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Author(s)	Ito, Minako Abe; Lin, Hsing-Juh; O'Connor, Mary I et al.
Citation	Marine ecology progress series, 675, 1-21 https://doi.org/10.3354/meps13884
Issue Date	2021-09-30
Doc URL	https://hdl.handle.net/2115/83645
Rights(URL)	https://creativecommons.org/licenses/by/4.0/
Type	journal article
File Information	m675p001.pdf

Hokkaido University Collection of Scholarly and Academic Papers : HUSCAP

Vol. 675: 1–21, 2021
https://doi.org/10.3354/meps13884

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published September 30

FEATURE ARTICLE

Large-scale comparison of biomass and reproductive phenology among native and non-native populations of the seagrass *Zostera japonica*

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ABSTRACT: Large-scale analysis along latitude or temperature gradients can be an effective method for exploring the potential roles of light and temperature in controlling seagrass phenology. In this study, we investigated effects of latitude and temperature on seagrass biomass and reproductive seasonality. *Zostera japonica* is an intertidal seagrass with a wide latitudinal distribution expanding from tropical to temperate zones in its native range in Asia, with an additional non-native distribution in North America. We collated available data on phenological traits (timings of peak biomass or reproduction, durations of biomass growth and reproductive season, and maximum biomass or reproductive ratio) from publications and our own observations. Traits were compared among geographic groups: Asia-tropical, Asia-temperate, and North America-temperate. We further examined relationships between traits and latitude and temperature for 3 population groups: Asian, North American, and all populations. Our analysis revealed significant variation among geographic groups in maximum biomass, peak reproductive timing, and maximum reproductive ratio, but not in other traits. Maximum biomass and peak reproductive timing for Asian and all populations were significantly correlated with latitude and temperature. Maximum biomass was highest at mid-latitudes or intermediate temperatures and decreased toward distribution range limits, and peak reproductive timing occurred later in the year at higher latitudes or cooler sites. North American populations showed shorter growth durations and greater reproductive ratios at higher latitude. Different responses observed for North American populations may reflect effects of introduction. Our study demonstrates potential variation among geographic regions and between native and non-native populations.

Intertidal seagrass bed of *Zostera japonica* at its maximum biomass in summer, at Crescent Beach, BC, Canada.

Photo: Minako Abe Ito

KEY WORDS: Seasonality · Life history · Latitude · Temperature · Introduced species · Climate change

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Publisher: Inter-Research · www.int-res.com

1. INTRODUCTION

Seagrasses are marine angiosperms that form extensive meadows in shallow coastal environments, which are known as seagrass beds (Hemminga & Duarte 2000). Seagrass meadows provide multiple important ecosystem services and are recognized as one of the most valuable habitats in the world (Costanza et al. 1997). Despite their importance, seagrasses are rapidly declining worldwide due to various types of anthropogenic stressors and disturbances that act at different scales (Orth et al. 2006, Waycott et al. 2009). While most stressors and disturbances generally affect seagrasses at local scales, ongoing climate change is considered to substantially impact seagrasses globally. Increased temperatures are expected to shift seagrass distribution to higher latitudes, alter growth rates and other physical functions, and change sexual reproduction patterns (Short & Neckles 1999, Duarte 2002, Hyndes et al. 2016). To predict future changes in seagrass meadows and to promote effective conservation, it is important to understand how life history traits of each seagrass species vary with environmental conditions.

Seagrasses maintain their populations through both vegetative growth and sexual reproduction (Hemminga & Duarte 2000, Kendrick et al. 2012). Abiotic factors such as temperature, light, and nutrients play key roles in regulating both vegetative growth and flowering in seagrasses (Lee et al. 2007). The relative importance of these factors varies among species and location. For example, the seagrass *Posidonia oceanica* exhibits growth patterns that are primarily controlled by large-scale variation in the solar cycle and are less affected by local environmental variability (Alcoverro et al. 1995, Marbà et al. 1996). Pergent-Martini et al. (2005) found that the effects of nutrients on *Zostera noltii* growth and biomass vary among locations. Other studies found that seagrass growth dynamics are more strongly affected by temperature than irradiance (Lee et al. 2005, Hosokawa et al. 2009). Variation among the findings of studies conducted at local scales makes it difficult to generalize effects of abiotic factors on seagrass phenology (the timing of recurring life history events).

Large-scale analyses covering broad environmental gradients are effective tools for understanding how abiotic factors affect the phenology of terrestrial species (e.g. Zhang et al. 2004, Primack et al. 2009, Gill et al. 2015), and such approaches are increasingly used to study marine species (Racault et al. 2012, Tala & Chow 2014, James et al. 2015). Furthermore, such large-scale analyses can be useful for predicting species' responses to ongoing or historical climate change through space-for-time substitution (Fukami & Wardle 2005, Buyantuyev et al. 2012). The amount of light available on a certain day of the year depends on latitude; temperature also shows a high correlation with latitude but varies more with local influences (Lalli & Parsons 1997). Therefore, studies that encompass wide latitudinal ranges could lead to insights on both light and temperature effects.

To date, several studies covering wide latitudinal ranges have been conducted for seagrass biomass, a proxy for growth condition, and reproduction. Duarte (1989) found that temperate seagrasses commonly showed unimodal patterns of biomass throughout the year, with peak biomass occurring in summer, with the timing of peak biomass influenced by its latitudinal distribution. Comparisons of multiple *Zostera* species revealed latitudinal influences on flowering duration and peak timing (Phillips et al. 1983, Ramage & Schiel 1998, Nakaoka & Aioi 2001, Dos Santos & Matheson 2017). Recent studies of *Z. marina* revealed that biomass and flowering patterns are strongly influenced by latitude and temperature; biomass and flowering peaks occurred earlier for low-latitude/warmer populations, while growth and flowering durations are constant across latitude (Clausen et al. 2014, Blok et al. 2018). However, tropical seagrasses show different characteristics in their seasonal pattern which are occasionally independent from light and temperature and are instead affected by factors such as riverine influence, tidal exposure, or water motion (Erftemeijer & Herman 1994, Huong et al. 2003). Furthermore, intertidal seagrass species are suggested to be more susceptible to change in temperature and/or light than subtidal species (Marbà et al. 1996). In fact, manipulative experiments testing light and temperature effects on intertidal species suggested that seagrass growth rate is a function of duration of exposure to warm temperature, and light is not the dominant factor controlling growth (Shafer & Kaldy 2014, Kaldy et al. 2015b). Although there is an increasing understanding of general phenological patterns observed in seagrasses, species-specific responses to global factors are not well investigated for intertidal and/or tropical seagrasses.

Among species belonging to the genus *Zostera*, whose distribution is mostly restricted to temperate ocean regions, *Z. japonica* has an exceptionally wide native distribution range extending from the tropical coast of Vietnam (10° N) to Kamchatka, Russia (55° N) on the western coast of the Pacific Ocean (Green & Short 2003). In addition to its native habitat, *Z. japonica* also extends its distribution to the eastern coast of

the Pacific Ocean in North America, where it is believed to have been introduced to that region with the Pacific oyster (Harrison & Bigley 1982). Non-native populations often show different traits (i.e. higher growth rate, extended flowering duration, higher reproductive output) than their native populations, suggesting trait changes during introduction processes (Mason et al. 2008, Leffler et al. 2014). However, introduction effects on phenology are context dependent; some non-native species maintain phenological traits from their native habitats even after being introduced to new region (Godoy et al. 2009), whereas other non-native species show higher phenological plasticity, enabling them to adapt to environmental change (Zettlemoyer et al. 2019). Observations of both native and non-native populations could therefore provide insights for how *Z. japonica* phenological traits are affected by introduction. Due to its wide latitudinal distribution in its native region, additional habitat in its non-native region, and habitat preference for fluctuating intertidal environment, *Z. japonica* is considered an ideal organism for large-scale analyses on latitudinal and temperature effects on its phenological traits.

The aim of this study was to examine broad-scale variation in phenology of the intertidal seagrass *Z. japonica* throughout its distributional range. We systematically reviewed and synthesized data from published literature on *Z. japonica* phenological traits (biomass and reproductive traits). Synthesized data were further analyzed to test for variation among different geographic groups, namely Asia-tropical, Asia-temperate, and North America-temperate, and evaluated for the effects of latitude and temperature. Through our analyses, we specifically tried to answer the following 3 questions: (1) How do *Z. japonica* phenological traits vary among geographic groups? (2) How are the traits influenced by latitude or temperatures? and (3) Is there a difference between native and non-native populations, suggesting an introduction effect?

2. MATERIALS AND METHODS

2.1. Data collection and synthesis

We systematically reviewed research articles to build a dataset for assessing seasonal changes in seagrass biomass and/or reproduction. We used ISI Web of Science to conduct the literature search by using seagrass species names as key words. Considering past changes in taxonomic identity, we also included currently unaccepted species names as search terms. Final key search terms were: 'Zostera japonica' OR 'Zostera nana' OR 'Zostera americana'. To include articles written in Japanese, we used J-STAGE (www.jstage.jst.go.jp) to collect additional articles. For searches on J-STAGE, 'Zostera japonica' and the Japanese name 'koamamo' were used. Both literature searches on the Web of Science and on J-STAGE were conducted on 26 January 2020. Searches resulted in 137 articles from the Web of Science and 220 from J-STAGE. Cross-referencing articles revealed additional papers, including a study written in Korean (Ok & Lee 2014). In addition to data collected from research articles, we used seasonal data collected by our research group to minimize gaps in the data coverage for the analysis (Table S1 in the Supplement at www.int-res.com/articles/suppl/m675p001_supp.pdf). To our knowledge, no seasonal data were available for populations in Russia, which is the northern range limit of *Zostera japonica*.

