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Reproductive strategy of the intertidal seagrass *Zostera japonica* under different levels of disturbance and tidal inundation

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A B S T R A C T

Zostera japonica populations along the coastline of the northwestern Pacific Ocean are declining, mainly due to anthropogenic and natural disturbances. Although reproductive strategy is an important factor in achieving population persistence, changes in the reproductive strategy of *Z. japonica* under anthropogenic disturbances and tidal stresses are largely unknown. Thus, the duration and frequency of flowering, reproductive effort, potential seed production, and seed density in sediments were measured at three study stations (undisturbed upper, undisturbed lower, and disturbed stations), which were classified based on the levels of inundation stress and clamming activity, in monospecific meadows of *Z. japonica* on the southern coast of Korea. The flowering duration was approximately six months in the disturbed station, with disturbance due to clam harvesting, whereas the duration was about five months in the undisturbed lower station, and only three months in the undisturbed upper station. The maximum flowering frequency was 25.5% in the disturbed station, which was approximately 4- and 2-fold higher than in the undisturbed upper (6.1%) and lower (12.3%) stations, respectively. A similar trend in reproductive effort was also found among the three study stations. Potential seed production was 7850, 6220, and 1560 seeds m^{-2} in the disturbed, undisturbed lower, and undisturbed upper stations, respectively. The annual maximum seed density in sediments was also higher in the disturbed and undisturbed lower stations than in the undisturbed upper station, but the densities were relatively low (ranging from 71 to 254 seeds m^{-2}) at all three study stations. It was found that the allocation to sexual reproduction was highest in the disturbed station, followed by the undisturbed lower station, and lowest in the undisturbed upper station, suggesting that sexual reproduction in *Z. japonica* tends to be enhanced under disturbed and inundated environmental conditions for population persistence.

1. Introduction

Significant losses and declines of seagrass meadows, mainly due to natural and anthropogenic disturbances, have been reported worldwide (Short and Wyllie-Echeverria, 1996; Waycott et al., 2009). Although natural events such as strong cyclones and diseases can contribute to the decline of seagrass meadows, the majority of seagrass declines are related to anthropogenic disturbances (Short and Wyllie-Echeverria, 1996; Case and Ashman, 2005; Hammerstrom et al., 2006). Intertidal seagrasses, such as *Zostera japonica* and *Z. noltii*, are probably much more vulnerable to natural and human-induced disturbances because of their primary distribution (Ferraro and Cole, 2011; Park et al., 2011; Kim et al., 2016). Anthropogenic disturbances such as coastal constructions, dredging, reclamation, and fishing activities (e.g., clam harvesting) can lead to seagrass declines in the intertidal zone (Everett et al., 1995; Dawes et al., 1997; Lee, 1997; Creed and Amado Filho, 1999; Badalamenti et al., 2006; Erftemeijer and Lewis, 2006).

The distribution, production, and morphology of intertidal seagrasses are also affected by intertidal stresses such as tidal exposure, extreme temperatures, light fluctuation, and desiccation (Lee et al., 2005; Kim et al., 2016). Seagrasses in the upper intertidal zone undergo several hours of exposure to the air during low tide, and thus experience extreme temperatures, high photoinhibitory irradiance, and desiccation stress, whereas seagrasses in the lower intertidal zone suffer competition with subtidal species, decreased light availability, and physical disturbances caused by tidal currents

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(Leuschner et al., 1998; Cabaço et al., 2009; Van Der Heide et al., 2010; Kim et al., 2016). Thus, environmental stresses on the intertidal seagrass plants will vary along a vertical gradient in the intertidal zones. Intertidal stresses also appear to cause variability in the reproductive strategy of intertidal seagrasses along the vertical intertidal gradient (Harrison, 1982; Yabe et al., 1996; Ramage and Schiel, 1998). These differences in reproductive strategy may be attributed to the different periods of exposure to air during low tide (Bayer, 1979; Phillips et al., 1983; Pettitt, 1984; Cabaço et al., 2009).

Seagrasses can reproduce both asexually via clonal growth and sexually via flowering and seed production (den Hartog, 1970). Asexual reproduction is the dominant process that sustains seagrass populations because new shoot recruitment through sexual reproduction has an extremely low success rate in existing populations (Hemminga and Duarte, 2000). However, sexual reproduction may be essential for the maintenance and recovery of seagrass meadows in highly disturbed conditions, and will ultimately improve the resilience to disturbances (Marbà and Walker, 1999; Rasheed, 2004; Greve et al., 2005; Lee et al., 2007; Kim et al., 2016; Qin et al., 2016). Seagrasses tend to reallocate their resources and energy from vegetative organs to reproductive organs under natural and anthropogenic disturbances (Park et al., 2011; Henderson and Hacker, 2015). Consequently, seagrasses exhibit an enhanced reproductive effort in disturbed or stressful environments (Phillips et al., 1983; Marba and Duarte, 1995; Park et al., 2011; Cabaço and Santos, 2012). Although many studies have focused on the growth dynamic or recovery process of the intertidal seagrass *Z. japonica* along the coastline of the northwestern Pacific Ocean (Lee et al., 2005, 2006; Park et al., 2011; Kim et al., 2016), few studies have investigated changes of reproductive strategies in response to physical disturbances and stressful environments.

