



Eelgrass (*Zostera marina*) Trait Variation Across Varying Temperature-Light Regimes

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Abstract

Seagrass trait variation, which results from both local genetic adaptation and phenotypic plasticity, has important effects on ecosystems. Physical drivers underlie these processes and are important determinants of trait variation. Despite this, few studies examine multivariate predictive relationships between sets of physical drivers and sets of seagrass traits. Here, we use redundancy analysis to define this relationship for eelgrass *Zostera marina*, using traits that represent bed structure, morphology, and physiology and physical drivers that emphasize light conditions and temperature variability on different time scales. We found a relationship between plant size (i.e., leaf length and width, rhizome width, number of leaves) and shoot density that dominated the trait variation. Specifically, as temperatures became warmer, more variable, and light was less limiting, plants became smaller (shorter, narrower, and fewer leaves, thinner rhizomes) but beds became denser. Plant biomass (leaf area index), which increased with decreasing temperature variability and bottom light, further refined this relationship. Overall, temperature variability (i.e., daily temperature range, heat accumulation, time in the optimal temperature range, and tidal and meteorological variability), as well as bottom light, were important predictors of eelgrass traits. We further identified three distinct temperature-light regimes across which traits differed; these included the cool low variability temperature regime with low light, the warm high variability temperature regime with high light, and the intermediate case between these endpoints. Our study identifies specific temperature and light drivers that define certain eelgrass traits and provides a multivariate statistical model that can be used to predict eelgrass trait values from known physical conditions.

Keywords Traits · Principal component analysis (PCA) · Multivariate regression · Atlantic ocean · Temperature regime · Photosynthetically active radiation (PAR)

Introduction

Seagrass traits, measurable features that determine overall fitness and performance, are shaped by both their evolutionary history and response to current environmental conditions (Duffy et al. 2022). Defined here to include individual plant features (i.e., size, physiology) and population-level attributes (i.e., shoot density, leaf area index), plant traits

are generally considered important determinants of plant community dynamics and functioning (Cadotte et al. 2011; Lavorel et al. 2011). Seagrasses typically inhabit highly variable physical conditions, and respond to environmental forcing by adjusting their morphology, physiology, and population attributes to maintain optimal performance (Lee et al. 2007). While evolutionary history constrains the upper and lower bounds of seagrass trait responses to changing environments, local adaptation and phenotypic plasticity are important determinants of trait values within these bounds (King et al. 2018; Pazzaglia et al. 2021; Duffy et al. 2022). Physical drivers underlie these processes, which often result in highly variable trait values, both within and among seagrass species (Maxwell et al. 2014; Soissons et al. 2018). Despite physical processes playing a key role in determining seagrass trait values, these relationships have not been fully explored. Here, we do so for *Zostera marina*, a common temperate seagrass that inhabits a broad range of environmental

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conditions and is typically characterized by high trait variability, across both large and small spatial scales (Krumhansl et al. 2021; Duffy et al. 2022).

In the marine nearshore, seagrasses are subjected to highly variable and dynamic physical conditions. Localized phenomena such as solar heating, riverine input, meteorological events, and tidal circulation all interact with complex coastlines, seabed bathymetry, and offshore oceanographic processes to create highly heterogeneous environments over quite small geographic separation (Wong and Dowd 2021). Seagrasses respond to changing nearshore conditions through both long-term adaptation and phenotypic plasticity, which can alter trait expression and distributions to ultimately enhance fitness (Pazzaglia et al. 2021; Nguyen et al. 2023). While many different physical processes influence seagrass traits, temperature and light are considered dominant drivers (Lee et al. 2007; Krumhansl et al. 2021). Seagrasses can respond to light limitation by increasing leaf length, width, or leaf chlorophyll content and by decreasing shoot density, all of which improve light capture and maintain photosynthetic processes (Collier et al. 2007; Enríquez et al. 2019; Wong et al. 2020). Responses to heat stress include increased production of carbohydrates and heat-shock proteins to protect cellular components and decreased biomass to reduce the respiratory burden (Gu et al. 2012; Krumhansl et al. 2021; Wong and Dowd 2023). Temperature and light also act together to influence key processes, such as photosynthesis, where temperature modulates the photosynthetic response to underwater irradiance (Marsh et al. 1986; Bulthuis 1987; Lee et al. 2007).

Temperature and light regimes in the nearshore are dominated by multiple sources of variability that act across a broad range of time scales. We emphasize time scales from hours to months (i.e., sub-seasonal to seasonal time scales), but interannual and decadal variability may also be important. Underwater light is strongly influenced by seasonal and daily light cycles, although light attenuation by depth, runoff, suspended sediments, and phytoplankton may also be important. While light variability other than the seasonal and diurnal signal is highly stochastic, sources of water temperature variability are more regular and operate across well-known time scales. For example, hourly and daily temperature variations result from solar heating/nighttime cooling of shallow waters, tidal advection, and restrictions in water flow and flushing due to coastal morphology. Weekly to monthly temperature variations result from seasonal heating/cooling and events such as wind-driven coastal upwelling (Petrie et al. 1987). Various sources of temperature variability were previously shown important for seagrass performance (Krumhansl et al. 2021; Wong and Dowd 2023). These can be represented not only by common summary metrics (mean or median), but also by metrics such as heat accumulation, daily temperature range, thermal exceedances, and tidal

variability (Krumhansl et al. 2021; Wong and Dowd 2023). Furthermore, temperature is a particularly useful variable to consider as not only does it directly affect seagrasses, but it also acts as a proxy variable for many other physical drivers at a site.

Elucidating predictive relationships between dominant physical drivers and seagrass traits is key to understanding the seagrass trait variability that is often evident even across small spatial scales (Krumhansl et al. 2021). An important focus is on establishing predictive multivariate relationships between sets of physical drivers and sets of seagrass response traits. These relationships can be best determined, and made interpretable, using constrained ordination techniques such as redundancy analysis (RDA). RDA uses multivariate regression to identify the relationship between multiple predictors and multiple response variables, followed by unconstrained ordination (i.e., principal component analysis, PCA, on the predicted response) to reduce dimensionality and aid in interpretation. Here, the central rationale is that plant traits should be examined together (i.e., as a multivariate response) because the suite of relevant physical drivers interact to affect the full trait ensemble collectively. Surprisingly, only a few studies use constrained ordination to establish predictive multivariate statistical relationships between sets of seagrass traits and sets of physical drivers (Ainley et al. 2016; Boyé et al. 2022). Most examine the response of a single seagrass trait to a single physical driver (e.g., Collier et al. 2007; Enríquez et al. 2019) or a single trait to multiple drivers (e.g., Krumhansl et al. 2021). Studies also sometimes use unconstrained ordination (i.e., PCA, multidimensional scaling (MDS)) to identify trait patterns across sites, linking these to the environment through correlations (e.g., Andrews et al. 2023). Furthermore, most seagrass trait-driver studies do not include metrics that capture the variability of physical drivers on multiple time scales, relying instead on basic summary metrics such as mean seasonal values.

In this study, we incorporate these aspects to determine the multivariate predictive relationship between dominant temperature-light drivers and eelgrass (*Zostera marina*) traits, on the Atlantic coast of Canada. Previously, we used a single trait-multiple driver approach and found that *Z. marina* traits strongly varied across dominant temperature-light regimes, and that different sources of short-term temperature variability were particularly important for individual trait responses (Krumhansl et al. 2021; Wong and Dowd 2023). Here, we extend that work by identifying the multivariate predictive relationship between comprehensive sets of seagrass traits and sets of temperature-light drivers. This approach allows the collective response of the seagrass traits to be examined and identified when multiple temperature and light drivers act concomitantly, as they do in field settings. Furthermore, our approach will identify the specific combinations of seagrass traits most responsive

to a particular set of physical drivers and also the specific sources of temperature and light variability important for seagrass traits. We aim for a robust and general relationship by including multiple years of data and by encompassing the range of conditions temperate *Z. marina* typically inhabits in our region. Specifically, we use multi-year field data of temperature, light, and *Z. marina* traits, to (i) quantify trait variation in *Z. marina*, based on bed structure, plant morphology, and physiological condition; (ii) characterize the different short-term temperature and light variables at each field site using high sampling rate time-series data collected in situ; (iii) develop a multivariate predictive model using redundancy analysis (RDA) to formally relate the collective response of seagrass traits to a set of temperature and light drivers; and (iv) identify the specific temperature and light variables and the specific set of seagrass traits that best define the observed relationship. We further present a general conceptual model relating *Z. marina* traits to temperature-light regimes, with the intention that this will be useful to inform coastal management actions.

