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Authors: Zhang, Pei D., Liu, Yan S., Guo, Dong, Li, Wen T., and Zhang, Qian

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Seasonal Variation in Growth, Morphology, and Reproduction of Eelgrass *Zostera marina* on the Eastern Coast of the Shandong Peninsula, China

Pei D. Zhang[†]*, **Yan S. Liu**[†], **Dong Guo**[‡], **Wen T. Li**[†], **and Qian Zhang**[†]

[†]College of Fisheries
Ocean University of China
Qingdao 266003, P.R. China

[‡]Liaoning Ocean and Fisheries Research Institute
Dalian 116023, P.R. China

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ABSTRACT

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Seasonal dynamics of *Zostera marina* were monitored monthly in Swan Lake of Shandong Peninsula, China, by examining plant density, morphology, weight, and environmental factors from February 2009 to January 2010. The greatest values for shoot size and weight were obtained in summer and the smallest values in winter and early spring. Reproductive shoots appeared in late March and developed into fruits in mid-June. Fruits were fully developed into mature seeds in mid-July. Reproductive shoot size and weight exhibited clear seasonal patterns with maximum values in May for leaf length, inflorescence length, and leaf width and in June for shoot length and shoot weight. The density of reproductive shoots ranged from 4 to 40 shoots m^{-2} with an average of 22.4 ± 12.8 shoots m^{-2} (mean ± 95% confidence interval) in July 2009. The average number of spathes per reproductive shoot was 18.9 ± 3.3, with 7.8 ± 0.7 seeds per spathe, and the mean seed dry weight was 3.2 ± 0.4 mg. Seasonal variations in shoot density and aboveground tissue dimensions correlated positively with water temperature. This study presents the first quantitative data on the seasonal dynamics of *Z. marina* in China.

ADDITIONAL INDEX WORDS: *Seagrass, shoot dynamics, environmental factor*.

INTRODUCTION

Seagrass meadows are considered to be one of the most important shallow marine ecosystems for humans, because they play a major role worldwide in the marine ecology of coastal and estuarine areas, supporting finfish, shellfish, and invertebrate communities, as well as filtering coastal waters, dissipating wave energy and anchoring sediments (Costanza *et al.*, 1997; Green and Short, 2003; Heck, Hays, and Orth, 2003; Lemmens *et al.*, 1996; Orth, Heck, and van Montfrans, 1984).

Zostera marina (eelgrass) is the most common temperate species of seagrass throughout the Northern Hemisphere. It undergoes both asexual, clonal reproduction with rhizomes and sexual reproduction with flowers and seeds (den Hartog, 1970). Vegetative development through clonal growth has been reported to be the main process for maintenance and establishment of seagrass meadows (Alexandre *et al.*, 2006; Plus, Deslous-Paoli, and Dagault, 2003; Rasheed, 2004). Flowering events and seed survival have been considered important mechanisms for maintaining genetic diversity, and possibly the only way to colonize bare sediments or disturbed areas (Alexandre *et al.*, 2006; Marbà and Walker, 1999; Orth *et al.*, 2000). The balance between the two types of reproduction varies from meadow to meadow, even within the same species, ranging from monoclonal (no sexual contribution) to populations where every sampled shoot came from a different seed (Arnaud-Haond *et al.*, 2005; Coyer *et al.*, 2004; Olsen *et al.*, 2004). *Zostera marina* eelgrass dominates the north temperate Pacific, occurring around the Pacific Rim from Japan, Korea, and China to the northern Bering Sea and down to the Gulf of California, with other *Zostera* species centred in east Asia (Short *et al.*, 2007). In China, eelgrass can be found in the coastal areas of Shandong, Liaoning, and Hebei provinces (Liu *et al.*, 2011). In recent years, however, many populations of *Z. marina* have declined due to both natural and anthropogenic disturbances (Guo, 2010). Although seasonal variations of shoot growth, morphology, and reproduction in *Z. marina* have been well described for the coast of Japan (Aioi and Nakaoka, 2003; Hasegawa, Hori, and Mukai, 2007; Morita *et al.*, 2007, 2010; Tanaka *et al.*, 2008; Watanabe, Nakaoka, and Mukai, 2005), these topics have not been previously studied in China.

