Environmental predictors of Seagrass Phenotype Variability in a Temperate Lagoon Ecosystem.

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Abstract

Seagrass ecosystems provide essential services but have declined worldwide due to human and natural influences. Thermal stress from diurnal and seasonal fluctuations, coupled with climatic factors, impact seagrass productivity and distribution. To survive in dynamic environments, plants must adapt or acclimate. Following concerning declines, environmental factors responsible for spatial and temporal variability were investigated in a dwarf eelgrass (*Zostera capensis*) habitat within a temperate lagoon. Significant differences in shoot densities, leaf size, and biomass of *Zostera* populations near the mouth and at the end of the lagoon were observed, with distinct seasonal responses. Severe diebacks were observed in summer with subsequent recovery under favourable conditions. Generalized additive mixed modelling revealed seagrass densities to be primarily (> 80%) predicted by water temperature, turbidity, and exposure. Those exposed longer during low tide exhibited a small-leaved morphotype in higher densities. Conversely, deeper intertidal stands supported a sparser large-leaved morphotype. These traits represent a phenotypic response enabling populations to acclimate to the prevailing environmental conditions, altering their characteristics and interactions. Large-leaved populations supported higher epiphyte loads and faunal diversity compared to small-leaved populations. High gene flow suggested that morphotypic variations are predominantly phenotypically based rather than genetically driven. Trends in *Zostera* cover within the lagoon reveal greater declines closer to the mouth, implying a concurrent decline in associated macro-epifaunal communities dependent on large-leaved populations. With climate change-induced warming, further decreases in *Zostera* and ensuing loss of large-leaved populations are expected, with likely negative repercussions on associated epifaunal communities and other trophic levels within the system.

1. Introduction

A fundamental focus in the fields of ecology and conservation remains the understanding of factors that contribute to patterns in species distribution, abundance and demography, across their distributional ranges (Parmesan 2006; Burgess et al. 2020). Differences in species characteristics (e.g. size and shape) and abundance can stem from broad variations in evolutionary histories which are frequently evidenced in genetic diversity (Oliva et al. 2014). Additionally, the abundance and structure of plants can be influenced by diverse environmental conditions that fluctuate both spatially and temporally (Mascaró et al. 2014). Seagrass ecosystems experience consistent variations in their environment that differ over time and space. Confined to nearshore subtidal and intertidal zones in tropical and temperate waters, they are influenced by air and water temperatures, among other factors, and have evolved to live in varying environments evident by their global spread (Den Hartog 1970). They persist in oscillating environments which can lead to fluctuations in the overall biomass and densities of seagrass, as well as affect their reproductive output (Wabnitz et al. 2008). However, both tropical and temperate seagrasses have optimal conditions in which growth and photosynthesis are at their peak (Niu et al. 2012). Even within these geographical limits, fluctuations as well as extreme temperature shifts pose a threat to seagrass acclimation and survival.

Of the many factors influencing seagrass growth, productivity is mainly controlled by temperature, light, and nutrient availability (Short 1987; Ralph et al. 2007; C. J. Collier et al. 2012). These key elements coupled with the hydrodynamics of a system affect the spatial distribution of seagrasses (Schanz and Asmus 2003; Uhrin and Turner 2018) and regulate biochemical processes that underpin growth and reproduction (K. S. Lee et al. 2007; Qin et al. 2020; Vercaemer et al. 2021)). Several studies have been conducted to determine the effects of fluctuating temperatures (Campbell et al. 2006; M. S. Koch et al. 2007), light limitation (Koch and Erskine 2001; Mvungi et al. 2012), extreme tidal exposure (Unsworth et al. 2012; Petrou et al. 2013), excess nutrients (Frankovich et al. 2009; Baggett et al. 2010) as well as their interactions with biodiversity (Blake and Duffy 2012; Eklöf et al. 2012) in a range of seagrass ecosystems with the aim of understanding seagrass-environment dynamics. Such investigations, however, have been lacking in *Zostera capensis* habitats in South Africa.

