



Recolonization Dynamics of Warm Affinity *Halophila nipponica* in a Temperate Seagrass Meadow With *Zostera marina*

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Because *Halophila nipponica* has only recently been reported in the temperate coastal waters of the northwestern Pacific, the recolonization dynamics of this species have not yet been investigated in temperate seagrass meadows. *H. nipponica* typically occurs in monoculture or in mixed meadows with *Zostera marina*, the most abundant seagrass species in this region. In this study, un-bordered and bordered gaps (0.5 × 0.5 m) were created in a mixed seagrass meadow of *H. nipponica* and *Z. marina* at Namhae Island on the southern coast of Korea to compare recolonization dynamics of the two species. Un-bordered gaps were marked using only a steel stake at each corner, while the margins of the bordered gaps were blocked to a sediment depth of approximately 20 cm using stainless steel blades to prevent penetration of seagrass rhizomes. Shoot densities of *Z. marina* and *H. nipponica* were measured in the gaps and in natural reference plots to estimate percent recolonized. In the bordered gaps, a few *Z. marina* seedlings and *H. nipponica* fragments were observed during winter, but no shoots of either species survived to the end of experiment. In the un-bordered gaps, the density of *H. nipponica* increased rapidly, with approximately 60% recovery after 2 months and reaching 85% after 10 months through only asexual reproduction via clonal growth. By contrast, recolonization of *Z. marina* was much slower than that of *H. nipponica*, with only approximately 25% recovery after 10 months through vegetative growth and recruitment of a few seedlings. Thus, small fast-growing *H. nipponica* rapidly recolonized, compared to relatively large slow-growing *Z. marina* in the small-size gaps. Asexual reproduction was the principle reproductive mechanism for the recolonization of both *Z. marina* and *H. nipponica* at the study site. According to our results, gaps created naturally and anthropogenically in mixed seagrass meadows may be primarily recolonized by *H. nipponica* rather than *Z. marina*, leading to a change in the seagrass ecosystem structure in Korean coastal waters.

Keywords: asexual reproduction, climate change, gap, *Halophila nipponica*, recolonization, *Zostera marina*

INTRODUCTION

Seagrasses are both economically and ecologically important components of coastal and estuarine ecosystems (Hejnowicz et al., 2015; Dewsbury et al., 2016; Unsworth et al., 2019). However, significant losses of seagrass habitats have recently been reported from many parts of the world (Orth et al., 2006a; Waycott et al., 2009; Short et al., 2014). The disappearance of seagrass meadows has occurred at a rate of 110 km² yr⁻¹ worldwide since 1980, and the rates of decline have recently accelerated (Waycott et al., 2009). These declines are related to both natural and anthropogenic disturbances such as storms, algal blooms, climate change, fishing activity, coastal construction, and reclamation (Rasheed, 2004; Brodersen et al., 2018; Chefaoui et al., 2018). Such disturbances can create small and/or large gaps in seagrass meadows (Paula et al., 2004; Rasheed, 2004; Neckles et al., 2005). In tropical and subtropical coastal waters, considerable attention has been given to the recovery and recolonization of seagrasses after disturbances of varying scales (Meehan and West, 2000; Morris and Virnstein, 2004; Olesen et al., 2004; Paula et al., 2004; Rasheed, 2004; Walker et al., 2006), however, only a few studies have examined the recolonization in mixed seagrass meadows of temperate seagrasses after disturbances.

Seagrasses can reproduce both sexually through seed production and asexually via clonal growth, but the reproductive efforts of these plants vary widely among species (Hemminga and Duarte, 2000). Seagrass meadows are commonly sustained by clonal growth, which is a key reproductive strategy for the recovery and recolonization of disturbed areas (Rasheed, 2004; González-Correa et al., 2005; Boese et al., 2009). However, sexual reproduction through flowering and seedling establishment is also an important process for the maintenance and recolonization of seagrass meadows (Greve et al., 2005; Lee et al., 2007a; Jarvis et al., 2012). Although flowering frequency and seedling survival rate of seagrasses are typically low, rapid recolonization via sexual reproduction has been observed after large-scale disappearances of seagrasses in some geographical regions (Paula et al., 2004; Orth et al., 2006b; Jarvis and Moore, 2010; Kim et al., 2014). In addition, a two-step seagrass recolonization process has been reported in disturbed areas, whereby shoot density increases via sexual reproduction through seedling establishment during the initial phase, followed by the expansion of seagrass meadows via asexual reproduction through lateral shoot production (Plus et al., 2003; Greve et al., 2005; Lee et al., 2007a; Jarvis et al., 2012). The relative contribution of sexual and asexual reproduction to the maintenance and/or recolonization of seagrass meadows may vary among geographical regions, disturbance scale, and species (Cabaço et al., 2012; Kim et al., 2014; Sherman et al., 2018).

Recolonization of gaps in seagrass meadows is governed by growth strategies of surrounding species (Rollon et al., 1999; Olesen et al., 2004; Rasheed, 2004). Small seagrass species, which are characterized by high growth and rhizome elongation rates, generally play a role as early colonizers in the small-scale disturbed area. The species in genus *Halophila*, *Cymodocea*, and *Halodule*, referred to as pioneer species (guerrilla strategy), have lower resistance, but ability to recolonize rapidly through

vegetative growth via asexual reproduction in the disturbed areas (Rollon et al., 1999; Olesen et al., 2004; Rasheed, 2004). On the other hand, relatively larger, slow-growing seagrasses such as genus *Thalassia* and *Enhalus* are considered as the latest recolonizer, referred to as climax species (phalanx strategy), in the disturbed areas due to slow horizontal extension rates (Rollon et al., 1999; Olesen et al., 2004). In the mixed seagrass meadows, the disturbed areas were firstly recolonized by smaller, fast-growing pioneer species, and then were eventually displaced by larger, slow-growing climax species (Congdon et al., 2019; Furman et al., 2019). Thus, recolonization pattern is greatly influenced by the traits of the adjacent seagrass.