Swan Lake (Yuehu) is a small inlet system located on the coast of the Shandong Peninsula, China. The tidal basin (*i.e.* the lagoon) is separated from the open sea (*i.e.* Rongcheng Bay and the Yellow Sea) by a 2.5-km-long sand spit that lies to the east of the lagoon (Wei and Zhuang, 1997). The entrance channel connecting the lagoon with the open sea is 132 m wide at its narrowest part (Jia, Gao, and Xue, 2003). Now, a major part of Swan Lake is covered with seagrasses (*Z. marina* and *Zostera japonica*). Fisheries are major human activities in Swan Lake and adjacent coastal areas, with intensive aquaculture of a clam (*Ruditapes philippinarum*). However, the ecosystem is considered relatively healthy, with extensive eelgrass meadows developed in Swan Lake. In the present study, we examined the annual variation in shoot growth, morphology, and reproductive effort for a population of *Z.*

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*Corresponding author: zhangpdsg@ouc.edu.cn

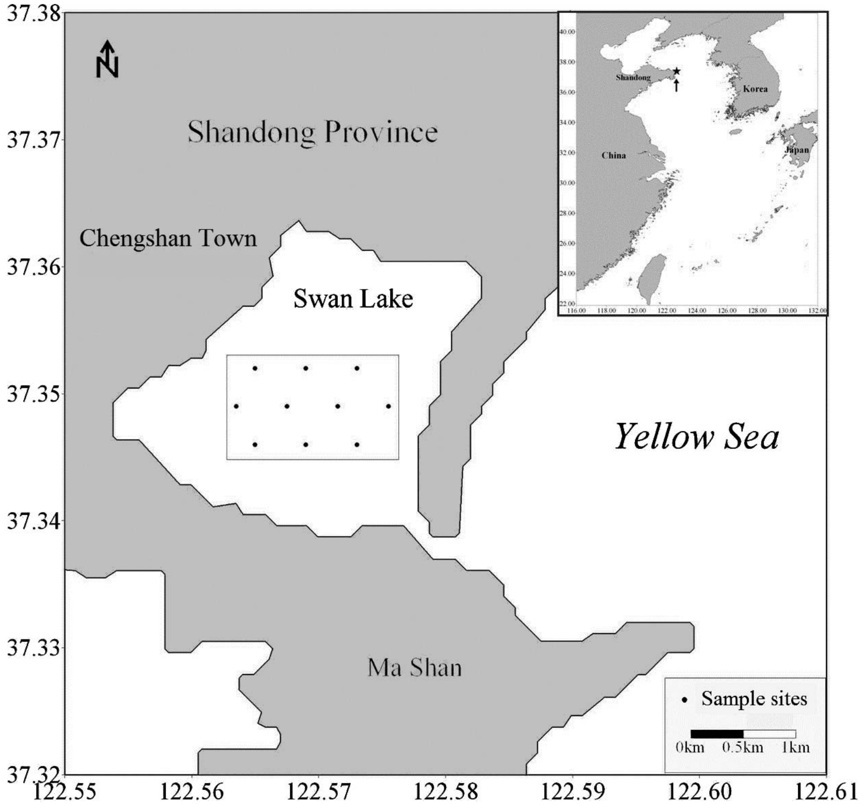

Figure 1. Location of Swan Lake. Ten permanent sampling stations, represented by dots, were established for periodical census and collection of *Z. marina* at 0.45-km intervals in three rows over an area of 1.35 km^2.

marina in Swan Lake and related these to seasonal trends in environmental parameters at the eastern end of Shandong peninsula, China, which have never been examined previously.

METHODS

The environment of Swan Lake was largely natural before the 1970s. Although there are no precise data for the abundance of *Z. marina*, anecdotal reports, fishery practices, and local historical knowledge indicate that *Z. marina* was very abundant in Swan Lake in the early 1970s. In 1979, the entrance to the lagoon was artificially closed for aquaculture purposes, but the closure caused rapid sediment accumulation within the entrance channel, which reduced water exchange (Gao *et al.*, 1998). The eelgrass beds were almost completely eliminated by the end of 1982 because of poor water exchange. An immediate effect of the loss of *Z. marina* was the elimination of the commercial finfish, shellfish, sea cucumber (*Stichopus japonicus*), and octopus (*Octopus variabilis*) fisheries and the disappearance of Whooper Swan (*Cygnus cygnus*) that fed exclusively on *Z. marina*. The upper part of the artificial dam was removed in 1986. As a result, the ecosystem of the lagoon gradually recovered, and the seagrass beds became re-established. Now, *Z. marina* is the dominant seagrass species, and it is estimated to occupy about 2.0 km^2, mostly distributed in the middle of the lake (Figure 1).