Atmospheric carbon dioxide (CO_2) levels have increased by 47% from 18th century preindustrial levels of ~ 280 ppm (parts per million) to an annual average of 420.13 ppm by 2023 (Lan et al. 2023) attributed mainly to anthropogenic activities. This rate of increase is an order of magnitude faster than has been historically documented, and concentrations are higher than that recorded for the last few million years (Monastersky 2013). The ocean acts as a carbon sink, absorbing nearly a third of atmospheric carbon (Friedlingstein et al. 2022; Zhang et al. 2022; Vashist et al. 2023), thus curbing the consequences of even greater CO_2 levels on the Earth's climate. Oceanic absorption of CO_2 leads to chemical changes in seawater that include acidification (reduced pH) and increases in total dissolved inorganic carbon (DIC), while reducing saturation levels of calcium carbonate and carbonate ion (Doney et al. 2009). Surface ocean pH is 0.1 units lower than preindustrial levels (pH 8.2) (Orr et al. 2005) and is predicted to drop by a further 0.14 to 0.5 by 2100 under current anthropogenic CO_2 emission rates (Caldeira and Wickett 2005; Gattuso et al. 2015). Elevated CO_2 has been shown to have a positive effect on growth and photosynthesis of several seagrass species, since seagrasses are carbon-limited under prevailing DIC levels in the ocean (Koch et al. 2013; Borum et al. 2016; Olsen et al. 2018). As a result, it is expected that there will be overall increases in productivity and biomass under conditions of reduced water column pH (B. Duarte et al. 2018). However, the response of seagrasses to acidification varies depending on the species, as well as their capacity to utilize different forms of DIC. This response is further influenced by various factors, such as nutrient availability, quality of light exposure, and competition (Koch et al. 2013; Cox et al. 2015; Olsen 2018).

Anthropogenic activities have led to the intensification of eutrophic conditions in shallow coastal and estuarine environments, resulting in reduced availability of light and promotes anoxic (no oxygen) or hypoxic (low oxygen) conditions (Howarth et al. 2011). These conditions are amplified in warm water when oxygen solubility is lower (Shaffer et al. 2009), while respiration of organic matter is enhanced (Quiñones-Rivera et al. 2010; Rabalais et al. 2010). Prolonged anoxia leads to increased sulfide levels in the sediment, while hypoxia in the water column affects the internal oxygen conditions of seagrasses, both of which have detrimental effects on photosynthetic rates, metabolism, and growth (Koch et al. 2007; Povidisa et al. 2009; Raun and Borum 2013). Die-offs have been reported for seagrass meadows

under hypoxic conditions (Holmer and Bondgaard 2001, (Shields et al. 2018) and the suggested reasons for this include a combination of intrusion of sediment sulfide and anoxic plant tissue, exacerbated by a greater demand for oxygen in warmer water to meet respiratory needs (Mascaro et al. 2009)(Koch et al. 2001, Koch et al. 2007). Since nearshore environments receive a higher output of organic matter from fluvial and estuarine sources than the open ocean, local scale variability in dissolved oxygen is higher in coastal compared to oceanic waters (Soetaert et al. 2006; Gilbert et al. 2010). Seagrasses are adapted anatomically and physiologically to contend with submersion as gases are efficiently diffused by well-formed aerenchyma tissue in the leaves, and oxygen loss through the root system is well buffered (Papenbrock 2012; Brodersen et al. 2018). However, prolonged hypoxic and anoxic conditions retard growth (Holmer and Bondgaard 2001), resulting in the eventual loss of seagrass habitats (Hall et al. 2016). Restoration of these important systems depends on interventions that reduce eutrophication and improve water quality.

Several factors, often acting collectively, are deemed responsible for the decline of seagrasses worldwide (Orth et al. 2006; Short et al. 2006; Waycott et al. 2009) which include eutrophication and coastal development, trophic interactions, and storm events linked to climate change (Short et al. 2006). Both natural and anthropogenic activities, therefore, influence various processes responsible for seagrass meadow dynamics (Orth et al. 2012; Pollard and Greenway 2013). These activities can alter the stability of an ecosystem, which is sometimes easily detected in catastrophic events such as storms, cyclones and floods (Pollard and Greenway 2013), or are so subtle that immediate detection is eluded, and the change is incremental (Marbà et al. 2004). Investigating the causes of seagrass decline is often initiated only once substantial habitat loss has occurred and even then the source of the decline is difficult to isolate. Changes that lead to lower productivity and even habitat loss may have severe implications on associated species and important ecosystem services (Duarte 2002; Orth et al. 2006; Barbier et al. 2011). Understanding environmental influences is therefore essential to identifying and detecting key drivers of seagrass growth, distribution and decline, and to particularly detect inconspicuous change.

