



Environmental drivers of flowering in the genus *Zostera* and spatio-temporal variability of *Zostera muelleri* flowering in Australasia

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Abstract

1. Seed-based seagrass restoration strategies demand precise understanding of the environmental drivers influencing flowering. Flowering varies across diverse spatial and temporal scales, yet environmental drivers' effects on these dynamics have received less attention. Lack of knowledge regarding this life-history stage limits the advancement of seed-based restoration efforts, especially the establishment of shore-based seagrass nurseries to enhance seed production.
2. A systematic literature review on the flowering of the genus *Zostera* was conducted to develop a conceptual model that links influential environmental drivers with flowering. Additionally, a case study using existing survey data supplemented by additional field surveys was designed to explore the spatio-temporal variability of flowering along the latitudinal gradient in Australasia for the species *Zostera muelleri*. Predictive models for flowering times were developed using regional climatic variables, following hypotheses generated from long-term mesocosm observations.
3. The review identified the direct and/or indirect effects of temperature, light, tidal variation, nutrients, salinity and grazing pressure on flowering dynamics. Four categories of flowering variables were identified based on their implications on restoration, namely, timing, abundance, the ratio between reproductive and vegetative growth and morphological characteristics. The spathe densities varied significantly among sites along the latitudinal gradient. While first ($r^2 = 0.71$) and peak ($r^2 = 0.68$) flowering times showed significant correlation with latitude, first

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Funding information

Manuja Lekammudiyanse was supported by a CQUniversity International Excellence Scholarship, Australian Government Research Training Program Scholarship and CSIRO Postgraduate Scholarship (top-up scholarship and operating budget). Megan Saunders was supported by a Julius Career Award from CSIRO. Rod Connolly and Michael Sievers acknowledge funding support from the Global Wetlands Project (GLOW), supported by a charitable organization that neither seeks nor permits publicity for its efforts. Michael Sievers was funded by an Australian Research Council (ARC) Discovery Early Career Researcher Award (DE220100079). Dana Clark and Anna Berthelsen were supported by the Cawthron Institute, the Westpac New Zealand Government Innovation Fund, a Catalyst Seeding Fund Grant, Port Nelson and OneFortyOne New Zealand. Rachel Hooks was supported by a scholarship from Nelson City Council and Breanna Hindmarsh was supported by a scholarship from Ngā Pae o te Māramatanga.

flowering was equally predicted by mean winter air temperature and mean winter solar radiation ($r^2 = 0.73$), whereas peak flowering time was best predicted by mean winter air temperature ($r^2 = 0.60$).

4. Accurate predictions of flowering times can improve conservation outcomes by enabling restoration practitioners to forecast flowering times and subsequent wild seed harvesting. The strong correlation between flowering times and climatic variables suggests future shifts in flowering times under climate change are likely, which is crucial knowledge for maintaining the contribution of restoration projects to seagrass conservation.

KEYWORDS

conceptual model, latitude, restoration, seagrass flowering, solar radiation, spatio-temporal variability, temperature, *Zostera*

1 | INTRODUCTION

Seagrasses are marine angiosperms, defined by the production of flowers that contribute to the genetic diversity and resilience of meadows. By producing viable seeds that germinate and grow into new plants or remain dormant in a seed bank, flowering helps ensure the persistence of populations in the face of natural and anthropogenic environmental change, such as declines in water quality, extreme temperatures, coastal development and dredging and storm events. Seagrass phenology can be influenced by various environmental factors (e.g. temperature, light, tidal variation and nutrients) (De Cock, 1981c; Johnson et al., 2017; Sherman et al., 2018; Qin et al., 2020; von Staats et al., 2021). Depending on the relative contribution of environmental drivers, the flowering pattern can vary spatially and temporally. Large-scale spatial variability is expected to be linked with regional, seasonal variation in environmental conditions (e.g. changes in temperature and day length) (Blok et al., 2018; Phillips et al., 1983), and site-specific environmental conditions (e.g. nutrients, tidal height and physical disturbances) may drive small-scale variability (Campey et al., 2002; Cook, 1983; Durako & Moffler, 1987; Inglis & Smith, 1998). Spatio-temporal variation in seagrass flowering and related drivers has not been adequately investigated to predict the flowering cycle for most Australasian seagrass species (York et al., 2017; Zabarte-Maeztu et al., 2023).

Information on the phenology of *Zostera* Linnaeus, 1753 was systematically explored to identify possible environmental drivers that can be linked to flowering. Such an understanding provides important insights into the functioning of coastal seagrass ecosystems and better informs key stages of seed-based restoration efforts, such as timing for flower and seed collections, which can

contribute strongly to seagrass conservation. Knowing the drivers of flowering is also of great benefit for designing and operating cost-effective seagrass seed nurseries that can support restoration. Most *Zostera* species have a high potential for restoration in terms of domestication in nurseries, and rewilding is viable because large numbers of seeds can be produced over a prolonged period (van Katwijk et al., 2021).

This review focused on the genus *Zostera*, which is globally distributed and widely studied in relation to phenology. This monoecious genus produces photosynthetic flowering shoots that usually grow above the canopy to facilitate pollen dispersal (Ackerman, 2006; Follett et al., 2019). Each shoot consists of multiple flattened spathes (also called a spadix, an adjusted leaf sheath attached to the axis) from which flowers emerge as small anther-like structures (De Cock, 1980). Spathes have five maturity stages, namely, developing spathe (with no styles erected), erecting styles out of the spadix, curving styles after pollination, maturing seeds and releasing seeds when the spathe starts withering (De Cock, 1980; Infantes & Moksnes, 2018; von Staats et al., 2021). The plant's flowering potential is thought to relate to the plant's maturity, and the flowering period may depend on the plant's resource availability (Johnson et al., 2017). Flowering shoots usually first appear and mature close to the main stem and continue to progress towards the end of the shoot (De Cock, 1980). *Zostera* flowers produce negatively buoyant seeds inside the spathes following pollination (De Cock, 1980). Flowering shoots can be harvested for seed-based restoration efforts when the spathes develop seeds (Infantes & Moksnes, 2018; Tan et al., 2023).

The flowering process may be linked to external factors (e.g. temperature, light, tidal variation and nutrients) and plant genetics (Wang et al., 2019; Zhang et al., 2016). Depending on the

environmental conditions and the resources allocated to flowering, the flowering duration can vary and may result in spatial and temporal variations of flowering even within a relatively small geographic space of the same climatic region (Smith et al., 2016; Suonan et al., 2017). However, the environmental drivers that trigger or inhibit the flowering of *Zostera* have yet to be sufficiently demonstrated, limiting the capacity to accurately predict flowering phenology under different scenarios. This review analysed the literature on natural *Zostera* phenology and developed a conceptual model for *Zostera* flowering by analysing the suite of environmental variables either putatively or causally linked to flowering. A pathway for future phenological studies is also provided.

Supporting this review, a large-scale case study was conducted in Australia and New Zealand to document the spatio-temporal variability of the flowering of *Zostera muelleri* along the latitudinal gradient in Australasia and to determine which environmental factors appear most linked to its timing. While previous studies of the relationship between temperature and the timing of flowering have used mean annual air temperatures (Blok et al., 2018; Ito et al., 2021), here the impacts of water temperature and solar radiation were also considered. In addition, this study concentrated on winter environmental conditions, which extended mesocosm experiments have shown to determine the timing of *Z. muelleri* flowering (Lekammudiyanse et al., 2022; Lekammudiyanse et al., 2023a).

2 | METHODS

2.1 | Literature search methodology

Peer-reviewed publications were searched with no time constraints on the indexed scientific databases Scopus, Web of Science and CSIRO journals. Standardized keyword combinations (seagrass, submerged aquatic vegetation, flower, inflorescence, sexual reproduction, spathe) were used with Boolean and wildcards (i.e. seagrass OR submerged aquatic vegetation AND flower* OR inflorescen* OR sexual reproduc* OR spathe). The resulting papers were excluded if they were non-English or unavailable in full text. Duplicate records were removed, and cross-referencing was conducted during the systematic search, providing 706 unique publications. To be included, a publication had to meet the following criteria: (a) study on the genus *Zostera*, (b) it addressed the topic of seagrass flowering, (c) it discussed environmental variables driving flowering and (d) it discussed temporal changes in flowering. Data were extracted from the 59 studies that met these criteria to build a database of information describing flowering phenology and proposed/demonstrated causal environmental variables, which were subsequently used to construct a generalized conceptual model of *Zostera* flowering. Studies that explored the flowering variabilities during discrete anthropogenic disturbances (e.g. effects of clam harvesting and manual clearance) were not considered in building the generalized conceptual framework.

2.2 | Case study: *Z. muelleri* flowering in Australasia

2.2.1 | Data collection

Data on flowering times were assembled from literature and from existing surveys by the authors, supplemented by additional field surveys, which also collected data on flowering intensity using a specifically designed protocol (Supporting Information, Protocol for field data collection – *Zostera muelleri* flowering). As per this protocol, two flowering measurements were taken (i.e. number of flowering shoots per quadrat and number of spathes in three randomly selected flowering shoots) by walking from the high tide level to the low tide level of the meadow monthly over the flowering season. These measurements were used to calculate the average number of spathes in a square metre (hereafter known as the density of spathes). The density of spathes during peak flowering months (where the highest densities were recorded) was used for the analysis. Three flowering measurements were taken at each level of the upper, middle and lower tidal levels of the meadow to find which intertidal zone is better for flower collection. Spathe density data were available at two tropical and five subtropical intertidal meadows in Queensland, Australia, and two temperate meadows in New Zealand during the peak flowering months in the 2020–2021 flowering seasons (Figure 1). These sites continue to be monitored by the authors.

2.2.2 | Data analysis

In each study, the timing of the first flowering was represented as the day number of the given year. As the timing of flowering in the case study was not always available as precise dates, the middle day of the particular month recorded was used in the analyses (Blok et al., 2018). We hypothesized that *Zostera* flowering across Australasia would be triggered by the coldest temperatures expected to occur in the Austral winter (June–August), based on fine-scale observations of seagrass flowering over 5 years (2018–2022) from mesocosm systems at the Coastal Marine Ecosystems Research Centre, CQUniversity (Lekammudiyanse et al., 2022, Figure S1). The relationships between first/peak flowering and three different aspects of the winter regional climate—air temperature, water temperature and solar radiation—was explored. Climatic data were extracted from the closest weather stations (available as daily minimum and maximum) and ERA5 climate data (available as hourly gridded data) (Hersbach et al., 2019).