For each research article, we first skimmed through the abstract for relevant information pertaining to our study. With the relevant articles, we then collated data on seagrass biomass and reproductive seasonality. To ensure a standard quality of data, we further filtered the articles based on the following criteria: (1) articles must contain one or more variables on phenological traits and where and how they were collected (see Section 2.2. for details), (2) only data collected *in situ* are used and data from laboratory experiments are excluded to assure a strong influence from environmental conditions, and (3) if an article is based on a manipulative experiment, only data from the control or untreated samples are used. If an article contained more than 1 year of data, the data were either merged or separated into multiple datasets, depending on whether the number of data points available per year exceeded 5 or not (see Section 2.2 for descriptions). If an article contained data from more than a single site, data from each site were analyzed separately to increase spatial heterogeneity in the dataset. Therefore, some articles contributed more than 1 dataset in the compiled data (Table 1).

After systematic review and quality control, we collated 24 articles and 7 datasets from our research group on seagrass phenological traits, covering a wide range in latitude and temperature, and from both native and non-native populations (Table 1, Fig. 1; Table S1). Compiled datasets were divided into 3 groups based on the geographic distribution of *Z. japonica*: the Asia-tropical group consists of native populations at latitudes $<30°$ N in Asia, the Asia-temperate group includes native populations at latitudes

Table 1. List of studies included in the analysis for seagrass biomass and reproduction. Numbers of data for seagrass biomass and/or reproduction that are noted as a single study may contain data from several locations or several years. Dashes mean no data from the study were used in the analysis

Geographic group Study site	Latitude (°N)	Annual temp (°C)	Sampling years	No. of data for Biomass	No. of data for Reproduction	Reference
North America-temperate						
Boundary Bay, BC	49.1	10.3	1978	1	1	Harrison (1982a)
Boundary Bay, BC	49.1	10.2	2017–2018	1	1	This study
Roberts Bank, BC	49.0	10.3	1980–1981	3[a]	3	Bigley & Harrison (1986)
Roberts Bank, BC	49.0	10.3	1979–1981	4	8	Harrison (1982b)
Roberts Bank, BC	49.0	10.3	1987	1	1	Nomme & Harrison (1991)
Roberts Bank, BC	49.0	10.0	2017–2018	1	1	This study
Padilla Bay, WA	48.5	10.5	1989–1990	1[a]	–	Thom et al. (1995)
Willapa Bay, WA	46.6	10.5	2004	6	6	Ruesink et al. (2010)
Willapa Bay, WA	46.4	10.1	2009–2010	2[a]	–	Wheatcroft et al. (2013)
Yaquina Bay, OR	44.6	10.8	2001–2003	2	2	Kaldy (2006)
Yaquina Bay, OR	44.6	10.8	1999–2000	7	–	Larned (2003)
Asia temperate						
Notoro-ko, Japan	44.1	6.3	2018	1	1	This study
Notoro-ko, Japan	44.0	6.2	2018	1	1	This study
Akkeshi-ko, Japan	43.0	6.5	2018	1	–	This study
Swan Lake, China	37.4	12.2	2011–2013	1	2	Zhang et al. (2015)
Sungbondo Isl., Korea	37.2	11.8	2001–2002	3	3	Lee et al. (2005)
Ena Bay, Japan	35.1	15.8	2007–2009	5[a]	–	Koshikawa et al. (2009)
Tateyama Bay, Japan	35.0	15.9	2004–2005	1	1	Inoue et al. (2006)
Koje Bay, Korea	34.8	13.9	2004–2006	3	–	Kim et al. (2016)
Koje Bay, Korea	34.8	13.9	2003–2005	3	1	Park et al. (2011)
Koje Bay, Korea	34.8	13.9	2015–2016	5	3	Suonan et al. (2017)
Mikawa Bay, Japan	34.8	15.6	2011–2012	3	3	Kamohara et al. (2015)
Dadae Bay, Korea	34.7	14.2	2001–2002	1	1	Lee et al. (2006)
Sagumi Bay, Korea	34.3	13.9	2008–2011	2	1	Ok & Lee (2014)
Ago Bay, Japan	34.3	16.1	2003–2004	2	1	Abe et al. (2012)
Tanabe Bay, Japan	33.7	16.5	2004–2005	3	2	Uede (2007)
Asia tropical						
Hsiangshan, Taiwan	24.8	21.4	2007–2008	3	3	This study
Kaomei, Taiwan	24.3	22.0	2007–2008	3	3	This study
Lai Chi Wo, Hong Kong	22.5	22.2	1995–1996	1	1	Fong et al. (1998)
San Tau, Hong Kong	22.3	22.8	1993–1994	1[b]	1	Lee (1997)
Ha Long Bay, Vietnam	20.9	22.9	1999–2001	1[c]	1	Huong et al. (2003)

[a]Data for density were used instead of above-ground biomass (AGB); [b]Data for ash-free dry weight were used instead of AGB; [c]Data for total biomass were used instead of AGB

>30° N in Asia, and the North America-temperate group includes non-native populations in North America. Spatial and temporal variations in the datasets differed greatly among geographic groups; the Asia-tropical and North America-temperate groups showed a narrower range of latitudinal and temperature variation compared to the Asia-temperate group, while the North America-temperate group showed the largest variation in temporal scales spanning from 1978 to 2018 (Tables 1 & 2, Fig. 1). The North American group only included temperate populations, as there are no reports on non-native *Z. japonica* distributed in tropical areas. In southern Japan, seagrass species composition drastically changes from temperate to tropical around 30° N (Kawano et al. 2012) and thus 30° N was selected as the cut-off point between tropical and temperate regions.

2.2. Biomass and reproductive trait acquisition

Differences in seagrass biomass and reproduction seasonality among geographic groups or populations were evaluated in the form of timings of peak biomass/reproduction, durations of biomass growth/reproductive season, and maximum biomass/reproductive ratio observed. Biomass was used as a proxy reflecting seagrass vegetative growth. From each

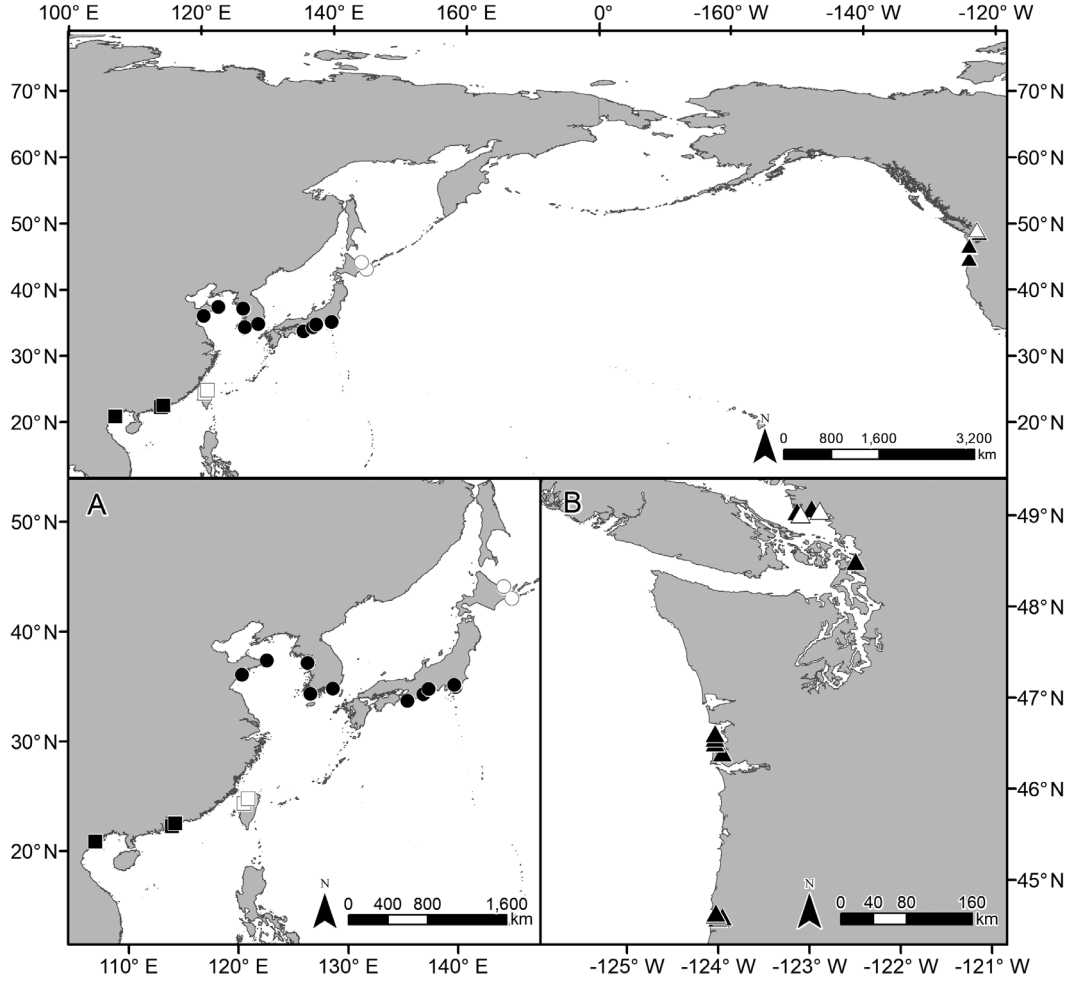

Fig. 1. Study locations, enlarged for (A) native *Zostera japonica* populations from Asia and (B) non-native populations from North America. Different symbols represent different geographic groups: Asia-tropical (square), Asia-temperate (circle), and North America-temperate (triangle), where filled symbols represent data from the literature review and open symbols from our unpublished data (available in Table S1)

article, we extracted data from tables or the main text whenever possible. If data were only available in a figure and not provided in any numerical form, we used a web-based graphical digitizer to extract data (WebPlotDigitizer version 4.2; Rohatgi 2019). After assigning fixed values, acquired from the original figure and calibrating the digitizer axes, we used manual methods to extract each data point from the figure by directly clicking on the graph.