Description of the Study Area

The study was carried out in Swan Lake on the eastern coast of Shandong Peninsula, China (37.3382°–37.3588°N, 122.5551°–122.5793°E; Figure 1). The lake is a tidal basin or lagoon with an area of 4.8 km^2. Water depth is mostly less than 1.5 m, measured at mean sea level, with a maximum water depth of around 3.5 m at high water on spring tides. The tidal range, measured at the entrance to the lagoon, is 1.15 m on springs and 0.64 m on neaps. The floor of the lagoon is generally dominated by fine-grained material, with mud and sandy mud covering around 40% of the lagoon area, with variable mud content. The remainder of the lagoon area is covered by muddy sand, with a mud content of 20–50% (Jia, Gao, and Xue, 2003). Local historical data show that annual average air temperature in Swan Lake is 12°C, and the highest and lowest air temperature values are attained in August and February, respectively. Days of water temperature higher than 30°C during a year are no more than 10 days, and average of water temperature in winter is about 1.5°C.

Field Procedure and Data Collection

In this study, 10 permanent sampling stations were established at 0.45-km intervals in three rows for periodic census and collection of *Z. marina*; they were located in the subtidal zone of the *Z. marina* bed over an area of 1.35 km^2

(Figure 1). A permanent buoy was fixed to the seabed using steel stakes to mark each station.

Biological Measurements of Shoots

Shoot density, morphology, and individual shoot weight at Swan Lake were monitored monthly for 12 months from February 2009 to January 2010. To estimate shoot density, four 0.25×0.25-m quadrats were haphazardly placed within 20 m of each sampling station to count the number of shoots, and the measurements were converted to shoots per unit area values (shoots m^{-2}). Shoot morphology was monitored on samples of 30–50 intact shoots. For this purpose, 3–5 intact shoots were collected at each sampling station. Shoots were collected carefully by hand to avoid damage to belowground structures, and samples were rinsed thoroughly in seawater to remove sediments, shells, and other debris.

Samples were placed in sealed polythene bags, stored on ice, transported to the laboratory, and kept at 4°C before sorting for analysis. Samples were sorted and cleaned with gauze to remove epiphytes; then, leaf length, leaf width, sheath length, internode length, internode diameter, and root length were measured. Sections of leaf, root, and rhizome material were cut with a razor blade and rinsed in deionized water. Subsamples were dried at 60°C for 48 hours to obtain above- and belowground tissue weight.

Biological Measurements of Reproductive Shoots

Reproductive shoots were monitored monthly at each sampling station from March 2009 to July 2009. Ten intact reproductive shoots were collected by hand at each sampling station, and the spathes of reproductive shoots were examined. Their maturation stage was recorded to estimate the time elapsed between maturation stages. Spathe maturity was classified according to the maturation scale developed by Alexandre *et al*. (2006). The maturation of the flowers inside the spathes was divided into six stages: 0, undefined flowers inside the immature inflorescence; I, flowers aligned on a single stem and sheath closed; II, mature females erected outside sheath for fertilization; III, filiform pollen released by mature males (anther dehiscing); IV, fertilized females, thecae empty (if still present); V, presence of fruits (Va, small embryos inside the female flowers; Vb, fully developed fruit; Vc, white fruit presents a thin coat; Vd, greenish-blue fruit with a hard brownish-black coat: seed stage).

Three to five reproductive shoots of eelgrass with inflorescences containing developed or developing seeds were collected monthly by hand at each sampling station from May 2009 to July 2009. Reproductive shoots were separated from their root systems and placed in sealed polythene bags, stored on ice, transported to the laboratory, and kept at 4°C before analysis. Samples were cleaned with gauze to remove epiphytes. Leaf length, leaf width, inflorescence length, and shoot length of reproductive shoots were measured; then, each reproductive shoot was dried at 60°C to constant weight. The plant reproductive effort was estimated by the density of reproductive shoots, number of spathes per reproductive shoot, and number of seeds per spathe in July 2009. To estimate reproductive shoot density, six 0.5×0.5-m quadrats were haphazardly placed within 10 m of each sampling station to count the number of reproductive shoots.

Biological Measurements of Seeds

Reproductive shoots with mature seeds were harvested from each sampling station by hand in late July 2009. Seeds were manually extracted from fruits, stored in natural seawater, returned to the laboratory, and held at 4°C before analysis. Seed length, diameter, number of longitudinal ribs, and wet weight were determined individually in a random subsample of 50 seeds, after blotting each seed rapidly on a paper towel. Then seeds were dried at 60°C to constant weight with a precision of 0.1 mg.