A set of univariate linear regression models was developed for the timing of first and peak flowering with the predictors mean winter air temperature, mean winter water temperature and mean winter solar radiation (the significance level was tested with $P < 0.05$). Though the environmental variables were assumed to correlate with latitudes strongly, their relationships with the latitudes were also tested to ensure the applicability of regional climatic variables as predictors of flowering times (Figure S2). Because the predictors are highly correlated

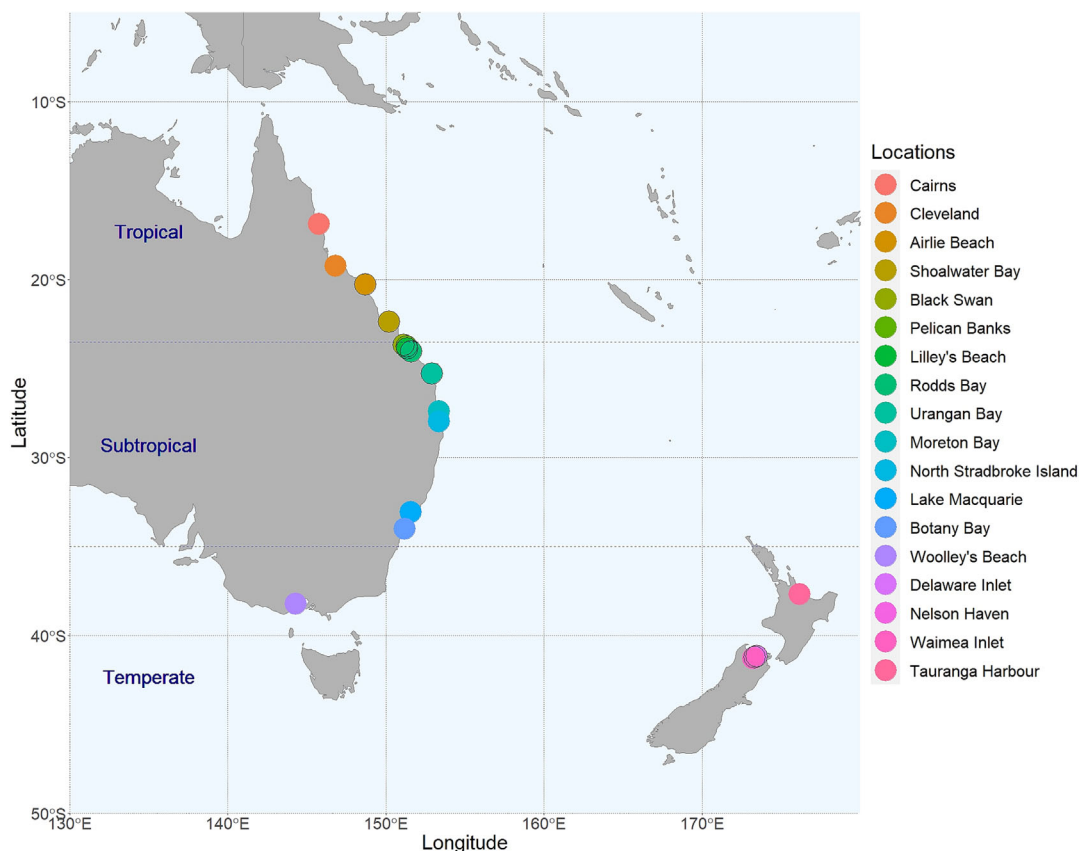


FIGURE 1 Locations from which *Z. muelleri* flowering time data for Australasia were collected. Dots with circles are denoted for the sites that have both flowering density data and timing data.

(Figure S3), univariate models were built to explore the effect of individual environmental variables. Variation in the density of spathes was tested with two-way analysis of variance (ANOVA) with two fixed factors (i.e. site and intertidal depth level). The requirements of ANOVA were checked with normalized q-q residual plots and Shapiro–Wilk's test ($P < 0.05$). Spathe density at the lower level of the Delaware Inlet site was detected as an outlier, and hence, it was removed from the analysis. Data remained heterogenous even after transformation, so a more conservative significant level was considered (i.e. $P < 0.01$) (Kutner et al., 2004; Underwood et al., 1997). All simulations were performed in R version 4.2.1 (Team, 2020), and data were plotted with ggplot2 (Wickham et al., 2016).

3 | RESULTS

3.1 | Systematic review results

The flowering variables were categorized and the database organized by species, experiment type, environmental variables, flowering metrics and the locations of these studies (Tables 1 and 2). Most studies (>80%) were conducted in the northern hemisphere, focusing mainly on *Zostera marina* Linnaeus, 1753 (Figure 2). Other studies

were focused on *Zostera noltei* Hornemann, 1832 (synonym *Zostera noltii*), *Z. muelleri* Irmisch ex Ascherson, 1867 subsp. *capricorni* (Ascherson) S.W.L. Jacobs, 2006, *Zostera japonica* Ascherson and Graebner, 1907 (unaccepted synonym *Zostera americana* den Hartog, 1970), *Zostera caespitosa* Miki, 1932, *Zostera capensis* Setchell, 1933, and *Zostera nigricaulis* (J. Kuo) S.W.L. Jacob and D.H. Les, 2009 (synonym *Heterozostera nigricaulis*) (Figure 2).

3.2 | Flowering variables

Seagrass flowering was measured using variables representing timing, flowering shoot/spathe density, the ratio between reproductive and non-reproductive shoots/biomass and morphological characteristics of flowering based on their importance in restoration (Table 1). The most common flowering variable in measuring spatial and temporal variabilities was flowering shoot or spathe density (i.e. number of flowering shoots or spathes per unit area) (Cabaço et al., 2009; Infantes & Moksnes, 2018; Morita et al., 2010; Potouroglou et al., 2014). From a harvesting point of view, abundance variables will be important (Infantes & Moksnes, 2018) and to predict the harvesting times, knowing the duration of seagrass flowering is useful (Blok et al., 2018). Resource allocation in flowering can be measured

TABLE 1 Types of flowering variables garnered from the literature.

Category	Flowering variable
Timing of flowering	<ul style="list-style-type: none"> -Probability/presence of flowering -Days of flowering (number of days to first and peak flowering) -Duration of flowering -Degree of decomposition of inflorescence -Number of days to inflorescence becomes visible
Density of flowering	<ul style="list-style-type: none"> -Number of flowering shoots per unit area (density of flowering shoots) -Number of spathes per unit area (density of spathes)
Ratios of flowering	<ul style="list-style-type: none"> -The proportion of spathe biomass to shoot biomass -Number/percentage of reproductive shoots to total shoots -Percentage of reproductive shoot biomass to total shoot biomass (reproductive effort) -The ratio between ovaries and shoot -Sex ratio (proportion of female and male flowers)
Morphology of flowering	<ul style="list-style-type: none"> -Height/length of flowering shoot -Length of spathe -Number of spathes per flowering shoot -Branches per flowering shoot -Number of spathes per branch -Total number of spathes on the 1st branch -Number of female and/or male flowers per spathe -Number of unfertilized flowers per spathe -Stage of spathe development

by the flowering ratio and morphological characteristics (Jackson et al., 2017; Wang et al., 2019). Combining variables from these categories will be beneficial in measuring, interpreting and applying the spatial and temporal variations in flowering. In addition, a combination of flowering variables might be a good indicator of physical disturbance as the alterations of reproductive efforts are strongly linked with the natural/anthropogenic factors regardless of the type of disturbance (Cabaco & Santos, 2012).

3.3 | Effects of abiotic factors

3.3.1 | Water temperature

In most previous studies, water temperature was identified as the most influential environmental variable related to triggering and defining the stages of the flowering cycle (De Cock, 1981c; Phillips et al., 1983; Potouroglou et al., 2014; Qin et al., 2020; Silberhorn et al., 1983). Temperature thresholds that trigger flowering are thought to be similar across latitudinal gradients based on differences in flowering times observed (Silberhorn et al., 1983). Conversely, some studies suggested that the threshold temperature across

latitudes is different due to the adaptation to local temperature regimes (Phillips et al., 1983). For instance, some *Zostera* species, like *Z. marina* in northern latitudes, are found to flower even at very low temperatures (e.g. at 0.3°C) (Silberhorn et al., 1983). In comparison, southern populations are associated with higher threshold temperatures (e.g. at 17°C), suggesting that temperature thresholds can vary among the populations along the latitudinal gradient (Qin et al., 2020; Silberhorn et al., 1983).

In the northern hemisphere, *Z. marina* flowering typically starts later than in most southern populations. Blok et al. (2018) showed that the formation of flowers is likely to be delayed by approximately 12 days with a 1°C increase in annual temperature increment. Such differences in the timing of flowering have also been recorded in southern hemisphere waters where tropical and subtropical *Zostera* populations start flowering in mid-winter while the flowering season begins in late spring to early summer in temperate populations (Lekammudiyanse et al., 2022; Rasheed, 1999; Smith et al., 2016). In contrast, differences in the timing of flowering have been observed even within the same latitudinal region where early flowering was observed in relatively warm areas compared with colder areas (Phillips et al., 1983; Qin et al., 2020; Vercaemer et al., 2021). This might be due to the differences in receiving the required temperature to trigger flowering. Differences in flowering times in the same latitudinal region further emphasized that temperature appears to be more important than day length differences.

Plants are usually thought to tolerate a range of temperature thresholds, with higher temperature thresholds likely to lower flower production (McMillan, 1980). In contrast, a longer duration of threshold temperatures is expected to compromise prolonged flowering events (Qin et al., 2020), which might be due to the difference in resource allocation between plant growth and flower production (Lee et al., 2007; Zimmerman et al., 2017). Therefore, temperature thresholds of flowering are unlikely to be found without considering the thermal tolerances and ambient temperature conditions within its local distributional range. This creates challenges in designing experiments to find the temperature triggers of flowering. Such temperature thresholds are available mainly for *Z. marina* (De Cock, 1981c; Phillips, Stewart Grant & Peter Mcroy, 1983; Silberhorn et al., 1983) and are rare for other species.

