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Photosynthesis and whole-plant carbon balances of warm affinity *Halophila nipponica* and cold affinity *Zostera marina* in relation to water temperature rise: implication for future geographic distribution

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Climate change associated sea surface temperature rise could significantly affect the physiology, and consequently geographic distribution of seagrasses. Photosynthetic and respiratory responses of warm affinity *Halophila nipponica* and cold affinity *Zostera marina* to a change in water temperature (7–26°C) were investigated to estimate whole-plant carbon balance for prediction of the future geographic distributions of these seagrasses in the northwestern Pacific region. It was hypothesized that *H. nipponica* and *Z. marina* showed distinctly different patterns of carbon balance with changes in water temperature. Photosynthetic and respiratory rates of *H. nipponica* and *Z. marina* generally increased with increasing water temperature, except for I_c and I_k of *H. nipponica* and α of *Z. marina*. *H. nipponica* showed high P_{max} and α values, which could support a greater respiratory demand related to the higher proportion of non-photosynthetic tissues (~67%), compared with *Z. marina* (~34%). The whole-plant carbon balance of *Z. marina* remained positive throughout the experiment, although it decreased to nearly zero during the high water-temperature period. *H. nipponica* exhibited a negative carbon balance during winter and early spring, which corresponded with severely limited growth at water temperatures< 15°C. These results suggest that increases in water temperature, particularly during winter, in relation to continuous climate change, could induce substantial changes in the seagrass ecosystem structure and corresponding changes in coastal ecosystem services in the temperate coastal waters of the northwestern Pacific region. The results of this study will provide valuable information on the effective management and conservation of coastal and estuarine ecosystems under ongoing climate change.

KEYWORDS

carbon budget, climate change, *Halophila nipponcia*, photosynthesis, *Zostera marina*

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1 Introduction

Coastal and estuarine seagrass ecosystems are significantly affected by global climate change (Thomson et al., 2015; Chefaoui et al., 2018; Duarte et al., 2018). The annual sea surface temperature in the Northern Hemisphere is predicted to increase by approximately 0.05°C to 0.5°C decade^{-1} by the end of the 21st century (Alexander et al., 2018); this warming is amplified in shallow coastal waters (Oczkowski et al., 2015). Rising seawater temperatures induced by global climate change could—directly and indirectly—affect the physiology, behavior, and life cycles of marine organisms (Poloczanska et al., 2013; Birchenough et al., 2015). The tropicalization of temperate marine ecosystems has been pronounced worldwide; these climate-regime shifts are causing a geographical redistribution of marine organisms, such as the poleward expansion of tropical/subtropical marine biota (Vergés et al., 2014; Hyndes et al., 2016; Wernberg et al., 2016; Cavanaugh et al., 2019; Osland et al., 2021). Seagrasses are a specialized group of flowering plants adapted to the marine environment that form highly productive ecosystems, thereby offering numerous ecological, economical, and social services to shallow coastal areas (Dewsbury et al., 2016; Nordlund et al., 2018; Unsworth et al., 2019). Increased water temperature has contributed to northward range extension, phenological changes, and shifts in the species composition of seagrasses in many geographical regions (Kim et al., 2009; Virnstein and Hall, 2009; Shields et al., 2019; Gerakaris et al., 2020).

Seagrass species in the genera *Zostera* and *Phyllospadix* are mainly distributed on soft sediments and rocky substrata, respectively, from the intertidal zone to a water depth of ~25 m in the northern parts of the western Pacific Region (Lee et al., 2018; Yoshida et al., 2019; Park et al., 2020; Xu et al., 2021). Most seagrasses inhabiting the coastal waters of the northwestern Pacific are low-temperature-adapted species, with optimal growth during spring and a significant reduction in growth during the summer high water-temperature period (Kikuchi et al., 2001; Lee et al., 2005; Park and Lee, 2009). *Halophila nipponica* was first reported in temperate regions of the Japanese archipelago in 2006, and it was observed on the southern coast of the Korean peninsula in 2007 (Kuo et al., 2006a; Kuo et al., 2006b; Uchimura et al., 2008; Kim et al., 2009). Several *H. nipponica* meadows are currently present on the southern coast of Korea and in the Japanese archipelago (Kuo et al., 2006a; Kuo et al., 2006b; Lee et al., 2018). *H. nipponica* exhibits a distinctly different growth pattern from the pattern of temperate seagrasses, such as *Zostera* spp. and *Phyllospadix* spp., in this region (Lee et al., 2005; Park and Lee, 2009; Kim et al., 2012). The optimal growth temperature for *H. nipponica* is approximately 25°C, and there is no growth inhibition during the high water-temperature conditions in summer. Productivity is severely restricted at water temperatures< 15°C (Kim et al., 2012). The growth pattern of *H. nipponica* indicates that this species possesses the tropical/subtropical growth characteristics of the genus *Halophila* (Kim et al., 2012). The persistence of warm affinity *H. nipponica* in the northern part of the western Pacific Region is presumably permitted by the warm Kuroshio Current in this region (Uchimura et al., 2008; Kim et al., 2009); it may also be related to the continuous climate change-induced increase in water temperature.

Carbon balance, which is determined on the basis of carbon assimilation by photosynthesis and carbon consumption *via* respiration, is a potential indicator of a plant's response to environmental change (Collier et al., 2011; Marín-Guirao et al., 2013; Moreno-Marín et al., 2018). The photosynthesis–irradiance (P–I) relationship is required to assess the carbon balance. When photosynthesis exceeds the carbon demands from respiration and growth, seagrass maintains a positive carbon balance, whereas plants will exhibit a negative carbon balance when the carbon demands cannot be met through photosynthesis (Lee et al., 2007). Because of structural characteristics, the carbon balance of seagrasses is more complex than the carbon balance of phytoplankton or algae. A large proportion of seagrass biomass is allocated to below-ground tissues, which are supported by leaf photosynthesis, indicating that seagrasses have a high light requirement (Lee et al., 2007; Tanaka and Nakaoka, 2007). Because below-ground tissues can significantly affect the carbon balance of the entire seagrass plant, the contribution of below-ground tissues should be considered when estimating the carbon balance of seagrasses.

Photosynthetic processes of seagrasses, which are affected by various environmental factors, exhibit considerable seasonal variations (Beca-Carretero et al., 2018; Moreno-Marín et al., 2018). The metabolic rates of seagrasses are particularly sensitive to variations in water temperature; they typically increase with increasing water temperature (Lee et al., 2007). Seagrass usually requires more light under high water-temperature conditions to maintain a positive carbon balance, suggesting that reduced light availability is more harmful to seagrass growth during the high water-temperature period in summer (Staehr and Borum, 2011; Said et al., 2021). The parameters of the P–I relationship also vary among and within species (Tanaka and Nakaoka, 2007; Collier et al., 2011; Burkholz et al., 2019). Thus, seasonal photosynthetic and respiratory responses to various irradiance and temperature conditions should be examined to assess the whole-plant carbon balance of each seagrass species; such information eventually could be used to predict the fate of each seagrass species in the context of global climate change.

In this study, we examined the photosynthetic and respiratory responses of two seagrasses, cold affinity *Z. marina* and warm affinity *H. nipponica*, to various water temperature conditions; we aimed to predict the fates of these species in the context of continuous increases in seawater temperature conditions in the northwestern Pacific Ocean. We hypothesized that, compared with the cold affinity *Z. marina*, the warm affinity *H. nipponica* would exhibit a more positive carbon balance in higher water-temperature conditions. The whole-plant carbon balance on areal basis can be estimated by considering seasonal photosynthetic production in relation to irradiance and temperature, respiration, and tissue biomass. Therefore, we measured seasonal P–I curves, dark respiration rates of above- and below-ground tissues, biomass, as well as *in situ* water temperature and underwater irradiance. This study will provide valuable information for prediction of the future geographic distributions of these seagrass species, as well as effective management and conservation of coastal ecosystems in the northwestern Pacific region in the context of continuous global climate change.