Environmental Parameters

Water temperature (°C) and underwater photosynthetic photon flux density (PPFD) were recorded continuously every 30 minutes throughout the study period using HOBO pendant temperature/light data loggers (Onset Computer Corp.), which were placed underwater 20 cm from the seabed. Measured water temperature was averaged daily. Light intensity (lux) measured by the HOBO data logger was converted to PPFD (μmol photons m^{-2} s^{-1}) by concurrent quantum measurements using an LI-250A data logger and an LI-193SA spherical quantum sensor (Li-Cor Inc.). A regression analysis was performed to convert the light intensity to PPFD ($y = 0.017x + 100.2$, $r^2 = 0.83$). Daily PPFD (mol photons m^{-2} d^{-1}) was calculated as the sum of the quantum flux over each 24-hour period.

Statistical Analysis

All values are reported as mean ± 95% confidence interval. Statistical analyses were performed using the SPSS Windows Program (Release 13.0, SPSS Inc.). Seasonal variations of shoot density, morphology, and individual weight data were analyzed by one-way analysis of variance (ANOVA). When a significant difference was observed, the means were analyzed by Tukey-Kramer tests to establish significant differences among them. Data were tested for normality and homogeneity of variance to meet the assumptions of parametric statistical analysis. The relationships between environmental parameters and shoot density, morphology, and individual weight were estimated using curve estimation, and the significances of these regressions were tested using ANOVA. For this purpose, measured water temperature and PPFD was averaged monthly. Significance level was set at $\alpha = 0.05$.

RESULTS

Clear seasonal variations in water temperature and PPFD and in shoot density, dimension, and weight of *Z. marina* in Swan Lake are showed in Figures 2–6. Curve estimation suggests that shoot density and aboveground tissue dimensions of *Z. marina* in Swan Lake are positively correlated with water temperature.

Water Temperature and PPFD

Water temperature showed a typical seasonal variation pattern (Figure 2A), with the highest value of 26.8°C in August 2009 and the lowest value of –1.0°C in February 2009. Underwater irradiance also exhibited a clear seasonal variation (Figure 2B). PPFD was highest during late spring and summer and lowest in the middle of fall. Monthly average

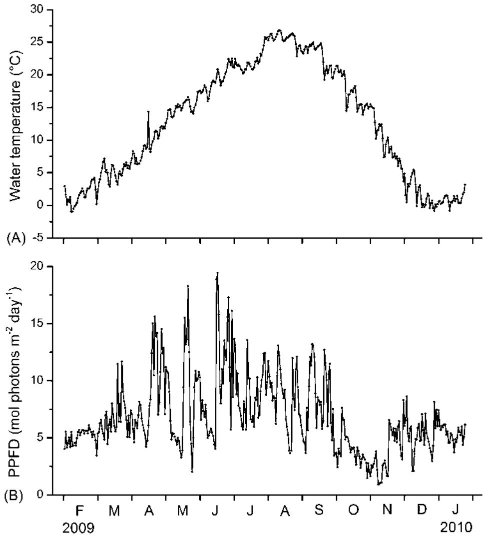

Figure 2. Seasonal changes in water temperature (A) and underwater photosynthetic flux density (PPFD) (B) during the experimental period from February 2009 to January 2010. Measurements were recorded continuously every 30 min. Measured water temperature was averaged daily. Daily PPFD was calculated as the sum of the quantum flux over each 24-h period.

water temperature and underwater irradiance changed significantly ($p < 0.01$) with sampling month.

Density, Morphology, and Individual Weight of Shoots

The shoot density of *Z. marina* showed significant ($p < 0.05$) seasonal variation, with the maximum value of 437 shoots m^{-2} in June and the minimum value of 190 shoots m^{-2} in January (Figure 3). Shoot dimensions also exhibited a clear seasonal variation ($p < 0.05$). Leaf length, leaf width, sheath length, and root length were greatest in July (summer) and least in December–March (from winter to early spring), ranging from 6.1 to 39.8 cm for leaf length, 0.24 to 0.68 cm for leaf width, 2.7 to 13.9 cm for sheath length, and 3.12 to 5.36 cm for root length (Figures 4A–C, 4F). Internode length was greatest in July and least in February–April, with monthly averages between 0.54 and 2.00 cm (Figure 4D), whereas internode diameter ranged from 0.23 cm in December to 0.38 cm in July (Figure 4E).