Antecedent conditions and fluctuations within the temperature range are also likely to affect flowering times. High temperatures tend to result in the plant allocating resources more towards vegetative growth as a response to withstanding thermal stress and thus may result in delays in flowering due to fewer resources for flower production (Zimmerman et al., 1989; Zimmerman et al., 2017). When temperature fluctuations are frequent and reach extremely high temperatures beyond the plant's photosynthetic temperature threshold, plants tend to stress quickly, even within a day, hindering the flowering potential of the plant (Qin et al., 2020; Vercaemer et al., 2021). Therefore, differences in flowering times can be expected even among closely located populations if they experience different temperature fluctuations (Qin et al., 2020).

TABLE 2 Summary of studies that report on *Zosteraceae* flowering phenology and its links to environmental variables.

Study type	Country	Continent/region	Location	Environmental factors	Studied temporal variability
<i>Zostera marina</i>					
Review	-	North America, Europe and Asia	-	Water temperature	No
Review	-	North America, Europe and Asia	-	Intertidal stresses	Yes
Field	USA	North America	Core and Back Sounds, North Carolina.	Current speed, wave exposure, tidal depth	No
Field	USA	North America	Long Island, New York	Sediment nutrients	No
Field	USA	North America	Phillips Island and Morgans Island	Temperature, salinity, nutrients	Yes
Field	USA	North America	Chesapeake Bay, Virginia	Sediment nutrients	No
Field	USA	North America	Chesapeake Bay, Virginia	Temperature, salinity	No
Field	USA	North America	Gulf of Maine	Tidal depth	No
Field	USA	North America	Lummi Bay	Tidal depth, tidal amplitude, sediment nutrients	No
Field	USA	North America	Crown Beach	Mesograzing	No
Field	USA	North America	Willapa Bay, Washington	Tidal elevation	No
Field	USA	North America	Humboldt Bay	Herbivore grazing	Yes
Field	Canada	North America	Boundary bay	Intertidal depth	Yes
Field	Alaska	North America	Grant Point in Izembek Lagoon	Sediment nutrients	No
Field	Canada	North America	Atlantic coast of Nova Scotia	Temperature, tidal depth, sediment type, water current, light	Yes
Field	Netherlands	Europe	Bergen op Zoom and Grevelingen	Tidal depth, temperature	No
Field	Netherlands	Europe	Zandkreek	Intertidal depth	Yes
Field	Ireland	Europe	Cadiz Bay and Kilkieran Bay and Ballysadare Bay	Temperature	Yes
Field	Portugal	Europe	Ria de Aveiro lagoon	Temperature, light, salinity	Yes
Field	Germany	Europe	Island of Sylt	Abundance of meiofauna	No
Field	France	Europe	Roscoff	Tidal depth	Yes
Field	Denmark	Europe	Archipelago of South Funen	Tidal depth	Yes
Field	UK	Europe	Isles of Scilly	Temperature	Yes
Field	-	Europe	Kiel Bight, Baltic Sea	Sedimentation	Yes
Field	Korea	Asia	East and south coasts of Korea	Temperature, light, nutrients	Yes
Field	Korea	Asia	Jindong Bay, Korea	Temperature	Yes
Field	Korea	Asia	Koje Bay, Korea	Nutrients	Yes
Field	Korea	Asia	Deukryang Bay and Dongdae Bay	Nutrient, light	Yes
Field	Korea	Asia	Koje Bay	Sediment and water column nutrients	Yes
Field	China	Asia	Coastal areas of North China	Nutrients	Yes

TABLE 2 (Continued)

Study type	Country	Continent/region	Location	Environmental factors	Studied temporal variability
Field	China	Asia	Allian Bay, north China	Tidal depth, light	Yes
Field	China	Asia	Swan Lake of Shandong Peninsula	Temperature, light	Yes
Field and laboratory	Sweden	Europe	Wallhamn, Swedish NW coast	Water temperature, tidal depth, light	Yes
Laboratory	USA	North America	San Francisco Bay, California	Mesograzers	No
Laboratory	Netherlands	Europe	Grevelingen	Daylength, temperature	No
Laboratory	Netherlands	Europe	Bergen op Zoom	Daylength, temperature	Yes
Laboratory	Netherlands	Europe	Bergen op Zoom	Temperature	Yes
Laboratory	Japan	Asia	Ago Bay	Seed germination, temperature	Yes
<i>Zostera noltei</i> (synonym <i>Zostera nolii</i>)					
A review	-	Europe	-	Intertidal stresses	Yes
Field	Portugal	Europe	Ria de Aveiro lagoon	Salinity, organic matter, sediment size	Yes
Field	Ireland	Europe	Cadiz Bay in southern Spain and Kilkieran Bay and Ballysadare Bay	Temperature	Yes
Field	Portugal	Europe	Ria Formosa lagoon	Intertidal depth	Yes
Field	Italy	Europe	Lagoon of Venice	Tidal depth	No
Field	Netherlands	Europe	Zandkreek	Intertidal depth	Yes
Field and laboratory	Portugal	Europe	Ria Formosa lagoon	Sediment burial and erosion	Yes
<i>Zostera muelleri</i>					
A review	-	Australia	-	Intertidal stresses	Yes
Field	Australia	Australia	Victoria Point, Moreton bay	Tidal depth	Yes
Field	Australia	Australia	Botany Bay and Port Hacking	Water temperature	Yes
Field	Australia	Australia	Moreton Bay	Megaherbivore grazing	Yes
Field	New Zealand	Oceania	Tauranga Harbour	Intertidal zones	Yes
Field and laboratory	New Zealand	Oceania	Kaikoura Peninsula	Intertidal depth, plant cover, site characteristics, light, salinity, temperature	Yes
Laboratory	Australia	Australia	Gladstone	Megaherbivore grazing	Yes
<i>Zostera japonica</i>					
A review	-	North America and Asia	-	Temperature	No
Field	USA	North America	Idaho Point in Yaquina Bay, Oregon	Sediment temperature	Yes
Field	USA	North America	Yaquina Bay	Sedimentation	Yes
Field	Canada	North America	Boundary bay, Canada	Intertidal depth	Yes

(Continues)

TABLE 2 (Continued)

Study type	Country	Continent/region	Location	Environmental factors	Studied temporal variability
<i>Zostera caespitosa</i>					
Field	Korea	Asia	Jangmok Bay	Temperature, light, salinity, water column nutrients	Yes
<i>Zostera capensis</i>					
Laboratory	Kenya	Asia	Shimo la Tewa	Temperature Day length	No
<i>Zostera nigricaulis</i> (synonym <i>Heterozostera nigricaulis</i>)					
Field	Australia	Australia	Port Phillip Bay	Algae cover	Yes

TABLE 2 (Continued)

Study type	Timing	Abundance	Ratio	Morphology	Reference
<i>Zostera marina</i>					
Review	✓				Blok et al. (2018)
Review			✓		Cabaco & Santos (2012)
Field			✓		Fonseca & Bell (1998)
Field				✓	Jackson et al. (2017)
Field		✓		✓	Jarvis et al. (2012)
Field		✓	✓	✓	Johnson et al. (2017)
Field		✓			Johnson et al. (2021)
Field		✓	✓	✓	von Staats et al. (2021)
Field	✓	✓			Yang et al. (2013)
Field				✓	Reynolds et al. (2012)
Field		✓			Ruesink et al. (2012)
Field		✓			Shaughnessy et al. (2021)
Field		✓	✓		Harrison (1982)
Field		✓			Short (1983)

TABLE 2 (Continued)

Study type	Timing	Abundance	Ratio	Morphology	Reference
Field	✓	✓	✓	✓	Vercaemer et al. (2021)
Field	✓	✓		✓	De Cock (1981a)
Field		✓			Harrison (1993)
Field	✓				Azcárate-García et al. (2022)
Field		✓		✓	Guerrero-Meseguer et al. (2022)
Field		✓			Hellwig-Armonies (1988)
Field		✓		✓	Jacobs & Pierson (1981)
Field			✓	✓	Olesen et al. (2017)
Field		✓			Potouroglou et al. (2014)
Field		✓		✓	Munkes et al. (2015)
Field		✓	✓	✓	Qin et al. (2020)
Field		✓	✓		Qin et al. (2020)
Field		✓		✓	Qin et al. (2021)
Field		✓	✓		Suonan et al. (2022)
Field		✓			Lee et al. (2005)
Field			✓		Wang et al. (2019)
Field	✓	✓			Xu et al. (2020)
Field			✓	✓	Zhang et al. (2016)
Field and laboratory	✓	✓		✓	Infantes & Moksnes (2018)
Laboratory			✓		Carr & Boyer (2014)
Laboratory	✓				De Cock (1977)
Laboratory			✓		De Cock (1981b)
Laboratory		✓	✓		De Cock (1981c)
Laboratory		✓		✓	Morita et al. (2010)
<i>Zostera noltei</i> (synonym <i>Zostera noltii</i>)					
A review			✓		Cabaco & Santos (2012)
Field		✓	✓		Ankel et al. (2021)
Field	✓				Azcárate-García et al. (2022)
Field		✓			Cabaço et al. (2009)
Field		✓		✓	Curriel et al. (1996)
Field		✓			Harrison (1993)
Field and laboratory		✓			Cabaco & Santos (2007)
<i>Zostera muelleri</i>					
A review			✓		Cabaco & Santos (2012)

TABLE 2 (Continued)

Study type	Timing	Abundance	Ratio	Morphology	Reference
Field		✓	✓	✓	Conacher et al. (1994)
Field		✓	✓		Inglis & Smith (1998)
Field		✓	✓		Peterken & Conacher (1997)
Field		✓		✓	Dos Santos & Matheson (2017)
Field and laboratory		✓		✓	Ramage & Schiel (1998)
Laboratory	✓	✓	✓	✓	Lekammudiyanse et al. (2022)
<i>Zostera japonica</i>					
A review	✓		✓		Ito et al. (2021)
Field		✓			Kaldy (2006)
Field		✓	✓		Henderson & Hacker (2015)
Field		✓	✓		Harrison (1982)
<i>Zostera caespitosa</i>					
Field	✓		✓	✓	Lee et al. (2005)
<i>Zostera capensis</i>					
Laboratory	✓				McMillan (1980)
<i>Zostera nigricaulis</i> (synonym <i>Heterozostera nigricaulis</i>)					
Field		✓		✓	Smith et al. (2016)