2 Materials and methods

2.1 Environmental parameters

Continuous measurements of *in situ* underwater photon flux density (PFD) and water temperature were conducted from July 2010 to August 2011 at the study site on Namhae Island, near the southern coast of Korea. Underwater PFD was monitored at 15-min intervals in a mixed seagrass meadow using the Odyssey photosynthetic irradiance recording system (Dataflow Systems, Christchurch, New Zealand). The light sensor was regularly cleaned at 4-week intervals to minimize fouling by epiphytes and sediment. Before deployment at the study site, the Odyssey sensor was calibrated by the collection of concurrent quantum measurements for 1 week using the LI-1400 data logger and LI-193SA spherical quantum sensor (Li-Cor, Lincoln, NE, USA). Daily PFD (mol photons m^{-2} day^{-1}) was calculated as the sum of quantum flux across a 24-h period. Water temperature was monitored every 15 min using a HOBO StowAway Tidbit temperature data logger (Onset Computer Corp., Bourne, MA, USA), and measured values were averaged daily. The PFD and water temperature loggers were deployed at the canopy level of *Z. marina*, approximately 20 cm above the sediment.

2.2 Seagrass collection

H. nipponica and *Z. marina* shoots were collected seasonally at the study site on Namhae Island (34°43′40″N, 128°02′07″E). *H. nipponica* was distributed in slightly deeper water depths of ~2–7 m relative to the mean lower low water, whereas *Z. marina* occurred at water depths of ~1–4 m relative to the mean lower low water (Kim et al., 2020b). Shoots of both seagrass species were collected at water depths of ~2.5–3 m in the mixed seagrass meadow. Whole seagrass materials including leaves, rhizomes, and roots were carefully collected by hand in early April, June, and late August (*in situ* water temperatures of ~9, 16, and 24°C, respectively), then transported to the laboratory in a cool box filled with seawater and ice to maintain the ambient seawater temperature during the sampling times. The shoots were thoroughly cleaned of dead tissues, epiphytes, and sediment using filtered seawater. Seawater for incubation experiments was collected from the study site in early April, June, and late August and filtered through a glass microfiber filter (47 mm GF/C^{TM}, Whatman,Piscataway, NJ, USA). The collected seawater conditions, including nutrient concentrations and salinity, were presented in Supplementary Table 1. Before incubation experiments, the seagrasses were progressively acclimated to the target temperature by ~1°C per day during sampling times (7 and 10°C in April, 14 and 18°C in June, and 22 and 26°C in August) under saturation irradiance (~450 µmol photons m^{-2} s^{-1}; Lee et al., 2007) from a 14:10 light:dark cycle for 1 or 2 days. The target temperatures for the experiment fell within the range of seasonal water temperature variations at the study site, which ranged from 7.5 to 25.9°C (Kim et al., 2020b). We attempted to conduct all incubation experiments at each target temperature when the field temperature conditions closely matched the respective target temperatures. All incubation experiments were performed within 3 days of seagrass specimen collection.

2.3 Measurements of photosynthetic and respiration rates

Incubation experiments (n = 4) were conducted in a temperature-controlled growth room at the following temperatures: 7 and 10°C in April, 14 and 18°C in June, and 22 and 26°C in August. Photosynthetic O_2 evolution was measured using a 2-mm oxygen dipping probe with coated sensor foil connected to a four-channel fiber optic oxygen transmitter (OXY-4 mini; PreSens Precision Sensing GmbH, Regensburg, Germany). Before taking measurements, each O_2 probe was calibrated using a conventional two-point calibration method, following the instruction manual of OXY-4 mini (www.presens.de). The calibration was performed using oxygen-free water (0% air saturation) and air-saturated water (100% air saturation). The seawater in the incubation chambers was purged with N_2 gas to reduce the initial O_2 concentration to approximately 20% of saturation, and maintained O_2 concentrations within the range of approximately 20% to 80% saturation throughout the experiment. For each species, one or two intact *H. nipponica* or *Z. marina* plants were placed inside a transparent cylindrical chamber made of Plexiglass. The chambers had a diameter of 6.5 cm and a height of 10 cm for *H. nipponica*, and a height of 40 cm for *Z. marina* (n = 4 for each species). To prevent diffusion limitation, the seawater in all incubation chambers was continuously stirred using a magnetic stirrer. A photosynthesis vs. irradiance curve (P–I curve) was obtained under nine light level steps (0 to 875 µmol photons m^{-2} s^{-1}) with a light-emitting diode lamp and reflector; each step lasted 10–20 min after the slope of the dissolved oxygen exhibited linear stabilization. The net chamber photosynthetic rate was determined from the slope by linear regression analysis of the oxygen value recorded at each light level. The gross photosynthetic rate (P_G) at each light level was calculated using the net chamber photosynthetic rate (P_N) and the chamber respiration rate (R; 0 µmol photons m^{-2} s^{-1} in light level), then normalized to leaf biomass (µmol O_2 g^{-1} DW min^{-1}):

$$P_G = \frac{P_N - R}{\text{leaf biomass}}$$

P–I curves were fitted to the data using the hyperbolic tangent function of Jassby and Platt (1976):

$$P = P_{max} \times \tanh\left(\frac{\alpha I}{P_{max}}\right)$$

where P_{max} is the maximum gross photosynthetic rate, α is the light-limited slope of the P–I curve, and I is irradiance. Saturation and compensation irradiances were determined as P_{max}/α and $-R/\alpha$, respectively (Herzka and Dunton, 1997). The daily photosynthetic production (P) was calculated by using the daily average irradiance for each day and the parameters obtained from the P–I curve corresponding to each temperature treatment (7, 10, 14, 18, 22, and 26°C). These parameters were applied to the respective day based on the range of *in situ* water temperature, which was categorized as follows: ≤ 8°C, 8–12°C, 12–16°C, 16–20°C, 20–24°C, ≥ 24°C, respectively (Supplementary Table 2). Then the daily photosynthetic production was integrated ($P_{G(\text{integrated})}$).

2.4 Whole-plant carbon balance

The whole-plant carbon balance was defined as the net photosynthetic production on an areal basis ($P_{\text{N-areal}}$). Whole-plant carbon balance was estimated using seagrass biomass, dark respiration, and daily integrated photosynthetic production. All seagrass materials, including above- and below-ground tissues, inside a haphazardly thrown quadrat (0.2 × 0.2 m; n = 4) were collected to measure biomass from July 2010 to June 2011. The seagrass samples were rinsed in tap water to remove epiphytes and sediment, separated into above- and below-ground tissues (leaves + sheath and rhizome + roots, respectively), and dried at 60°C to constant weight. The samples were weighed and converted to per unit area estimates (g dry weight m^{-2}).

To measure the dark respiration rate of each seagrass tissue (n = 4), above- and below-ground tissues were incubated in cylindrical chambers for 1 h under dark conditions at the projected temperatures (7, 10, 14, 18, 22, and 26°C). After incubation, the seagrass tissues were dried at 60°C to constant weight. Dark respiration rates were normalized to the dry weight of each seagrass tissue and are expressed as μmol O_2 g^{-1} DW min^{-1}.