Atmospheric carbon dioxide (CO₂) concentrations have risen by 40% since preindustrial levels, and concomitantly, sea surface temperature (SST) has gradually increased (IPCC, 2013). According to the 5th report of the IPCC, global SST has risen by 0.11°C per decade over the last 40 years and is expected to increase by an additional 2.6–4.8°C by 2100 (IPCC, 2013). This warming trend in the world's oceans could directly and indirectly affect the physiological function, behavior, and life cycle of all resident organisms, leading to changes in body size, phenology, and biotic interactions including competition and predation (Yamano et al., 2011; Doney et al., 2012; Poloczanska et al., 2013). Recently, climate-driven regime shifts of temperate marine ecosystems have been reported around the world; these shifts are characterized by the poleward expansion of the distribution of tropical and/or subtropical marine organisms (Vergés et al., 2014; Hyndes et al., 2016; Wernberg et al., 2016). Seagrasses are important foundation species in coastal waters, and the distributional range expansion and phenological changes of seagrasses have also been observed in many geographical regions (Diaz-Almela et al., 2007; Kim et al., 2009; Virnstein and Hall, 2009; Gorman et al., 2016).

The Korean peninsula is located in the temperate region of the northwestern Pacific Ocean. In the coastal waters of Korea, nine seagrass species, including five *Zostera*, two *Phyllospadix*, *Ruppia maritima*, and *Halophila nipponica*, have been reported on soft sediments and rock substrata within the intertidal zone to a water depth of about 15 m (Lee et al., 2018). Although species in the genus *Halophila* are predominantly distributed in subtropical or tropical waters, a *H. nipponica* meadow was observed on the south coast of Korea in 2007 for the first time (Kim et al., 2009, 2012). Several *H. nipponica* meadows have since been discovered along the southern coast of Korea, and they typically occur as monocultures or mixed with *Z. marina*, the most abundant seagrass species in Korea (Kim et al., 2012; Lee et al., 2018). *H. nipponica* in temperate regions of the Japanese archipelago was first described as a new species in 2006, but has been previously treated as *H. ovalis* since early 1900s (Kuo et al., 2006). Thus, *H. nipponica* is considered as endemic species in warm temperate waters of Korea and Japan influenced by the Kuroshio Current (Uchimura et al., 2008; Kim et al., 2009) whereas *Z. marina* has been considered as a low-temperature adapted seagrass species (Lee et al., 2005, 2007b). Because optimum growth temperature for *H. nipponica* was approximately 25°C in summer when *Z. marina* underwent significant thermal stress (Kim et al., 2012) differences in temperature optima may be

partly responsible for recolonization pattern of these two species after disturbances. Varying scales of seagrass loss caused by both natural and anthropogenic disturbances are common in seagrass meadows, but the process of recolonization in mixed seagrass meadows containing both warm and cold affinity species is poorly understood in temperate coastal waters. We compared the recolonization dynamics of warm affinity *H. nipponica* and cold affinity *Z. marina* in gaps created in mixed seagrass meadows to predict the resilience of these two species to habitat disturbances. We also investigated the relative importance of sexual and asexual reproduction of both seagrass species during recolonization.

MATERIALS AND METHODS

Study Site

The study site (34°43'40–N, 128°02'07–E) was located at Namhae Island on the southern coast of the Korean peninsula (**Figure 1**). The tidal regime is semi-diurnal with a maximum tidal range of approximately 3 m during spring tide (Tide Tables for the coast of Korea, Korea Hydrographic and Oceanographic Administration¹). Sediments are mainly characterized by fine sand and silts with less than 3% organic content in sediments. Two seagrass species, *H. nipponica* and *Z. marina*, exhibit a distinct vertical zonation at the study site. *Z. marina* is distributed in slightly shallow water (~1 to 4 m relative to the mean lower low water; MLLW), whereas *H. nipponica* occurs at water depths of ~2 to 7 m relative to MLLW. This study was conducted in a mixed seagrass meadow of *H. nipponica* and *Z. marina* with a water depth of approximately 2.5–3 m relative to MLLW from September 2010 to July 2011.