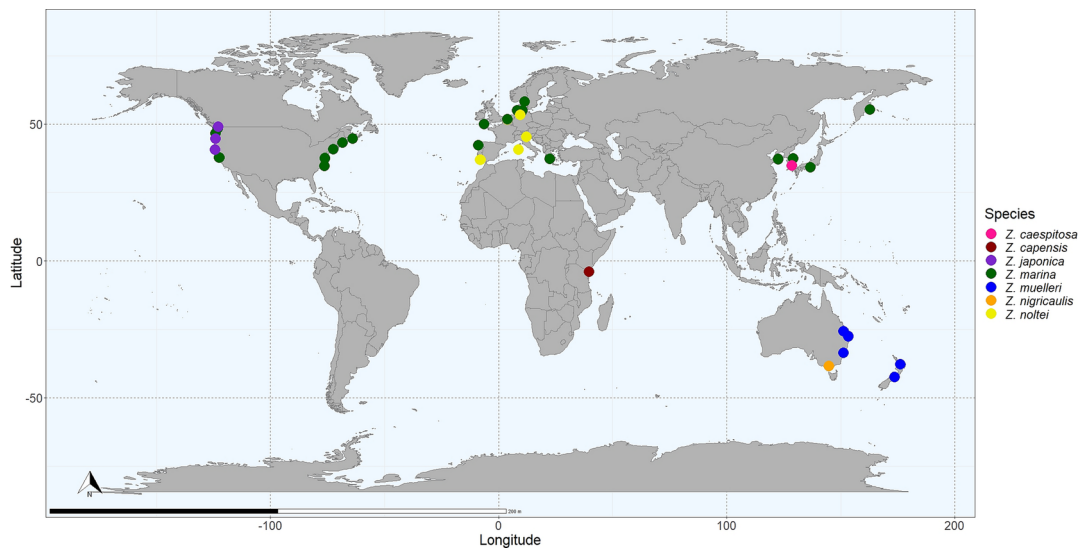


FIGURE 2 Locations of studies examining the phenology of *Zostera* and related environmental drivers.

3.3.2 | Light

Light levels also affect the flowering of *Zostera*. Low irradiance levels resulting from algal blooms, deeper water or high turbidity may reduce or inhibit flowering shoot development in *Zostera*. The long-term decline in light levels along urban coastlines where turbidity is consistently elevated above historical levels can decrease the plant's investment in sexual reproduction, even in nutrient-rich waters (Johnson et al., 2017). Along the tidal depth gradient, light intensities decrease, and in many estuarine and coastal habitats, tidal depth and the associated light limitation are considered the most important factor in limiting the vertical distribution of *Zostera* (Fonseca et al., 1983; Koch, 2001; Krause-Jensen et al., 2000).

In deeper subtidal water, low light conditions can delay flowering. If the light level received is below the light compensation point, carbohydrate production may be diminished (Ruiz & Romero, 2001). As a result, the above-ground biomass and shoot densities are reduced, but canopy height can increase, which could reduce the potential of self-shading while also assimilating greater amounts of light energy (Collier et al., 2007; Dennison, 1987; Krause-Jensen et al., 2000; Olesen et al., 2017). In such cases, it appears plants can invest their resources towards sexual reproduction, resulting in increased flowering acutely or seasonally (Kim et al., 2014; McMillan, 1982; Olesen et al., 2017; Phillips et al., 1983; Silberhorn et al., 1983; van Lent & Verschuure, 1994). However, prolonged light reduction at deeper depths can reduce the resource investment in flowering, which might be the reason for observed delays in flowering times, low flowering densities and lengthening of the flower maturation periods in deeper water (von Staats et al., 2021). At shallower depths, light regimes are supposed to be more favourable and thus may result in higher flowering intensities (von Staats et al., 2021). In addition, heavy epiphytic fouling of seagrass leaves by

filamentous macroalgae can reduce the available light and thus result in lower flowering intensities in shallow waters (Infantes & Moksnes, 2018). However, low light conditions resulting from algal phytoplankton blooms may not affect the triggering of flowering, which is thought to be driven primarily by temperature (Qin et al., 2020).

Across the intertidal zone, light is unlikely to be a limiting factor, but oversaturated light during low tides can cause photo-inhibition and stop plant metabolism (Petrou et al., 2013; Pollard & Greenway, 2013). In the lower intertidal zone, light can be attenuated by re-suspended sediments from turbulent flows during high tides (Adams et al., 2016; Coles et al., 2007). Some studies have observed that plant sexual reproduction tends to increase acutely with environmental stressors in the intertidal zone, but it is unclear whether these acute responses are related to tidal fluctuation and/or the light limitation or their interaction (Fonseca & Bell, 1998; Potouroglou et al., 2014).

Unlike light intensity, the effect of the duration of the photoperiod was unclear. Shorter photoperiods (i.e. in winter) were found to inhibit the formation of reproductive shoots of some *Zostera* species (e.g. *Z. novazelandica*), even at preferable temperatures (Ramage & Schiel, 1998), suggesting that the flower development inhibited by short photoperiod may reduce the longevity of the meadow by limiting sexual reproduction. Conversely, some studies suggest that the photoperiod may not determine the reproductive periodicity over the latitudinal gradient as the populations are expected to be acclimatized and adapted to regional light regimes (Blok et al., 2018; McMillan, 1980; McMillan, 1982; Silberhorn et al., 1983). This might be due to the absence of the phytochrome C gene in *Zostera* plants (e.g. *Z. marina*) that are linked to the photoperiod control of flowering, suggesting that the photoperiod may play a minor role in the timing of flowering (Olsen et al., 2016).

3.3.3 | Tidal variation

Tidal variation can affect *Zostera* flowering, with intertidal seagrasses often subject to desiccation stress, hydrodynamic removal or sedimentation with tidal movements (Fonseca & Bell, 1998; Koch, 2001; Vermaat, 2009). The stressors associated with tidal variation vary across the intertidal depth gradient, typically greatest at landward intertidal levels.

At shallow intertidal depths, plants are exposed for extended hours during low tides, resulting in high desiccation stress and photo-inhibition from light over-saturation (Ralph et al., 2007; Silva & Santos, 2003). These stresses change the plant's physiology and mechanical strength. For instance, 5 h of aerial exposure reduced the photosynthetic rate of *Z. noltii* by 50% due to the loss of water content in plant tissues (Leuschner et al., 1998). In extreme conditions, long-term desiccation stress can shred the leaves, resulting in short canopies in the intertidal zone (Boese et al., 2003; Vermaat et al., 1993). The desiccation stress can vary depending on the groundwater seepage, self-shading by plant cover, shielding by algae, air temperature and wind speed. For instance, *Z. noltii* was found to tolerate extremely high air temperatures (e.g. 40°C) for 6 h of daily tidal exposure when the plant cover is dense (e.g. >75% cover) (De Fouw et al., 2016). During the exposure, plants can facilitate the photosynthetic rate by enhancing the carbon dioxide assimilation when the plant's tissues remain moist (Petrou et al., 2013; Pollard & Greenway, 2013). At lower intertidal depths, the desiccation stress is likely less due to relatively short-term ariel exposure, providing more favourable conditions for plant growth (Van Lent et al., 1991). In addition, during high tide, the intertidal zone may experience low light conditions due to turbulent flows with re-suspended sediments that are likely to attenuate the light (Adams et al., 2016; Coles et al., 2007).

Plant sexual production sometimes shows slight increases with the changes in environmental stressors in the intertidal zone (Fonseca & Bell, 1998; Potouroglou et al., 2014). For instance, Fonseca & Bell (1998) observed a 5% increase in flowering shoots with a 10-fold increase in wave exposure index, calculated from wind velocities. The weak correlation ($r^2 = 0.29$) between the percentage of flowering shoots and wave exposure suggested that wave exposure might not significantly influence flowering (Fonseca & Bell, 1998). In addition, intertidal meadows show patchiness in flowering over scales of metres to tens of metres and vary temporally (Campey et al., 2002; Conacher et al., 1994; Inglis & Smith, 1998). This might be due to the plant's adaptability in allocating resources towards sexual reproduction and vegetative growth in disturbed regimes (Mony et al., 2011; Nelson et al., 2007). Observed spatial and temporal variation in flowering may also be linked to local environmental conditions as well as plant genetic factors (Campey et al., 2002; Clavier et al., 2011; Cook, 1983; Durako & Moffler, 1987; Inglis & Smith, 1998). For instance, Olesen et al. (2017) observed increased flowering in mid-intertidal levels, and Ramage & Schiel (1998) noted increased flowering in lower intertidal depths and tide pools where the desiccation stress is expected to be lowest. In

contrast, Cabaço et al. (2009) observed no differences in flowering at different heights of the intertidal zone, and Harrison (1982) noted some temporal changes at different intertidal zones. These reported changes might be due to the antagonistic or synergistic effects of the stressors in the intertidal zone, where the combination of stressors may have less impact than the effects of the individual stressor (i.e. antagonistic effect) or vice versa (i.e. synergistic effect) (Brown et al., 2014). The previous contradictory findings emphasize the need for further studies on the factors driving the patchiness of flowering in the intertidal zone.

At subtidal depths, desiccation stress is absent, but light might be a crucial factor. Particularly at deep depths, limited light availability is found to reduce and delay flowering (Olesen et al., 2017). However, light may not be limited at shallow depths, where conditions are thought to be more favourable for plant growth and flower production (Inglis & Smith, 1998; von Staats et al., 2021). However, contrasting observations are reported by von Staats et al. (2021), where less flowering was observed in shallow subtidal depths than at deeper depths. This might be due to the differences in the timing of the observations or the physical damage of mature flowering shoots by hydrodynamic disturbances, which are expected to be more pronounced in shallow depths (Krause-Jensen et al., 2000). Further research that employs manipulative experiments will be helpful in determining the effects of light limitation in subtidal depths while controlling the covarying factors that hinder the direct influence of light.