To estimate gross and net photosynthetic production on an areal basis, daily integrated photosynthetic production ($P_{G(\text{integrated})}$) and dark respiration (R_D) of the above- and below-ground tissues (R_a and R_b, respectively) were multiplied by areal seagrass biomass (Herzka and Dunton, 1998). The R_D values obtained for each temperature treatment (7, 10, 14, 18, 22, and 26°C) were applied to the corresponding day, depending on the range of *in situ* water temperature, which were categorized as follows: ≤ 8°C, 8–12°C, 12–16°C, 16–20°C, 20–24°C, ≥ 24°C, respectively (Supplementary Table 2):

$$P_{\text{G-areal}} = P_{G(\text{integrated})} \times B_a$$

$$R_{\text{D-areal}} = (R_a \times B_a + R_b \times B_b) \times 24$$

$$P_{\text{N-areal}} = P_{\text{G-areal}} + R_{\text{D-areal}}$$

where $P_{\text{G-areal}}$ and $P_{\text{N-areal}}$ are gross and net photosynthetic production (mg C m^{-2} day^{-1}) on an areal basis, respectively; $R_{\text{D-area}}$ and B are dark respiration (R_a and R_b; mg C m^{-2} min^{-1}) and areal biomass (B_a and B_b; g DW m^{-2}) of the above- and below-ground tissues, respectively. Photosynthetic and respiratory quotients of unity were assumed to be 1 mol O_2 = 1 mol C (Herzka and Dunton, 1998).

2.5 Statistics

All values are presented as means ± standard errors, and statistical analyses were conducted using SPSS 23.0 software (SPSS Inc., Chicago, IL, USA). Significant differences among water temperatures in terms of photosynthetic parameters (e.g., P_{max}, α, I_c, and I_k) and the dark respiration rates of above- and below-ground tissues were determined by one-way analysis of variance. One-way analysis of variance was also performed to detect differences in PFD and water temperature among the sampling months. The data were subjected to evaluations of normality and homogeneity of variance to determine whether they met the assumptions of parametric statistics. If necessary, the data were log- or square-root-transformed. p-values< 0.05 were considered statistically significant. Means were analyzed by the Student-Newman-Keuls test to determine where differences were present.

3 Results

3.1 Underwater PFD and water temperature

Daily average PFD exhibited considerable fluctuation, and the monthly average PFD exhibited a significant (p< 0.001) difference according to sampling time (Figure 1A; Table 1). The monthly average PFD tended to increase during spring and summer, then decrease during fall and winter; it ranged from 3.9 mol photons m^{-2} day^{-1} in February 2011 to 19.3 mol photons m^{-2} day^{-1} in August 2010. Water temperature varied in a seasonal manner, with the highest temperature (25.9°C) in September 2010 and lowest temperature (7.5°C) in February 2011 (Figure 1B). The annual mean water temperature at the study site during the experimental period was 15.8°C.

3.2 Photosynthetic and respiration rates

The P–I curves for whole plants of *H. nipponica* and *Z. marina* varied according to water temperature (Figure 2). P–I curves for both seagrass species showed a general pattern of rapid increases in gross photosynthesis with increasing light intensity at low irradiance; maximum gross photosynthesis was reached at high irradiance. There was no evidence of photoinhibition at high irradiance (Figure 2).

The maximum gross photosynthetic rates (P_{max}) of both seagrass species significantly (p< 0.001) differed among water temperature treatments and tended to increase with increasing water temperature (Figure 3A; Table 1). The P_{max} value of *H. nipponica* ranged from 6.5 μmol O_2 g^{-1} DW min^{-1} at 7°C to 18.5 μmol O_2 g^{-1} DW min^{-1} at 26°C; the P_{max} value of *Z. marina* ranged from 2.2 μmol O_2 g^{-1} DW min^{-1} at 10°C to 6.6 μmol O_2 g^{-1} DW min^{-1} at 26°C. The photosynthetic efficiency (α; μmol O_2 g^{-1} DW min^{-1}/μmol photons m^{-2} s^{-1}) of *H. nipponica* significantly (p<

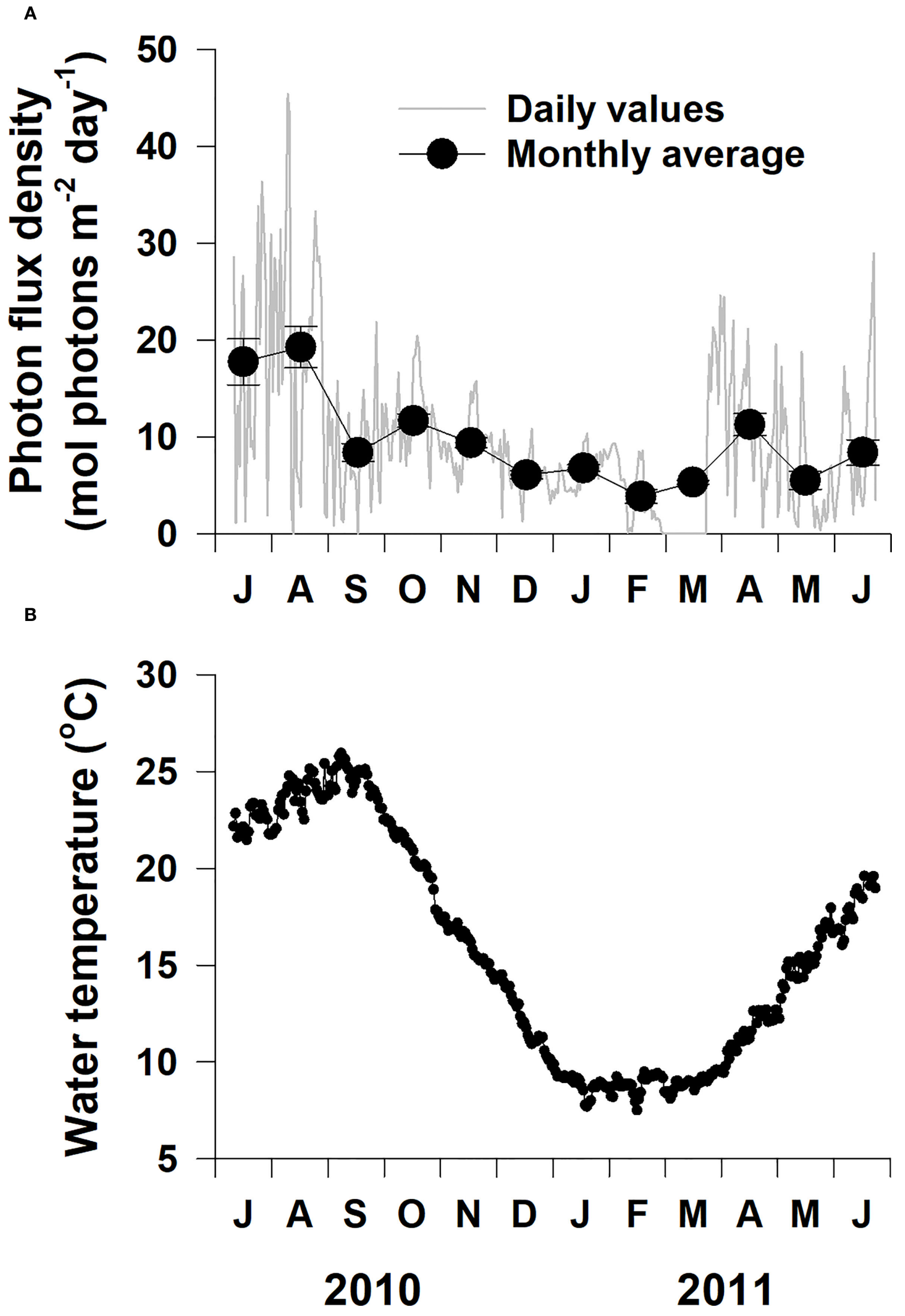

FIGURE 1
Underwater photon flux density **(A)** and water temperature **(B)** at the study site on the southern coast of Korea from July 2010 to June 2011.