Experimental Design

In September 2010, eight experimental gaps (0.5 × 0.5 m) were created in the mixed seagrass meadow at the study site to examine the recolonization of *H. nipponica* and *Z. marina*. The seagrass meadows in the study site was close to a small port, and thus the gap size of 0.25 m² was similar scale to gaps caused by anchoring and boat propeller scarring, which were frequently occurred at the seagrass meadows in this area. Gaps were created by carefully removing all seagrass tissues to minimize sediment loss. Four of the gaps were only marked using a steel stake at each corner (hereafter, the un-bordered gaps), allowing seagrass recolonization by both sexual and asexual reproduction through seedling recruitment and clonal growth, respectively (**Figure 1**). The margins of the other four gaps were blocked to a sediment depth of approximately 20 cm using stainless steel blades to prevent penetration of seagrass rhizomes (hereafter, the bordered gaps), allowing recolonization by only seedling recruitment (**Figure 1**). Shoots of *H. nipponica* and *Z. marina* in the experimentally created gaps were counted monthly using a grid quadrat (0.5 × 0.5 m) divided into 25 sub-quadrats (0.1 × 0.1 m). Any rhizomes growing over the steel blades of the bordered gaps from the surrounding meadow

were removed. Four reference plots were placed at the same tidal level of the experimental gaps to estimate the percent recolonized, which was calculated by dividing shoot density in the gap by average shoot density in the reference plots for each species. All reference plots and experimental gaps were assigned at random. This study was conducted for only 11 months due to a devastating typhoon in August 2011 that destroyed all experimental materials.

Underwater Irradiance and Water Temperature

Underwater photon flux density (PFD) was monitored using an Odyssey photosynthetic irradiance recording system (Dataflow Systems Ltd., Christchurch, New Zealand) every 15 min at the study site from September 2010 to July 2011. The Odyssey sensor was pre-calibrated using an LI-1400 data logger and an LI-193SA spherical quantum sensor (Li-Cor) and was regularly cleaned to minimize fouling. Daily PFD (mol photons m⁻² d⁻¹) was calculated as the sum of quantum flux over each 24 h period. *In situ* water temperature was monitored every 15 min at the study site using StowAway Tidbit temperature data loggers (Onset Computer Corporation, Bourne, MA, United States), and the measured water temperatures were averaged daily.

To detect the warming trend of water temperatures during summer periods on the southern coast of Korea over the last 50 years, water temperature data were obtained from the Korea Oceanographic data center of the National Fisheries Research & Development Institute², which has monitored water temperature since 1961 at a buoy station, located approximately 40 km from the study site. The yearly number of days with water temperatures exceeding 20°C and 25°C were counted from the 1960 to 2000s.

Statistical Analyses

Values are represented as means ± SEs. Normality and homogeneity of variance were tested for the assumptions of parametric statistics. For each species, a one-way analysis of variance (ANOVA) was used to compare significant differences in shoot density of *H. nipponica* and *Z. marina* among reference plots and bordered and un-bordered gaps at the same sampling months. Bordered and un-bordered gaps were separately analyzed due to distinctly different dynamics to test the difference of percent recolonized between two species. Significant difference in percent recolonized between *H. nipponica* and *Z. marina* was analyzed using a repeat-measures ANOVA, with the species as the between-subject factor and the month as the within-subject factor. When sphericity assumption was violated, we used Huynh-Feldt epsilon adjusted *F* values and probabilities. Underwater irradiance and water temperature were each compared among sampling months by one-way ANOVA, with daily total irradiance and average water temperature as samples. If significant differences ($\alpha = 0.05$) were detected among variables, the Student-Newman-Keuls (SNK) test was performed to determine where significant differences occurred. All statistical analyses were performed using SPSS statistics 20.