Tidal effects on flowering may further be associated with sedimentation. At high levels of sedimentation, an acute increase in flowering might be expected as a stress-responsive mechanism (Henderson & Hacker, 2015). For instance, in a study on *Z. japonica*, Henderson & Hacker (2015) observed that sites with low mean monthly sediment deposition (~0.2 cm) during the flowering season produced fewer flowering shoots than the sites with a high mean monthly sediment deposition (~0.4–0.7 cm). However, high levels of sedimentation over a long duration can substantially reduce the flowering shoot density (Cabaco & Santos, 2007) and can even result in failures in recolonization (Zabarte-Maeztu et al., 2023). On the other hand, sedimentation can negatively affect macroinvertebrate communities that support flowering by grazing epiphytic algae (Siciliano et al., 2019). With these contradictory results, it is difficult to conclude how sedimentation and hydrodynamics affect *Zostera* flowering. Therefore, further investigation is required to understand the variations of flowering observed under the influence of sedimentation and related hydrodynamic stresses. When designing field experiments to test the relationship between flowering and intertidal depth, it will be important to consider the changes in depth gradient resulting from sedimentation or erosion.

3.3.4 | Nutrients

The effects of nutrients on the flower development of *Zostera* can be direct or indirect. As observed by Suonan et al. (2022), the sexual reproduction of *Z. marina* increased by 1.5- to 4.6-fold under

nutrient-rich conditions. Also, Guerrero-Meseguer et al. (2021) found a strong correlation between *Z. noltei* flowering and sediment with high silt and clay content ($r^2 = 54\%$). Sediments with high organic matter content that supply inorganic phosphorus and nitrogen via mineralization can promote flowering (Ankel et al., 2021; Guerrero-Meseguer et al., 2021; Middelburg et al., 1997). This could be the reason for the extended flowering period observed in Ria de Aveiro, where the organic matter content was high (Ankel et al., 2021). For the initial development of flowering shoots, water column nutrients such as ammonium, nitrite, nitrate and phosphate and sediment sulphide can positively influence flowering, whereas water column, suspended solids and sediment heavy metals such as copper, lead, cadmium, arsenic and mercury may negatively impact flowering (Wang et al., 2019). However, spathe development is more likely to be affected by short-term elevations of sediment nutrients such as ammonium (Johnson et al., 2017). Adequate levels of nutrients may increase the biomass of reproductive shoots; however, their role in developing reproductive shoots may be regulated by other environmental factors, like the light that drives plant growth (Johnson et al., 2017; Qin et al., 2020). For instance, Qin et al. (2020) observed light reduction by algal growth during the upwelling of nutrient-rich water; however, the indirect effects of nutrients on *Zostera* flowering are not clearly evident. Additional nutrients may stimulate the growth of algae that compete with plants for light (Kim et al., 2014; McGlathery, 2001).

3.3.5 | Salinity

The effect of salinity on *Zostera* flowering has not been explicitly tested in field experiments, yet some inferences can be drawn from the salinity data presented in some studies. For instance, Jarvis et al. (2012) noted that flowering started when the salinity is low, and Lee et al. (2005) and Guerrero-Meseguer et al. (2022) noted no significant differences in salinity when the flowering starts. Effects of salinity might be linked with rainfall. Reduction in salinity has previously been thought to affect flowering based on the observations of stimulated flowering and vegetative growth in low-salinity waters in laboratory cultures (Ramage & Schiel, 1998). However, the effects of salinity on the trade-off between vegetative growth and flowering are not clear, suggesting that salinity might be a less influential driver in the presence of other environmental drivers, such as temperature (Phillips, Stewart Grant & Peter Mcroy, 1983). For instance, Ramage & Schiel (1998) observed that the flower production of *Z. novazelandica* (now known as *Z. muelleri*) increased by 1.5 times at 17% salinity compared with normal seawater salinity (i.e. 33%), where flowering was found to be inhibited at 70% salinity.

Low salinity, however, is crucial for seed germination where freshwater pulses have been found to substantially trigger seed germination under the presence of favourable conditions (e.g. burial depth and temperature) (Blackburn & Orth, 2013; Cumming et al., 2017; Greve et al., 2005; Jørgensen et al., 2019; Moore et al., 1993). The effects of salinity might depend on other factors

related to rainfall. For instance, in the subtropical waters of Australia, dilution of coastal waters from rainfall-induced runoff may not be common as most frequent rains occur in summer when the plants are usually not reproductive. Therefore, the effects of rainfall-induced salinity may not influence or probably only have a minor influence on the flowering of *Zostera* in such regions. However, future changes in rainfall pattern caused by climate change may further affect flowering via flood waters that carry sediment and nutrient loads (Suonan et al., 2022) and pollutants like pesticides and herbicides. Rainfall can also increase water turbidity and reduce light availability, leading to flowering reductions (Munkes et al., 2015). Such flooding events are expected to restrict the light available for seagrass growth on Australia's east coast (Great Barrier Reef Marine Park Authority, 2018). Conversely, groundwater seepage from rainfall can enhance flower production by keeping intertidal plants moist during exposure or submerged in tidal pools (Dos Santos & Matheson, 2017).

3.4 | Effects of biotic factors

3.4.1 | Grazing

The effects of grazers can be either direct or indirect. Their foraging patterns can alter biomass, shoot density and morphological characteristics (e.g. shoot height); variability in flowering; and thus changes in meadow structure (Lal et al., 2010). For instance, amphipods were found to preferentially consume flowering shoots rather than vegetative shoots, resulting in substantially damaged flowering shoots (approximately 85%), where the damage is prominent in the late stages of spathe development (Reynolds et al., 2012). On the other hand, other mesograzers can indirectly support plant growth by grazing epiphytic algae (Carr & Boyer, 2014), which may further facilitate flower production.

The effects of megaherbivore grazing (e.g. dugongs, turtles and geese) are likely to differ from other grazers. Grazer foraging patterns modify the structure of the meadow by altering primary production, species composition and structural complexity of microhabitats, facilitating the nutrient cycle and also changing the geomorphology of the meadow (Aragones et al., 2006; Christianen et al., 2014; Skilleter et al., 2007). Unlike mesograzers, megaherbivores often remove a large amount of aboveground seagrass material (Aragones et al., 2006; Bakker et al., 2016; Preen, 1995; Rivers & Short, 2007). Their frequency of visit is thought to be dependent on the plant recovery times at the local scale following the grazing (Aragones & Marsh, 1999; Scott et al., 2020a; Scott et al., 2020b); however, large herds of megaherbivores can cause the collapse of the meadow entirely (Christianen et al., 2014; Skilleter et al., 2007). On the other hand, their grazing can benefit plant growth by providing spaces for new shoots to emerge by removing epiphytes and old leaves (Christianen et al., 2012) or facilitating the plant's morphological traits that support survival under grazing pressure (Ruesink et al., 2012). At monospecific meadows, intense grazing is often expected during peak flowering periods as the plants with flowering shoots and seeds are more digestible and richer in

nutrients (Dall et al., 1992; Peterken & Conacher, 1997). The consumable seeds become viable while passing through the digestive track of herbivores, and dispersing them beyond the parent meadow can facilitate genetic connectivity among populations (Sumoski & Orth, 2012; Tol et al., 2016; Tol et al., 2017; Tol et al., 2021).

Megaherbivore grazing can also influence nutrient cycling by exporting seagrasses away from their original habitats (Christianen et al., 2012). In terrestrial ecosystems, the nutrient addition returns via the urine and faeces of herbivores; however, such returns might not be prominent in seagrass habitats where their faecal matter is usually exported away from the grazed area (Balazs et al., 1993). As estimated, the nitrogen and phosphorus exported by turtles are 13 and 1.4 mgm⁻² day⁻¹, respectively (Christianen et al., 2012); however, the effects of the nutrient transfer via megaherbivores on flowering have not been examined.

3.5 | Conceptual model for *Zostera* flowering

From the systematic review, the links between environmental variables and *Zostera* flowering were identified (Figure 3). Based on the conceptual model, temperature, light, nutrients, genetic factors and herbivory grazing can directly or indirectly affect flowering. For instance, tidal variation can affect flowering directly and indirectly by limiting light availability. Similarly, the indirect effects of nutrients might be expected via light limitation due to excess algal growth. The direct effects of environmental variables have been reported well, and the interactive effects are rarely evident in *Zostera* phenology literature.

3.6 | Flowering variability in Australasia

3.6.1 | Spatial variability of flowering

Field data collected across 10 intertidal meadows on the east coast of Australia and New Zealand in the 2020–2021 flowering seasons revealed a relatively low spathe density at temperate sites

(i.e. Delaware Inlet and Nelson Haven) than at tropical (i.e. Airlie Beach and Shoalwater Bay) and subtropical sites (i.e. Black Swan, Pelican Banks, Lilley's Beach, Rodds Bay and Urangan Bay) (Figure 4, Table 3). The significantly different spathe density among sites suggests that the flowering intensity may relate to the local environmental conditions. No significant differences in spathe densities were observed among intertidal depths within sites (Figure 4). However, compared with the lower and upper levels, the spathe density in the middle level in most sites was relatively high, probably due to the middle level having the most favourable environmental conditions with regard to the combination of desiccation stress and light limitation (Olesen et al., 2017). The highest spathe density was reported at Lilley's Beach, where the density of spathes in the mid-intertidal level exceeded 800 m⁻². This unusually high spathe density may result from adaptation to the high wave energy environment (Andrews et al., 2023). Such high spathe density was noted at this site during another monthly field survey conducted to understand the spatio-temporal variability of flowering in subtropical intertidal meadows (Lekammudiyanse et al., 2023b).

3.7 | Temporal variability of flowering

Based on the data collected along the latitudinal gradient of Australasia, flowering starts in the Austral winter months in tropical and subtropical regions, whereas flowering in the temperate region begins in late spring. The peak flowering times are observed approximately 2 months after the first flowering across the region, although this was not consistent across all sites (e.g. Cairns in North Queensland in Australia) (Figure 5). The onset of flowering always began after the lowest mean monthly temperatures across all sites (Figure 5). The flowering period was longer in tropical and subtropical regions (up to 6 months) than in temperate regions (3 months). Inter-annual variations in the timing of first flowering were noted in some locations within the same climatic region (e.g. Moreton Bay and Gladstone in subtropical Australia), suggesting that temporal climate variability plays a role in determining the timing of flowering.