In South Africa, there are a few remaining locations where the dominant seagrass species, *Zostera capensis*, forms monospecific stands creating important habitats in estuaries and coastal environments. One notable example is Langebaan Lagoon, which supports multiple large stands *Z. capensis*, a dwarf eelgrass listed by the IUCN (The World Conservation Union) as “Vulnerable” because of its restricted range and declining population trend (Short et al. 2011). The extent of seagrass cover in the lagoon has undergone changes over time. Seagrass cover in the tidal lagoon was estimated at ~ 58 ha in 1960 and reported to have declined to 22 ha by 2009 (Pillay et al. 2010), however, by 2014 cover was assessed to be 85.8 ha (Adams 2016). To enhance our understanding of how *Z. capensis*, a temperate seagrass species, responds to fluctuating environments and anticipated climate extremes, it is important to comprehend its natural variability and identify the effects of key environmental factors. One way to achieve this is by assessing seasonal influences on morphometric parameters, which can shed light on the species' adaptive strategies and acclimation to different environmental conditions.

This study documents the spatial and temporal patterns of distribution in *Zostera capensis* in Langebaan Lagoon and identifies environmental factors influencing variability in seagrass density, biomass and morphometrics. This is a critical step in understanding natural and anthropogenic influences, and essential to establishing monitoring and restoration initiatives. Monitoring seagrass distributional patterns as well as tracking environmental parameters, are a prerequisite to understanding natural dynamism, while allowing for detection of trends and anomalies. The prolonged effects of anomalies can cause shifts in ecosystem stable states, alter ecosystem function and lead to loss of productivity and biodiversity (Duarte 2002; Dennison 2009; Winters et al. 2011; Fraser et al. 2014). Knowledge of the influence of environmental factors therefore aids in identifying the effects of natural and human-induced stress along with the effectiveness of conservation measures. Furthermore, results can be used to inform predictions of environmental effects under future climate change scenarios (Orth et al. 2006, Short et al. 2007).

2. Methods

2.1.1. Study area and site selection

Langebaan lagoon is a protected area located on the west coast of South Africa (100 km north of Cape Town). At ~ 15 km in length and 4 km maximum width, it opens into the ocean through a large bay (Saldanha Bay) to the north that supports an industrial port (Fig. 1). Benthic substrate in the lagoon comprises sandy sediment with macroalgae, salt marsh grass *Spartina* sp. and seagrass *Zostera capensis* as dominant macrophytes (Schils et al. 2001). The lagoon experiences semi-diurnal tides and an average spring tidal range of 1.4 m (Day 1981). Seagrass populations were assessed at five sites within the lagoon selected based on historical spatial descriptions (Day 1959) supported by satellite imagery (Landsat time-lapse: 1984–2012) that confirmed consistent seasonal and/or interannual cover albeit with a high degree of variability. Sites experienced different emergence periods during low tide while the average water depth at high tide was estimated at 2 m at Centre Banks, 1.5 m at Klein Oesterval and Oesterval, and 1 m at Bottelary and Geelbek (Flemming 1977). Maximal astronomical tidal range in South Africa is 2 m and as a result estuarine systems have been described as micro-tidal (Whitfield 1992). *Zostera* produces short-leaved and large-leaved morphotypes under varying environmental conditions observed at specific sites.

2.1.2. Seagrass Field Sampling

Since seagrass cover varied at each site, samples were taken according to the total number of beds/ patches present. For example, Oesterval had ~ 20 beds and 10 were sampled while beds at Klein Oesterval and Bottelary ranged from three to five in which case three beds were sampled each season. Centre Banks and Geelbek had one continuous seagrass stand > 200 m long, and here samples were taken every 50 m. Seagrass shoots were collected randomly from each bed using a corer (10 cm diameter x 15 cm; 0.008 m^2; n = 5) during spring low tide when plants were completely exposed, over four austral