¹www.khoa.go.kr

²http://kocdc.nfrdi.re.kr

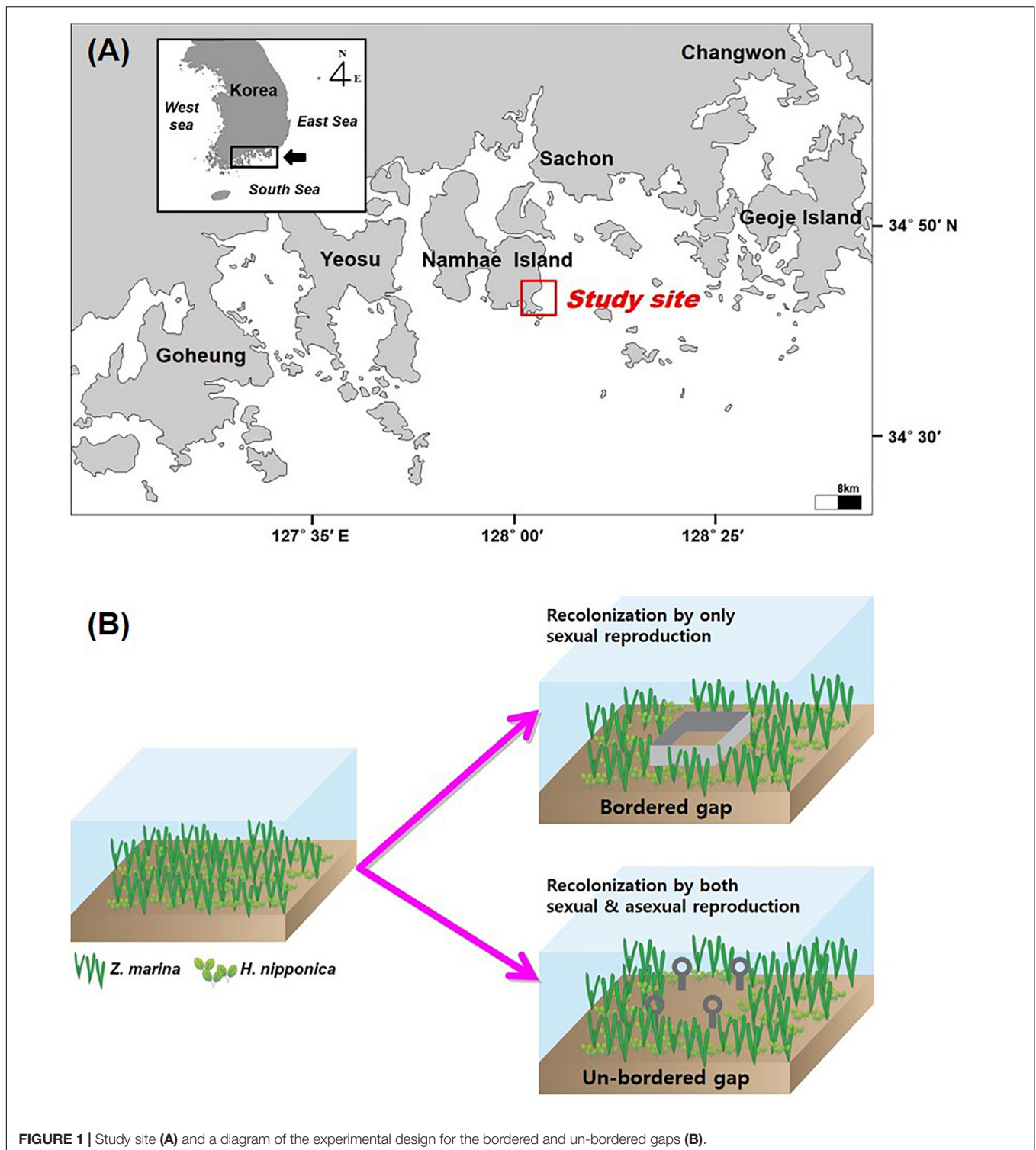


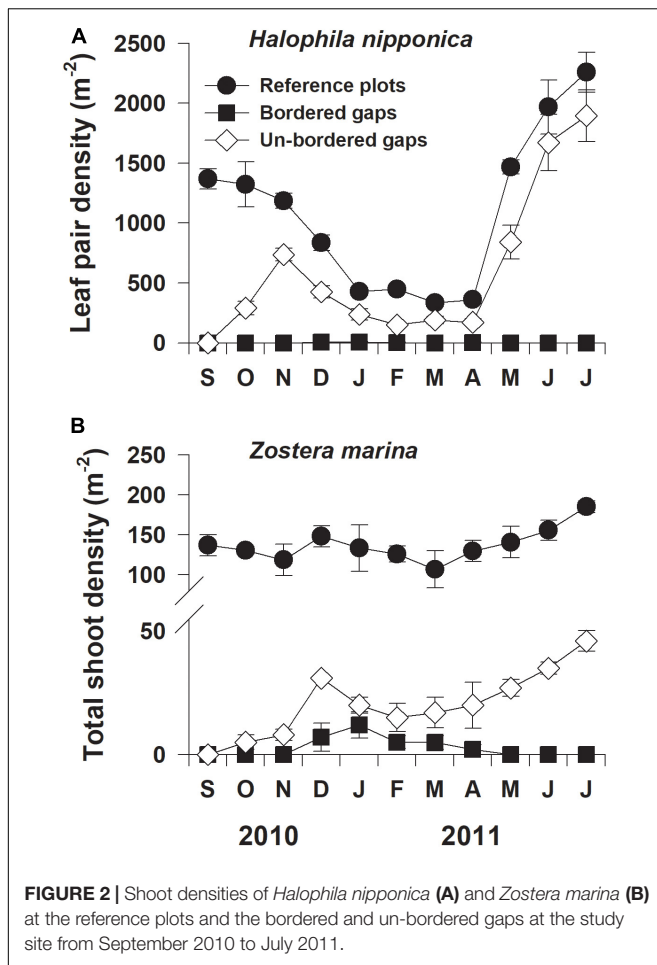
FIGURE 1 | Study site **(A)** and a diagram of the experimental design for the bordered and un-bordered gaps **(B)**.

RESULTS

Shoot Density

Shoot densities of both *H. nipponica* and *Z. marina* in the reference (control) plots exhibited significant seasonal variation,

with the highest values (2259 and 185 shoots m^{-2} , respectively), occurring in July 2011 and the lowest values (335 and 107 shoots m^{-2} , respectively), occurring in March 2011 (**Figure 2**). In the experimentally created gaps, shoot densities of both seagrass species increased more rapidly in the un-bordered gaps than in



the bordered gaps (Figure 2). The density of *H. nipponica* in the un-bordered gaps increased rapidly during the first 2 months of the experiment, after which densities did not significantly differ from those in the reference plots after 9 and 10 months of the experiment ($F_{2,9} = 41.740$, $p = 0.231$ and $F_{2,9} = 73.196$, $p = 0.104$, respectively; Figure 2A). However, in the bordered gaps, *H. nipponica* did not recolonize via seedling recruitment during the experimental period. The shoot density of *Z. marina* in the un-bordered gaps increased during the experimental period, but a few seedlings of *Z. marina* were only observed in the bordered gaps during winter (Figure 2B). In the bordered gaps, a few *H. nipponica* shoots developed from plant fragments, and seedlings of *Z. marina* were observed in random locations during winter and spring (Supplementary Figure S1). In the un-bordered gaps, however, both *H. nipponica* and *Z. marina* initially recolonized at the periphery of gaps by asexual lateral shoot formation via rhizome branching (Supplementary Figure S2).