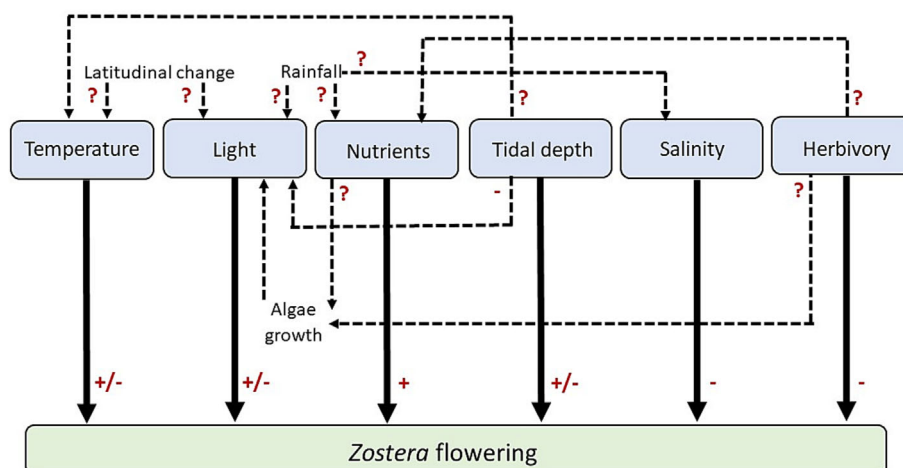


FIGURE 3 Conceptual model describing the reciprocal linkages between environmental variables and *Zostera* flowering based on empirical studies. Solid and dashed lines denote direct and indirect pathways, respectively. The direction of change (i.e. '+', '-', or '+/-' where the latter is context dependent) indicates the predicted changes in flowering when the environmental variable increases. The question mark (i.e. '?') indicates the pathways that are not studied well.

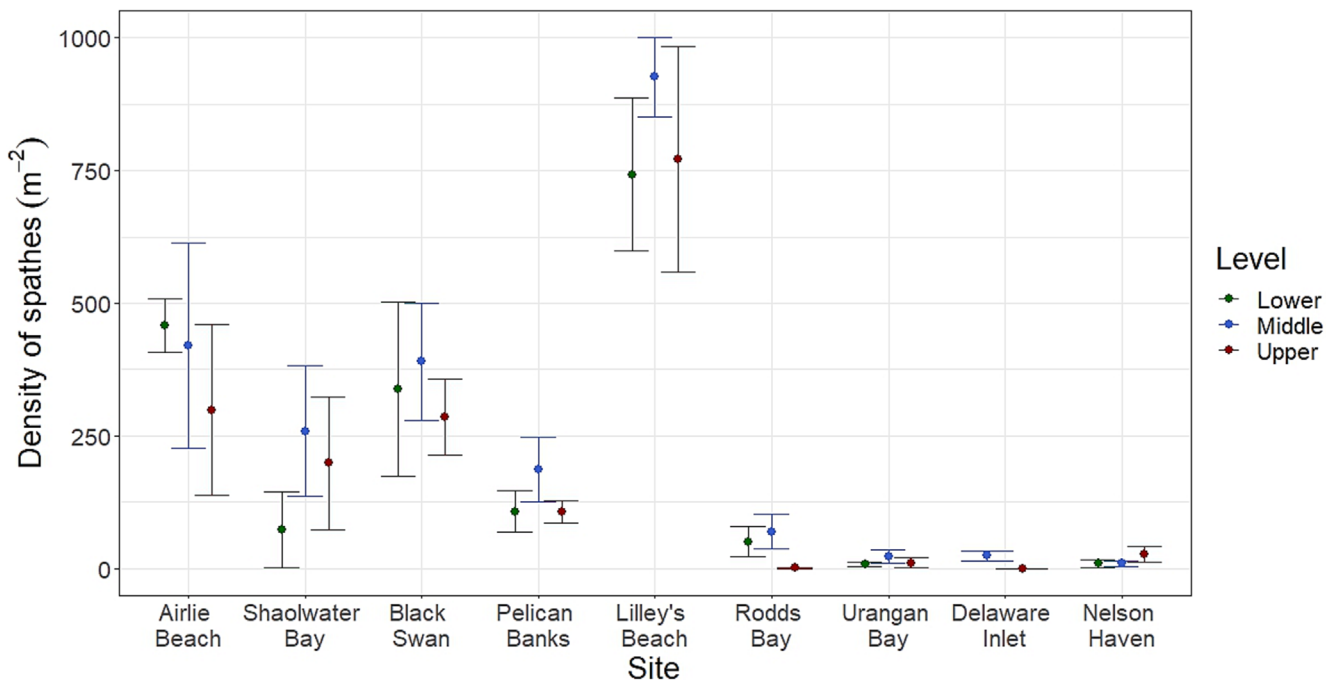


FIGURE 4 Variations in spathe density of *Z. muelleri* among intertidal levels during the peak flowering month (mean, SE, $n = 3$).

TABLE 3 Two-way ANOVA testing the effects of three intertidal levels (upper, middle and lower) on the density of spathe ($n = 3$, $P < 0.01$).

	Density of spathes			
	df	Mean Sq	F	P
Intertidal level	2	33,779	1.321	0.275
Site	8	595,239	23.281	<0.001
Intertidal level * Site	16	26,903	1.052	0.421
Residuals	53	25,567		

Abbreviation: ANOVA, analysis of variance.

Both first and peak flowering times showed a significant negative relationship with mean winter climatic conditions (Figure 6). Clear latitudinal variations in the first and peak flowering times were noted ($r^2 = 0.71$ and $r^2 = 0.68$, respectively), where earlier flowering times were recorded in locations with higher winter temperatures and solar radiation (i.e. typically low latitudes) (Figure 6, Table 4). As may be expected, the three regional climatic variables considered were significantly correlated with latitude ($r^2 = 0.89$ – 0.97) (Figure S2). Of the three climatic variables, mean winter air temperature and solar radiation had the strongest relationships with the first flowering time ($r^2 = 0.73$) (Table 4). Mean winter water temperature showed a weaker relationship with the first flowering ($r^2 = 0.67$) (Table 4). Mean winter air temperature was a significantly better predictor of peak flowering ($r^2 = 0.60$) than mean winter water temperature ($r^2 = 0.55$) and solar radiation ($r^2 = 0.50$). Based on the model coefficients, the timing of first and peak flowering was advanced by approximately ~ 10 and ~ 8 days with each 1°C increase in mean winter air temperature, respectively (Table 4). Also, a 1 Wm^{-2} increase in mean winter solar

radiation and 1°C increase in mean water temperature advanced the first flowering by 1 and 10 days, respectively, and peak flowering by 8 and 1 days, respectively (Table 4).

3.8 | Reconstructing and predicting flowering based on prior climatic conditions

The strong correlation between winter climate and the timing of first flowering suggests that it may be possible to predict the commencement of wild flowering and manipulate the timing of flowering in seagrass nurseries. As the three climate factors considered are highly correlated, it is difficult to determine which is most responsible for the timing of flowering. In particular, air temperature and solar radiation explain identical fractions of the variability in the timing of first flowering. However, a multivariate model including all three factors did not significantly improve the variance explained, suggesting that it is only one factor impacting the timing of flowering. To illustrate how this information may be applied, the relationship between mean winter air temperature alone was used to estimate how the timing of wild flowering may have changed along the Australian east coast over the previous 50 years (Figure 7). The historical air temperature used to reconstruct the first flowering times was taken from the same ERA5 dataset discussed above. The figures show the strong latitudinal gradient in the timing of the first flowering and significant variations from year to year. Notably, a trend towards earlier flowering from 1950 to the present is apparent, driven by warming air temperatures over the same period. The potential future change in the timing of flowering could be estimated similarly using climate projections.

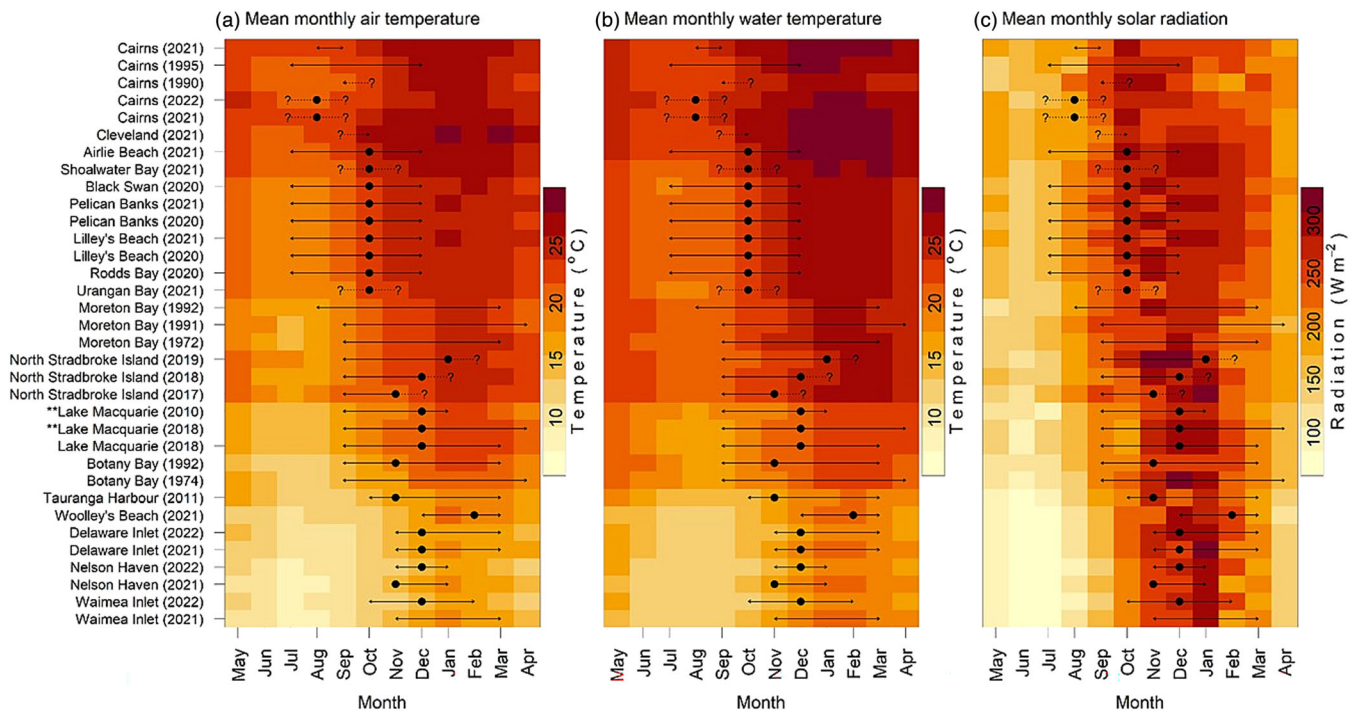


FIGURE 5 Variation of *Z. muelleri* flowering and associated mean winter climatic conditions: (a) mean monthly air temperature, (b) water temperature and (c) solar radiation along the latitudinal gradient in the particular year. Dots indicated the peak flowering time. Solid lines showed the sites with both first and peak flowering information available, and the dashed line denoted the sites that only have peak flowering information available. Subtidal locations are marked by asterisks.