Table 2. Range of latitude and temperature of 3 geographic groups of *Zostera japonica*. For each variable, values for each group are summarized as minimum–maximum (mean ± SD). Kruskal-Wallis test and post hoc Dunn test examined the variation in these variables among groups. Data are also available in graphical form in Fig. S1

Variable	North America-temperate (NAtemp)	Asia-temperate (Atemp)	Asia-tropical (Atrop)	Kruskal-Wallis test p	Post hoc Dunn test
Latitude (°N)	44.6–49.1 (47.2 ± 1.9)	33.7–44.1 (35.7 ± 2.6)	20.9–24.8 (23.7 ± 1.4)	<0.001	NAtemp > Atemp > Atrop
Annual air temp. (°C)	10.0–11.2 (10.5 ± 0.3)	6.2–16.5 (13.8 ± 2.7)	21.4–22.9 (22.0 ± 0.6)	<0.001	NAtemp < Atemp < Atrop
Summer air temp. (°C)	14.7–16.8 (15.8 ± 0.9)	15.2–25.3 (22.9 ± 2.4)	26.9–28.4 (27.5 ± 0.5)	<0.001	NAtemp < Atemp < Atrop
Winter air temp. (°C)	4.0–7.2 (5.4 ± 1.2)	−4.9–7.7 (4.1 ± 3.4)	15.0–16.9 (15.7 ± 0.6)	<0.001	NAtemp = Atemp < Atrop

For the expected unimodal annual biomass pattern, we can analyze biomass seasonality by fitting quadratic equations to seasonal data, based on the method described by Clausen et al. (2014). The peak biomass timing was determined using the *x*-coordinate of a parabola vertex and the growth duration using 2 parabola roots (Clausen et al. 2014). Start and end of biomass growth season corresponded with 2 parabola roots, and therefore the number of days between the 2 roots was considered the growth duration. To minimize uncertainty in estimated relationships, we used a minimum of 5 datapoints per dataset. Although a quadratic fit can be applied to any variable that shows a unimodal pattern, we only used data on dry weight of above-ground biomass (AGB) whenever available to maintain consistent biological measurements in the data. However, these strict limitations would result in reduced analytical power and hence we also used other variables such as total biomass, ash-free dry weight, and density, but only if AGB was not provided in the article. The quadratic fit performed well with our dataset, with a mean and median r-squared value (r^2) of 0.79 and 0.81, respectively. However, we excluded data with a criterion of $r^2 = 0.65$, as suggested in studies of unimodal curve fitting (Frisén 1986, Murtaugh 2003). We retained approximately 85% (62 out of 73) of all datasets, and there was no obvious bias in regional groups or latitude/temperature that showed a poor quadratic fit.

For the comparison of maximum biomass, we used values obtained from the articles rather than using values estimated from the quadratic equation. For maximum biomass, we used AGB if available; if not, AGB was calculated from data on total biomass and either of above- to below-ground biomass ratios or below-ground biomass, whichever was available. Most data on AGB were presented in g m^{-2}, and if not, units were converted to g m^{-2} to make direct comparisons possible. For the sites with multiple years of observations, only the maximum biomass observed per site was used in the analysis.

Seagrass biomass was reported quantitatively in most of the articles, making it possible for us to conduct analysis using the quadratic fit. However, seagrass sexual reproduction was usually only reported when reproductive shoots were present, and the absence of reproductive shoots was rarely stated, making it impossible to apply the quadratic fit to annual datasets. There are a variety of ways to report seagrass reproduction: reproductive shoot density, biomass, ratio (both density- or biomass-based) or verbally (presence/absence). For a verbal statement like 'Sexual reproduction is also limited to a brief period in the year, between March and May' (Lee 1997, p. 190), we were unable to extract any information other than timing and duration of the reproductive season since there was no statement about the reproductive peak or maximum reproductive ratio. Nonetheless, we included information to increase sample size and analytical strength. We did not include different reproductive stages (i.e. spathe emergence, flowering, or fruiting) due to limited information available in most articles.

For the duration of the reproductive season, we used the number of days between the start (i.e. when a reproductive shoot was first observed) to the end (i.e. when a reproductive shoot was last observed) of the year. When data were available in verbal form, we used mid-month (15th day of the month) as the date, unless the article stated an early or late period in a certain month, in which case the 5th and 25th day of the month were used, respectively.

We extracted or calculated reproductive ratio from the articles. There are 2 common methods to calculate reproductive ratio: density-based or biomass-based. We used both ratio types for analysis of reproductive ratio. If both types were available from the same study, we used only density-based data. Maximum reproductive ratio observed per site was used in the analysis.

2.3. Latitude and temperature data

Geographical coordinates, or latitude and longitude, of each site were directly obtained from the original publications. When authors of the original publications did not provide the coordinates, we georeferenced them from maps or text in the publications. Based on the obtained site coordinates, we extracted site-specific air temperatures from WorldClim Version 2 (www.worldclim.org; Fick & Hijmans 2017), as a monthly mean temperature over a 30 yr period (1970–2000). Although the analyzed temperature data spanned 30 yr, we confirmed that there was no consistent trend in temperature during this period or between old and recent temperature from the same study sites with large temporal variation (Roberts Bank and Boundary Bay, Canada; data not shown). Similarly, water temperature data were derived from MODIS-Aqua 11 µm daytime sea surface temperature (NASA 2014), as monthly mean temperatures from 4 July 2002 to 25 January 2020. Both WorldClim and MODIS-Aqua were accessed on 26 January 2020.

Intertidal seagrasses are influenced by both air and water temperatures (Lee et al. 2005). However, only

air temperature was used for analysis in this study, due to its high correlation with water temperature measured *in situ* and scientific support from previous research. Among the articles we examined, 6 publications reported water temperatures measured *in situ* (Lee et al. 2005, 2006, Park et al. 2011, Zhang et al. 2015, Kim et al. 2016, Suonan et al. 2017). When on-site water measurements were compared with extracted air and water temperatures, half of the sites showed higher correlations with extracted air temperatures while the other half showed higher correlations with extracted water temperatures (data not shown). Across studies with on-site temperatures, average coefficient of determination was also high between on-site temperatures and extracted air temperature ($n = 6$, $r^2 = 0.80$). Additionally, Clausen et al. (2014) showed that air temperature has a significant effect on the seasonality of subtidal populations of the seagrass *Z. marina*. Therefore, we can justify using air temperature data to test for a correlation between temperature and intertidal seagrass seasonality.

From monthly mean temperatures, we calculated the annual mean (average from January to December), summer mean (June to August), and winter mean (December to February) for each site. These values were used in the rest of our analyses. We conducted a separate analysis for each mean temperature variable, to evaluate and distinguish the effects of temperatures in different seasons.

Prior to our analysis, the relationships between latitude and each temperature variable were investigated (Figs. S1 & S2). As expected, we found a high negative correlation between latitude and temperature (Pearson's correlation analysis), where increases in latitude were associated with decreases in temperature. While the amount of light available and photoperiod are determined exclusively by latitude, substantial variation in temperature is attributable to other local factors (Clausen et al. 2014), and thus comparison of latitude with temperature allowed us to differentiate the influence of light vs. temperature. Additionally, relationships between variables differed significantly among seagrass geographic groups. The North America-temperate group showed a reversed relationship that summer temperature increases as latitude increases, since it is driven by coastal upwelling events along the western coast of North America (Bograd et al. 2009). Among-group variation in latitude and temperature relationship would enable us to distinguish the primary driver of variation in phenological traits.

We initially used photosynthetically available radiation (PAR) data from NASA MODIS-Aqua for a measure of light availability in terms of total radiation received in a day. However, analysis using PAR is not presented because it was mostly consistent with our latitude analysis (data not shown) and did not yield new findings. Therefore, we only used latitude as a proxy for light availability in terms of daylength (total hours of sunlight).

2.4. Statistical analysis and inference

All analyses were performed in R version 3.6.2 (R Core Team 2019). We expected significant among-group variation for traits affected by latitude/temperature or altered during introduction. To assess whether phenological traits differ among the 3 geographic groups, we conducted a non-parametric Kruskal-Wallis rank sum test for each trait. The non-parametric test was chosen because all trait variables violated assumptions for parametric tests; data were not normally distributed and/or showed non-homogeneous variances among groups. To evaluate the effect size of each among-group variation, eta-squared based on the *H*-statistic was also calculated for a Kruskal test using the 'kruskal_effsize' function in the R package 'rstatix' (Kassambara 2020). Eta-squared is calculated as sums of squares for the effect of interest divided by the total sums of squares (Cohen 1973), and magnitudes of effect are interpreted as follows: 0.01 to <0.06 (small effect), 0.06 to <0.14 (medium), and ≥0.14 (large) (Maher et al. 2013, Kassambara 2020). When a significant ($p < 0.05$) effect of geographic group was found, we performed Dunn's multiple comparison test to examine which group or groups showed the significant difference, using the 'dunnTest' function in the R package 'FSA' (Ogle et al. 2020), with the p-value adjusted using the Benjamini-Hochberg method.