Materials and Methods

Study Sites

To determine the relationship between seagrass (*Z. marina*) traits and dominant physical drivers, we used data of seagrass traits, water temperature, and light (specifically, underwater photosynthetically active radiation, PAR) from sites along the Atlantic coast of Nova Scotia, Canada (Table 1, Fig. 1). Data from three different sampling years (2017, 2021, 2022) were used. A full suite of sites were sampled in 2017 ($n=10$), with a subset of these sampled in 2021 ($n=7$) and 2022 ($n=8$). Two additional sites were sampled in 2022 that were not sampled in other years (i.e., Fish Peddler and Crescent Beach). In 2017 and 2021, both deep and shallow locations at several sites were sampled where large depth gradients were evident (i.e., Sambro, Taylor Head, Sacrifice Island (both years); Cable Island, Croucher Island (2017 only)). Further, in 2017, one site with contrasting sediment types was sampled for both a muddy and sandy location (i.e., Port Joli). Note that we included these multi-year data to ensure the generality of observed patterns, accounting for potential effects of sampling year and varying site combinations in the statistical analyses (see below).

Field sites were chosen to represent the range of physical conditions that temperate *Z. marina* beds inhabit, including warm, shallow, protected waters with mud-silt sediments to cooler, deeper, more exposed waters with sand-gravel sediments (Wong 2018; Krumhansl et al. 2021). These sites differed in their temperature regime,

underwater light, depth, bottom slope, exposure, water currents, and sediment type. Previous work indicated the importance of temperature and light variables for seagrass traits and furthermore the importance of using multiple metrics of variability, in particular for temperature (Krumhansl et al. 2021; Wong and Dowd 2023). Based on these results, we use physical drivers representing several different seasonal and sub-seasonal temperature and light metrics that are important in the marine nearshore.

Temperature

Yearly temperature time series were obtained at each site using temperature data loggers (TidbiT v2, Onset Computer Corporation). Loggers were deployed on the sea bottom and recorded temperature every 15 min. Temperature metrics were calculated from these records and included the following: median temperature, maximum growing degree day (GDD), median daily temperature range, proportion of time spent in the optimal temperature range (OTR) for photosynthesis, standard deviation (SD) of the tidal and meteorological bands, and proportion of variation in the meteorological band relative to the total variance. Most metrics were calculated for the main growing season, between June 1 and September 15. The exception was GDD which was calculated as the maximum value at the end of the growing season. Temperature loggers at some sites (Port l'Hebert, Lower Three Fathom, Port Joli) were sometimes exposed during low tides (as were the seagrass beds), resulting in both higher and lower temperatures ($> 30\text{ }^{\circ}\text{C}$ or below freezing) than if the loggers remained submerged. We retained these temperatures in the time-series records since it is what the seagrass bed experienced, and extreme air temperatures have been demonstrated to impact seagrasses (Park et al. 2016).

Calculations of the temperature metrics were as follows. Median temperature was determined as the median of the temperature time series at each site for the growing season. The daily temperature range was the median of the daily difference in the 90th and 10th temperature percentiles across the growing season. Time in the OTR was the proportion of time spent between 5 and 23 $^{\circ}\text{C}$ for the growing season. The lower limit of 5 $^{\circ}\text{C}$ was chosen as this is where the photosynthesis to respiration ratio (P:R) for *Z. marina* peaks (Marsh et al. 1986), while the upper limit of 23 $^{\circ}\text{C}$ is the mean optimal temperature for photosynthesis (Lee et al. 2007). We used this temperature range to determine time spent in generally suitable temperature conditions, but acknowledge that plant responses to these limits may be influenced by temperature history. GDD was calculated for each sampling year as follows:

Table 1 Field sites (a), physical drivers (b), and *Z. marina* traits (c) used in the analyses and shown in figures. All physical drivers and response traits were measured at each field site

	Abbreviation
(a) Field sites	
Cable Island Deep	Cab-D
Cable Island Shallow	Cab-SH
Croucher Island Deep	CR-D
Croucher Island SH	CR-SH
Crescent Beach	CresB
Fish Peddler	FishP
Lower Three Fathom	L3F
La Have	LH
Mason's Island	MA
Port l'Hebert	PH
Port Joli Muddy	PJ-M
Port Joli Sandy	PJ-S
Sacrifice Island Deep	Sac-D
Sacrifice Island Shallow	Sac-SH
Sambro Deep	Sam-D
Sambro Shallow	Sam-SH
Taylor Head Deep	TH-D
Taylor Head Shallow	TH-SH
(b) Physical drivers	
Bottom photosynthetically active radiation	BotPAR
Total duration above the daily light saturation	Hsat
Light attenuation coefficient	KD
Median temperature	MedT
Growing degree day	GDD
Daily temperature range	DTR
Proportion time in the optimal temperature range	OTR
Standard deviation of the tidal temperature band	SDtidal
Standard deviation of the meteorological temperature band	SDmeteo
Proportion of total temperature variation in the meteorological band	PropMetvar
(c) <i>Z. marina</i> traits	
Vegetative shoot density	VegDen
Leaf area index	LAI
Reproduction shoot density	ReproDen
Number lateral shoots	Numlat
Rhizome water soluble carbohydrates	WSC
Total leaf chlorophyll concentration	TotChl
Number of leaves per shoot	Numleaves
Length of leaf 3	L3
Width leaf three	W3
Rhizome width	RW

$$GDD = \sum_{t=1}^n GDD_t$$

where

$$GDD_t = \frac{T_{max} + T_{min}}{2} - T_{base}.$$

Here, the GDD at each time interval t (day) is calculated by subtracting a base temperature (T_{base}) from the mean of the daily maximum (T_{max}) and minimum (T_{min}) temperatures, and these values are then cumulatively summed across each yearly temperature record to yield total heat accumulation (Neuheimer and Taggart 2007). Maximum GDD was extracted for the end of the growing season (September 15). The T_{base} of 5 °C was used because this is where the P:R ratio peaks, similar to our calculations for time in the

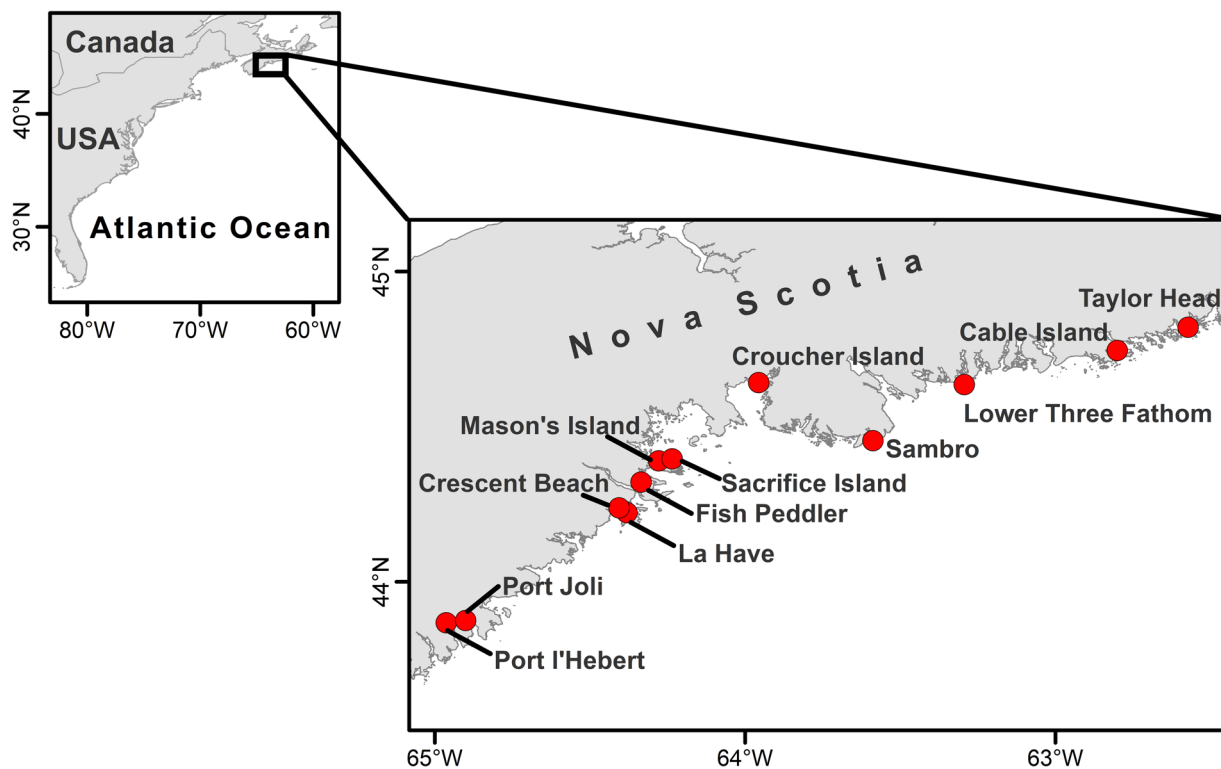


Fig. 1 Field sites on the Atlantic coast of Nova Scotia, Canada

OTR. Although a maximum temperature cap is sometimes imposed for land plants, we did not do so here, as the P:R ratio for *Z. marina* remains above 1 for temperatures up to 35 °C (i.e., beyond the observed temperatures in this study).