0.001) differed among temperatures, ranging from 0.0233 at 10°C to 0.0610 at 26°C; however, the photosynthetic efficiency of *Z. marina* did not significantly (p = 0.405) differ among water temperature treatments (Figure 3B; Table 1). The compensation and saturation irradiance (I_c and I_k, respectively) for *H. nipponica* did not significantly (p = 0.372 and p = 0.305, respectively) differ according to water temperature, whereas I_c and I_k for *Z. marina* exhibited significant ($p < 0.001$ and $p < 0.01$, respectively) differences among water temperature treatments (Figures 3C, D; Table 1).

Significant (all $p < 0.001$) differences among water temperature treatments were observed for the dark respiration rates of the above- and below-ground tissues of *H. nipponica* and *Z. marina* (Figure 4; Table 1). Dark respiration (µmol O_2 g^{-1} DW min^{-1}) of the *H. nipponica* above-ground tissues ranged from −0.84 at 7°C to −3.13 at 26°C, whereas dark respiration of *Z. marina* ranged from −0.32 at 10°C to −1.11 at 26°C (Figure 4). The dark respiration rates of below-ground tissues of *H. nipponica* and *Z. marina* were also highest (−2.36 and −0.9 µmol O_2 g^{-1} DW min^{-1}, respectively)

TABLE 1 Results of one-way ANOVA testing the significant difference in underwater photon flux density (PFD) and water temperature among sampling months (M) and the effects of water temperatures (T) on maximum gross photosynthetic rate (P_{max}), photosynthetic efficiency (α), compensation irradiance (I_c), and saturation irradiance (I_k), and dark respiration (R_D) of *Halophila nipponica* and *Zostera marina*.

Parameters	Factor	df	M.S.	F	p-value
Underwater PFD	M	11	16.239	15.440	<0.001
Water temperature	M	11	29.353	940.743	<0.001
Halophila nipponica					
P_{max}	T	5	87.061	13.776	<0.001
α	T	5	0.001	8.269	<0.001
I_c	T	5	893.583	1.153	0.372
I_k	T	5	9532.952	1.313	0.305
R_D (above-ground)	T	5	0.205	13.459	<0.001
R_D (below-ground)	T	5	0.202	17.889	<0.001
Zostera marina					
P_{max}	T	5	0.142	26.185	<0.001
α	T	5	0.000	1.083	0.405
I_c	T	5	0.205	11.399	<0.001
I_k	T	5	0.608	4.508	0.008
R_D (above-ground)	T	5	0.158	34.275	<0.001
R_D (below-ground)	T	5	0.341	35.779	<0.001

at 26°C, whereas they were lowest at 10°C and 7°C (−0.55 and −0.16 µmol O_2 g^{-1} DW min^{-1}, respectively). The dark respiration rates of above- and below-ground tissues for both species tended to increase more rapidly at higher temperatures (18–26°C) than at lower temperatures (7–14°C). Compared with *Z. marina*, the above- and below-ground tissues of *H. nipponica* required more respiratory carbon demands during water temperature treatments (Figure 4).

3.3 Seagrass biomass

Although total, above-, and below-ground biomasses of *H. nipponica* and *Z. marina* exhibited distinct seasonal variations, both species had slightly different seasonal patterns (Figures 5A–C). Total and above-ground biomasses of *H. nipponica* were highest during summer (July–August 2010) and lowest during early spring (April); below-ground biomass increased during fall and decreased during winter and spring (Figures 5A–C). Total, above-, and below-ground biomasses of *Z. marina* were highest during early summer (June 2011) and lowest during fall and winter (Figures 5A–C). The proportion of *H. nipponica* below-ground to total biomass ranged from 47.3% on July 2010 to 86.5% on March 2011, whereas the corresponding proportion for *Z. marina* ranged from 23.1% on June 2011 to 53.1% on February 2011 (Figure 5D). Below-ground *H. nipponica* and *Z. marina* biomasses constituted 67.0% and 34.0% of the total corresponding biomasses, on average, during the experimental period.

3.4 Whole-plant carbon balance

The daily *H. nipponica* and *Z. marina* carbon balance at the study site fluctuated more in spring and summer than in winter (Figure 6). The carbon balance of both species tended to increase when the PFD increased during summer. The monthly average carbon balance in *H. nipponica* was positive in July, August, and October 2010, as well as June 2011; it was negative during the other months (Figure 6A; Table 2). The monthly *Z. marina* carbon balance was positive throughout the experimental period; it was highest (100.0 mg C m^{-2} day^{-1}) during July 2010 and lowest (0.5 mg C m^{-2} day^{-1}) during February 2011 (Figure 6B; Table 2).

4 Discussion

4.1 Seasonal photosynthetic and respiratory activities

Contrary to expectations, the two seagrass species, warm affinity *H. nipponica* and cold affinity *Z. marina*, did not show distinctly contrasting photosynthetic and respiratory responses to increasing water temperature in the present study. Photosynthesis generally increases with increasing temperature up to a specific temperature, then decreases at higher temperatures (Pedersen et al., 2016; Collier et al., 2017; Beca-Carretero et al., 2018). The high water temperatures that impact seagrass photosynthesis are distinct in temperate and

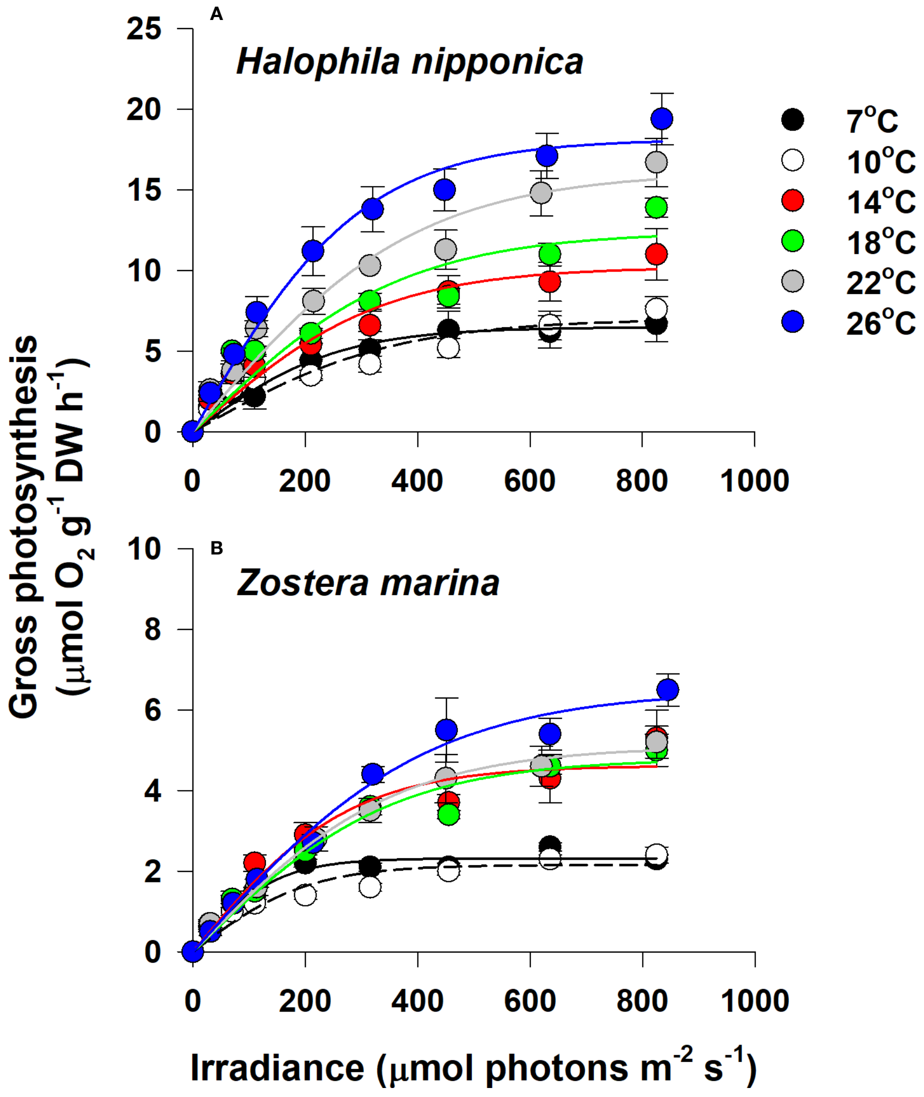

FIGURE 2
Gross photosynthesis–irradiance curves for *Halophila nipponica* **(A)** and *Zostera marina* **(B)** at the various water temperature treatments. The temperature treatments of 7 and 10°C, 14 and 18°C, and 22 and 26°C were implemented in early April, June, and late August, respectively. Values are means ± SE (n = 4).