seasons: autumn (April), winter (July), spring (October) and summer (January). Random sampling allowed for areas with high and low shoot densities to be sampled. Cores were gently rinsed in the field to remove sediment and faunal epibionts then placed in a bag before being transported to the University of Cape Town for analyses. In the lab, shoots and leaves were counted and the average width and length of 20% of the longest leaves in each core were measured. Algal epiphytes were gently scraped off leaves into pre-weighed petri dishes using the back of a scalpel blade. Thereafter, shoots were separated from root/rhizomes and dried at 60^{o}C to a constant dry weight (~ 12 hours). This short drying period is due to the small shoots/leaves and low biomass characteristic of this species. Shoots were then weighed to obtain aboveground dry weight (g m^{-2}). Epiphyte dry weight was measured after drying at 60^{o}C till constant weight was reached (~ 11 hours).

2.1.3. Environmental Variables

Measurements of temperature, pH, turbidity, salinity, dissolved oxygen and chlorophyll a (chl a) were taken monthly at each site over 12 months during a similar time of day at spring high tide, using a handheld multiparameter probe (Conductivity Temperature Depth profiler, Model: YSI 6820 V2-2V). During low tide, all sites were assumed to be subjected to the same solar irradiance intensity, however since sites occurred at varying depths when the tide was high, the duration for which they were exposed varied. Direct measurements of light were not recorded in the field, instead turbidity was measured as a proxy for water column irradiance since suspended particulate matter can influence light levels reaching seagrass plants (Waycott et al. 2009; C. J. Collier et al. 2012). Beds were assigned an exposure level based on average emergence time during spring low tide and distance (m) from the high water mark. Beds were classified as ‘high shore’ if they were within 10 m of the spring high water mark, ‘mid shore’ between 10–50 m and ‘low shore’ if greater than 50 m.

2.2. Statistical Analyses

Multi-panel scatterplots and correlation analyses indicated strong collinearity between temperature and pH (Spearman Rs = 0.87, p = 0.001), leaf and shoot densities (Spearman Rs = 0.92, p = 0.001) as well as leaf length and leaf width (Spearman Rs = 0.85, p = 0.001). Therefore, leaf density, leaf width and pH were excluded from the analyses so as not to confound the observed variation (Lipovetsky and Conklin 2001).

2.2.1. Environmental Parameters

To statistically relate the effects of environmental conditions to seagrass metrics, 2-tailed Pearson correlations were carried out between these variables and the seasonal average (three months), compared to a one month lag preceding the seagrass sampling event. One month was assumed a reasonable response time for a small-leaved seagrass such as *Zostera capensis* since a similar species *Z. noltei* was observed to delay its response to seasonal fluctuations in this period relative to a large-leaved species *Z. marina* (Marbà et al. 1996). Correlations were higher between seagrass metrics and seasonal averages of environmental variables compared to measurements recorded one month prior (refer to supplementary material for correlation results), implying that seasonal environmental factors

were better predictors of growth responses in *Z. capensis*. This was the case for all environmental variables apart from dissolved oxygen which showed a slightly stronger and significant correlation to leaf length and width in the preceding month (-0.58 and − 0.61 respectively) than over the season (-0.47 and − 0.53 respectively). Given that this difference was marginal, seasonal averages of all environmental variables were used to predict responses in seagrass metrics.

2.2.2. Multivariate Analyses

The effects of “season” (fixed factor: four levels) and “site” (random factor nested within season: five levels) on variation in three seagrass morphological metrics (leaf length, shoot density and aboveground biomass (referred to as seagrass biomass) and epiphyte biomass were assessed using PERMANOVA + for PRIMER (Plymouth Routines in Multivariate Ecological Research, version 6; Clarke and Gorley 2006). A visual appraisal of site differences in seagrass metrics was done using ordination techniques (non-metric multi-dimensional scaling (MDS) and principal coordinates (PCO)). Vectors correlating environmental variables were overlain on PCO plots. Seagrass variables were 4th root transformed to down weight the influence of large variances, and differences were calculated as Euclidean distances. ‘Bed’ was used as the sampling unit representing the mean of five replicate samples.