The temperature time series data were separated into different frequency bands to identify temperature variation on time scales related to seasonal, meteorological, and daily/tidal processes. This was done by the following time series decomposition:

$$T(t) = T_{seas}(t) + T_{met}(t) + T_{tidal}(t)$$

where t is the time, $T(t)$ is the observed temperature series at a site, $T_{seas}(t)$ is the seasonal cycle, $T_{met}(t)$ is the meteorological variations, and $T_{tidal}(t)$ includes daily and tidal temperature fluctuations. First, the seasonal cycle, $T_{seas}(t)$, at each site was determined using a smoothing spline applied to the portion of $T(t)$ during the growing season. The de-seasonalized time series was then obtained by subtracting the spline-fitted seasonal cycle from the original temperature time series, or $T_{anom}(t) = T(t) - T_{seas}(t)$, where $T_{anom}(t)$ refers to the temperature anomaly time series. The meteorological band was determined by applying a low pass digital filter to the temperature anomaly time series, $T_{anom}(t)$, to isolate time series features with periods greater than 48 h (using “signal” R package; Priestley 2004). This yields

the meteorological band time series, $T_{met}(t)$, which includes processes that occur between 48 h and ~60 days, such as temperature changes related to wind-driven upwelling. The tidal frequency band was then determined by subtracting the meteorological band from the temperature anomaly (i.e., $T_{tidal}(t) = T_{anom}(t) - T_{met}(t)$). It includes tidal variations in temperature and daily heating/cooling, both of which operate on time scales < 48 h. We then calculated the standard deviation within the meteorological (i.e., the standard deviation of $T_{met}(t)$) and tidal bands (i.e., $T_{tidal}(t)$) for use in our analyses. We also calculated the proportion of variance in the meteorological band time series $T_{met}(t)$ relative to the total variance in the temperature anomaly time series $T_{anom}(t)$.

The temperature metrics used represent relatively distinct components of the overall temperature signal that occur on time scales ranging from hours to months. Median temperature represents the overall seasonal heating and cooling of waters, while GDD represents heat accumulation across the year. Daily temperature range accounts for variability from localized processes (i.e., solar heating and tidal flushing). Time in the OTR accounts for variability associated with temperature exceedances outside of thermal thresholds. SD of the tidal band reflects the temperature variability on short time scales < 48 h (e.g., tidal flushing, solar heating), while SD of the meteorological band indicates temperature variability from longer-term processes (48 h to ~60 days; e.g.,

wind-driven upwelling events). Finally, the proportion of total temperature variance attributed to the meteorological band provides an indication of the importance of these longer-scale events relative to shorter frequency events such as daily and diurnal tides, overtides, and daily heating/cooling.

Underwater Photosynthetically Active Radiation (PAR)

Underwater PAR (400–700 nm) was measured at each site using PAR sensors (DEFI2-L, JFE Advantech Co., Ltd.). Two sensors were deployed concurrently at the same location within each seagrass bed, one at the bottom and the other higher in the water column. The distance between the two sensors remained fixed and was either 0.5 or 1 m apart depending on the site depth (sensors were 0.5 m apart at shallower sites). Sensors were oriented upwards towards the water surface to measure downwelling irradiance and recorded at 1-min intervals. In 2017, sensors were deployed for 2 weeks in July while in 2021 and 2022 sensors were deployed for the entire growing season. To ensure that light metrics were comparable among years and because PAR sensors often fouled after ~1 month, we only used data from the last 2 weeks of July for all years. Prior to analyses, PAR data were low-pass filtered (using the R package “signal”) to remove high-frequency signals less than 20 min related to focused light on the sensor surface from surface ripples and episodic blockage of the sensor by leaves or detritus. Low light values ($20 \mu\text{mol m}^{-2} \text{s}^{-1}$) that typically occurred at night were also removed, as well as values from the top sensor that were less than the bottom sensor (likely due to measurement errors at lower light levels).

These processed data were used to calculate the median bottom PAR from the bottom sensor for the 2-week period in July. The paired bottom and top sensors allowed for the light attenuation coefficient (K_d) to be also calculated for each recording interval as follows:

$$K_d = \frac{1}{z_2 - z_1} \ln \frac{I_{z_1}}{I_{z_2}}$$

where I_z is the PAR at depth z , with z_1 and z_2 being the depth of the sensor closer to the surface and the bottom sensor, respectively. Daily median K_d was then calculated from these data. K_d values from 2017 included only the absorption properties of the water column, as sensors were placed in open patches in the seagrass beds, whereas 2021 and 2022 values were more influenced by the seagrass canopy. We elected to use 2017 values across our multi-year analyses, as these best represent water column attenuation. Our previous work indicates little inter-annual variability in K_d relative to site differences (Wong and Dowd 2021).

Because growth and survival of *Z. marina* are more closely correlated with daily light period than absolute light intensity, we also calculated the total duration above the daily light saturation point (H_{sat}) for the year (Dennison and Alberte 1985). To do so, we modelled the daily PAR reaching the water surface across the year using the diurnal light equation of Vollenweider (1965) at 30-min intervals. This equation requires day length estimates, which we determined based on the latitude of the field sites and solar declination (Brock 1981; Kirk 2011), and also daily maximum incident PAR, which we determined from a polynomial relationship of annual surface light data obtained from a nearby surface buoy (LOBO-0010). This buoy was centrally located for the field sites, with large-scale light patterns (i.e., clear sky and clouds) expected to be generally similar across this distance. Values of daily surface PAR were reduced by 10% to account for reflectance at the water surface (Madden and Kemp 1996). These data were used with site-specific K_d and depth to calculate H_{sat} (total hours per year) at the bottom of the seagrass bed, based on a saturation irradiance (I_k) of $250 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Lee et al. 2007; Wong unpublished data). As for K_d , we expected the general within-site patterns in H_{sat} to be similar across years, and so we used the same site-specific values for all years in the analyses.

Our suite of light metrics represents different sources of light variability that occur across different time scales. The median bottom PAR represents the overall seasonal signal at the seagrass bed. K_d represents the light attenuation in the water column, with differences between sites being related to depth and events that affect water column constituents, such as wind-resuspension of bottom sediments. Finally, H_{sat} represents the amount of daily light saturation and combines light information across multiple time scales (i.e., seasonal, daily, weeks). In contrast to the temperature metrics, we have not considered variability in underwater PAR in this study since it was determined (via spectral analysis) to be very similar across the study sites.

Characterizing Seagrass Traits

Seagrass traits related to bed structure, plant morphology, and physiological condition were measured during the peak summer biomass (mid-July to mid-August) each sampling year. Ten sampling stations within each seagrass bed were haphazardly distributed at approximately the same depth. Stations were located at least 10 m apart and 2 m from any seagrass-bare sediment interface. Sampling was conducted using snorkeling or scuba diving depending on site depth.

At each sampling station, the number of vegetative and reproductive shoots was determined within a $0.25 \text{ m} \times 0.25 \text{ m}$ or $0.5 \text{ m} \times 0.5 \text{ m}$ quadrat, respectively. Three mature vegetative shoots were collected with 5 cm or more live rhizome and refrigerated for 1–2 days prior

to processing for morphological metrics. In the laboratory, the number of leaves per shoot was determined by counting all broken and full leaves that were emerged from the sheath. Leaf lengths were measured as the distance from the meristem at the base of the shoot to the leaf tip, and leaf widths were measured midway along the leaf. Leaf area (single-sided) per leaf was determined by multiplying each leaf length by its corresponding width. The total leaf area per shoot was calculated by summing the leaf area across all leaves in that shoot. The number of lateral shoots per shoot that were attached between rhizome nodes 1 and 4 was counted. Rhizome width was measured laterally in the middle of the third rhizome internode. The leaf area index (LAI, m^2 leaf area per m^2 bottom area) was determined for each quadrat by multiplying the mean total leaf area (one-sided) per shoot by the shoot density.