We expected significant relationships between latitude or temperature and traits influenced by light and temperature, and expected that the trends would differ between native and non-native populations, if the traits are altered during introduction. To test whether there is a difference between native and non-native groups, we analyzed Asian and North American populations separately. Due to limitations in data from the tropical region, we could not conduct a separate analysis for the tropical populations. Prior to the main analysis, we compared trends between the Asian populations with and without the tropical group; combining of the tropical group would significantly decrease explanatory power (R^2) if trends differ between the tropical and temperate

groups, whereas combining would strengthen explanatory power if trends are consistent. Combining the tropical and temperate Asian groups did not significantly reduce explanatory strength, but rather increased strength in most cases, indicating a similar trend among the Asian populations. Furthermore, we investigated latitude and temperature effects on all populations by combining Asian and North American populations together, to evaluate if *Z. japonica* as a species shows consistent trends across its entire distributional range. Hence, we focused on comparison among native and non-native populations (Asian vs. North American populations), and all populations for evaluation of latitude/temperature effects. To evaluate the effects of latitude and annual, summer, and winter mean temperature parameters on seagrass biomass and reproduction, and to examine how trends differ among population groups, we performed linear and quadratic regression analyses.

To assess latitude and temperature effects on phenological traits, we first examined if the regression model with latitude or temperature was better than the null model without the explanatory variable. The best regression model was selected based on Akaike's information criterion corrected for small sample size (AICc) using the 'dredge' function in the R package 'MuMIn' (Barton 2019). If the models with predictors were better than the null models (ΔAICc > 2), we then compared AICc for linear and quadratic models and selected the best models; quadratic models were only selected if their ΔAICc was lower than the linear models. For each trait, the best predictor among latitude and temperature was determined based on adjusted r-squared (R^2) values; the parameter with the highest R^2 was selected as the most influential variable for variation in the phenological traits. Significance of fit based on the p-value and goodness of fit using an adjusted r-squared value (R^2) were used for the examination. Cohen (1988) suggested that R^2 values are interpreted as follows: 0.26 (substantial), 0.13 (moderate), and 0.02 (weak). In this sense, results with $R^2 > 0.13$ were considered significantly addressing a good fit. When the quadratic model was selected as the best model, we solved the quadratic equation to calculate the latitude/temperature value where the quadratic maximum/minimum occurs.

3. RESULTS

Compiled datasets covered a wide latitudinal range, from 20.9 to 49.1° N. Annual mean air temperature ranged from 6.2 to 22.9°C, summer mean air temperature ranged from 14.7 to 28.4°C, and winter mean air temperature ranged from −4.9 to 16.9°C (Tables 1 & 2). Latitude and temperature were significantly different among seagrass geographic groups except for the winter temperature between the North America-temperate and Asia-temperate groups (Table 2; Fig. S1).

3.1. Comparisons of biomass and reproductive traits among geographic groups

Mean ± SD peak biomass timing for Asia-tropical, Asia-temperate, and North America-temperate groups were day of year (DOY) 174.9 ± 90.3, 207.4 ± 38.3, and 209.7 ± 28.5, respectively, and the differences among the groups were not significant (Kruskal-Wallis test: chi-squared [χ^2] = 2.67, df = 2, p = 0.26, eta-squared [η^2] = 0.01; Fig. 2A). Average growth duration for Asia-tropical, Asia-temperate, and North America-temperate groups were 192.6 ± 54.6, 207.2 ± 68.1, and 199.6 ± 62.8 d, respectively. Variations in growth duration were not significantly different among the groups (χ^2 = 0.14, df = 2, p = 0.93, η^2 = −0.03; Fig. 2B). Maximum biomass showed significant differences among the groups (χ^2 = 23.38, df = 2, p < 0.001, η^2 = 0.44; Fig. 2C). Average maximum biomass was significantly higher in Asia-temperate (154.0 ± 75.1 g m^{-2}) than North America-temperate (60.0 ± 27.6 g m^{-2}; Dunn's test p < 0.001) and Asia-tropical groups (42.6 ± 20.5 g m^{-2}; p < 0.001). The difference between Asia-tropical and North America-temperate groups was not significant (p = 0.33).

Peak reproductive timing was significantly different among geographic groups (χ^2 = 23.76, df = 2, p < 0.001, η^2 = 0.44; Fig. 2D). The peak reproductive timing was earliest for the Asia-tropical group (DOY 119.9 ± 22.1), followed by the Asia-temperate (DOY 183.5 ± 57.1) and lastly the North America-temperate group (DOY 231.3 ± 31.2). All differences between each pair of groups were significant (Asia-tropical vs. Asia-temperate: p < 0.05; Asia-tropical vs. North America-temperate: p < 0.001; Asia-temperate vs. North America-temperate: p < 0.01). Average reproductive duration for Asia-tropical, Asia-temperate, and North America-temperate groups was 125.6 ± 86.0, 135.7 ± 51.0, and 106.5 ± 45.6 d, respectively. Among-group variation in reproductive duration was not significant (χ^2 = 2.39, df = 2, p = 0.30, η^2 = 0.01; Fig. 2E). For reproductive ratios, we performed analyses with and without data from Park et al. (2011) for Koje Bay, where 63% of shoots flowered in the first year after clamming activity (Fig. 2F; Fig. S3). Origi-

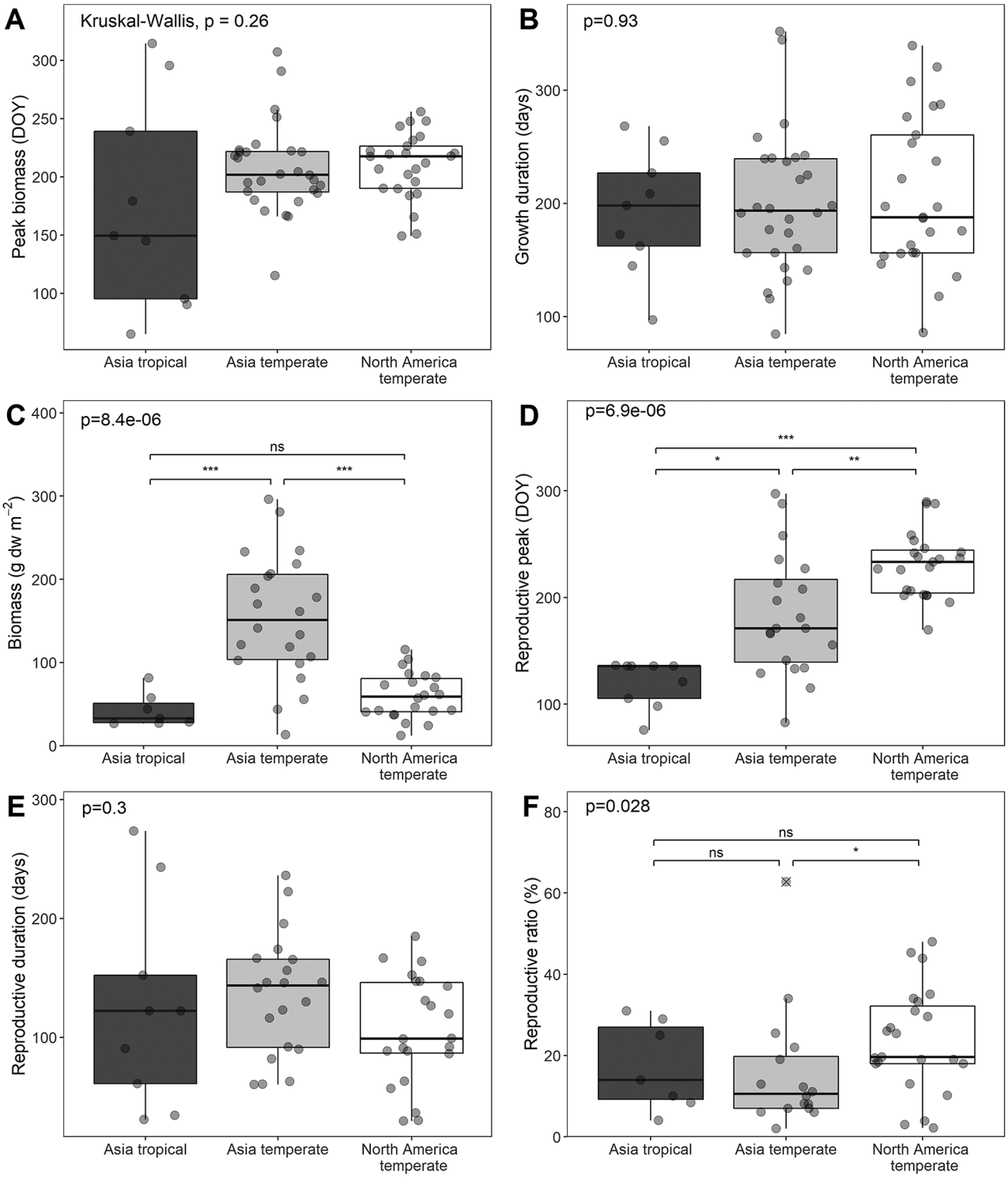

Fig. 2. Comparison of biomass and reproductive traits among *Zostera japonica* geographic groups for: (A) peak biomass timing by day of year (DOY), (B) growth duration, (C) maximum biomass, (D) peak reproductive timing, (E) reproductive duration, and (F) maximum reproductive ratio. A crossed circle in (F) represents an outlier removed from the analysis. Boxes delimit upper and lower quartiles, the horizontal line within the box is the median, and the whiskers above and below the box indicate the interquartile range. Dots represent the actual values observed for each group. Results from the Kruskal-Wallis rank sum test are presented in the top-left corner of each plot, and significance of the post hoc Dunn's test results is indicated as: ns: not significant ($p > 0.05$); *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

nal data including this outlier showed marginally significant variation of reproductive ratio among geographic groups (χ^2 = 5.07, df = 2, p = 0.08, η^2 = 0.07; Fig. S3), however, when we removed the outlier, the trend became significant (χ^2 = 7.13, df = 2, p < 0.05, η^2 = 0.12; Fig. 2F). Mean reproductive ratios for each group were 17.3 ± 10.8% for Asia-tropical and 23.6 ± 12.9% for North America-temperate groups, whereas the Asia-temperate group had values of 15.9 ± 15.1 and 12.7 ± 8.7% with and without the outlier, respectively. Analysis without the outlier revealed a significant difference between the Asia-temperate and North America-temperate groups (p < 0.05), but not between the other combinations (Asia-tropical vs. Asia-temperate: p = 0.35, Asia-tropical vs. North America-temperate: p = 0.44; Fig. 2F).

