Ministry of Oceans and Fisheries, Korea (Project titles: 'Long-term changes in structure and function in the marine ecosystems of Korea' and 'Development of blue carbon information system and its assessment for management').

Funding Information Additional support was provided by China Scholarship Council (CSC; No. 201608260099) to L-Z Qin.

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