Rhizome water-soluble carbohydrates (WSC) and total leaf chlorophyll concentration were also determined. Rhizome WSC were extracted from a 5-cm piece of rhizome sampled from the three shoots used for morphological measurements. Extractions were done using 80% ethanol and WSC was quantified using the phenol sulfuric acid method in a microplate assay. One additional shoot collected during sampling was used to determine total chlorophyll concentration (chlorophyll a + b). A 20-mm section from the middle of leaf 3 was collected and frozen at -80°C until processed. Chlorophyll was extracted using an acetone and dimethylsulfoxide solution, and chlorophyll a and b concentrations were determined using a spectrophotometer. See Wong et al. 2020 for further details.

Statistical Modelling

Statistical approaches were focused on assessing the ability of physical drivers to predict the overall suite of plant traits. We used a combination of unconstrained (principal component analysis) and constrained (redundancy analysis) ordinations to examine how the collective set of seagrass properties changed across physical conditions defined by the temperature and light metrics.

Unconstrained ordination via principal component analysis (PCA) was used to understand and identify the temperature-light regimes and how they varied across sites. We included all temperature and light metrics described above (median bottom PAR, median K_d , H_{sat} , median temperature, GDD, time in the OTR, daily temperature range, SD tidal and meteorological band, and proportion of total variation in the meteorological band). Note that all metrics differed per year, with the exception of H_{sat} and median K_d , where the same representative values were used across years (see above). We then also used PCA to identify seagrass traits (vegetative and reproductive shoot density, LAI, total number of leaves per shoot, length and width of leaf 3, number

lateral shoots, rhizome width, rhizome WSC, total leaf chlorophyll content) that explain trait variation across sites. Predictor variables (temperature-light regimes) did not exhibit multicollinearity (correlations near one in absolute value), a feature important for regression-based studies. For both analyses (temperature-light regimes and seagrass traits), one PCA was carried out for each sampling year (2017, 2021, 2022) to provide insight into how patterns may change across different years and with different site combinations. Scores associated with each physical or seagrass metric were used to identify specific metrics that best explained the variance. The ordination was visualized by plotting the loadings of each temperature-light metric or seagrass trait as vectors. Vector length indicated their relative importance, vector direction their association with axis 1 or 2, and angles between vectors the correlation between metrics (where smaller angles indicate higher positive correlation). The site scores (i.e., the principal component axes scores for replicate samples at each site) were plotted as points within the multivariate space defined by principal component axes 1 and 2. The temperature-light or seagrass loadings were scaled proportionally to the eigenvalues, while site loadings were left unscaled (Oksanen 2016). Location of site loadings relative to the principal component axes indicates their association with the gradients these axes represent. Both physical and seagrass metrics were standardized prior to use in the PCAs. PCAs were carried out using the package “vegan” in R Studio (2021.09.01).

Constrained ordination was then used to establish the multivariate predictive statistical relationship between the seagrass traits (response variables) and temperature-light metrics (explanatory variables). We used redundancy analysis (RDA), a technique that combines both ordinary least squares multivariate regression and unconstrained ordination (PCA) to determine the relationship between the multivariate sets of response and explanatory variables. Multivariate regression is first implemented where the matrix of response variables Y (containing measured plant traits) is regressed on the matrix of explanatory variables X (containing physical drivers), resulting in a matrix of fitted values, or predicted response, $\hat{Y}$. PCA is then applied to the $\hat{Y}$ matrix to reduce dimensionality and increase interpretability, and the resultant loadings define the RDA axes. These are interpreted as being the aspects of seagrass traits that can be predicted by the temperature-light metrics. We used all replicate data from the three sampling years within a single analysis, and so implemented partial RDA where the linear effect of X on Y was adjusted for the effects of the covariate Year. The RDA was scaled so the explanatory and response loadings were proportional to the eigenvalues. The significance of the overall RDA and of each axis was determined using permutation tests (Legendre et al. 2011). The proportions of the variance in seagrass metrics explained by the covariate

year (conditioned variance), the explanatory temperature-light variables (constrained variance), and variance unaccounted for (unconstrained variance) were identified. The RDA results were visualized by plotting the scores for the explanatory temperature-light metrics and seagrass response traits as vectors and the site scores as points. Vector length indicates their relative importance for defining the RDA axes (seagrass response traits) or importance of predictors for these seagrass metrics (explanatory temperature-light metrics), direction indicates their association with the RDA axes, and the cosine angle projections between all vectors (response or explanatory) reflects their approximate linear correlation. Site scores are presented as LC (linear combination) scores, which are the correlations of the principal components of $\hat{Y}$ with the explanatory variables. There is only one LC score per site because, although there were replicate stations sampled for plant traits at each site, replicate temperature or light metrics at each station were not available nor would they be meaningful. Location of site scores relative to the RDA axes indicates their association with the varying seagrass traits represented by those axes, and right-angled projections of points onto response vectors approximate their values for that RDA-based metric.

Results

Characterizing Temperature-Light Regimes Across Seagrass Sites

The principal component analyses (PCAs) indicated that sites strongly varied with respect to their temperature-light conditions in a consistent manner across sampling years (Fig. 2). The PCAs accounted for 73 to 77% of the variance in the data using the first two PCs across all years. PC1 accounted for 50 to 56% of the total variance and was consistently defined by all temperature metrics except for the SD of the meteorological band. Loading of light metrics on PC1 was inconsistent across years, with median K_d important for 2017 and 2021 and bottom PAR and H_{sat} important for 2022. PC2 accounted for 21 to 27% of the variance in the data. Temperature processes that defined PC2 included the SD of the meteorological band in all years and the proportion of total variance in the meteorological band in 2021. Similar to PC1, light metrics were more variable in their loadings on PC2, with bottom PAR and/or H_{sat} important for 2017 and 2021 and K_d important for 2022.

The location of sites along the temperature-light regimes represented by the first two PC axes was consistent across years (Fig. 2). Port Joli (muddy and sandy), Port l'Hebert, Lower Three Fathom, and Mason's Island were all defined by relatively higher temperature, heat accumulation, and temperature fluctuations compared to the remaining sites,

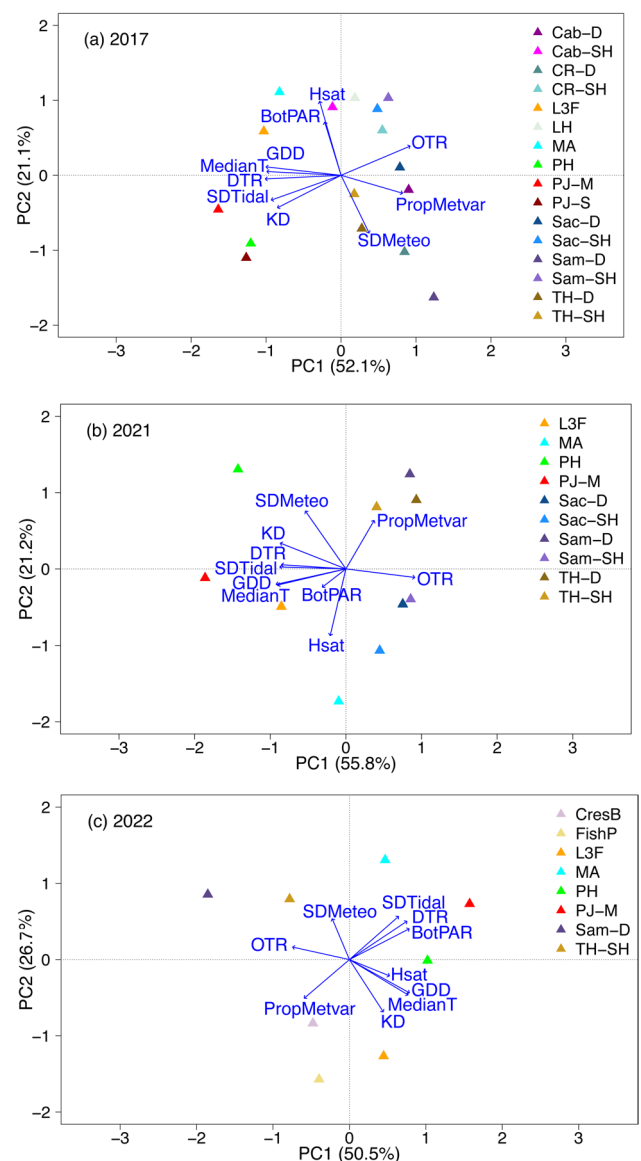


Fig. 2 Principal component analyses of the light and temperature metrics characterized at each site for **a** 2017, **b** 2021, and **c** 2022. Loadings of the metrics are indicated by the ends of the vectors. See Table 1 for site and physical driver abbreviations

as well as higher K_d . These sites all tended to be more shallow with higher mud/silt content in sediments relative to other sites. Although K_d was high at these sites, a result of easily resuspended bottom sediments, PAR remained high relative to deeper sites because of the shallow depths. Within this group of sites, Port Joli consistently had the highest temperature and the largest temperature variability, followed by Port l'Hebert and Lower Three Fathom, while Mason's Island had the lowest temperature and smallest temperature variability. Mason's Island was further differentiated by having the lowest K_d and being the least influenced by the meteorological band. Sites outside of this cluster were all

relatively cooler with less heat accumulation and smaller temperature fluctuations, lower K_d , and higher variability across the meteorological band. Of these sites, deeper locations (i.e., Sambro Deep, Cable Island Deep, Sacrifice Island Deep, Taylor Head Deep) were cooler with less temperature fluctuations and less bottom PAR than the shallower locations. Sambro Deep consistently had the coldest temperatures and lowest heat accumulation across all years relative to other sites.