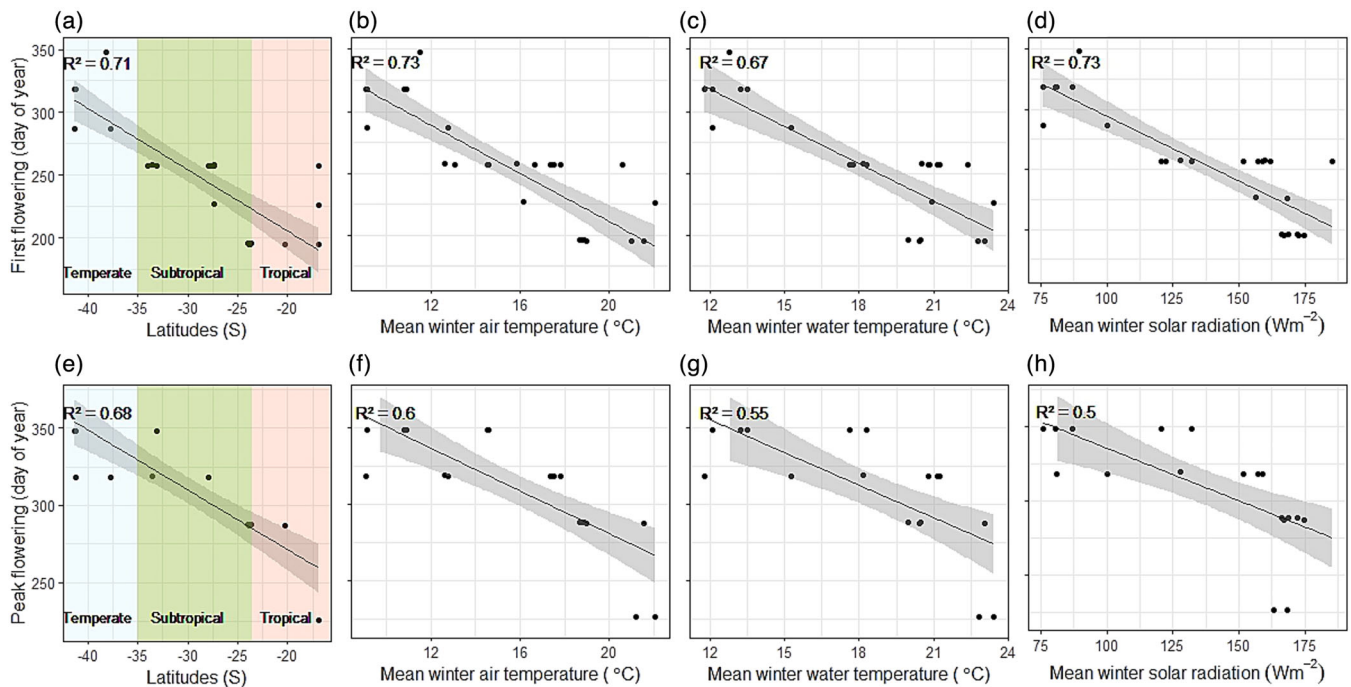
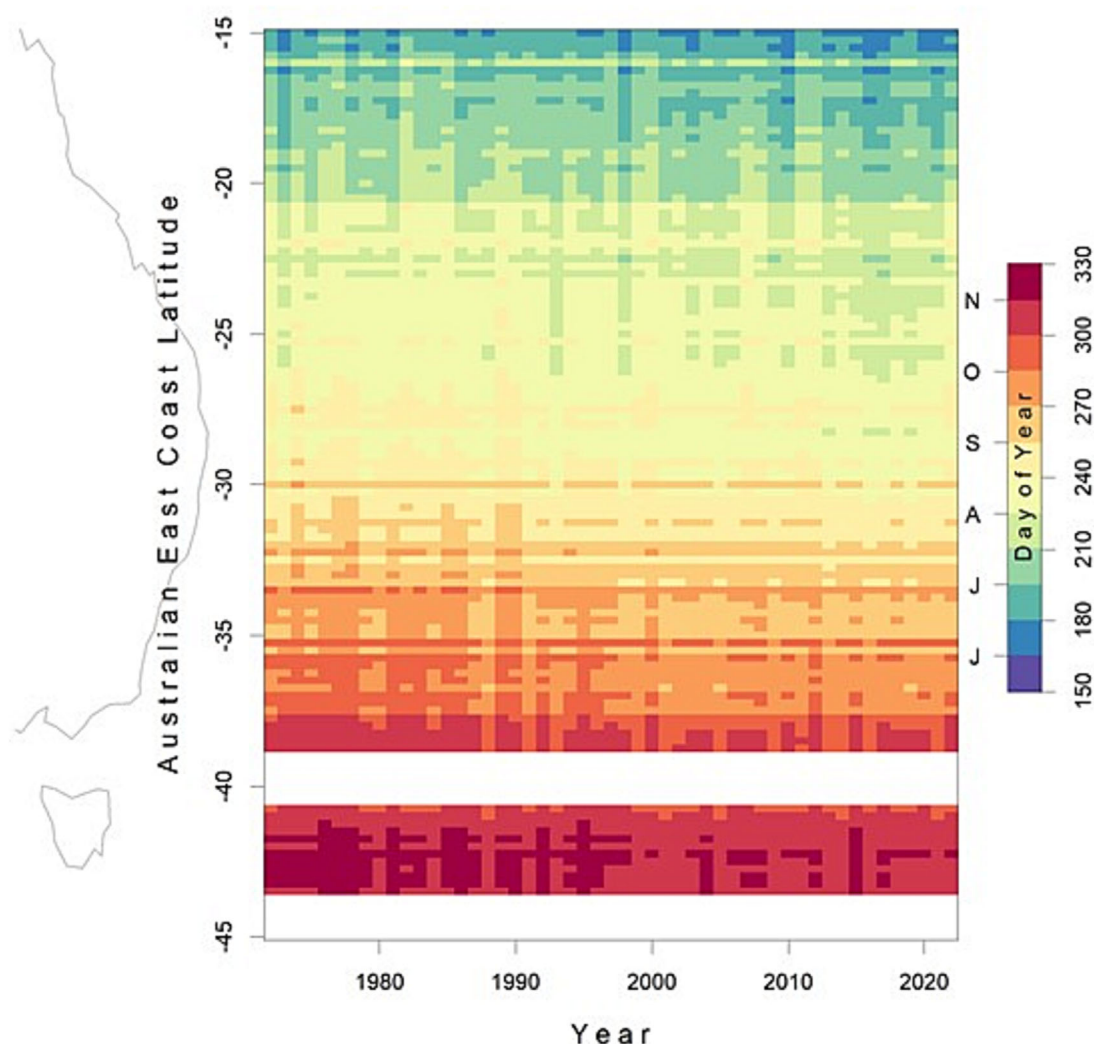


FIGURE 6 Timing of first and peak flowering of *Z. muelleri* on the East coast of Australia and in New Zealand as a function of latitude, mean winter air temperature, water temperature and solar radiation. Figures (a)–(d) and (e)–(h) represent the models built for first and peak flowering times, respectively.

TABLE 4 Relationships between the flowering times and climatic variables.

Flowering variables (y)	Predictor variables (x)	Model	P value	R ²
First flowering time (days of the year) n = 30	Latitude (°S)	$y = -4.89x + 107.30$	<0.001	0.71
	Mean winter air temperature (°C)	$y = -9.74x + 405.96$	<0.001	0.73
	Mean winter water temperature (°C)	$y = -10.01x + 438.17$	<0.001	0.67
	Mean winter solar radiation (Wm ⁻²)	$y = -1.07x + 402.15$	<0.001	0.73
Peak flowering time (days of the year) n = 22	Latitude (°S)	$y = -4.23x + 185.88$	<0.001	0.68
	Mean winter air temperature (°C)	$y = -7.73x + 435.07$	<0.001	0.60
	Mean winter water temperature (°C)	$y = -8.10x + 460.80$	<0.001	0.55
	Mean winter solar radiation (Wm ⁻²)	$y = -0.81x + 422.35$	<0.001	0.50

**FIGURE 7** A reconstruction of the timing of the first flowering of *Z. muelleri* along the latitudinal gradient as determined from the relationship to mean winter air temperature.

4 | DISCUSSION

4.1 | Summary of the review

The review synthesized the *Zostera* flowering phenology literature to provide an understanding of the likely underlying drivers of

Zostera flowering. The proposed conceptual framework classified the direct and indirect pathways of environmental factors that affect flowering, which will be beneficial for developing future hypotheses and designing experiments. The framework allows the inclusion of additional mechanisms that arise from future flowering studies.

As noted in the review, temperature fluctuations in conjunction with temperature thresholds are critical for triggering flowering; however, daily temperature fluctuations have rarely been considered in phenological studies due to the limitations of fine-scale long-term observations and simulated experiments. Past laboratory-based studies suggested that temperature is the primary influencer on flowering relative to other environmental variables (e.g. light); however, it is unknown which temperature thresholds and/or their fluctuations trigger flowering. Further studies with fine-scale measurements are required to trigger the flowering in nurseries and accurately predict the flowering times locally under global warming scenarios.