Percent Recolonized and Contribution of Asexual and Sexual Reproduction to Recolonization

The percent recolonized of *H. nipponica* in the un-bordered gaps was significantly ($F_{1,6} = 37.431$, $p < 0.01$) higher than

that of *Z. marina* (Figure 3). In the un-bordered gaps, the percent recolonized of *H. nipponica* was approximately 60% after 2 months of the experiment, reaching 85% after 10 months (Figure 3A). In the bordered gaps, *H. nipponica* exhibited a less than 2% of recolonized shoots during winter months (December to February), but no shoots were observed at the end of experiment (Figure 3C). The percent recolonized of *Z. marina* in the un-bordered gaps increased to approximately 25% after 10 months (Figure 3B). Although a few seedlings of *Z. marina* were observed in the bordered gaps during winter and spring, no seedlings survived after 8 months of the experiment (Figure 3D).

Halophila nipponica only recolonized by asexual reproduction through rhizome branching and vegetative tissue fragment propagules from the adjacent meadow (Figures 3A,C). Although the bordered gaps did not allow rhizome expansion from the adjacent meadow, vegetative tissue fragments of *H. nipponica*, which developed to new shoots, were observed in the bordered gaps (Figure 3C). *Z. marina* only recolonized via seedling recruitment during winter and early spring in the bordered gaps, but recolonized by both sexual reproduction via seedling recruitment and asexual reproduction through penetration of rhizomes from the adjacent meadow in the un-bordered gaps (Figures 3B,D). No seedlings of *Z. marina* successfully established as adult shoots in the experimentally created gaps (Figures 3B,D); thus, the relative contribution of asexual reproduction to the recolonization of *Z. marina* was much higher than that of sexual reproduction at the study site.

Underwater Irradiance and Water Temperature

Daily underwater irradiance significantly ($F_{10,321} = 7.614$, $p < 0.001$) varied among sampling times (Figure 4A). Monthly average underwater irradiance was highest in July 2011 (11.9 mol photons $m^{-2} d^{-1}$) and lowest in February 2011 (3.9 mol photons $m^{-2} d^{-1}$), with an average value of 8.1 mol photons $m^{-2} d^{-1}$ during the entire experimental period (Figure 4A). Water temperature exhibited clear ($F_{10,322} = 806.797$, $p < 0.001$) seasonal variation, ranging from 7.5°C in mid-February 2011 to 25.9°C in early September 2011 (Figure 4B).

Summer water temperatures have gradually increased on the southern coast of Korea since the 1960s (Figure 5). The yearly number of days when daily water temperature exceeded 20°C was approximately 109 days during the 1960s, whereas the number of days was approximately 116 days during the 2000s (Figure 5A). The yearly numbers of days when daily water temperature exceeded 25°C were approximately 10 days during the 1960s and 26 days during the 2000s (Figure 5B).

DISCUSSION

Seagrass Recolonization by Sexual and Asexual Reproduction

The recolonization of seagrasses following destruction caused by various disturbances has been reported in many