Characterizing Seagrass Traits Across Sites

The PCAs indicated strong separation of sites based on seagrass traits across all years, despite high trait variability within sites (Fig. 3). The first three PCs accounted for 61 to 70% of the variance in seagrass traits across all years. PC1 accounted for 28 to 39% of the variance across sites and was strongly defined by morphological traits (i.e., total number of leaves, leaf length and width, rhizome width) and bed structure traits (vegetative and reproductive shoots, lateral shoots, LAI), although the structural traits loaded inconsistently across years. PC2 accounted for 15 to 18% of the variance in plant traits, with bed structure traits (mainly vegetative shoot density, LAI) consistently loading across all 3 years. PC3 (not shown) accounted for 12 to 15% of the total variance in seagrass traits and was defined mainly by WSC and leaf chlorophyll in 2017 and 2021 and reproductive shoot density and LAI in 2022. When compiled, these results indicate that a relationship between plant size (leaf length and width, rhizome width, number of leaves) and bed structure (shoot density, lateral shoots) dominates the trait variance, where plant size decreases as shoot density or LAI increases. This relationship was further modulated by variation in vegetative shoot density and LAI, with some influence from physiological traits.

Across all years, sites consistently aligned along the trait variation represented by the first two PC axes (Fig. 3). Plants at Port Joli, Port l'Hebert, Mason's Island, and Lower Three Fathom had the lowest number of leaves per shoot, the shortest and narrowest leaves, and the thinnest rhizomes. Within this group, these morphological traits had lowest values at Port Joli and highest values at Lower Three Fathom. These sites further differed in bed structure traits, with vegetative shoot density and LAI being consistently highest at Port l'Hebert across all years and Port Joli showing the highest interannual variability in these traits. Seagrass beds at the remaining sites tended to have a higher number of leaves, longer leaf lengths and widths, and thicker rhizomes. When a deep and shallow location was sampled at the same site, these morphological traits tended to be relatively higher at the deep locations, particularly at Sambro, Sacrifice Island, and Croucher Island. Bed structure traits further differentiated deep from shallow locations, with shallow locations

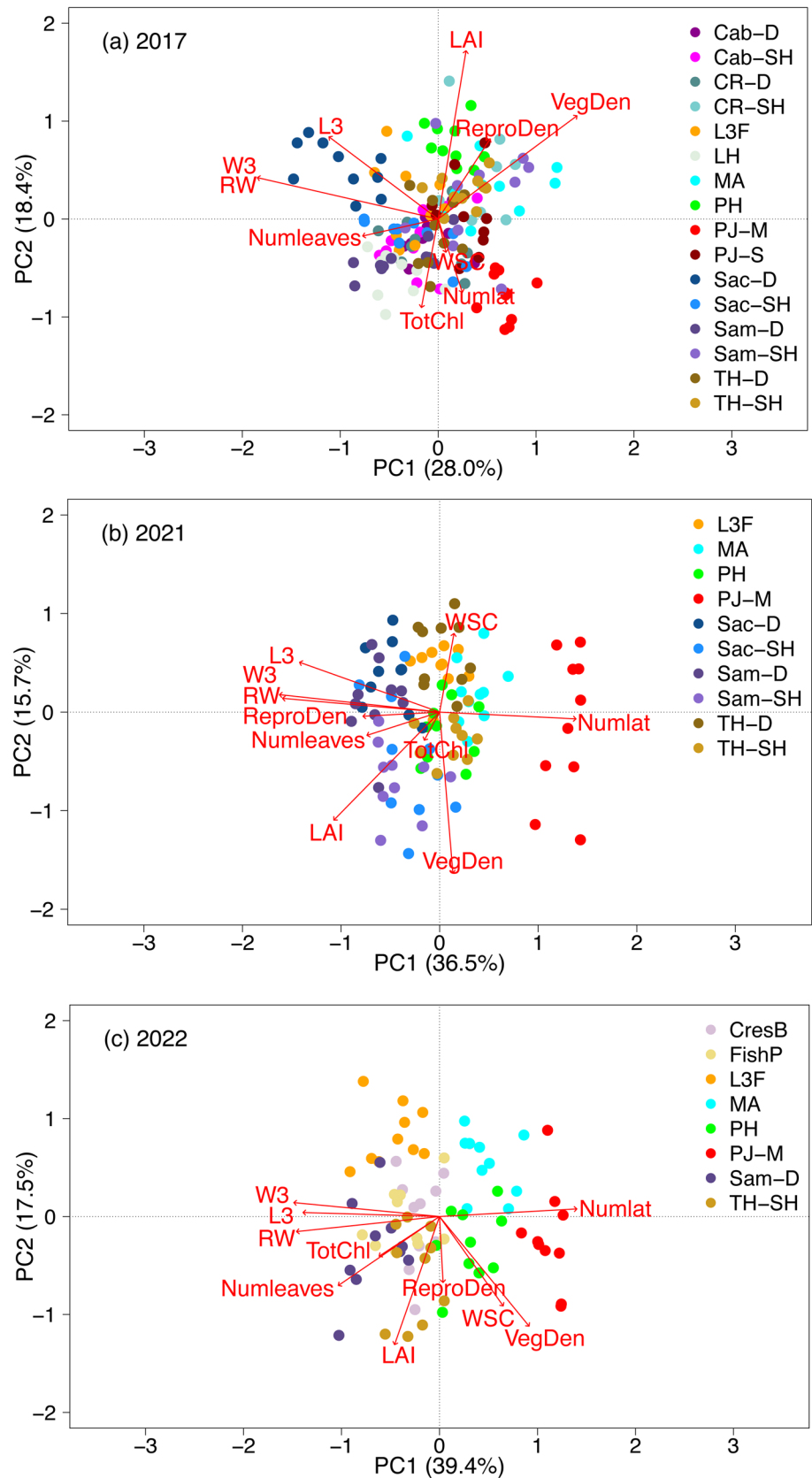
having the highest LAI and vegetative shoot density. High within-site variability in seagrass traits was evident for most sites across all years.

Relationship Between Seagrass Traits and Physical Drivers

The partial redundancy analysis (RDA) indicated that 30.8% of the total variance in seagrass traits was predicted by temperature-light regimes (Fig. 4). Unconstrained variance not explained by temperature-light conditions was 65.5%, while variance related to the covariate sampling year was 3.6%. While the unconstrained portion is high, this largely reflects replicate variability within sites, as no systematic patterns in the multivariate regression residual plots were observed. The overall RDA model was highly statistically significant ($F_{10,328} = 15.4$, $p = 0.001$), and the first five of the ten constrained axes were significant ($p \leq 0.006$). Of the constrained portion of the model, the first RDA axis accounted for 54% of the variance in seagrass traits predicted by the explanatory temperature and light variables. The first RDA axis was strongly defined by predicted vegetative shoot density, lateral shoots, and rhizome WSC, which all increased from the negative to the positive side of RDA1, and also the morphological traits (number of leaves per shoot, leaf length and width, rhizome width), which all decreased (Fig. 5). These trait patterns were predicted by median temperature, temperature variability (i.e., SD tidal band, daily temperature range), heat accumulation (i.e., GDD), thermal exceedances (i.e., time outside OTR), and light availability (i.e., bottom PAR), which all increased from the negative to the positive side of RDA1. RDA2 accounted for 24% of the total variance in seagrass traits and was defined primarily by predicted LAI, but also vegetative shoot density, lateral shoots, and morphological traits (excluding number of leaves) which loaded on both RDA1 and RDA2. LAI, vegetative shoot density, and leaf length increased from the positive to the negative side of RDA2, while lateral shoots and the other morphological traits decreased. These trait patterns were predicted by SD in the meteorological band, which increased from the positive to the negative side of the axis, and heat accumulation and bottom PAR, which decreased. RDA 3 and RDA 4 (not shown) explained 8 and 5% of the variance in seagrass traits predicted by the explanatory variables, respectively. RDA 3 was defined primarily by leaf length, which was predicted to increase from the negative to the positive side of the axis as K_d , median temperature, and time outside the OTR increased. RDA 4 was defined by total leaf chlorophyll, which was predicted to increase with decreasing H_{sat} and increasing SD meteorological band, when moving from the negative to the positive side of the axis.