3.2. Effects of latitude and temperature on biomass and reproductive traits

Variation in biomass and reproductive traits were compared along latitude and temperature gradients, and relationships between traits and latitude or temperature were examined through regression analysis and model selection (see Figs. 3 & 4). The best models were selected based on AICc for each pair of biomass or reproductive traits and latitude or temperature, which are summarized in Table 3. Additional information on linear and quadratic regression models is provided in Table S2.

Peak biomass timing was not affected by latitude or temperature in any geographical group (R^2 < 0.13 for all combinations; Fig. 3A–D, Table 3; Table S2). For peak biomass timing, the model fits were statistically significant or marginally significant (p < 0.05) for Asian and all populations in linear regression models, but the linear models were not selected as the best model (Table S2). Growth durations for the North American populations were negatively correlated with latitude and summer mean temperatures (latitude: $F_{1,23}$ = 14.99, p < 0.001, R^2 = 0.37; summer mean: $F_{1,23}$ = 5.71, p < 0.05, R^2 = 0.16; Fig. 3E,G; Table S2) and positively with annual and winter mean temperatures (annual mean: $F_{1,23}$ = 4.87, p < 0.05, R^2 = 0.14; winter mean: $F_{1,23}$ = 6.36, p < 0.05, R^2 = 0.18; Fig. 3F,H; Table S2). Among parameters affecting variation in growth duration in the North American populations, latitude is the strongest predictor; growth duration decreases by 22.45 d per 1° of latitude north (Fig. 3E, Table 3). Growth durations of the Asian and all populations were not affected by latitude or temperature (p > 0.05, R^2 < 0.13; Fig. 3E–H, Table 3; Table S2).

For maximum AGB, significant relationships between latitudes/temperatures and biomass were observed in the quadratic regression for Asian and all populations, but not for the North American populations (Fig. 3I–L, Table 3; Table S2). For the Asian populations, the biomass peaked at latitude 34.4° N ($F_{2,26}$ = 12.37, p < 0.001, R^2 = 0.45) and at 13.5, 21.9, and 4.3°C for annual, summer, and winter mean temperatures, respectively (annual mean: $F_{2,26}$ = 13.73, p < 0.001, R^2 = 0.48; summer mean: $F_{2,26}$ = 14.09, p < 0.001, R^2 = 0.48; winter mean: $F_{2,26}$ = 11.92, p < 0.001, R^2 = 0.44). For all populations, the biomass peaked at latitude 36.9° N ($F_{2,48}$ = 18.85, p < 0.001, R^2 = 0.42), at 15.7°C for annual mean temperature ($F_{2,48}$ = 12.27, p < 0.001, R^2 = 0.31), and at 21.7°C for summer mean temperature ($F_{2,48}$ = 20.80, p < 0.001, R^2 = 0.44). Winter mean temperature did not explain variation in AGB for all populations due to an R^2 value below our threshold of 0.13 ($F_{2,48}$ = 3.93, p < 0.05, R^2 = 0.10). Among latitude and temperatures, summer mean temperature was the strongest predictor for maximum biomass in both Asian and all populations (Table 3).

Peak reproductive timing was significantly affected by latitude in all geographic groups, and in contrast, temperature effects were only observed for Asian and all populations (Fig. 4A–D, Table 3; Table S2). An increase in latitude delayed the reproductive peak timing, with 4.8 and 4.3 d per 1° latitude for the Asian and all populations, respectively (Asia: $F_{1,27}$ = 10.90, p < 0.01, R^2 = 0.26; all: $F_{1,50}$ = 45.89, p < 0.001, R^2 = 0.47; Fig. 4A). For the North American populations, reproductive peak timing showed a unimodal relationship with latitude ($F_{2,20}$ = 7.49, p < 0.005, R^2 = 0.37); however, an unrealistic U-shaped curve within a small latitudinal range with large residuals, represented in Fig. 4A, suggests that the model was statistically overfitted without ecological significance. Temperatures were correlated with reproductive peak timing for both Asian and all populations, yet the relationships were varied. Annual mean temperatures showed significant negative relationships with reproductive peak timing in the Asian and all populations, where we found that a 1°C increase in temperature advanced timing by 6.7 and 8.8 d for the Asian and all populations, respectively (Asia: $F_{1,27}$ = 12.17, p < 0.01, R^2 = 0.29; all: $F_{1,50}$ = 43.07, p < 0.001, R^2 = 0.45; Fig. 4B). Summer mean temperatures showed a quadratic relation with reproductive peak timings, where the quadratic maximum occurred at 20.1 and 16.5°C for the Asian and all populations, respectively (Asia: $F_{2,26}$ = 7.57, p < 0.005, R^2 = 0.32; all: $F_{2,49}$ = 24.30, p < 0.001, R^2 = 0.48; Fig. 4C). Finally, winter mean temperatures showed a negative linear rela-

Table 3. Best regression models for biomass and reproductive traits selected based on Akaike's information criterion corrected for small sample size (AICc). Estimate ± SE are noted for quadratic and/or linear coefficients and the intercept of selected models. Null indicates that neither linear nor quadratic models were selected. Dashes indicate that the estimate was not applicable to the selected model. Within each trait, the environmental variable with the highest explanatory strength (R^2) is **bolded**

Phenological trait	Asian populations					North American populations					All populations				
Environmental variable	Model	Quadratic (SE)	Linear (SE)	Intercept (SE)	R^2	Model	Quadratic (SE)	Linear (SE)	Intercept (SE)	R^2	Model	Quadratic (SE)	Linear (SE)	Intercept (SE)	R^2
Biomass peak															
Latitude	Null	–	–	–	–	Null	–	–	–	–	Null	–	–	–	–
Annual mean	Null	–	–	–	–	Null	–	–	–	–	Null	–	–	–	–
Summer mean	Null	–	–	–	–	Null	–	–	–	–	Null	–	–	–	–
Winter mean	Null	–	–	–	–	Null	–	–	–	–	Null	–	–	–	–
Growth duration															
Latitude	Null	–	–	–	–	Linear	–	**–22.5 (5.8)**	**1259.8 (272.1)**	**0.37**	Null	–	–	–	–
Annual mean	Null	–	–	–	–	Linear	–	86.2 (39.0)	–701.2 (411.7)	0.14	Null	–	–	–	–
Summer mean	Null	–	–	–	–	Linear	–	–33.8 (14.2)	734.7 (221.1)	0.16	Null	–	–	–	–
Winter mean	Null	–	–	–	–	Linear	–	27.1 (10.7)	54.2 (61.9)	0.18	Null	–	–	–	–
Maximum biomass															
Latitude	Quadratic	–1.2 (0.3)	82.5 (18.9)	–1251.1 (298.6)	0.45	Null	–	–	–	–	Quadratic	–0.7 (0.1)	51.7 (9.3)	–778.0 (167.4)	0.42
Annual mean	Quadratic	–2.1 (0.5)	56.5 (14.3)	–218.0 (108.5)	0.48	Null	–	–	–	–	Quadratic	–2.3 (0.5)	69.1 (14.0)	–386.7 (100.7)	0.31
Summer mean	Quadratic	**–4.4 (0.9)**	**192.8 (38.7)**	**–1922.7 (432.1)**	**0.48**	Null	–	–	–	–	Quadratic	**–3.0 (0.5)**	**130.0 (22.3)**	**–1222.5 (219.4)**	**0.44**
Winter mean	Quadratic	–1.1 (0.3)	9.5 (4.6)	148.2 (17.4)	0.44	Null	–	–	–	–	Null	–	–	–	–
Reproductive peak															
Latitude	Linear	–	4.8 (1.5)	9.5 (47.6)	0.26	Quadratic	**11.1 (3.0)**	**–1051.7 (281.1)**	**25123.7 (6631.2)**	**0.37**	Linear	–	4.3 (0.6)	24.2 (25.7)	0.47
Annual mean	Linear	–	–6.7 (1.9)	272.0 (32.3)	0.29	Null	–	–	–	–	Linear	–	–8.8 (1.3)	312.5 (19.1)	0.45
Summer mean	Quadratic	–1.8 (0.7)	72.5 (29.5)	–534.7 (333.4)	0.32	Null	–	–	–	–	Quadratic	**–1.1 (0.4)**	**36.2 (17.3)**	**–82.5 (174.5)**	**0.48**
Winter mean	Linear	–	**–5.3 (1.3)**	**201.6 (12.8)**	**0.35**	Null	–	–	–	–	Quadratic	–0.4 (0.1)	–	220.7 (7.9)	0.38
Reproductive duration															
Latitude	Null	–	–	–	–	Null	–	–	–	–	Null	–	–	–	–
Annual mean	Null	–	–	–	–	Null	–	–	–	–	Null	–	–	–	–
Summer mean	Null	–	–	–	–	Null	–	–	–	–	Null	–	–	–	–
Winter mean	Null	–	–	–	–	Null	–	–	–	–	Null	–	–	–	–
Reproductive ratio															
Latitude	Null	–	–	–	–	Linear	–	**3.5 (1.7)**	**–146.7 (79.7)**	**0.14**	Null	–	–	–	–
Annual mean	Null	–	–	–	–	Null	–	–	–	–	Null	–	–	–	–
Summer mean	Null	–	–	–	–	Null	–	–	–	–	Null	–	–	–	–
Winter mean	Null	–	–	–	–	Null	–	–	–	–	Null	–	–	–	–