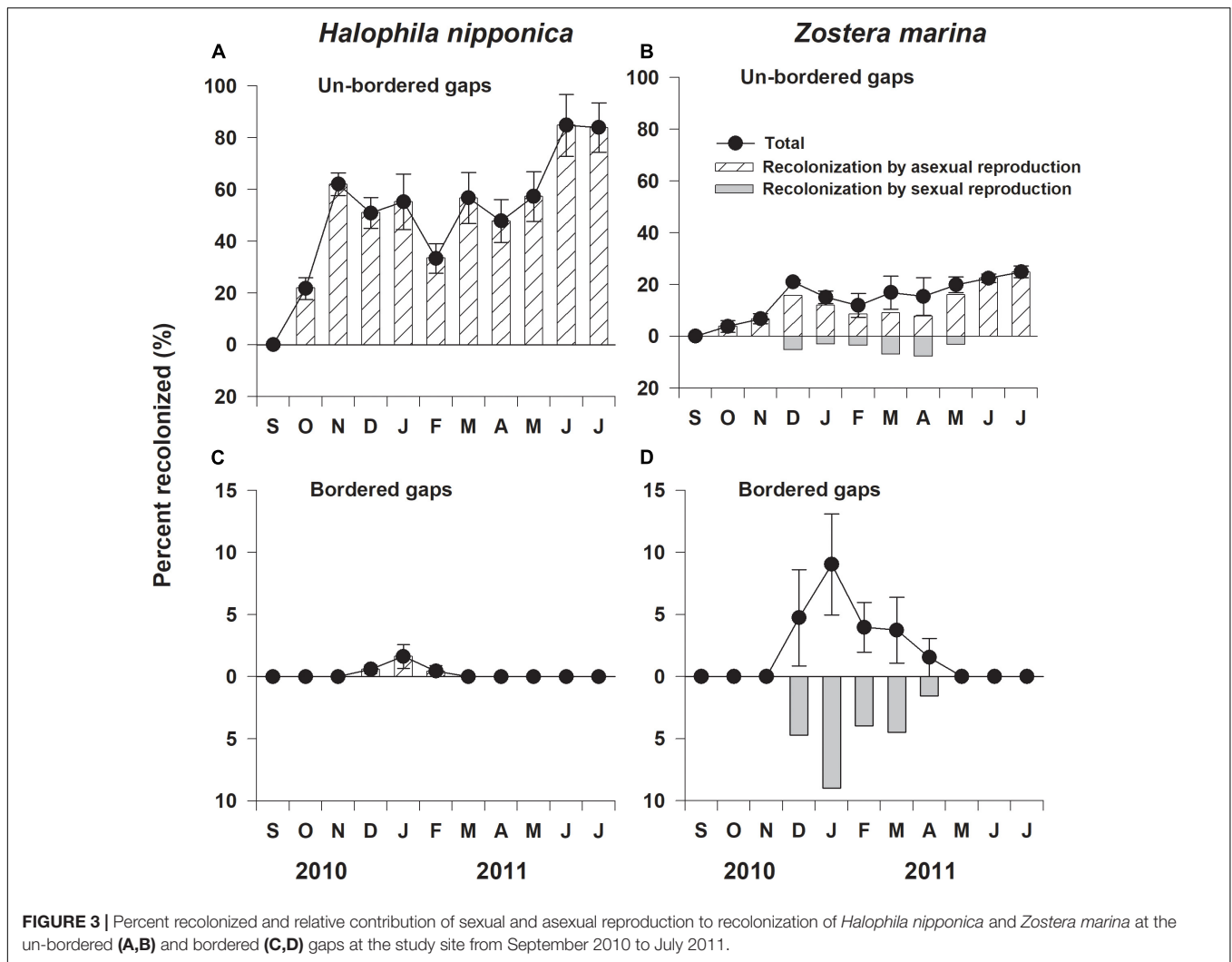
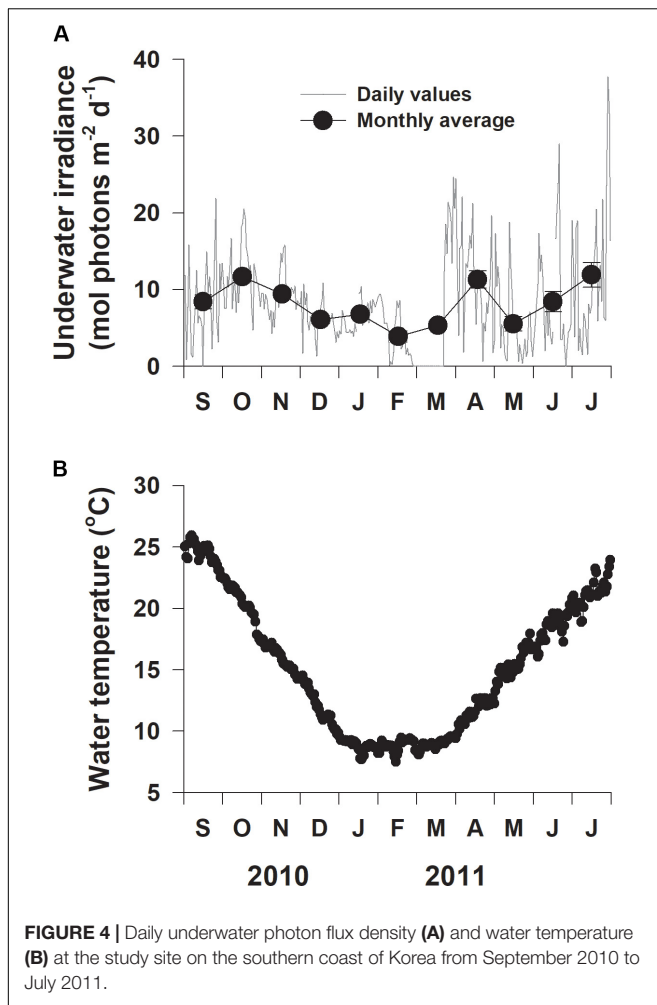


FIGURE 3 | Percent recolonized and relative contribution of sexual and asexual reproduction to recolonization of *Halophila nipponica* and *Zostera marina* at the un-bordered (A,B) and bordered (C,D) gaps at the study site from September 2010 to July 2011.

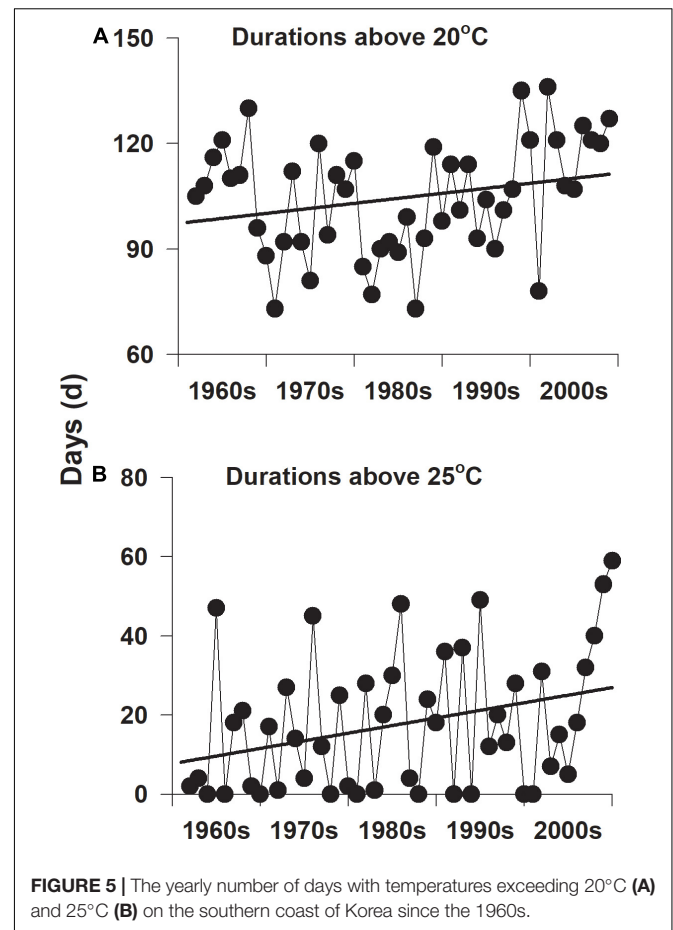
geographical regions (Morris and Virnstein, 2004; González-Correa et al., 2005; Greve et al., 2005; Orth et al., 2006b; Lee et al., 2007a; Park et al., 2011). Asexual reproduction functions as a primary mechanism for the expansion and recolonization of disturbed seagrass meadows (Olesen et al., 2004; Boese et al., 2009; Park et al., 2011). In a multi-species tropical seagrass meadow, shoot density and above-ground biomass in artificially created gaps recovered to the level of un-manipulated control plots within 10 months through asexual reproduction (Rasheed, 2004). After seagrass loss due to mechanical damage caused by a barge grounding in a shallow reef lagoon in the Philippines, approximately 450 m² of seagrass vegetation recolonized, and the majority of the net increase in seagrass cover occurred via rhizome penetration from the surrounding seagrass meadow (Olesen et al., 2004). In the present study, although a few seedlings of *Z. marina* were observed in the gaps, asexual reproduction was the main mechanism for seagrass recolonization within the artificially created gaps in the mixed seagrass meadow of *Z. marina* and *H. nipponica*. The recolonization of