Our RDA results identify a plant size-density relationship that dominated the trait variance similar to that

Fig. 3 Principal component analyses of *Z. marina* traits characterized at each site for **a** 2017, **b** 2021, and **c** 2022. Loadings of the metrics are indicated by the ends of the vectors. See Table 1 for site and trait abbreviations



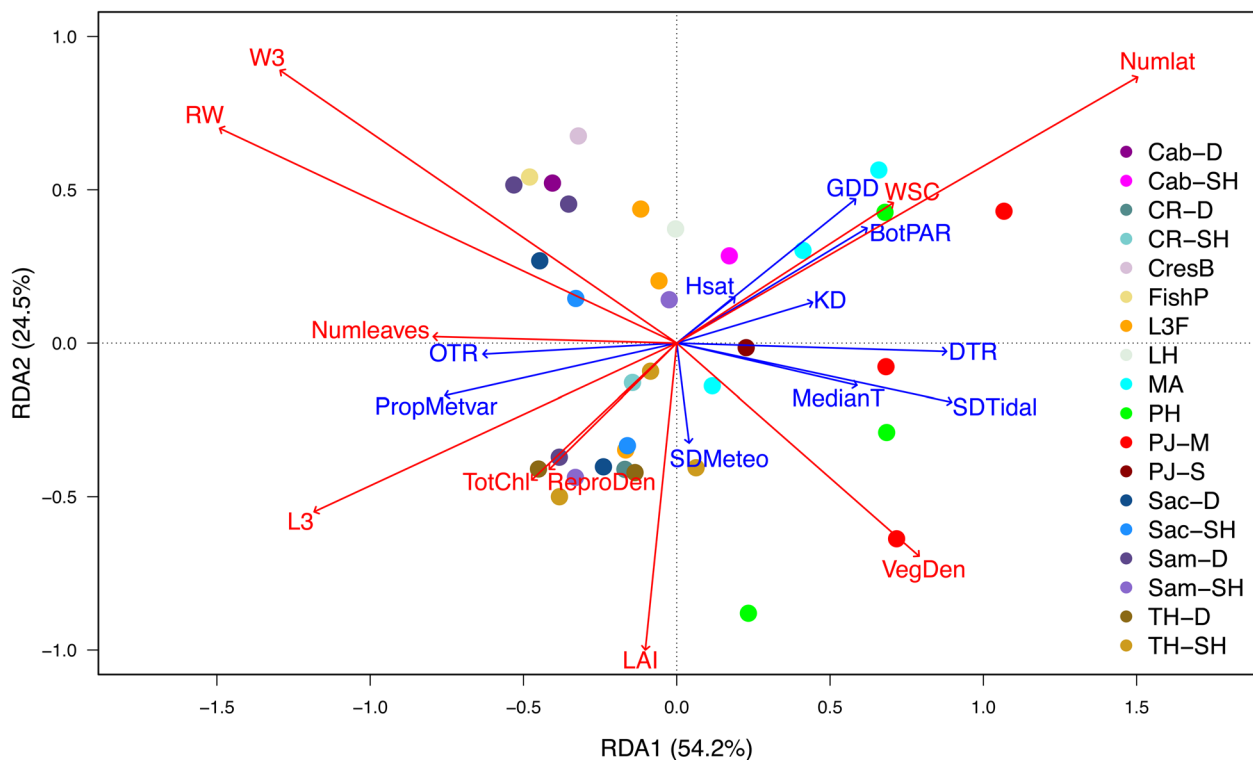
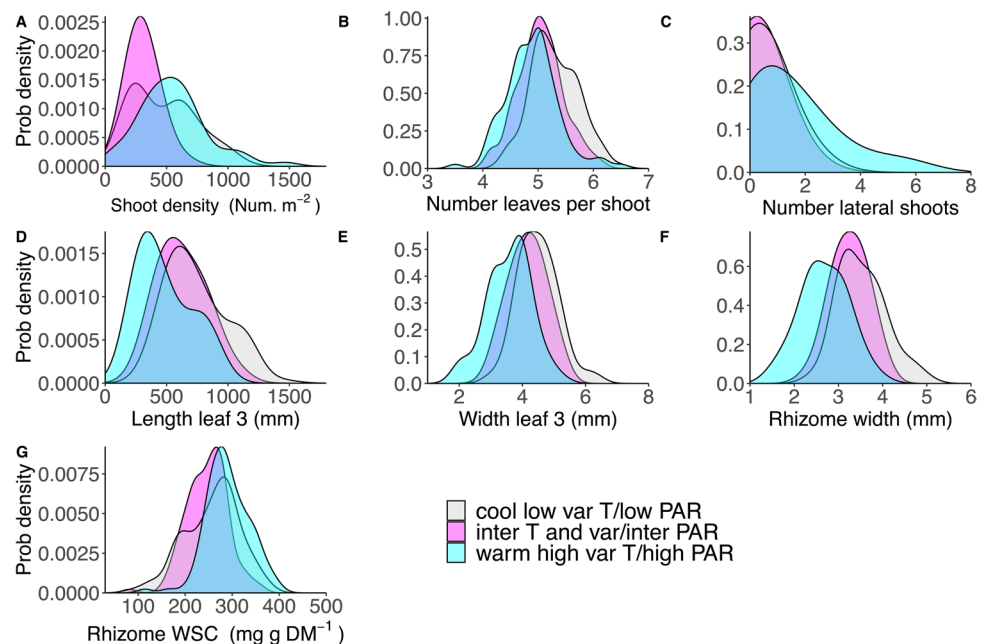


Fig. 4 Partial redundancy analysis illustrating the multivariate predictive relationship between seagrass traits (response variables in red) and the temperature and light metrics (explanatory variables in blue). RDA1 and RDA2 are defined by seagrass trait values predicted by the temperature and light metrics and explained 30.8% of the total vari-

ance in the data. Percent of unconstrained variance was 65.6%, and percent explained by the covariate year was 3.6%. LC (linear combination) scores for sites indicate the correlation between the principal components of the predicted trait values and the explanatory variables. See Table 1 for site, driver, and trait abbreviations

Fig. 5 Kernel density plots of *Z. marina* traits grouped across three different temperature-light regimes, as defined by RDA1. Blue = warm highly variable temperature regime, with high bottom PAR; pink = intermediate temperature and variability, with intermediate bottom PAR; grey = cool less variable temperature regime, with low bottom PAR. Prob, probability; WSC, water soluble carbohydrates; PAR, photosynthetically active radiation



observed for the PCA of plant traits, but we now also identify the important environmental predictors of this relationship. Specifically, when temperatures were warmer, more variable, with more time outside of optimal conditions, and bottom light was high, plant size (i.e., leaf length and width, rhizome width, number of leaves) decreased as bed structure (i.e., shoot density, lateral shoots) increased. Variability in this relationship was related to plant biomass (per area bottom, represented by LAI) and vegetative shoot density, which increased with less heat accumulation, more variability in the meteorological band, and less bottom PAR.

The LC (linear combination) scores of sites along the dominant RDA1 were used to categorize sites into 3 different groups defined by their temperature-light conditions and associated seagrass traits (Fig. 5). The first site group had the highest LC scores on RDA1 and was categorized as having warm, highly variable temperature, and frequent thermal exceedances, with high PAR (hereafter “warm highly variable temperature regime with high light”). This group included Port Joli (muddy and sandy), Port l’Hebert, Mason’s Island, and Cable Island Shallow. The second site group had mid-range LC scores on RDA1 and was categorized as having intermediate temperature, temperature variability, and exceedances and intermediate bottom PAR (hereafter “intermediate temperature regime with intermediate light”). This group included La Have, L3F, Croucher Shallow, Taylor Head Shallow, Sacrifice Shallow, and Sambro Shallow. The third site group had the lowest LC scores on RDA1 and was categorized as having cool, less variable temperature, few thermal exceedances, and low bottom PAR (hereafter “cool less variable temperature regime with low light”). Sites included Sambro Deep, Cable Deep, Sacrifice Deep, Taylor Head Deep, Fish Peddler, and Crescent Beach.