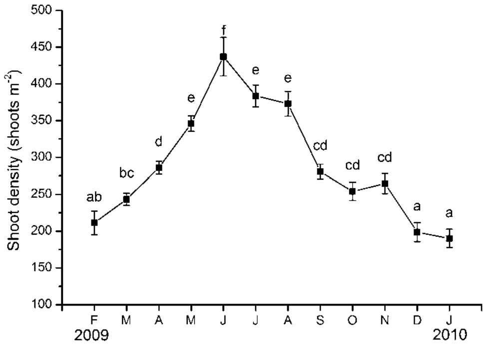

Figure 3. Seasonal change in shoot density of *Z. marina* at Swan Lake from February 2009 to January 2010. Data are means ± 95% confidence intervals. Different letters above bars indicate significant differences ($p < 0.05$).

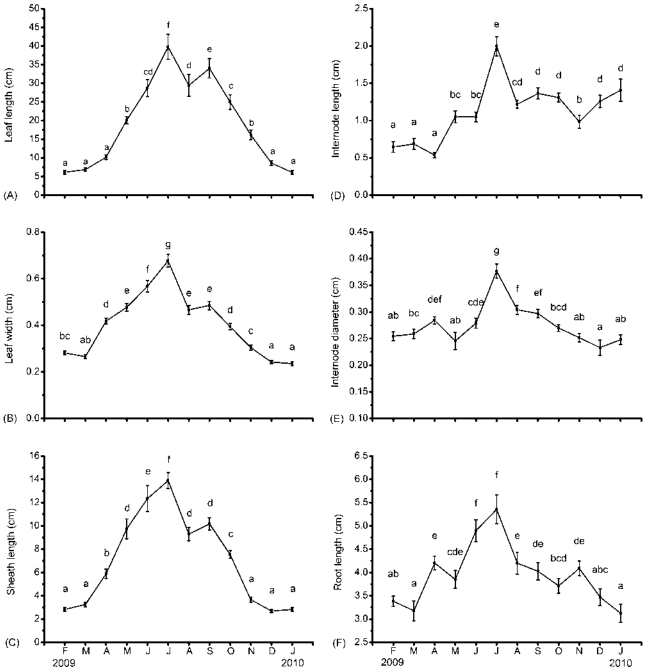

Figure 4. Seasonal changes in shoot dimensions of *Z. marina* at Swan Lake from February 2009 to January 2010: (A) leaf length, (B) leaf width, (C) sheath length, (D) internode length, (E) internode diameter, and (F) root length. Other details as in Figure 3.

Individual shoot weight showed clear seasonal variations with significant peaks in July (Figures 5A–C). The aboveground tissue weight and total weight of shoots in sampling months from November to April were significantly lower ($p < 0.05$) than those of shoots in sampling months from July to September. The highest aboveground tissue weight and total shoot weight occurred in July 2009, whereas the lowest values occurred in February 2009. The belowground tissue weight exhibited a similar trend to the aboveground tissue and total shoot weights, but the weight was far less than those of aboveground tissues and total shoots. The belowground tissue weight of shoots in February and March was significantly lower ($p < 0.05$) than that of shoots in sampling months from June to October. In the meantime, individual shoot weight, calculated from means, decreased rapidly about 70% from July to August.

Density, Morphology, and Weight of Reproductive Shoots

In our study site, the flowering period occurs from March to July and is characterized by the appearance of reproductive shoots, maturation, and the release of seeds. Reproductive shoots first appeared in late March (Stage 0), and developmental stages I and II were reached in late April and mid-May, respectively. The maximum proportion of reproductive shoots recorded (45–50% of total shoot density) was in May. Stages III