tropical seagrass species. *Halodule uninervis* and *Zostera muelleri*, which are generally regarded as tropical and temperate species on the Great Barrier Reef, respectively, have contrasting responses to increased water temperature (Collier et al., 2011). The photosynthetic rates and net carbon production of *H. uninervis* increase with water temperature up to 33°C; in *Z. muelleri*, those parameters rapidly decrease at 33°C. This result suggests that, compared with the tropical species *H. uninervis*, the temperate seagrass species *Z. muelleri* is more susceptible to increasing water temperature (Collier et al., 2011). In the shallow brackish water of Denmark, the maximum photosynthetic rates of *Z. marina* consistently increase from 5°C to 25°C and then decrease at 30°C and 35°C (Staehr and Borum, 2011). The photosynthetic rate of *Z. marina* on the west coast of Sweden consistently increases with increasing water temperature up to ~29°C; the Q10 values for the photosynthetic rate are ~4-fold higher at 10–20°C and 20–30°C than at 30–35°C, suggesting a decline in photosynthetic activity above 30°C (Rasmusson et al., 2019). The maximum net photosynthetic rate of *Z. marina* in Denmark also continuously increases up to 27°C (Hansen et al., 2022). Thus, optimal temperatures for photosynthesis in these *Z. marina* populations, which were distributed in higher latitudinal regions (55–58°N) than our study site, range from 25°C to 29°C. The threshold temperature for high-temperature stress in *Z. marina* occurred near its southern distribution limit (~37°N), located at similar latitude to our study site, was suggested to range from 26°C to 30°C (Hammer et al., 2018). Considering these results, the optimal temperature for *Z. marina* photosynthesis would be 26–30°C, regardless of the latitudinal location of the population. The highest water temperature treatment of 26°C in the present study may be within the optimal temperature range for *Z. marina* photosynthesis; thus, we did not observe any decline in photosynthetic activity at the highest

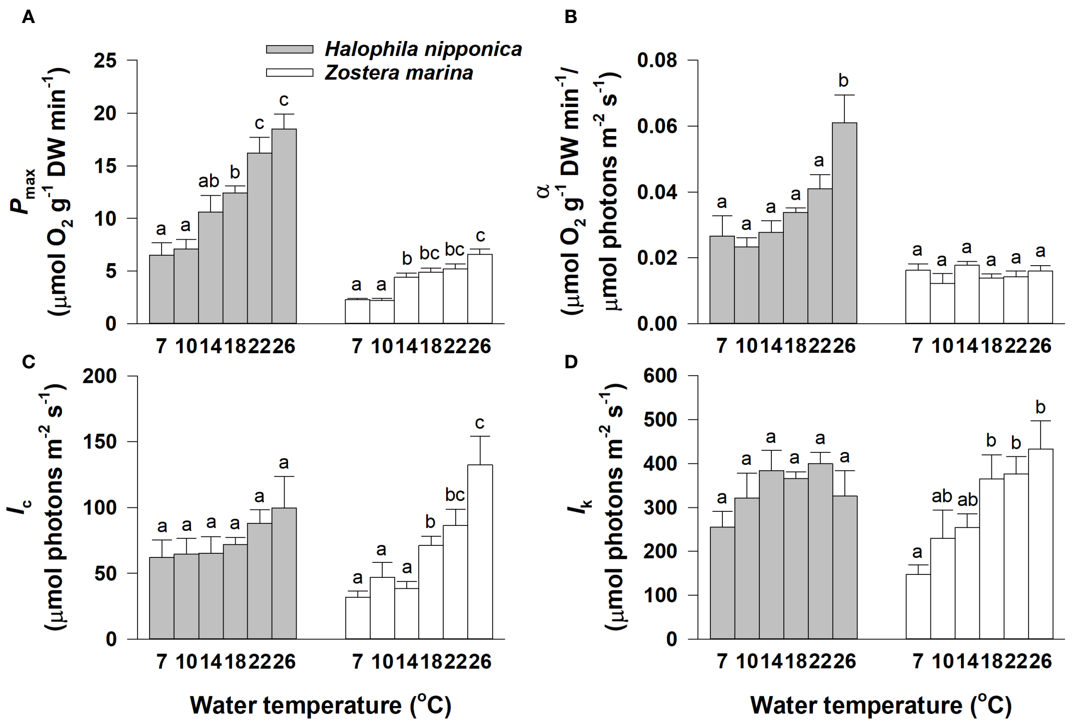

FIGURE 3
Maximum gross photosynthetic rate (P_{max}; **(A)**), photosynthetic efficiency (α; **(B)**), compensation irradiance (I_c; **(C)**), and saturation irradiance (I_k: **(D)**) for *Halophila nipponica* and *Zostera marina* at the various water temperature treatments. Different letters on the bars indicate significant ($p< 0.05$) differences. The temperature treatments of 7 and 10°C, 14 and 18°C, and 22 and 26°C were implemented in early April, June, and late August, respectively. Values are means ± SE (n = 4).

temperature treatment used in the present study. However, *Z. marina* biomass significantly decreased during the highest water-temperature (25–26°C) period in September at the present study site, although photosynthetic activity did not decrease under the highest water-temperature condition.

The optimal temperature for *Z. marina* growth in Korean coastal waters is between 15°C and 20°C; large decreases in growth are observed at higher water temperatures (Lee et al., 2005). However, our results indicate that the optimal temperature for *Z. marina* photosynthesis differs from the optimal temperature for the growth of this species. The optimal temperatures for photosynthesis in seagrasses are generally higher than optimal temperatures for the growth (Lee et al., 2007; Georgiou et al., 2016; Collier et al., 2017). This discrepancy may be related to the greater number of factors that affect plant growth, compared with photosynthesis (Lee et al., 2007; Said et al., 2021). Importantly, plant growth is the result of a combination of multiple factors, including nutrient availability and uptake, respiration, leaf senescence, and photosynthesis (Lee et al., 2007; George et al., 2018; Hammer et al., 2018; Moreno-Marín et al., 2018). Additionally, an alternative explanation could be the impact of temperature on biogeochemical processes occurring in the sediment (Sanz-Lázaro et al., 2011). Elevated temperatures can lead to an increased oxygen demand from seagrasses and microorganisms present in the sediment surrounding the below-ground tissues. This increased oxygen demand makes the plants more susceptible to *in situ* conditions characterized by anoxia and the presence of toxic sulfide (Holmer and Hasler-Sheetal, 2014; Hammer et al., 2018). Thus, *Z. marina* may have different optimal temperatures for growth and photosynthesis.