While trait distributions across these three temperature-light regimes had significant overlap, strong shifts in their central tendencies were evident (Fig. 5). The warm highly variable temperature regime with high light (blue curve) had the highest vegetative shoot density, number of lateral shoots, and rhizome WSC and the most reduced morphology (lowest number of leaves, leaf length and width, rhizome width) compared to the cool less variable temperature regime with low light (gray curve) or the intermediate temperature regime with intermediate light (pink curve). Trait distributions in the warm highly variable temperature regime differed most strongly from the other two regimes, although differences in trait distributions between intermediate and low temperature regimes were still evident. Sites with intermediate temperature and light had morphology (i.e., number of leaves, leaf length and width, rhizome width) and shoot density values that fell between the warm and cool temperature regimes, while this pattern was not evident for lateral shoots or rhizome sugars.

Discussion

Our results revealed the environmental variability that distinguishes small-ecotype, dense *Z. marina* beds from large-ecotype sparse beds. Specifically, we found that as temperatures warmed, became more variable, exceeded thermal tolerances, and light became more available, seagrass plants became smaller (i.e., shorter, narrower and fewer leaves, thinner rhizomes) but beds became denser. This plant size-shoot density relationship was further influenced by plant biomass (represented mainly by LAI), which increased when temperature variability, heat accumulation, and bottom light decreased. The observed trade-off between seagrass plant size and shoot density is a common paradigm (Vieira et al. 2018; Enríquez et al. 2019; Duffy et al. 2022). In fact, our results closely resemble those found in a global-scale study of *Z. marina* traits, where form (i.e., canopy height, sheath length and width, shoot density) ranged from tall sparse “forests” in the Pacific ocean to short dense “meadows” in the Atlantic ocean, with variability in this relationship linked to plant biomass (Duffy et al. 2022). Within our “meadow” type beds, we also observed a strong gradient in plant form and linked these patterns to biomass with certain temperature-light conditions being important drivers. The trade-off between plant size and density represents a self-thinning response, where fewer but larger plants allow adequate resource capture (Vieira et al. 2018; Enríquez et al. 2019). The self-thinning relationship is sometimes absent for clonal plants such as seagrasses, because clonal integration allows resource sharing that can increase biomass via increased plant size, density, or both (Olesen and Sand-Jensen 1994; Vieira et al. 2018). As is typical, the plant size-density relationship observed in our study was not perfect (Vieira et al. 2018), being strongly influenced by plant biomass and variable temperature and light conditions. Interestingly, structural responses to changing temperature-light regimes were dominant in our study despite the inclusion of physiological traits (i.e., rhizome sugars and leaf chlorophyll). Previous studies have similarly shown that larger-bodied seagrasses tend to adjust structure in response to light reduction, while smaller-bodied seagrasses adjust physiological processes (e.g., Olesen et al. 2002).

Our study showed that seagrass trait variability, characterized by the trade-off between plant size and shoot density, is strongly influenced by temperature and light conditions. High shoot densities observed in warm and highly variable temperature regimes with high PAR likely resulted from enhanced photosynthetic production. Photosynthesis scales with both temperature and light, at least until photosynthetic optimal temperatures, maximum

photosynthetic rates (P_{max}), or photoinhibition are reached (Marsh et al. 1986). Although thermal exceedances and high daily temperature ranges may have reduced photosynthesis to respiration (P:R) ratios, growth, or even survival of some eelgrass shoots (Marsh et al. 1986; Nejrup and Pedersen 2008; Wong and Dowd 2023), high shoot densities persisted at the warmer sites. This suggests enough bottom light was available to maintain carbon balance, even if plants were periodically thermally stressed, and consequently had higher light requirements (Lee et al. 2007). Higher densities may also reflect an enhanced growth response to anomalously warm temperatures, where plants emphasize clonal production rather than parental maintenance, as has been observed previously for *Z. marina* (DuBois et al. 2020). Reduced shoot density in cool and low light conditions indicates a reduction in self-shading to provide more resources (mainly light) for remaining individuals (Enríquez and Pantoja-Reyes 2005). Low bottom PAR resulted mainly from deeper water depth but was also due to higher light attenuation at certain shallow sites (i.e., Fish Peddler and Crescent Beach).

Enhanced leaf morphology (i.e., more leaves per shoot, longer and wider leaves) was also evident in cool low-light conditions, likely because these mechanisms enhance light capture in light-limited seagrasses (Lee et al. 2007; Wong et al. 2020). Thicker rhizomes in cool regimes suggest higher belowground biomass and better plant anchoring ability (Duarte 1991), important as cooler sites were often more exposed. In warm high light conditions, reduced morphology in plants indicates that bottom PAR was adequate, and plants did not need to enhance light capture through morphological changes. However, plants may have also reduced leaf and rhizome morphology in response to high temperatures and periodic exceedances of thermal thresholds in order to lessen respiratory burden and overall carbon requirements (Lee et al. 2005; Lee et al. 2007). LAI, a composite index of shoot density and leaf morphology that influenced the plant size-density relationship, increased with higher prevalence of meteorological events, lower heat accumulation, and lower bottom PAR. Here, LAI benefited from meteorological events such as wind-driven upwelling that can cool coastal waters and provide seagrasses thermal refuges from warming (Kim et al. 2020). Furthermore, it also reflected the enhanced morphological response to lower bottom PAR and lower heat accumulation. Finally, rhizome water-soluble carbohydrates (WSC) also responded to temperature-light drivers, with higher concentrations in warm highly variable temperature regimes with high light. Plants will typically increase WSC production to protect cellular components from thermal damage (Gu et al. 2012), a response previously observed for *Z. marina* (Wong et al. 2020; Wong and Dowd 2023).

A previous study indicates that both genetic evolutionary history and phenotypic plasticity in response to current environmental forcing are important determinants of eelgrass form and biomass (Duffy et al. 2022). While the legacy of evolutionary history strongly influences eelgrass traits in both Pacific and Atlantic oceans, environmental drivers are almost equally important, especially for Atlantic eelgrass populations (Duffy et al. 2022). This suggests that while the upper and lower bounds of eelgrass trait values are determined by its genetic history, variability within these bounds is related to phenotypic responses to current environmental conditions. Our study examined the importance of physical conditions in shaping eelgrass trait variability and aimed to identify important physical drivers. We focused on multiple types of short-term temperature and light variation that are characteristic of the nearshore and have been shown previously important for eelgrass (Krumhansl et al. 2020, 2021; Wong and Dowd 2021). We found that multiple types of temperature variation played a central role in defining eelgrass trait variation. These included not only a common summary metric (median temperature), but also those representing different aspects of short-term temperature variability (i.e., heat accumulation, daily temperature range, tidal variability, exceedances). These different temperature metrics allowed additional insights not evident from using median temperature alone. For example, the Fish Peddler and Lower Three Fathom sites had similar median temperature and heat accumulation as warm sites, but local horizontal temperature gradients were reduced because of their location within lagoons. This restricted the daily temperature ranges as tidal advection was limited and increased the influence of temperature variability from the meteorological band. Because temperature variability metrics had the highest RDA loadings, LC scores placed these sites within the cool with low variability temperature regime; this site grouping would likely have differed if temperature variability metrics had not been included.

In seagrass trait studies, temperature is a useful physical driver to include as it not only has direct effects on seagrasses, but also acts as a proxy for other physical drivers and site conditions. Nearshore temperature regimes are strongly shaped by localized conditions, such as depth, exposure, and tidal currents. For example, water temperature at Sambro Deep was typically cool with low variability, because deep well-flushed waters minimized daily solar heating. Its location on the open coast meant that high wind exposure enhanced horizontal mixing and reduced spatial temperature gradients, and high tidal advection from a nearby channel transported cold deep water inwards from the nearby offshore (Wong and Dowd 2021). These conditions not only affected the overall temperature signal, but also likely had their own effects on seagrass performance, such as enhanced nutrient delivery in high-flow environments.

Using the temperature regime is thus a useful proxy of overall site conditions because it integrates across the physical processes at a site while also being strongly associated with traits. Temperature is an easy, inexpensive, reliable, and spatially representative measurement, and thus can avoid difficult field measurements of many other variables (e.g., currents, fluxes) whose linkage to relevant processes can be difficult to disentangle.