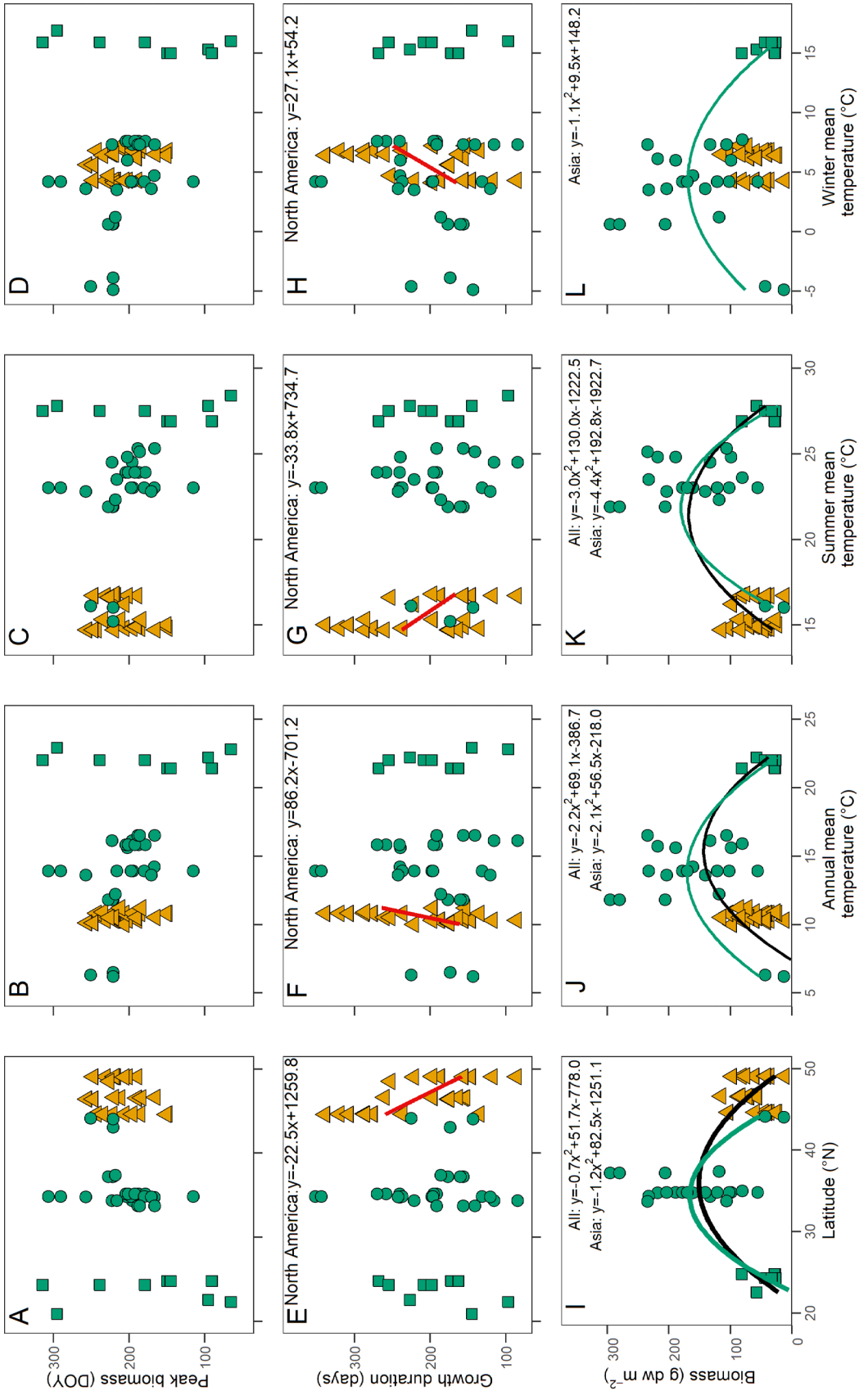

Fig. 3. Biomass variables in relation to latitudes and temperature. (A–D) Peak biomass timing by day of year (DOY), (E–H) growth durations, and (I–L) maximum biomass are compared to latitude (A,E,I), annual mean (B,F,J), summer mean (C,G,K), and winter mean (D,H,L) temperatures. Shapes represent different geographic groups: Asia-tropical (square), Asia-temperate (circle), and North America-temperate (triangle). Significant regression lines in panels (I–L) are green for the Asian populations, red for the North American populations, and black for all populations, with the equation at the top of each panel

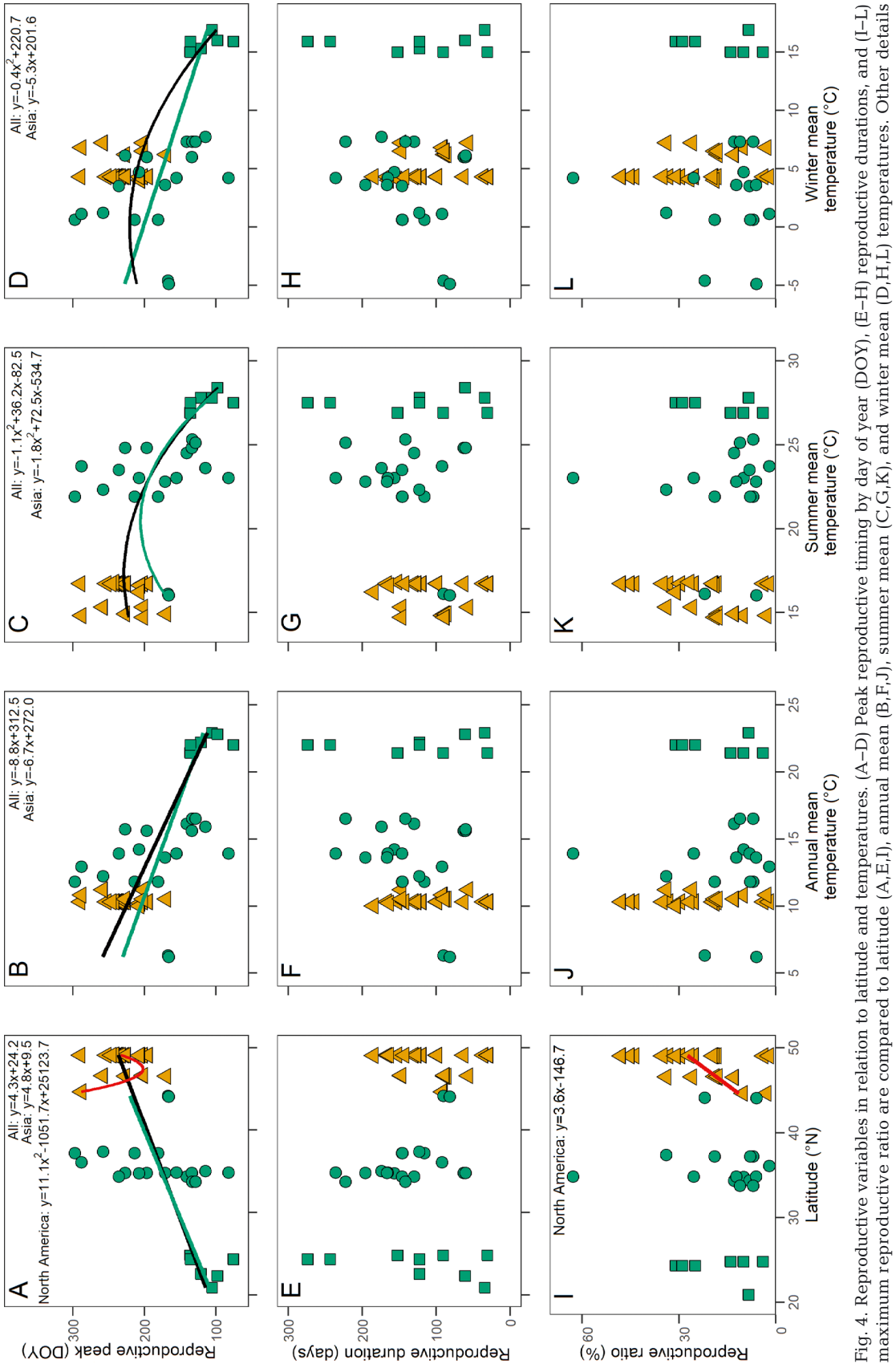

Fig. 4. Reproductive variables in relation to latitude and temperatures. (A–D) Peak reproductive timing by day of year (DOY), (E–H) reproductive durations, and (I–L) maximum reproductive ratio are compared to latitude (A,E,I), annual mean (B,F,J), summer mean (C,G,K), and winter mean (D,H,L) temperatures. Other details as in Fig. 3

tionship with the Asian populations ($F_{1,27}$ = 15.93, p < 0.001, R^2 = 0.35). A 1°C increase in temperature caused an earlier reproductive peak by 5.3 d, whereas the relationship was quadratic for all populations with the quadratic maxima at 0°C ($F_{1,50}$ = 32.65, p < 0.001, R^2 = 0.37; Fig. 4D). The strongest predictor for reproductive peak timing varied among groups: latitude for the North American populations, summer mean temperature for all populations, and winter mean temperature for the Asian populations (Table 3).