Underwater irradiance usually decreases during summer when *Z. marina* undergoes thermal stress in the *Z. marina* meadows on the southern coast of Korea (Park et al., 2009; Kim et al., 2014; Suonan et al., 2022). The decline in underwater irradiance at the level of the seagrass canopy is attributed to an augmentation in particulate organic matter, primarily originating from phytoplankton. This increase in particulate organic matter is linked to high temperatures, surface irradiance, and precipitation during the summer season (Ahn et al., 2006; Lee et al., 2017; Kim et al., 2019). Thus, *Z. marina* populations in this region experience high mortality because of high water temperatures and severe light restrictions during summer (Lee et al., 2005; Kim et al., 2014; Suonan et al., 2022). In the present study, the water temperature reached its highest point in September 2010, while underwater irradiance significantly decreased during the same period. This coincided with a dramatic decline in *Z. marina* biomass. Thus, the decline in biomass was likely caused by the combined effects of high water temperature and reduced light conditions at that time, rather than solely due to high water-temperature stress, because seagrasses require higher levels of irradiance under elevated water-temperature conditions (Lee et al., 2007; Ralph et al., 2007). This decline in *Z. marina* growth during summer may have contributed to the difference in optimal temperatures between photosynthesis and growth observed in this study.

Intra- and interspecies differences in photosynthetic parameters have been reported (Lee et al., 2007; Collier et al., 2017; Beca-Carretero

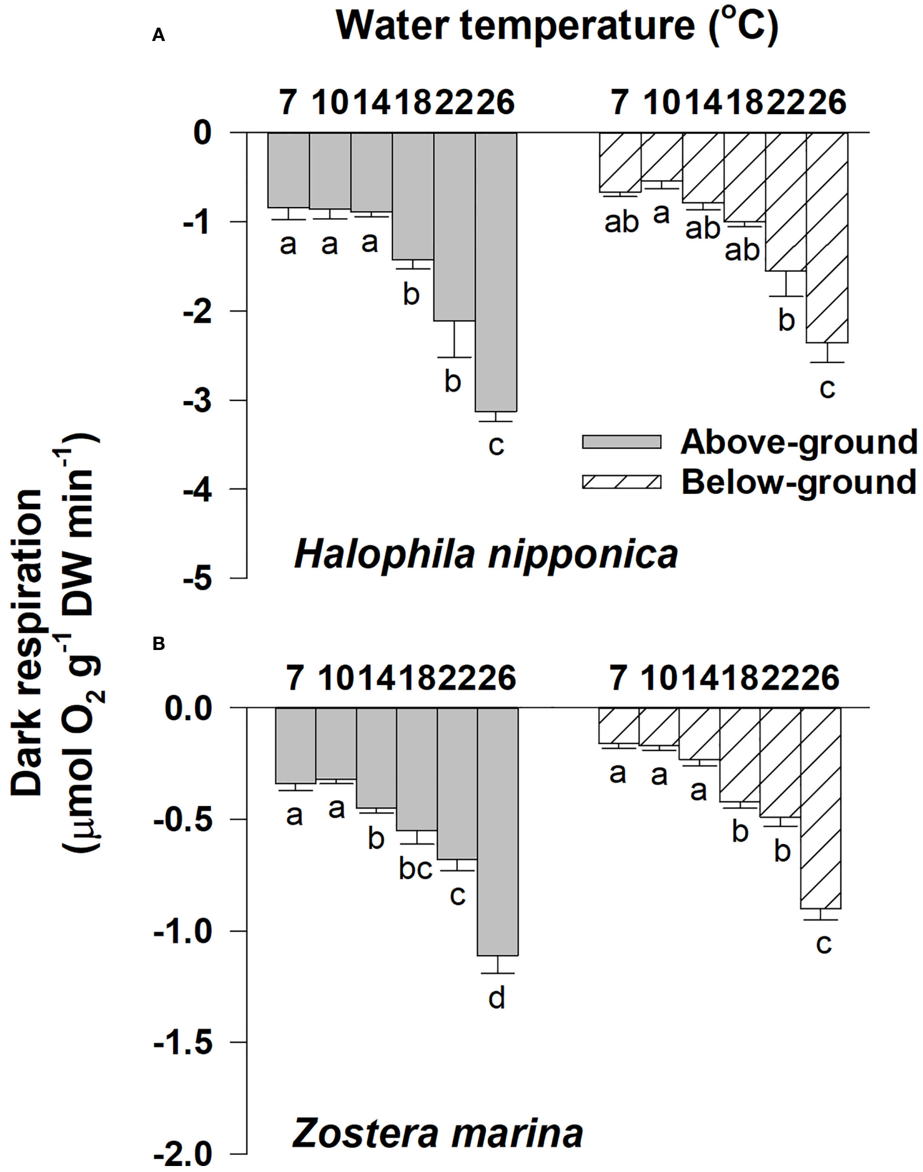

FIGURE 4
Dark respiration rates of above- and below-ground tissues for *Halophila nipponica* **(A)** and *Zoster marina* **(B)** at the various water temperature treatments. Different letters on the bars indicate significant ($p< 0.05$) differences. The temperature treatments of 7 and 10°C, 14 and 18°C, and 22 and 26°C were implemented in early April, June, and late August, respectively. Values are means ± SE (n = 4).

et al., 2018). Higher α and lower I_k, which can result in comparatively greater net photosynthesis, were identified in two *Amphibolis* species in Western Australia, compared with two *Posidonia* species in that region, thereby contributing to higher maximum *in situ* specific growth rates in the *Amphibolis* species (Masini and Manning, 1997). In the present study, the P_{max} and α values for *H. nipponica* were much higher than those values for *Z. marina*. Seagrass species in the genus *Halophila* are distributed over a wide range from tropical to temperate waters and have the greatest depth limit of > 85 m; these characteristics indicate that such species are extremely eurybiotic (den Hartog and Kuo, 2006; Short et al., 2007). Furthermore, *Halophila* species are opportunistic because of their rapid growth rate among seagrass species, as well as their ability to inhabit a wide array of environmental conditions. The proportion of below-ground to total biomass was much higher in *H. nipponica* (~67%) than in *Z. marina* (~34%) throughout the experimental period. Because of the higher biomass allocation to below-ground biomass relative to above-ground biomass, *H. nipponica* may have a greater respiratory demand, compared with *Z. marina*. The simultaneously higher P_{max} and α in *H. nipponica* than in *Z. marina* may constitute an acclimation mechanism to the higher respiratory demand in *H. nipponica*. Additionally, *Halophila* species are petiolate plants with elliptical or ovate blades along rhizomes or on distal nodes of an erect stem, which are more efficient at harvesting light compared with the strap-shaped or lanceolate leaves of seagrasses, such as *Z. marina*. These metabolic and morphological adaptations of *H. nipponica* could lead to similar I_c and I_k between the two seagrass species, although the respiration rate was higher in *H. nipponica* than in *Z. marina*.