Although multiple sources of temperature variability were important to define the trait-driver relationship observed in our study, we did not consider variability in underwater PAR as it was determined (via spectral analysis) to be very similar across sites. However, this feature may be relevant, particularly over very broad spatial scales, and could be considered in future studies. Regardless, we found that bottom PAR was the dominant light metric in the trait-diver relationship. Light attenuation (K_d) played only a minor role in determining seagrass trait values, loading on RDA 3, and mainly influencing leaf length (which increased as K_d increased). Although K_d was based on only 2 weeks of data, daily median light attenuation is quite stable across the growing season (Wong and Dowd 2021), so we consider it a good representative of overall attenuation properties at each site. While K_d itself was not an important driver of seagrass traits, its effects would have been included in the overall PAR signal. The total duration above light saturation (H_{sat}) was also not a strong driver of seagrass traits, even though daily light periods are more correlated with seagrass persistence than absolute light intensity (Dennison and Alberte 1985). We also calculated daily H_{sat} periods, but these were all > 6 h during the growing season, the minimum required for *Z. marina* growth and survival (Dennison and Alberte 1985), and so we did not include them in our analysis. H_{sat} was calculated using a common year record of incident surface light, combined with site-specific light attenuation properties from depth and water conditions. Although it ranged from ~2000 to 4000 h y^{-1} across the sites, it had only minimal effect, loading on RDA 4 and influencing only leaf chlorophyll (which increased as H_{sat} decreased). Bottom PAR appears to be relatively more important than K_d and H_{sat} in influencing morphological and structural bed traits, at least in our study.

Although we identified a strong relationship between eelgrass traits and temperature-light drivers, the inclusion of other drivers may have further improved our analysis. Nutrient availability can strongly influence seagrass traits, where nutrient addition can increase biomass, plant size, and productivity for nutrient-limited plants (Lee et al. 2007). However, consistent summer nitrogen content in leaves (Krumhansl et al. 2021) and minimal anthropogenic nutrient loading across our sites (Murphy et al. 2021) suggest that nutrients may not be a strong determinant of trait variability in our study. Sediment conditions may be more

important, as sediments ranged from muddy-silty with high organic content at warmer sites to sandy-gravelly with low organic content at cooler sites (Wong 2018; Krumhansl et al. 2020). Although these sediment differences are indirectly accounted for by temperature regime, high organic content in warm regimes may have still influenced seagrass traits through chronic exposure to high sulfide concentrations, which can reduce photosynthetic rate, shoot density, and root growth (Goodman et al. 1995; Pedersen and Kristensen 2015). Further, water velocity has long been shown to influence seagrass bed structure, growth, and morphology (Fonseca et al. 1983; Peralta et al. 2006; Yang et al. 2013). In the only other study to our knowledge that examines predictive multivariate statistical relationships between *Z. marina* traits and physical drivers using constrained ordination, water motion in addition to light and temperature improved the prediction of eelgrass traits in intertidal habitats (Boyé et al. 2022). Despite the potential role of additional physical drivers, our RDA model accounted for a reasonable portion (31%) of the trait variation, with the overall model and first 5 RDA axes being highly significant. While the proportion of unconstrained variance was relatively high (65%), our analysis of the multivariate regression and associated residuals indicated that this was mainly from high replicate variability. This is a fairly typical feature in RDA or other constrained ordination analyses for benthic community analysis when individual replicates are included (Wong 2018; Boyé et al. 2022).

Based on our study results, we developed a conceptual model (Fig. 6) that illustrates the relationship between temperature-light regimes and seagrass traits, encapsulating the plant size-shoot density relationship that dominated the observed trait variability and its environmental predictors. Physical conditions range from cool and low variability in temperatures, where PAR is also low, to those with warm and highly variable temperatures, where PAR is high (i.e., left to right in Fig. 6). Shoot density, lateral shoots, and rhizome sugars all increase when moving from cooler to warmer regimes, while morphological traits (number of leaves, leaf length and width, and rhizome width) all decrease. We also include additional traits that are known to vary across these conditions but were not consistently sampled in our study. These are aboveground to belowground biomass ratio (AGBM: BGBM) and bed fragmentation, which tend to be highest in warmer temperature regimes (Krumhansl et al. 2021; Wong and Dowd 2023). This conceptual model can provide broad initial insights into variations in trait distributions when physical conditions are known. When paired with habitat distribution maps (e.g., O'Brien et al. 2022), further application of the multivariate model could provide more detailed insights into large-scale patterns in *Z. marina* traits.

In conclusion, we identified and established a multivariate predictive relationship between certain temperature-light

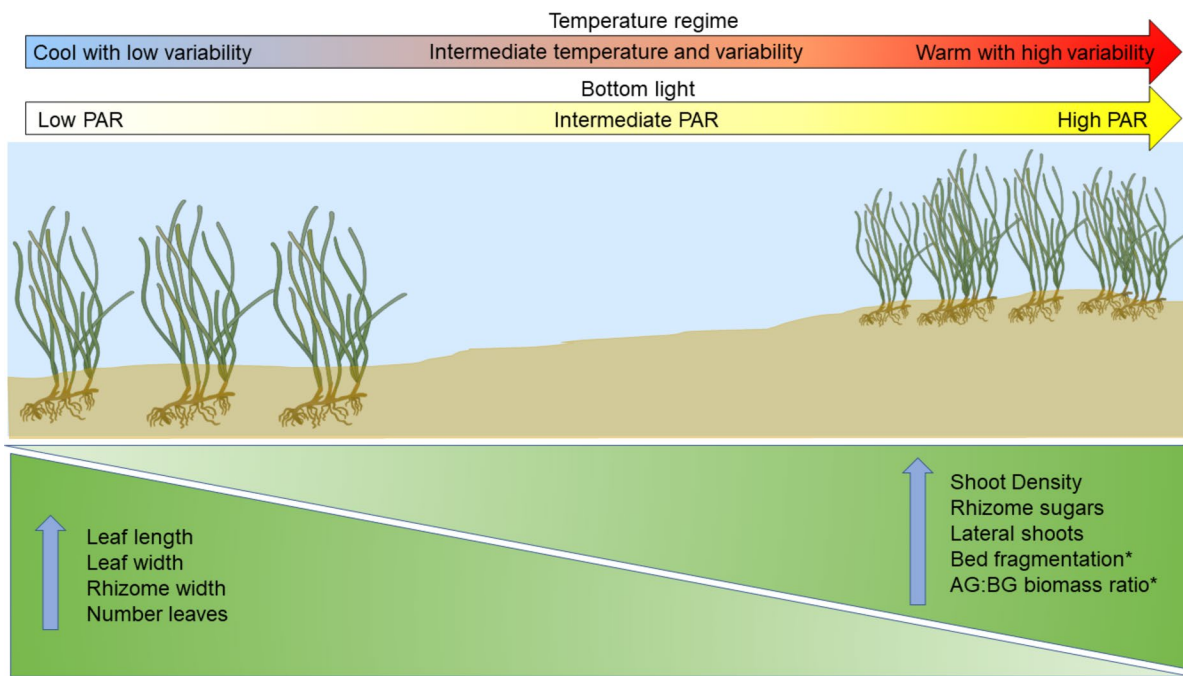


Fig. 6 Conceptual model illustrating *Z. marina* intraspecific trait variability across the temperature-light conditions it inhabits in Atlantic Canada. The temperature regime (blue/red arrow) represents a gradient from cool and least variable temperatures to warm and highly variable temperatures when moving left to right. The light regime

(white/yellow arrow) represents a gradient from low to high bottom PAR when moving left to right. Traits with an asterisk (*) indicate traits not sampled consistently in this study, but are included based on previously identified relationships. *Z. marina* image from <https://www.vims.edu/research/units/programs/sav/species/eelgrass.php>

processes and *Z. marina* trait variation. Trait variation was dominated by a trade-off between plant size and shoot density, where plants became smaller and beds denser as temperatures warmed, temperature variability increased, and bottom light increased. Several temperature processes were important predictors of traits and included daily temperature range, time in the OTR, heat accumulation, SD tidal band, and relative importance of the meteorological band, as well as median temperature. Bottom PAR was the only light metric important for traits, with light attenuation and duration of saturating photosynthetic light playing a more minor role. Redundancy analysis (RDA) proved useful to predict multiple seagrass traits (i.e., their collective multivariate response) from the suite of physical drivers. This predictive capacity is not available from other approaches (e.g., canonical correlation analysis) that focus on association between variables, not prediction. The dimension reduction aspect of RDA allowed insights into not only the overall response of seagrass traits to temperature-light drivers but also the specific traits and drivers important for this relationship. Furthermore, our analysis was strengthened by including multiple sources of temperature variability as predictors, which were shown to be key for defining traits. Both our conceptual and statistical models are valuable to predict trait distributions when physical conditions are known, providing insights into drivers of seagrass trait variability.

Such insights can support the development of management approaches that acknowledge and consider the heterogeneity in seagrass habitats observed in the nearshore.

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Data Availability The data that support the findings of this study are available from the authors or are publicly available on the Government of Canada Open Data Portal.

Declarations

Competing Interests M. Wong is an Associate Editor with Estuaries and Coasts. The authors declare no other competing interests.

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