Zostera japonica, which occurs typically in the intertidal zone, was originally distributed along the coastline of the northwestern Pacific Ocean, and was introduced to the Pacific coast of North America in the early 20th century (Harrison, 1982; Short, 1983). The distribution of *Z. japonica* has rapidly expanded along the Northeastern Pacific coast of North America, but in its original distribution areas on the coastline of the Northwestern Pacific Ocean, populations have frequently been disturbed by severe intertidal stresses and human activities such as clam harvesting (Park et al., 2011; Shafer et al., 2014; Kim et al., 2016). Clam harvesting is considered to be a major cause of seagrass declines in intertidal zones where clams are commercially important (Alexandre et al., 2005; Park et al., 2011; Guimarães et al., 2012; Choi et al., 2016; Kim et al., 2016; Qin et al., 2016). Clam harvesting can cause direct uprooting or shoot burial, and consequently contribute to losses of seagrass coverage (Short and Wyllie-Echeverria, 1996; Neckles et al., 2005; Park et al., 2011). Clam culture grounds are usually located in the intertidal zone, and occasionally overlap with *Z. japonica* beds along the coast of Korea (Park et al., 2011). Clam harvesting occurs during every spring when the tide is low, and thus the *Z. japonica* beds in the clam culturing grounds are disturbed annually by clamming activity (Park et al., 2011). In this study, we hypothesized that sexual reproduction will be enhanced in the disturbed area due to clamming activity and in the area with high intertidal stresses. We assessed the effects of the clamming activity and the environmental stresses in the different intertidal zones on the reproductive phenology and strategy of *Z. japonica*. Flowering duration, flowering frequency, reproductive effort, potential seed production, and sediment seed density were measured at the three study stations, with different levels of anthropogenic disturbance and intertidal stresses.

2. Materials and methods

2.1. Study site

This study was conducted in monospecific meadows of *Z. japonica* from May 2015 to November 2016. Three experimental stations, a disturbed station (due to clam harvesting) at Yongbuk (34°48′04″N, 128°35′02″E), and undisturbed upper and undisturbed lower intertidal stations at Yulpo (34°46′34″N, 128°35′45″E) were established at Koje Island on the southern coast of Korea (Fig. 1). The tidal regime is semidiurnal, with a tidal amplitude ranging from 2.5 m during the spring tide to 1.2 m during the neap tide in the three study stations (Tide Tables for the Coasts of Korea, Korea Hydrographic and Oceanographic Administration; http://www.khoa.go.kr). The three stations were characterized by a high sand content in the sediment. *Zostera japonica* meadows were located in the intertidal zone at all study stations. Two undisturbed study stations (i.e., the undisturbed upper and lower stations) were established along the vertical intertidal gradient within a meadow of *Z. japonica* in Yulpo, whereas only one disturbed station was established in Yongbuk, because the *Z. japonica* meadow in this area was relatively narrow in the vertical direction. The *Z. japonica* meadow in Yongbuk was located within a Manila clam culturing ground and was disturbed every spring by clam harvesting activity. Numerous *Z. japonica* shoots were removed or buried in sediment during clam harvesting in the disturbed station (Park et al., 2011). In contrast, the meadow in Yulpo was well protected, and no anthropogenic disturbances were observed in this area. The disturbed station in Yongbuk and the undisturbed upper and lower stations in Yulpo were located at approximately 60, 40, and 20 cm above the mean lower low water (MLLW), respectively.

2.2. Measurements of physical and chemical parameters

Temperature at the seagrass canopy level in the three study stations was monitored every 15 min throughout the experimental period from May 2015 to November 2016 using a Hobo data logger (Onset Computer Corp., Bourne, MA, USA) encased in waterproof underwater housing. The average daily values of the measured temperatures were calculated. Photon flux density (PFD) was monitored every 15 min in each station using an Odyssey photosynthetic irradiance recording system (Dataflow Systems Ltd., Christchurch, New Zealand). The logger was calibrated using an LI-1400 data logger and an LI-193SA spherical quantum sensor (Li-Cor, Lincoln, NE, USA). Daily PFD (mol photons m^{-2} d^{-1}) was calculated as the sum of the quantum flux over each 24-h period. Daily temperature and irradiance were averaged monthly. The tidal height at each station was measured when the study station began to be exposed to the air during low tide, and the air exposure time was calculated at each station using real-time tidal height data for the Korean coastline (Korea Hydrographic and Oceanographic Administration; http://www.khoa.go.kr). Monthly exposure time (h) was represented as the sum of total exposure time in each month.

To determine the inorganic nutrient concentrations in sediment pore water, eight replicate sediment samples were randomly collected to a sediment depth of approximately 13 cm using a syringe corer at each station. The samples were placed in ice and frozen pending laboratory analyses. Sediment pore water was obtained by centrifugation (8000 × g for 20 min) and used for the determination of dissolved inorganic nitrogen (NH_4^+ and $NO_3^-+NO_2^-$) and PO_4^{3-} concentrations after dilution with low-nutrient seawater (<0.1 μM). The NH_4^+, $NO_3^-+NO_2^-$, and PO_4^{3-} concentrations were measured using standard colorimetric techniques following the methods used by Parsons et al. (1984). Concentrations of $NO_3^-+NO_2^-$ were determined after running samples