Reproductive durations were not affected by latitude nor temperatures in any geographic groups (p > 0.05, R^2 < 0.13 in all combinations; Fig. 4E–H, Table 3; Table S2). For reproductive ratios, only the North American populations showed a significant positive effect of latitude ($F_{1,21}$ = 4.57, p < 0.05, R^2 = 0.14; Table 3, Fig. 4I), while all other combinations of geographic groups with latitude or temperature were not significant (p > 0.05, R^2 < 0.13; Fig. 4I–L, Table 3; Table S2). In North American populations, an increase of 1° latitude caused a 3.55% increase in reproductive ratio.

4. DISCUSSION

4.1. Seagrass biomass and growth

Generally, seagrass biomass peaks during summer and remains low during winter, while the date of peak biomass timing shows latitudinal variation (Duarte 1989, Hemminga & Duarte 2000). Studies on kelp production and reproduction suggested that environmental conditions during winter and summer temperatures are both important to their seasonality (Krause-Jensen et al. 2012, James et al. 2015). In our study, the intertidal seagrass *Zostera japonica* showed no geographical variation in peak biomass timing and growth duration, nor was it affected by latitude or temperature, except for the North American populations where latitude and temperature had significant effects on their growth duration. For the predominantly subtidal congener *Z. marina*, Clausen et al. (2014) found significant latitude and temperature effects on seagrass peak biomass timing, but the effects were not significant on growth duration. Average growth duration for *Z. japonica* was 201.6 ± 63.1 d, which is comparable to the growth duration reported for *Z. marina*, 192.6 d (Clausen et al. 2014). In their study, Clausen et al. (2014) suggested that the earlier start and earlier end of the growth season in southern populations, and the later start and later end in northern populations, resulted in an overall constant growth duration across latitudes. An analysis of the start or end of the growth season was outside the scope of our study, yet the lack of significant latitude/temperature effects on peak biomass timing in this study implies that *Z. japonica* biomass is controlled differently from *Z. marina*.

High spatial and temporal variation, especially in peak biomass timing, may have masked potential effects of global factors, such as latitude and temperature. Our results suggest that the northern distributed group tended to show delayed biomass peak timing (Figs. 2A & 3A–D; Table S2). However, high spatial and temporal variation within the group were observed. Peak biomass timing from the same site but from a different tidal zonation could differ as much as 87 to 95 d (Kim et al. 2016, Suonan et al. 2017). Even at the same location, observations from 2 consecutive years resulted in peak timing differences of 57 d in an undisturbed condition (Kaldy 2006) and up to 192 d when disturbed; biomass peaked in March–April in an undisturbed year and in late October in the year disturbed by clamming activity (Park et al. 2011). This high variation suggests relatively stronger local effects than factors showing effects at larger scales, such as latitude or temperature, due to the fluctuating intertidal environment, compared to the stable subtidal environment experienced by *Z. marina*. Local environmental conditions, such as disturbance, tidal exposure, and ocean currents, may certainly affect the observed variation in seasonality traits; however, with limited case studies investigating the effect of each condition and no evidence of latitudinal trends in disturbance, the analysis of local conditions remained outside of scope in this study.

Differences between temperate and tropical populations may have contributed to the observed variation in peak biomass timing and growth duration. In the tropics, stress from heat or desiccation is especially strong for intertidal seagrasses (Lin & Shao 1998, Björk et al. 1999, Lan et al. 2005). High within-group variation for the tropical region might be caused by an autumn–winter peak, instead of a spring–summer peak for the temperate region, which occurred after heat and desiccation stress during late spring to summer. To this extent, an autumn–winter peak may not have fit well with our analysis, which assumed a spring–summer peak. Furthermore, the tropical population growth is largely affected by the rainy season, salinity, turbidity, riverine influence, tidal exposure, or water motion (Erftemeijer & Herman 1994, Lee 1997, Fong et al. 1998, Huong et al. 2003), suggesting that seasonal fluctuations in temperature or light may not be the most important factors control-

ling the growth of intertidal seagrass in the tropics. For example, biomass and growth of the tropical seagrass *Thalassia hemprichii* increased during the monsoon season, in which heavy rain brings more terrestrial nutrients into the beds (Lin & Shao 1998, Lin et al. 2018). Future investigation on seagrass seasonality in tropical regions will help resolve this uncertainty.

In our analysis, *Z. japonica* showed significant variation among geographical groups and significant latitude and temperature effects on maximum biomass, where the maximum biomass was the highest at mid-distribution, mid-latitude, or intermediate temperature, and decreased towards the edge of its range distribution (Fig. 3I–L). To our knowledge, this relationship between biomass and latitude or temperature was not found in the well-studied congener *Z. marina*, or in any other seagrass species (Olesen & Sand-Jensen 1994, Nakaoka & Aioi 2001, Olesen et al. 2015), although the size of *Z. marina* shoots peaks at intermediate latitudes (Ruesink et al. 2018). In native *Z. japonica*, variation in maximum biomass was described best by a quadratic relationship between latitude and temperature, and peaked around 34.4° N latitude or 21.9°C in summer mean temperature; summer mean temperature was the most influential predictor for variation in biomass (Fig. 3I,K). The quadratic relationship indicates a substantial reduction in maximum biomass at both the northern/colder range limit as well as the southern/warmer range limit. A significant reduction in biomass caused by storms, waterfowl grazing, ice scouring, and freezing in winter was observed in northern *Z. japonica* populations (Harrison 1982a,b, Sato et al. 2020, M. A. Ito pers. obs.), whereas similar biomass reduction caused by heat and desiccation in summer was observed in southern populations (Lee 1997, Fong et al. 1998). Such stressors at both the northern/colder and southern/warmer range limits may have caused biomass reduction or change in growth patterns. However, such stressors have also been reported in other seagrass species, especially in the well-studied *Z. marina* (freezing or ice scour: Keddy & Patriquin 1978, Robertson & Mann 1984; summer heat or desiccation: Phillips et al. 1983, Orth & Moore 1986), although that species does not show significant biomass variation among latitude or temperature. Our new findings on latitude/temperature–biomass relationships address the potential risk of applying insight from one species to another.

Optimal and upper critical temperatures for growth rate, photosynthesis, and distribution of *Z. japonica* from both native and non-native regions have been reported in past studies. An investigation of temperature effects on *Z. japonica* growth rates revealed maximum growth around 18–23°C in native (Lee et al. 2005) and around 20°C in non-native populations (Shafer et al. 2008, Kaldy et al. 2015b). Similarly, Uede (2007) found that seagrass standing biomass increases significantly up to 20°C, and then drastically decreases at 25–28°C in its native region. Two experimental studies on upper critical temperatures for photosynthetic activity for this species reported an identical value of 29°C (Abe et al. 2009, Morita et al. 2010), which corresponds to the upper critical temperature for its native geographic range (Abe et al. 2009 and references therein). The optimal and upper critical temperatures demonstrated from our study, 22 and 28°C, respectively, agreed well with other studies. Additionally, Kaldy et al. (2015b) suggested that *Z. japonica* growth rate is a function of the duration of exposure to warm temperature (20°C) and implies that temperature predominantly drives the intertidal zonation pattern. Although an analysis of the temperature experienced during the seagrass growth season was outside of our research scope, Kaldy et al. (2015b) clearly highlights the importance of temperature effects on maximum biomass achieved by each population. Based on our results (Fig. 3K), most of the *Z. japonica* populations are suggested to be experiencing higher than optimum temperatures at least some of the time within the summer. Further arguments considering ongoing climate change and its effect on seagrass biomass are discussed in Section 4.4.

4.2. Seagrass sexual reproduction

Seagrass sexual reproduction shows a seasonal pattern with a later peak at higher latitude and lower temperature sites (Phillips et al. 1983, Nakaoka & Aioi 2001). Our analysis demonstrated strong latitude/temperature effects on peak reproductive timing of *Z. japonica*, but not on reproductive duration nor on maximum reproductive ratio. Average peak reproductive timing was significantly different among the geographic groups; the reproductive peak occurred in late spring for the Asia-tropical group, in early summer for the Asia-temperate group, and late summer for the North America-temperate group (Fig. 2D). Regression analysis using summer mean temperatures showed that a decrease in temperature delayed the peak timing of the Asia-tropical group, which plateaued around DOY 230 (Fig. 4C). This plateau corresponded with the late-summer peak for the North America-temperate group, suggesting that reproduction cannot happen later than this time-

point. Interestingly, this timing coincides with the timeframe during which coastal upwelling starts to relax in North America (Bograd et al. 2009). For successful sexual reproduction, seagrass must flower, produce fruit, and carry out seed maturation (Alexandre et al. 2006). The number of days needed for *Z. japonica* to complete its reproductive stages have not been documented, although one study on the closely related congener *Z. noltii* reported that 47 d were required for the whole flowering to fruiting process (Alexandre et al. 2006). If this period is applicable to *Z. japonica*, limits on peak reproductive timing may arise from necessity to complete its reproductive process before seasonal die-off in winter. Most of the studies screened here did not report reproductive stages, which prevented us from conducting detailed analyses on different stages.