Permutational multivariate analysis of variance (PERMANOVA; Anderson et al. 2008) was performed using sequential Type I Sums of Squares to test the null hypothesis of no differences among groups, on 9999 permutations generating a pseudo-F test statistic and corresponding P (perm) value (Anderson 2005). For acceptable contrasts for “site” and “season” factors, α was set at 0.05. To test for homogeneity in relative group spread by comparing average distance values of each observation to their group centroid, PERMDISP (9999 permutations) including *post hoc* pair-wise comparisons, were run (Anderson 2006; Anderson 2017). Thereafter, a similarity percentage breakdown analysis (SIMPER) on Euclidean distances was done to calculate the contribution of each seagrass variable to the observed dissimilarity between sites.

To determine the extent to which selected environmental factors contributed to variability in seagrass metrics, environmental predictor covariates that most strongly influenced the multivariate assemblage of seagrass variables, were assessed using a distance-based linear model (DistLM, with selection procedure ‘best’ and criteria ‘AIC’). DistLM calculates the proportion of variability contributed by each environmental variable and partitions variation in seagrass metrics according to univariate multiple regression models based on selected predictor variables (Anderson et al. 2008). In this assessment, all possible combinations of predictor variables were explored and the best models were selected based on Akaike’s information criterion (AIC) (Akaike 1974) and adjusted R^2 values. Small AIC values indicate a better model fit, with the lowest AIC value signalling the most efficient model to explain variation (Anderson et al. 2008).

2.2.3. Univariate Analyses

Environmental variables (water temperature, salinity, pH, turbidity, chlorophyll a and oxygen) were "normalised" before analysis by subtracting the mean from each value for each variable and then dividing by their standard deviation. This was necessary to bring environmental data which have different scales and units into proportion with each other in order to derive comparable outputs. Thereafter, two-factor ANOVAs of each environmental variable across "sites" (random) and "seasons" (fixed) were performed to test for localized differences, followed by Tukey multiple comparisons *post hoc* analyses. Similarly, two-factor ANOVAs were performed to test the effect of "site" and "season" on each seagrass metric followed by *post hoc* analyses (Tukey multiple comparisons).

One categorical (exposure level/shore height) and five continuous environmental variables (water temperature, salinity, turbidity, dissolved oxygen and chlorophyll a) and combinations thereof were tested as likely predictors of variation in seagrass metrics using generalized additive mixed models (GAMMs) (S. N. Wood and Augustin 2002). GAMMs allow for flexibility in modelling non-linear relationships and contain model functions constructed on a penalized regression-spline approach that incorporates smoothness selections in the estimation process (S. N. Wood 2017). The degree of smoothing provided by each smooth term is treated as a random effect and expressed as "effective degrees of freedom" (edf) estimated based on its variance in a mixed modelling structure (Wood 2017). Smoothers with high edf values (> 8) indicate a highly non-linear curve, while a straight line has an edf of 1 (Zuur et al. 2009, Wood 2017).

GAMMs were evaluated for each seagrass metric with "site" as a random effect, and included smoother functions for continuous environmental variables. Knots were selected incrementally to produce relationships that were biologically meaningful, and checked for over-specification (Wood 2017). Model assumptions were also assessed by inspecting diagnostic plots of random effects and residuals. Most parsimonious models were derived after evaluating the significance of the random effect in the full model. This was followed by determining optimal combinations of predictor variables by opting for low AIC values and high R^2 values, while selecting for only significant predictor variables in the final model. Models were configured on a Gaussian distribution with a maximum likelihood function (Zuur et al. 2009), and tested using the R package 'mgcv' (Wood and Scheipl 2015) within the "nlme" library (Pinheiro et al. 2016) using the R statistical software 3.6.0 (The R Development Core Team, 2015; www.r-project.org).

Significance for all tests was assessed at $\alpha < 0.05$, and variance is expressed as standard error (SE) of the mean. For each analysis, data were transformed (log or log x + 1) where necessary if assumptions for normality (Shapiro-Wilk's test) and homogeneity of variance (Levene's Test) were not met.

3. Results

3.1. Field observations on seagrass morphometrics and epiphyte biomass

a). Multivariate analyses

From PERMANOVA analyses, contrasts in seagrass metrics were significant across sites, and the interaction of site and season contributed slightly more to the explained variation than site only (Table 3.1). Despite sites being > 90% similar in the multivariate space (Fig. 3.1A) a spatial gradient was visually evident with distance from the lagoon mouth. Seasonal differences were not significant and accounted for the least variation (17%) which was confirmed visually except for a minor separation in variability of seagrass metrics at Centre Banks in summer (Fig. 3.1B). A large percentage (51%) of multivariate variation was unexplained.