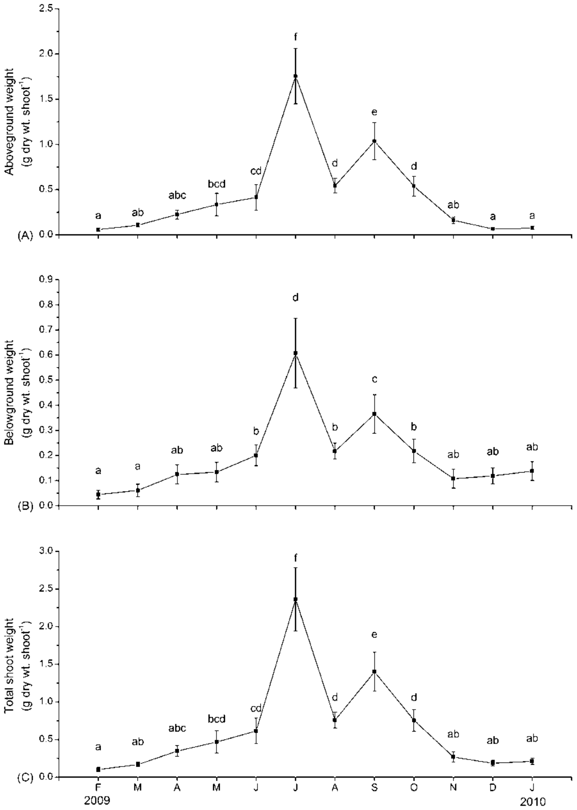

Figure 5. Seasonal changes in individual shoot weight of *Z. marina* at Swan Lake from February 2009 to January 2010: (A) aboveground weight, (B) belowground weight, and (C) total shoot weight. Other details as in Figure 3.

and IV appeared from mid-May to mid-June, and fruits (Stage V) were observed from mid-June, with a series of Stage V peaks through to mid-July. Fruits were fully developed into mature seeds (Stage Vd) in mid-July. Mature seeds from the reproductive shoots began to fall to the bottom sediments in mid-July. During the withering period from late July to August, biomass decreased and plants became shorter.

Reproductive shoot morphology exhibited significant changes over the reproductive season (Figure 6). Both leaf length and inflorescence length were greatest in May and then decreased rapidly in July (Figures 6A and 6C). The average leaf width was greatest in May and was significantly higher than in June and July; however, there was no marked difference between June and July (Figure 6B). Reproductive shoot length in June was significantly higher than in May and July (Figure 6D). The mean reproductive shoot weight showed a similar pattern of variation through the reproductive season, with the highest value in June and lower values in both May and July (Figure 6D).

The density of reproductive shoots ranged from 4 to 40 shoots m^{-2}, with an average of 22.4 ± 12.8 shoots m^{-2} in July 2009. The average number of spathes per reproductive shoot was 18.9 ± 3.3, with 7.8 ± 0.7 seeds per spathe. The potential seed production of *Z. marina* meadows in Swan Lake could be 3303 ± 573 seeds m^{-2}.

Seed Size and Weight

Length of *Z. marina* seeds at Swan Lake in late July 2009 ranged from 2.7 to 3.6 mm, with an average of 3.14 ± 0.08 mm. Seed diameter ranged from 1.3 to 1.9 mm, with an average of 1.65 ± 0.04 mm. Number of longitudinal ribs per seed ranged from 14 to 17, with an average of 15.3 ± 0.4. The mean wet weight and dry weight of seeds were 5.5 ± 0.5 mg and 3.2 ± 0.4 mg, respectively.

The Relationships between Environmental Parameters and Shoot Biological Parameters

Curve estimation showed that water temperature and shoot density displayed a positive linear relationship ($R^2 = 0.6$, $p < 0.01$). Water temperature and aboveground tissue dimension also exhibited clear linear relationships, and the correlation coefficients were all greater than 0.7 ($p < 0.01$). However, relationships between water temperature and belowground tissue dimensions and between water temperature and individual shoot weight were not significant ($p > 0.05$). Underwater irradiance and shoot density also revealed a similar linear relationship ($R^2 = 0.6$, $p < 0.01$). However, relationships between underwater irradiance and other shoot biological parameters were not significant ($p > 0.05$), except for leaf width and sheath length.

DISCUSSION

Seagrass productivity usually exhibits distinct seasonal variation, with rates increasing during spring and summer and decreasing during fall and winter (Dunton, 1994; Lee and Dunton, 1996; Lee, Park, and Kim, 2005; Vermaat, Hootsmans, and Nienhuis, 1987). This study presents the first quantitative data on the seasonal dynamics of *Z. marina* density, morphology, weight, and reproduction in China. Our results show that shoot density of *Z. marina* in Swan Lake gradually increased from February 2009 (211 shoots m^{-2}) to June 2009 (437 shoots m^{-2}) and then gradually decreased from June 2009 to January 2010 (190 shoots m^{-2}). A similar change also was found in Sango Bay in the vicinity of Swan Lake (Tang, 2013), but the annual average of shoot density (446 shoots m^{-2}) in Sango Bay was greater than that of shoot density in Swan Lake (289 shoots m^{-2}). This may be because of the difference in sampling sites in two studies. Sampling stations in our study were located in the subtidal zone of the *Z. marina* bed; however, sampling stations in the study of Tang (2013) were located in a sea cucumber aquaculture pond. Chen (2013) reported that shoot density of *Z. marina* in Qingdao Bay about 250 km south from Swan Lake and Sango Bay showed a clear seasonal variation, with the maximum value of 780 shoots m^{-2} in July and the minimum value of 284 shoots m^{-2} in November. The higher shoot density may be because the water temperature in Qingdao Bay (annual average of 15.3°C) was higher than that in Swan Lake (12.7°C) and in Sango Bay (10.9°C). Similar results were found in two bay systems on the south coast of the Korean peninsula (Lee, Park, and Kim, 2005). Total eelgrass shoot density exhibited a distinct seasonal variation, and the highest values were achieved during March and April in Kosung Bay and during May in Koje Bay. However, shoot density of *Z. marina* in Akkeshi Bay, northern Japan, did not show a clear seasonal pattern, with the maximum value of 580