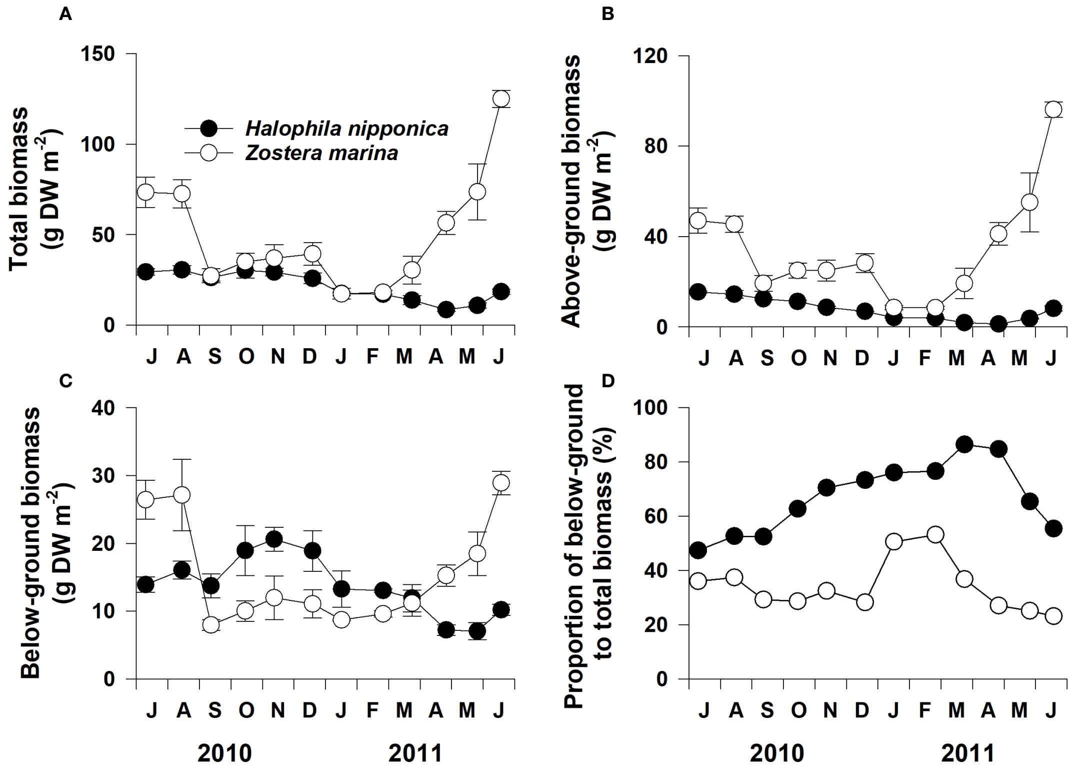

FIGURE 5
Total **(A)**, above- **(B)** and below-ground **(C)** biomass and proportion of below-ground to total biomass **(D)** for *Halophila nipponica* and *Zostera marina* at the study site on the southern coast of Korea from July 2010 to June 2011. Values are means ± SE (n = 4).

In the present study, the *H. nipponica* and *Z. marina* photosynthetic parameters generally increased with increasing water temperature. These results are consistent with previous findings (Herzka and Dunton, 1997; Staehr and Borum, 2011; Olivé et al., 2013; Georgiou et al., 2016). Low P_{max}, α, I_c, and I_k in *T. testudinum* were observed under low water-temperature conditions during winter; those photosynthetic parameters increased with increasing water temperature during the early spring and summer (Herzka and Dunton, 1997). Higher P_{max} and R for *Z. marina* and *Cymodocea nodosa* during spring and summer, along with higher P_{max}, I_c, and I_k for *Halophila stipulacea* at higher water temperatures, have also been reported (Staehr and Borum, 2011; Olivé et al., 2013; Georgiou et al., 2016). However, I_c and I_k of *H. nipponica* and α of *Z. marina* did not significantly differ among temperature treatments. The increases in I_c and I_k and a generally constant α of *Heterozostera tasmanica* with increasing water temperature are mainly affected by changes in P_{max} and dark respiration in response to increasing water temperature (Bulthuis, 1987). The α value for *H. johnsonii* in Florida is higher at higher temperatures (Torquemada et al., 2005), but the α value for *H. stipulacea* is higher at lower temperatures; this difference implies photo-acclimation to maximize carbon fixation under various environmental conditions (Georgiou et al., 2016). Overall, the results indicated that photosynthetic parameters were mainly controlled by changes in water temperature but did not always show a clear seasonal trend, suggesting acclimation to local environmental conditions.

4.2 Whole-plant carbon balance

Although many studies have been conducted regarding P–I relationships and respiration in seagrasses, most studies have simply estimated photosynthesis and respiration under various environmental conditions (Tanaka and Nakaoka, 2007; Staehr and Borum, 2011; Georgiou et al., 2016; Beca-Carretero et al., 2018; Said et al., 2021). Few studies have calculated the seasonal carbon balance of seagrass using the photosynthetic and respiration rates, biomass, and *in situ* underwater PFD (Table 2; Alcoverro et al., 2001). In the present study, the seasonal carbon balance, which reflects a plant's responses to environmental fluctuations throughout the year, was estimated *via* seasonal variations in photosynthesis, respiration, biomass, and underwater PFD.

Importantly, we found that the *Z. marina* carbon balance varied in a seasonal manner. It increased during the spring and early summer, then decreased during the fall and winter; these trends were related to seasonal variations in the P–I relationship. Although *Z. marina* did not have a monthly negative carbon balance throughout the experiment, the monthly average daily carbon balance decreased to nearly zero during the highest water-temperature period in September 2010. The growth of *Z. marina* in Korean coastal waters is usually greatest at water temperatures of 15–20°C during spring, then dramatically decreases during the high water-temperature period in summer (Lee et al., 2005; Park et al., 2009; Qin et al., 2020b; Suonan et al., 2022). *Z. marina* photosynthesis continuously increases up to 26°C, but biomass

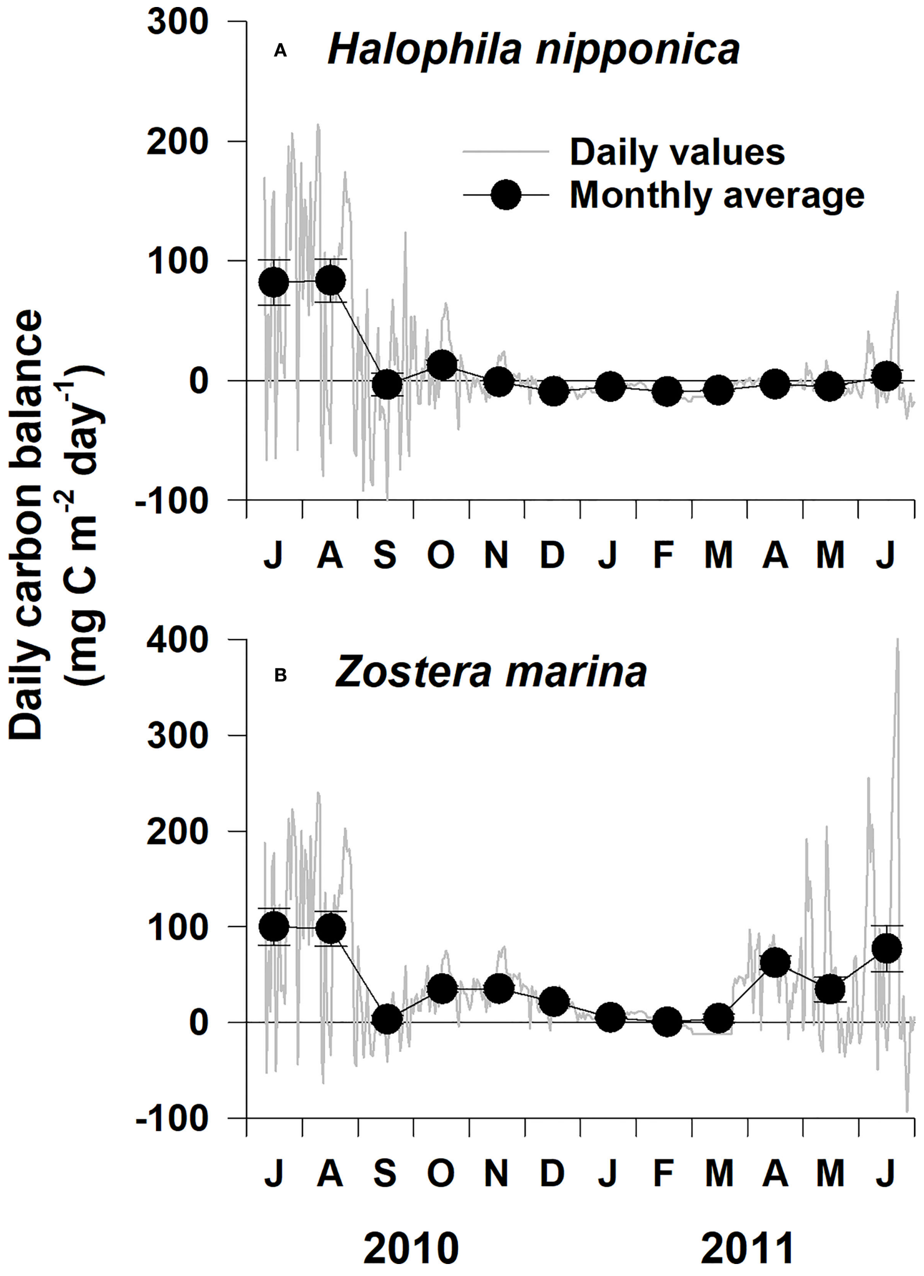

FIGURE 6
Daily and monthly average carbon balance for *Halophila nipponica* **(A)** and *Zostera marina* **(B)** at the study site on the southern coast of Korea from Jul 2010 to June 2011.