seagrasses was much faster in the un-bordered gaps than in the bordered gaps. At the end of the experiment, no seagrass shoots had established in the bordered gaps, in which asexual reproduction through penetration of vegetative shoots and roots from the surrounding seagrass meadows was prevented. By contrast, approximately 85% of *H. nipponica* and 25% of *Z. marina* recovered through asexual reproduction in the un-bordered gaps, in which recolonization was allowed through both sexual and asexual reproduction.

Sexual reproduction by seeds and seedling establishment is also an essential recolonization mechanism in large-scale disturbed areas (Plus et al., 2003; Greve et al., 2005; Lee et al., 2007b). Previous studies have documented the rapid recolonization of seagrass beds through the germination of seeds in the sediments following intense destruction caused by various disturbances such as algal blooms and anoxic events (Plus et al., 2003; Lee et al., 2007a). In the present study, *Z. marina* recolonized by both sexual and asexual reproduction during the initial phase of recovery in the experimentally



created gaps. Although a few seedlings of *Z. marina* were observed in both the bordered and un-bordered gaps during winter, no seedlings developed to adult shoots at the study site. Because seagrass seedlings are vulnerable to abiotic and biotic stresses, survival rates of *Z. marina* seedlings are often very low (Hauxwell et al., 2001; Greve et al., 2005). In the Yaquina River Estuary, a few seedlings of *Z. marina* were observed in experimentally created gaps, but none survived until summer (Boese et al., 2009). *Z. marina* seedlings emerging under a seagrass canopy usually exhibit very low survival rates (Marion and Orth, 2010). Less than 5% of *Z. marina* seedlings from germinated seeds developed to adult shoots at the shallow area in Jindong Bay on the southern coast of Korea (Kim et al., 2014). Thus, the lower contribution of sexual reproduction to the recolonization of *Z. marina* in the present study can be partially attributed to the generally low survival rates of seedlings. Sexual reproduction of *Z. marina* can be a potentially important mechanism, as seedlings were observed during the germination period at our study site. However, seedlings of *H. nipponica* were not observed in the experimentally created gaps throughout the experimental period; thus, sexual reproduction of this warm temperature-adapted seagrass species (Kim et al., 2012)



may rarely occur in temperate coastal waters, although fruits containing seeds of this species have been observed in this region (Kim et al., 2009).

Vegetative tissue fragments are often thought to serve as potential propagules for seagrass dispersal, as they can drift, root, and produce new shoots (Hall et al., 2006; Diaz-Almela et al., 2008; Stafford-Bell et al., 2015). Vegetative fragments of *Halodule wrightii* and *Halophila johnsonii* exhibited the ability to settle in mesocosm experiments, indicating that seagrass tissue fragments are able to disperse and recruit in new habitats or disturbed areas (Hall et al., 2006). Campbell (2003) also demonstrated that vegetative fragments of *Posidonia* species can recruit and colonize new areas. In the present study, in the bordered gaps where root and rhizome penetration into gaps was prevented, a few shoots of *H. nipponica* were observed during winter and early spring; these did not appear to be seedlings arising from seed germination because of their size. Shoots of *H. nipponica* growing over the borders of the gaps from the adjacent meadow may not be possible, as the growth of this species is severely limited during winter and early spring in this region (Kim et al., 2012). Because the seagrass meadow at the study site was located near a small port, boat grounding, anchor damage, boat propeller scarring, and fishing activity were frequently observed in

the meadow. These physical disturbances may result in the production of vegetative tissue fragments of *H. nipponica*, which can develop to new shoots. Thus, tissue fragments of *H. nipponica* can likely function as propagules that can disperse and colonize new habitats.