Table 3.1
PERMANOVA results based on Euclidean distances comparing seagrass variables (leaf length, shoot density, seagrass and epiphyte biomass) sampled across five sites (random) over four seasons (fixed). Effect size was calculated from the estimated contribution of components of variation for each factor. *P* values are significant at $\alpha < 0.05$ and in bold.

Source of variation	df	MS	Pseudo-F	*p*	Unique permutations	Effect Size
Season	3	8.18	2.06	0.092	9943	17%
Site	4	10.46	20.66	**< 0.001**	9929	53%
Season x Site	12	3.03	5.99	**< 0.001**	9902	54%
Residual	79	0.51				51%

The relative contribution of each morphological metric to site distinctions was determined in a SIMPER analysis. Shoot density contributed the highest proportion (> 60%) of variation to within and between differences for all sites with a few exceptions. At Bottelary, epiphyte biomass contributed more (41.85%) to variation than number of shoots (35.78%). Variation between seagrass metrics at Centre Banks vs Geelbek and Bottelary was explained more by leaf length than by shoot densities, which were evident in their spatial and temporal contrasts (Fig. 3.1).

b). Univariate analyses

Shoot densities differed significantly across sites ($F = 117.22$, $p < 0.001$) and seasons ($F = 75.5$, $p < 0.001$). Bottelary and Geelbek had similar means and the highest average densities of shoots compared to the other three sites (Fig. 3.2A). Average shoot densities were also similar at Oesterval and Klein Oesterval, while seagrass beds at Centre Banks were the least dense (Fig. 3.2A). The average lengths of seagrass leaves were also shorter at Geelbek and Bottelary compared to Centre Banks, Klein Oesterval and Oesterval (Fig. 3.2B). Summer produced the lowest shoot densities for all sites except Oesterval which had lowest densities in autumn (Fig. 3.2A). All sites generated longer leaves in autumn and winter, except for Centre Banks where leaves were shortest in winter and longest in summer and autumn (Fig. 3.2B). Average lengths of leaves differed significantly across sites ($F = 179.49$, $p < 0.001$) and seasons ($F = 29.29$, $p < 0.001$) due to variability in mean leaf lengths at all sites (Tukey HSD, $p < 0.05$).

Seagrass beds at Oesterval produced the highest average aboveground biomass (9.72 g dry wt m^{-2}) across all seasons, followed by Centre Banks (9.45 g dry wt m^{-2}) and Klein Oesterval (8.04 g dry wt m^{-2}). Seagrass biomass at Bottelary was comparable to sites closer to the mouth while biomass at Geelbek was consistently low over all seasons (Fig. 3.2C). Seagrass biomass differed significantly between sites ($F = 29.71$, $p < 0.001$) and seasons ($F = 57.23$, $p < 0.001$) due mainly to high variability between Geelbek and the other four sites (Tukey HSD, $p < 0.05$). On average seagrass biomass was lowest in summer in the lagoon and higher in autumn and winter (Fig. 3.2C).

In general, epiphyte biomass did not correlate with leaf length or density. Algae were found on seagrass leaves at Klein Oesterval over all seasons, while no algae were recorded at Oesterval, Centre Banks and Bottelary in winter, or from Geelbek during the entire sampling period (Fig. 3.2D). On average highest algal biomass was recorded on seagrass leaves at Centre Banks, followed by Bottelary, Oesterval and Klein Oesterval (Fig. 3.2D). These differences were significant across sites ($F = 7.12$, $p < 0.001$), seasons ($F = 22.03$, $p < 0.001$) and their interaction ($F = 8.22$, $p < 0.001$) due to variation in mean algal biomass between Geelbek and the other four sites (Tukey HSD, $p < 0.05$).