Average reproductive durations for *Z. japonica* and *Z. marina* appear similar, i.e. 121 and 128 d, respectively (*Z. japonica*: this study, *Z. marina*: Blok et al. 2018). *Z. japonica* showed constant reproductive duration among groups without latitude/temperature effects. For *Z. marina*, reproductive duration showed significant latitude/temperature effects as an earlier start of flowering for lower latitude/warmer populations, while end of flowering was constant along latitude/temperature (Blok et al. 2018). Although start or end flowering dates were not analyzed in the present study, contrasting results suggest that such events may have not occurred in *Z. japonica*.

Non-significant latitude and temperature effects on Asian or all population groups confirmed that the reproductive ratio in *Z. japonica* might be independent of large-scale factors, such as light or temperature, but may rather depend on local environmental conditions. When under stress, seagrass allocates more energy to sexual reproduction and thus reproductive effort can be used as an ecological indicator of environmental stress (Cabaço & Santos 2012, Kendrick et al. 2012). In this study, *Z. japonica* demonstrated relatively low (<20%) reproductive ratios for native populations, whereas non-native populations showed higher reproductive ratios, although the difference was only significant between the Asia-temperate and North America-temperate groups (Fig. 2F). An exceptionally high reproductive effort (63%), treated as an outlier in our analysis, was observed at a site with high anthropogenic disturbance by clam-harvesting activity (Park et al. 2011). In fact, experimental disturbance resulted in a negative correlation between flowering and vegetative biomass of non-native *Z. japonica* (Henderson & Hacker 2015), yet there was no observed negative relationship between reproductive effort and vegetative biomass in our study (Fig. S4C).

Compared to the vegetative growth (biomass results; Section 4.1), seagrass sexual reproduction was more strongly correlated with variation in latitude and temperature. This was also suggested by Blok et al. (2018, p. 88), who stated that 'sexual reproduction is more responsive to latitudinal climatic variation than seasonal biomass development' in *Z. marina*. Investigation of the direct relationship between biomass and reproduction remains outside of our scope; however, none of comparisons between peak biomass and reproductive timing, duration, or maximum output showed significant correlations in any geographic group (Fig. S4). These results highlight that drivers for biomass and reproduction might be different or have different mechanisms in *Z. japonica*.

4.3. Effects of introduction

Non-native *Z. japonica* populations in North America enabled us not only to extend latitude or temperature coverage, but also to investigate the potential effects of introduction on seagrass phenology. Among-group geographic comparisons resulted in significant differences between native and non-native groups for maximum biomass, peak reproductive timing, and reproductive ratio. Nonetheless, observed results must be cautiously interpreted because native and non-native groups differed in their latitudinal distribution. In this study, the non-native *Z. japonica* (North America-temperate) group covered only small latitudinal and temperature ranges compared to the native (Asia-tropical and Asia-temperate) groups (Table 2), reflecting their current and limited distribution in North America (Shafer et al. 2014). Furthermore, the eastern coast of the Pacific Ocean, which is inhabited by non-native *Z. japonica* populations, is strongly affected by seasonal coastal upwelling in summer (Bograd et al. 2009), and an inverse relationship between summer temperature and latitude was observed relative to what we observed in the western Pacific (Fig. S1). Differences in latitudinal distribution and latitude–temperature relationships in non-native populations may confound the observed results.

We found that non-native populations exhibited higher reproduction and shorter growth duration at higher latitudes, while other populations did not. Kaldy (2006) reported that sexual reproduction in non-native *Z. japonica* differed between southern populations in Oregon, where the timing and intensity of sexual reproduction was more variable than

among populations in British Columbia. Experiments on non-native *Z. japonica* demonstrated higher germination rates in warmer temperatures (15 and 20°C) compared to lower temperatures (10°C) (Kaldy et al. 2015a). In *Z. marina*, higher flowering ratios and longer reproductive durations were reported for lower temperature sites (Qin et al. 2020). Populations at northern cooler sites experiencing unfavorable germination but good flowering conditions may experience higher sexual reproduction as observed in this study, although effects of temperature were not significant. These interpretations, however, do not explain why this relationship is absent in native populations. The magnitude of environmental change effects on seagrass generally increases at higher latitude (Hemminga & Duarte 2000). The fact that non-native *Z. japonica* occurs at the upper end of latitudes where data were not available for native populations may explain why there are stronger abiotic effects at higher latitudes compared to introduction effects. Furthermore, coastal upwelling that only affects North American populations may moderate the latitudinal effect on growth duration. Kaldy et al. (2015b) suggested that non-native *Z. japonica* growth rate is highest at 20°C and decreased in lower temperature. Such low water temperature conditions caused by coastal upwelling may limit seagrass growth during summer. Further investigation will be possible once seasonality data on the northern-most native populations from Russia become available.

High reproductive ratios observed in non-native *Z. japonica* could have occurred during the introduction process, as it is one of the common characteristics for successful establishment and population growth of non-native species (Ruesink et al. 2010). *Z. japonica* has been established in North America since the 1970s; however, an invasion lag-phase (interval between non-native species becoming established and becoming fully invasive) is 20–30 yr on average, and some species show a lag-phase >40 yr (Sakai et al. 2001, Aikio et al. 2010), suggesting the possibility that *Z. japonica* is still in an invasion lag-phase. As stated earlier, reproductive ratios can be used as an ecological indicator of stress (Cabaço & Santos 2012). Kaldy & Shafer (2013) pointed out that a non-native population in Padilla Bay, WA, USA, is susceptible to the combination of heat stress and low salinity. Higher sexual reproduction observed in non-native groups indicates that non-native *Z. japonica* may be under stress while adapting to local environmental conditions in the introduced regions. Likewise, enhanced sexual reproduction was demonstrated in *Z. noltii* during its colonization stage (Cabaço et al. 2012), which suggests that non-native *Z. japonica* could be rapidly reproducing as they colonize new habitats.

Interestingly, latitude was a stronger predictor than temperature in North American *Z. japonica* populations, while temperature was always the strongest predictor for the Asian and all populations. It is known that *Z. marina* has lost its photo-recognition gene (Olsen et al. 2016); however, our results suggest that *Z. japonica* may retain some mechanism to recognize photoperiod. On the other hand, significant latitudinal correlation found in North American populations could be confounded with other environmental factors, such as coastal upwelling. Two of the northern-most study sites included in our analysis, Boundary Bay and Roberts Bank, Canada, are located in inner estuaries compared to other sites in North America that are located on the outer coast (Fig. 1). Upwelling intensity is generally weaker at northern sites (Bograd et al. 2009). Pawlowicz et al. (2019) showed that the Salish Sea, where the 2 sites are located, have a long water residence time, especially during the summer, and this long residence time could lead to warmer water temperatures being optimal for *Z. japonica* to grow. However, limited latitudinal and temperature coverage in the non-native region and limited knowledge on upwelling effects on seagrass will restrict further investigation. More data on seasonality from both northern and southern ranges will help clarify this uncertainty in the future.

4.4. Conclusions and future implications

Our study demonstrates that the effects of latitude and temperature on seagrass biomass and reproduction vary among analyzed traits and among geographic groups. Phenological traits with significant among-group geographical variation coincided with traits with significant latitude or temperature effects, highlighting the strong influences of globally controlled factors on maximum biomass and peak reproductive timing. In contrast, some traits showed significant latitude effects but only for the non-native group, suggesting an alteration in traits during the introduction process. Many of the results obtained from this study for *Z. japonica* differed from the previous findings of other seagrass species. Our new findings revealed the complexity of seagrass phenology under fluctuating intertidal environments, and highlight the importance of including data from tropical and non-native regions, which cannot be addressed in other seagrass species aside from *Z. japonica*.

Thus, we have presented the limitations of applying these findings to other species and the necessity of understanding species-specific phenological responses to changing abiotic factors.

Our study provides considerable insight in predicting how an intertidal seagrass species may respond to climate change. Large-scale analyses covering wide temperature ranges enabled us to use a space-for-time substitution approach to predict plant response to future climate change (Fukami & Wardle 2005, Buyantuyev et al. 2012). In this study, we found significant temperature effects on *Z. japonica* maximum biomass and peak reproductive timing. More than half of the studied populations are already experiencing higher temperatures than the growth optimum, and these populations are highly likely to experience substantial decreases in maximum biomass observed in the growth season. Furthermore, increases in temperature will push all tropical and some temperate populations beyond their upper critical temperatures. Our study suggests that climate change can cause detrimental reductions in biomass and may alter the range of *Z. japonica* in the future.

Acknowledgements. We thank Yung-Ji Huang and Shu-Chuan Hsiao for collecting seasonal data in Taiwan, and Mizuho Namba and Emily M. Adamczyk for their help with field surveys in Japan and Canada, respectively. We highly appreciate Emily M. Adamczyk and Kenji Sudo for constructive comments on an earlier draft. We thank 3 anonymous reviewers for their insightful and constructive comments that helped improve the manuscript. This research is partially funded by Tobitate Ryugaku JAPAN Nihondaihyou Program Scholarship to M.A.I., the 'Innovation and Development Center of Sustainable Agriculture' from The Featured Areas Research Center Program within the Higher Education Sprout Project by the Ministry of Education (MOE) of Taiwan to H.-J.L., an NSERC grant (#402006-13) awarded to M.I.O., and the Environment Research and Technology Development Fund (S-15 Predicting and Assessing Natural Capital and Ecosystem Services [PANCES]) by the Environmental Restoration and Conservation Agency, Japan, and JSPS KAKENHI (No.16H01792) to M.N.

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Editorial responsibility: Adriana Vergés, Sydney, New South Wales, Australia
Reviewed by: K.-S. Lee, J. Ruesink and 1 anonymous referee

Submitted: March 19, 2021
Accepted: August 30, 2021
Proofs received from author(s): September 27, 2021