significantly decreases when the water temperature is higher than 15–20°C in this region (Lee et al., 2005); these observations indicate a stronger effect of heat stress on biomass than on photosynthesis (George et al., 2018). Compared with changes in the physiological characteristics of *Z. marina*, reductions in shoot density and biomass because of high water-temperature conditions (25–30°C) are more evident in culture experiments (Nejrup and Pedersen, 2008; Kim et al., 2020a). Under high water-temperature conditions, seagrass requires more light to maintain a positive carbon balance; under reduced light conditions, seagrass is more sensitive to high water-temperature stress (Lee et al., 2007; Ralph et al., 2007). Thus, the significant light reduction during September 2010 may have caused a rapid decline in the carbon balance and, consequently, biomass of *Z. marina* at the study site, indicating that the effects of reduced light are more harmful in summer than in winter.

However, *H. nipponica* had a negative carbon balance for several months in the present study. The seasonal carbon balance pattern for *H. nipponica* was consistent with the *in situ* growth pattern of this species at the study site on the southern coast of Korea. The maximum growth of *H. nipponica* was observed during the highest water-temperature period in this region; no reduction in the growth of this species has been observed under high summer water-temperature conditions (Kim et al., 2012). The productivity of *H. nipponica* is severely restricted at water temperatures< 15°C,

TABLE 2 The carbon (C) balance of *Zostera marina* and species in genus *Halophila* reported under various conditions.

Species	C balance (mg C m^{-2} d^{-1})	Temperature (°C)	Conditions	Reference
Zostera marina	0–18.5^{a}	20	Manipulated H_{sat} lengths at 1.3 and 5.5 m depths	Dennison and Alberte (1985)
	−1.4–9.2^{a}	20	Transplants along depth gradients	Dennison and Alberte (1986)
	0.6–1.9^{b}	15	Enriched CO_2	Zimmerman et al. (1997)
	*−2–0^{b}	15	Simulated extreme winter light limitations	Alcoverro et al. (1999)
	8.1–62.0^{c}	15, 25	Three factorial experiments: light, temperature, & NH_4^+	Moreno-Marín et al. (2018)
	0.4–105.2	7–26	Seasonal C balance	This study
Halophila decipiens	100–500	Jun., Jul.	Based on *in situ* productivity	Josselyn et al. (1986)
Halophila ovalis	830–1380	May, Jul., Sep., Nov.	Based on *in situ* productivity	Erftemeijer and Stapel (1999)
Halophila nipponica	−10.8–82.1	7–26	Seasonal C balance	This study

*indicates values from figures.

^{a}mg C g^{-1} d^{-1}, ^{b}mmol C plant^{-1} d^{-1}, ^{c}mg C plant^{-1}.

and the winter minimum productivity lasts until May when water temperature increases to ~15°C (Kim et al., 2012). In the present study, the proportion of *H. nipponica* below-ground to total biomass rapidly increased by 86.5% during the low water-temperature periods in winter and early spring, leading to high respiratory demands in non-photosynthetic tissues. The high respiratory demands and lower photosynthetic performance during the low water-temperature periods may have contributed to the negative carbon balance in *H. nipponica* during these times. Although *H. nipponica* is widely distributed in temperate waters of Korea and Japan, this species is presumably less tolerant of low water temperatures, indicating that it is warm-adapted (Kim et al., 2012; Kim et al., 2020b). *H. nipponica* also had a negative carbon balance in September 2010, which may have been related to the low underwater PFD during this period. Because seagrass requires more light for a positive carbon balance under high water-temperature conditions, *in situ* underwater irradiance of< 10 mol photons m^{-2} day^{-1} during this time may have been insufficient to maintain a positive carbon balance. These results suggest that *Z. marina* is adapted/acclimated to the local temperature regime in Korean coastal waters, whereas *H. nipponica* growth is limited during low water-temperature periods in winter and early spring.

Our results indicate that the carbon balances of *H. nipponica* and *Z. marina* were not entirely consistent with their growth patterns in this study or previous studies (Lee et al., 2005; Kim et al., 2012). We could not find clear evidence regarding potential changes in seagrass ecosystem structure related to a continuous increase in water temperature in our study region. *Cymodocea rotundata* is distributed in a shallower zone than *Cymodocea serrulata* in the Indo-Pacific tropical region of southwestern Japan, although the I_c, I_k, and respiration rate are lower in *C. rotundata* than in *C. serrulata* (Tanaka and Nakaoka, 2007). The photosynthesis and respiration trends of *C. rotundata* and *C. serrulata* do not fully explain their depth distributions, suggesting that other factors influence the depth ranges of these two species (Tanaka and Nakaoka, 2007). The effects of temperature on photosynthesis in *Halophila ovalis*, a widely distributed species across both tropical and temperate regions, were inconsistent at similar geographical sites, suggesting that seagrass was acclimated to local environmental factors controlling photosynthesis (e.g., light, nutrients, depth, and fine spatial-scale differences in temperature) (Said et al., 2021). Thus, *in situ* growth patterns of seagrasses can be explained by a combination of numerous metabolic and environmental factors, rather than by photosynthesis and respiration rates alone.

Reductions in *Z. marina* growth and reproduction related to long-term increases in sea surface temperature, as well as seasonal temperature anomalies (e.g., marine heatwaves), have been reported in the study region in the northwestern Pacific Ocean (Kim et al., 2020a; Qin et al., 2020a; Qin et al., 2020b). These decreases in *Z. marina* growth during high water-temperature periods under *in situ* conditions were not fully explained by increased water temperature-induced changes in the patterns of photosynthesis and respiration. Our results showed that *Z. marina* photosynthetic and respiration rates significantly increased under the highest water-temperature treatments; consequently, *Z. marina* maintained a positive carbon balance at the highest water temperature. Because *H. nipponica* exhibited a negative carbon balance during low water-temperature periods in winter and spring, the severely restricted growth of *H. nipponica* during low water-temperature periods was explained by seasonal changes in photosynthesis and respiration. Thus, increases in water temperature, particularly during winter, related to continuous climate change will be advantageous for *H. nipponica* growth in this region. In a previous study, small fast-growing *H. nipponica* rapidly recolonized, in contrast to the large slower-growing *Z. marina* in disturbed areas (Kim et al., 2020b). The results of the present and previous studies suggest that the expansion of *H. nipponica* meadows is more rapid than the expansion of *Z. marina* under climate change-related increases in water temperature in the temperate coastal waters of the northwestern Pacific; such differences may lead to changes in coastal seagrass ecosystem structure such as primary production and blue carbon sequestration and corresponding changes in coastal ecosystem services in this region.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

SK and K-SL conceptualized the experiments. SK and HK performed the experiments. SK, ZS, FZ, and K-SL analyzed the results. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2023.1203809/full#supplementary-material

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