Recolonization of *Halophila nipponica* and *Zostera marina*

Small, fast-growing seagrasses such as species of the genera *Cymodocea*, *Halodule*, and *Halophila* are considered pioneer species, which rapidly colonize new habitats and/or recolonize disturbed seagrass meadows (Rollon et al., 1999; Olesen et al., 2004; Rasheed, 2004). These species are characterized by fast rhizome elongation rates and a high vegetative propagation capacity; thus, disturbed seagrass meadows are rapidly and efficiently recolonized by these pioneer species (Rollon et al., 1999; Olesen et al., 2004; Rasheed, 2004). *Halophila ovalis* was the most conspicuous early colonizer among six seagrass species in a mixed tropical seagrass meadow, in which the shoot density of *H. ovalis* reached up to 30-fold higher than pre-disturbance values within 6 months after disturbance (Rollon et al., 1999). *Syringodium isoetifolium* was also a rapid asexual colonizer of disturbed areas, in which the shoot density of this species reached the same level of the natural meadow within 2 months following the clearing of shoots (Rasheed, 2004). In the present study, *H. nipponica* exhibited very rapid recolonization in the experimentally created gaps. *H. nipponica* achieved approximately 60% recovery within 2 months after shoot clearing. However, the shoot density of *H. nipponica* in the experimentally created gaps decreased during winter and spring, because growth of this species is severely restricted at water temperatures less than 15°C (Kim et al., 2012). Nonetheless, *H. nipponica* achieved up to 85% recovery within 10 months after shoot removal in this study. Compared to *H. nipponica*, *Z. marina* showed relatively slow recolonization in the gaps and only achieved 25% recovery within 10 months after shoot removal.

Rollon et al. (1999) reported that the seasonal timing of disturbance did not affect recolonization patterns at mixed seagrass meadows in tropical waters; however, seasonality would likely more strongly affect the pattern of seagrass recolonization in temperate regions due to seasonal variability in seagrass growth. The growth of *Z. marina* is highest at around 15–20°C during spring and then dramatically decreases during high summer water temperature periods (Pastres et al., 2004; Lee et al., 2005; Nejrup and Pedersen, 2008; Park et al., 2009). Both sexual and asexual reproduction of *Z. marina* are more prevalent during winter and spring compared to summer periods (Kim et al., 2014; Qin et al., 2016). Previous studies have demonstrated that the vegetative shoot density of *Z. marina* rapidly increases during winter and spring through shoot recruitment via lateral shoot formation, but decreases during summer and fall due to transformation into flowering shoots and lower shoot recruitment rates during these seasons (Kim et al., 2008, 2014). High *Z. marina* seedling recruitment via seed germination also occurs during winter and early

spring in the temperate coastal waters of Korea and China (Kim et al., 2008, 2014; Qin et al., 2016; Xu et al., 2018). However, *H. nipponica* exhibits a different growth pattern relative to *Z. marina* along the coasts of this region (Kim et al., 2012; Park et al., 2017). Growth of *H. nipponica* is severely restricted at water temperatures below 15°C during winter and spring, and the highest growth occurs at the highest water temperature (~25°C) during the summer period in this region (Kim et al., 2012). The rhizome elongation rate of *H. nipponica* was approximately 1.4 cm apex⁻¹ day⁻¹ during summer, but much lower (0.1 cm apex⁻¹ day⁻¹) during winter (Kim et al., 2012). Because seasonal growth and reproduction distinctly differ between these two seagrass species in Korean coastal waters, the recolonization dynamics of *H. nipponica* and *Z. marina* would also likely exhibit seasonal differences. *Z. marina* would be expected to show more rapid recolonization during winter and spring when reproduction occurs through lateral shoot production and seedling recruitment is high (Kim et al., 2014; Qin et al., 2016). By contrast, *H. nipponica* would be expected to exhibit fast recolonization during summer, as it still possesses tropical growth characteristics (Kim et al., 2012; Park et al., 2017).

Strong evidence of increasing sea temperatures has been reported along the coasts of Korea and throughout the global oceans (Kim et al., 2009; IPCC, 2013). Water temperatures on the south coast of Korea have increased gradually over the last seven decades (Kim et al., 2009). The average water temperature during the coldest month has increased by 2°C, and the average annual water temperature has increased by approximately 1°C in coastal waters of Korea since the 1930s (Kim et al., 2009). In addition, the yearly numbers of days with daily water temperatures exceeding 20°C and 25°C have increased on the southern coast of Korea since the 1960s (Figure 4). The frequency and magnitude of catastrophic events, including typhoons and algal blooms, have also tended to increase gradually on the coasts of Korea over the last few decades (Kim K. et al., 2015; Kim Y. K. et al., 2015). Three consecutive strong typhoons led to the loss of more than 4 km² of *Z. marina* meadow in this region (Kim K. et al., 2015). The disappearance of *Z. marina* due to severe light reduction by a red tide algal bloom has also been reported in coastal waters of Korea (Lee et al., 2007a). These significant losses of *Z. marina* meadows in this region usually occur during summer when the maximum growth of *H. nipponica* was observed at the highest water temperature. Thus, the dominance of *H. nipponica* over *Z. marina* will likely strengthen in the temperate seagrass meadows in this region. Consequently, the structure of seagrass ecosystems will be altered within the coastal waters of the northwestern Pacific under conditions of ongoing climate change.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

SK, YK, and K-SL conceived and designed the experiments. SK and YK performed the experiments. SK, HK, and K-SL analyzed the results. All authors contributed to writing the manuscript and approved the submission.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2020.00500/full#supplementary-material>

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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.

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