Light is also recognized as an important factor in the flowering of *Zostera*, but the duration of light may not be a critical factor in triggering the flowering. However, with the establishment of seagrasses in nurseries to aid seed-based restoration, photoperiod may play an important role in keeping the plant growing during flower production. The role of light, the duration of the photoperiod and how both interact with temperature to affect the timing of flowering need further investigation. Manipulative experiments will not only help determine the relative effects of different factors on flowering but also help to disentangle the covarying factors that hinder clear causal interpretations from field-based monitoring studies.

Tidal variation was also found to affect flowering, where the differences in environmental stressors in intertidal and subtidal zones are likely to create offsets in phenology. This could influence the pollination success in a meadow and create genetically different subpopulations along the depth gradient (Kamel et al., 2012; Kim et al., 2017). The inconsistencies in previous findings suggest that further research is required to assess how the tidal variation and light limitation interact to affect flowering dynamics in intertidal and subtidal meadows (Cabaço et al., 2009). Individual effects of the tidal variation may be studied via field experiments, but the interactive effects of tidal variation and light limitation might need simulated experiment designs that isolate the other co-varying influential drivers (e.g. temperature, grazing and genetic factors).

Direct effects of nutrients on flowering were evident in field studies; however, indirect pathways of nutrients require further investigation. Simulation experiments might be helpful in this regard, where the controlled conditions isolate the influence of other influential environmental drivers. Also, further studies on the effects of salinity reduction by intense rainfall are required to understand the flowering patterns under future climate change scenarios.

Regarding the biotic factors, much of the knowledge on how grazing affects seagrass flowering phenology comes from experimentally cleared trials. Due to the effects of other environmental factors, it is difficult to determine whether grazing-induced observations are actually driven by megaherbivore grazing or other habitat conditions altered by disturbances (Rasheed, 1999; Rasheed, 2004; Ruesink et al., 2012). A recent simulation experiment has suggested that the megaherbivores can drive the *Zostera* flowering in terms of timing, abundance and ratio of flowering to non-flowering stems (Lekammudiyanse et al., 2022); however, the direct

and indirect effects of multiple grazing events on flowering require further investigation.

Overall, the studies on the reproductive strategy of the genus *Zostera* and associated driving factors were limited in that the majority have either considered only a small number of environmental drivers or were derived from either laboratory approaches or field observations. Most studies have not considered the interactive effects of environmental variables due to the lack of explicit differentiation of mechanistic pathways of environmental variables, which makes it difficult to test the interactions. Testing all potential drivers and their threshold levels in the distributional range is logistically challenging but necessary to understand the future resilience of a population. Further field studies that measure the different aspects of flowering are encouraged with simultaneous manipulative laboratory experiments that isolate the actual effects under controlled conditions. Such simulation experiments have advantages in terms of fine-scale measurements and high resolution, which may be beneficial in seagrass nurseries established to support restoration.

4.2 | Spatio-temporal variability of flowering in Australasia

This study showed that the timing of the first flowering of *Z. muelleri* along the latitudinal gradient is significantly correlated with the winter climatic conditions. On average, the timing of first flowering is advanced with increasing mean winter air temperature, water temperature and solar radiation at the approximate rate of 10 days for every 1°C increase in the air or water temperature or 1 day for every 1 Wm⁻² of solar radiation. However, the relationships between climatic variables and peak flowering times were not as strong as with first flowering, where unit increases in air and water temperatures advanced the peak flowering times by approximately 8 days. These results agreed with the earlier comparison of the timing of flowering of *Z. marina* and *Z. japonica* in the northern hemisphere, but their relationships with air temperature are substantially weaker than the flowering models (Blok et al., 2018; Ito et al., 2021). As hypothesized, flowering was found to be predicted by winter conditions, and hence, the mean winter climatic conditions better describe the flowering times than mean annual temperatures. This is likely to be because flower production is most strongly influenced by the climate during the winter and because annual averages include the months following flowering, which are unrelated to the environmental conditions preceding the onset of flowering. This study covered *Z. muelleri* populations in tropical, subtropical and temperate regions, and thus, the findings are likely to be extended across the entire population in Australasia. Because temperature is a key determinant of plant growth and development, the timing of flowering could be predicted from the model for the next decade(s) based on climate projections. For example, the relationship to air temperature was used to reconstruct first flowering times along the Australian east coast, where a trend towards earlier flowering is suggested to have occurred

over the preceding 50 years. The strong relationship between climatic variables and latitude (Figure S2) suggests that, when predicting the flowering times at broader scales, the latitudinal relationship is likely to be sufficient without requiring in situ climatic data.

Similar to the temperature, there was an equal relationship between the timing of first flowering and the mean winter solar radiation, suggesting that the high winter temperatures and/or solar radiation might be linked to advancing the flower triggering. As reviewed in this study, light is found to be an essential environmental factor for flowering, but the daylength might not be a critical factor in determining the flowering cycle (Blok et al., 2018; McMillan, 1980; McMillan, 1982; Silberhorn et al., 1983). *Zostera* plants have no phytochrome C gene that is linked to the photoperiod control of flowering, and hence, the populations are expected to be adapted to the local climate regimes (Olsen et al., 2016). In subtropical climates, low light intensities in winter ($<10.8 \text{ Wm}^{-2}$) were found to produce fewer flowers in *Z. muelleri* under simulated intertidal and subtidal conditions (Lekammudiyanse et al., 2023a). However, experiments will be required to establish causal relationships and, in particular, to discriminate between possible effects of light and temperature or test for their interactive effects.

Furthermore high spatial variability of spathe densities along the latitudinal gradient was observed. The spathe densities during the peak flowering season were independent of tidal level, suggesting that any flower collection events for restoration could theoretically be done across multiple depths. Some sites reported substantially high spathe densities (e.g. Lilley's Beach); however, high spathe intensities may not reflect the production of viable seeds, which is one of the major barriers in seed-based restoration (Vanderklift et al., 2020). Therefore, future research may usefully focus on exploring the likelihood of obtaining more viable seeds during peak flowering periods.

4.3 | Implications on seagrass conservation and future research directions

As the first comprehensive review and assessment of seagrass phenology in Australasia, this study provides a basis to inform seagrass seed-based restoration plans for *Z. muelleri*, many of which fit within a broader conservation and habitat management framework. Accurate predictions of flowering times enable restoration practitioners to plan flower collection activities with improved precision. Knowing when flowering events are expected can also facilitate a better alignment of natural reproductive cycles with seed-based supplements through restoration. This would likely enhance the success of important decisions required in restoration projects, such as critical periods to implement protective measures against disturbances that could disrupt flower production, seed dispersal and so on. In addition, knowledge of flowering times aids in sourcing seeds from various meadows to disperse across populations, which can enhance genetic connectivity and potentially increase the resilience of the local population to disturbance.

This study further highlighted the need for continued research in seagrass phenology to ensure the long-term sustainability and conservation of seagrass ecosystems. Based on the review, three priority research areas that require further investigation are proposed to support local and regional scale restoration and seagrass nursery setups.

1. Potential shifts in flowering times under climate change scenarios
 2. Applications of novel technologies in frequent monitoring of seagrass flowering cycle (e.g. drones)
 3. Possibility of triggering seagrass flowering artificially to encourage greater production of viable seeds
- Filling these research gaps will be important for developing adaptive management plans and understanding the natural dynamics of meadows. For instance, predicting how flowering times may shift is crucial to adjusting restoration projects and conservation strategies aligned with anticipated changes. Shifts in flowering times could also disrupt the interdependencies among populations and, ultimately, seagrass ecosystem functioning and resilience. Utilizing novel techniques to capture the finer-scale variations in the flowering cycle will allow researchers to improve modelling accuracy while providing advantages in covering large spatial areas and cost-effective monitoring of trends over long periods. Also, if it is possible to induce multiple flowering within a year under manipulative conditions, seagrass nurseries may supply sufficient seed volumes for restoration throughout the year. This will require an understanding of the conditions that are required to trigger the flowering artificially and keep the plant's seed production viable. A consistent supply of seeds will likely improve the conservation of seagrass habitats by enabling both short-term responses to threats (e.g. a rapid re-seeding of habitat after loss due to anthropogenic disturbance) and longer-term planning of larger-scale habitat restoration efforts where historical losses have been both extensive and prolonged.

In summary, the spatio-temporal models developed in this study provide a basis to predict the timing of *Z. muelleri* flowering, which is important information to guide management decisions and conservation efforts to protect the seagrass ecosystem and may be of considerable value under climate change scenarios. In addition, flowering can be used as an ecological indicator of environmental stress (Cabaco & Santos, 2012). As identified in the review, further studies that examine the direct and indirect effects of environmental variables on flowering are necessary to make seed-based restoration more effective and efficient, both now and under the influence of climate change. Applications of novel technologies that allow cheap and frequent monitoring of changes over time are encouraged. Simulation experiments that explore the artificial triggering and optimum conditions for flower production are also encouraged in designing seagrass seed nurseries that aid in restoration capacity.

AUTHOR CONTRIBUTIONS

Manuja U. Lekammudiyanse conducted the systematic review; designed the study; conducted field surveys on the east coast of Australia; analysed the data; prepared schematic diagrams, figures and

tables; and wrote the manuscript. Christopher Aiken helped in extracting and visualizing climatic data. Emma Jackson, Andrew Irving, Nicole Flint and Megan Saunders guided the project, contributed to revising the draft manuscript and provided editorial advice. Dana Clark, Anna Berthelsen, Breanna Hindmarsh and Rachel Hooks conducted field surveys in New Zealand. Other authors provided data about flowering times, and all authors reviewed and provided input into the manuscript.

ACKNOWLEDGEMENTS

We thank the team at the Coastal Marine Ecosystems Research Centre, CQUniversity, for laboratory operations. Open access publishing facilitated by Central Queensland University, as part of the Wiley - Central Queensland University agreement via the Council of Australian University Librarians.

CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest regarding the publication of this paper.

DATA AVAILABILITY STATEMENT

Data will be available upon request.

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How to cite this article: Lekammudiyanse, M.U., Saunders, M.I., Flint, N., Irving, A., Aiken, C., Clark, D.E. et al. (2024). Environmental drivers of flowering in the genus *Zostera* and spatio-temporal variability of *Zostera muelleri* flowering in Australasia. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 34(2), e4068. <https://doi.org/10.1002/aqc.4068>