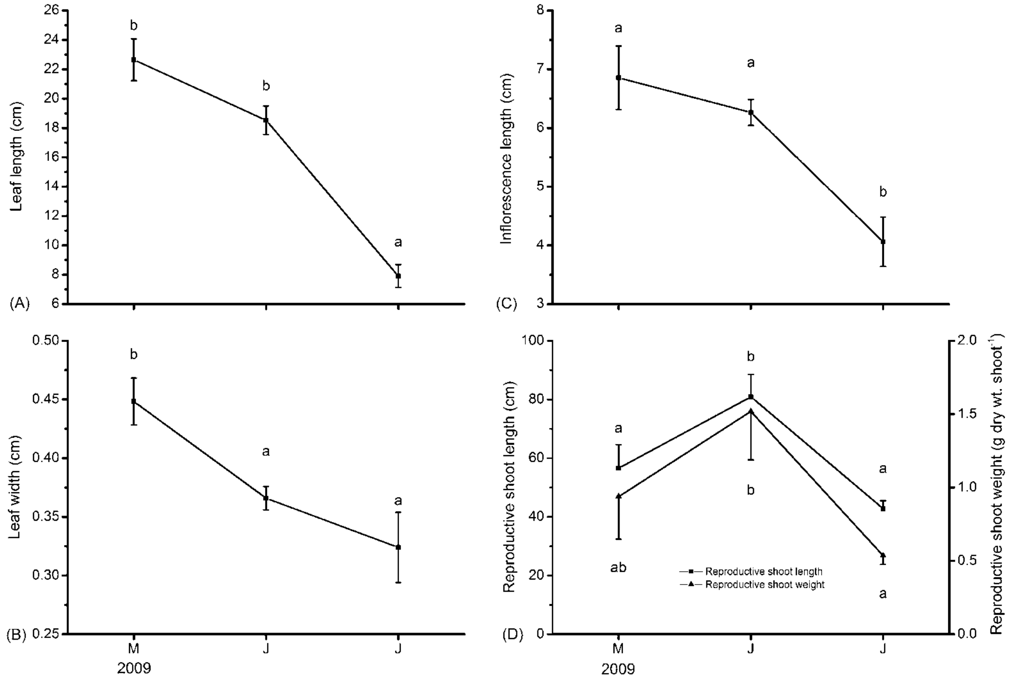

Figure 6. Seasonal changes in dimensions and weight of reproductive shoots of *Z. marina* at Swan Lake from May to July 2009: (A) leaf length, (B) leaf width, (C) inflorescence length, and (D) length and weight of reproductive shoots. Other details as in Figure 3.

shoots m^{-2} in December and the minimum value of 427 shoots m^{-2} in July (Watanabe, Nakaoka, and Mukai, 2005). This may be attributed to great difference in latitude.

Our results also show that shoot dimensions and weight of *Z. marina* in Swan Lake exhibited a clear seasonal variation, being greatest in summer and least in winter and early spring. Variations in shoot dimensions and weight of *Z. marina* in Sango Bay showed a similar seasonal trend (Liu, 2011); however, their dimensions were less than those of *Z. marina* in Swan Lake. The greatest weight of 1.44 g dry wt. shoot^{-1} was only 61% of that in Swan Lake. However, shoot dimensions in Qingdao Bay were greater than those in Swan Lake, with the greatest value of 130 cm in shoot height in July, which was 1.5 times higher than that in Swan Lake (Liu, 2011). Lee, Park, and Kim (2005) reported that shoot dimensions exhibited a clear seasonal variation in Koje Bayand Kosung Bay on the south coast of the Korean peninsula, which were significant greater than those in northern China. Similarly, Watanabe, Nakaoka, and Mukai (2005) also found that leaf length in Akkeshi Bay, northern Japan, was higher in summer than in winter, with an annual average of 86.2 cm, which was longer than that in Swan Lake. The inconsistent data in these studies may be attributed to differences in environmental conditions, especially for water temperature, and population variation.

Seasonal variation in seagrass productivity has been attributed to changes in various factors, such as underwater irradiance (Koch and Beer, 1996; Moore, Wetzel, and Orth, 1997) and water temperature (Duarte *et al.*, 2006; Orth and Moore, 1986). Watanabe, Nakaoka, and Mukai (2005) found that temporal variation in production was correlated with that of accumulated solar radiation for *Z. asiatica* and of water temperature for *Z. marina* in Akkeshi Bay, northern Japan. Lee, Park, and Kim (2005) indicated that seasonal variations in eelgrass shoot density, biomass, and leaf productivities in two bay systems (Koje Bay and Kosung Bay) on the south coast of the Korean peninsula were strongly correlated with water temperature. Also, Hosokawa, Nakamura, and Kuwae (2009) found that in an indoor experiment, leaf life span of *Z. marina* was negatively related to water temperature but not related to irradiance. Similarly, data in the present study showed that water temperature and shoot density and aboveground tissue dimensions displayed positive linear relationships, but only shoot density for underwater irradiance. These results indicated that water temperature is the most important factor determining seasonality of *Z. marina* in Swan Lake. Data in the present study also suggested that optimal water temperature for eelgrass growth in Swan Lake was about 15°–25°C during the midspring and early summer period. In our research site, a rapid decline of about 70% in shoot morphometry and biomass from July to August may occur because of development and bloom of reproductive shoot, epiphyte, and drift macroalgae (Hasegawa, Hori, and Mukai, 2007; Hootsmans and Vermaat, 1985; Tomasko and Lapointe, 1991).

Flowering events and seed survival have been considered important mechanisms in maintaining genetic diversity, possibly being the only way to colonize bare sediments or disturbed areas (Greve *et al.*, 2005; Lee *et al.*, 2007; Marbà and Walker, 1999; Plus, Deslous-Paoli, and Dagault, 2003). The reproductive biology and strategies of *Z. marina* have been well described, indicating that the reproductive processes are highly variable along its geographic distribution (De Cock, 1980; Meling-López and Ibarra-Obando, 1999; Morita *et al.*, 2007; van Lent and Verschuure, 1994). Variations are considerable in spatial and temporal patterns of the species' flowering and seed production, which have been related to latitudinal and local gradients (Ackerman, 2006) as well as genotypic variation of the populations (Cabaço and Santos, 2010; Walker, Olesen, and Phillips, 2001). Our study has shown that the potential seed production in *Z. marina* meadows in Swan Lake could be 3303 ± 573 seeds m^{-2}, indicating that the reproductive effort of *Z. marina* in our research site was higher than in Ago Bay, central Japan (Morita *et al.*, 2007), and in four populations (Fuzeta, Culatra, Barrinha and Armona) at the species' southern distribution limit in the eastern Atlantic, the Ria Formosa lagoon (Cabaço and Santos, 2010), but was lower than in populations from northern France (Jacobs and Pierson, 1981) and Canada (Keddy, 1987), suggesting that flowering shoots and seed traits are site-specific.

Several studies have found that temperature is the primary controlling factor in eelgrass reproduction (Granger *et al.*, 2002; Phillips, McMillan, and Bridges, 1983; Setchell, 1929). Our observations prove the conclusion and find that eelgrass flowers in Swan Lake first appeared in late March (Stage 0) at about 5°C and developed into stage II in mid-May at about 15°C. Mature seeds (Stage V) were observed in mid-July at a temperature of about 20°C, and seeds were released when temperatures were higher than 20°C. Similar results are also found in studies reported by Setchell (1929), De Cock (1981), and Silberhorn, Orth, and Moore (1983).

CONCLUSION

Shoot density, dimensions, and weight of *Z. marina* in Swan Lake, China, exhibited strong seasonal variation, with the maximal values in summer and minimal values in winter and early spring. Also, the dimensions and weight of reproductive shoots varied significantly during the three-month reproductive season, with maximal values in May for leaf length, inflorescence length, and leaf width, and in June for shoot length and shoot weight. Shoot density and aboveground tissue dimensions correlated positively with water temperature. The optimal water temperature for the growth of *Z. marina* in our research site was about 15°–25°C during the mid-spring and early summer period.

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