3.2. Spatial and Temporal Patterns in Environmental Variables

Langebaan lagoon exhibits an environmental gradient from the mouth to the upper reaches of the lagoon. Average water temperature increased with distance from the mouth, with temperatures at Bottelary and Geelbek being consistently warmer compared to Klein Oesterval and Oesterval (Table 3.2). Water temperature at Centre Banks was the lowest on average throughout the study period while the highest temperatures in the lagoon were recorded at Geelbek followed by Bottelary. Maximum temperature values were generally similar and lower near the mouth at Klein Oesterval, Oesterval and Centre Banks (Table 3.2). Water temperature differences were significant across sites ($F = 28.23$, $p < 0.001$), seasons ($F = 93.51$, $p < 0.001$) and their interaction ($F = 2.22$, $p = 0.015$) explained mainly by variation in means between Centre Banks, Bottelary and Geelbek (Tukey HSD, $p < 0.05$, Table 3.2). Mean temperatures differed across all seasons except for spring and autumn (Tukey HSD, $p < 0.05$).

Salinity levels between sites ($F = 13.39$, $p < 0.001$), seasons ($F = 8.74$, $p < 0.001$) and their interaction ($F = 9.75$, $p < 0.001$) differed significantly. Highest salinities were recorded at Geelbek and Bottelary while Centre Banks, Klein Oesterval and Oesterval had lower and similar averages (Table 3.2). Variation at the site level was explained by the significantly higher salinity at Geelbek compared to the other four sites (Tukey HSD, $p < 0.05$), while salinities across the remaining four sites remained homogenous. Seasonal variation was explained by the significant differences between salinities in summer and autumn, and summer and winter (Tukey HSD, $p < 0.05$, Table 3.2).

Water column pH levels differed significantly between sites ($F = 2.98$, $p = 0.022$), seasons ($F = 93.44$, $p < 0.001$) and their interaction ($F = 2.30$, $p = 0.011$). This was mainly due to pH at Oesterval being significantly different to levels at Centre Banks, Geelbek and Bottelary (Tukey HSD, $p < 0.05$). On average

pH at Geelbek was 0.33 levels higher i.e., more alkaline (8.2) compared to the other four sites, however Centre Banks experienced the greatest range in pH with a minimum of 6.9 in winter and a maximum of 9.7 in summer. All sites experienced alkaline conditions in summer compared to winter except for Klein Oesterval where alkalinity was higher in spring (Table 3.2).

Average water column turbidity was highest at Geelbek with maximum levels reaching almost five times higher than that of other sites (Table 3.2). This equates to much lower light levels in the water column. Average turbidity across the other four sites ranged from 5.73–8.57 NTUs. Turbidity differed significantly across sites ($F = 22.37$, $p < 0.001$) but not across seasons ($F = 2.48$, NS). The interaction between site and season was also significant ($F = 2.55$, $p = 0.005$) driven mainly by the high differences in turbidity between Geelbek and the other sites (Tukey HSD, $p < 0.05$, Table 3.2).

A generally high level of dissolved oxygen (DO) was recorded at Geelbek across all seasons with the highest value of 26.44 mg/L recorded in autumn. Centre Banks experienced lowest DO levels, while DO at Klein Oesterval, Oesterval and Bottelary were similar (Table 3.2). DO between sites differed significantly ($F = 6.75$, $p = 0.001$) due to differences in means between sites closer to the mouth (Centre Banks, Oesterval and Klein Oesterval) and those closer to the head (Geelbek and Bottelary) of the lagoon (Tukey HSD, $p < 0.05$, Table 3.2). Seasonal differences were not significant ($F = 1.8$, NS), while the interaction between sites and seasons were ($F = 4.32$, $p = < 0.001$).

Dissolved chlorophyll *a* (chl *a*) was significantly different at the site level ($F = 20.76$, $p < 0.001$) due to a higher mean recorded at Geelbek compared to the other sites (Tukey HSD, $p < 0.05$, Table 3.2). Average chl *a* was relatively stable at the other sites. No differences in chl *a* levels were observed between seasons ($F = 1.089$, NS) or the interaction between site and season ($F = 1.013$, NS).

From distance-based linear models, exposure contributed the greatest proportion of variation in seagrass metrics between sites (Table 3.3). This was followed by turbidity, oxygen, salinity and chlorophyll *a* (Table 3.3). Variability in seagrass metrics provided by temperature was 4.11%. PCO ordination confirmed these responses visually, as the longest trajectories indicating the strength of the Spearman correlations were provided by exposure, turbidity and oxygen (Fig. 3.3). The best model solution based on lowest AIC and highest R^2 values suggested that all six environmental variables contributed to the observed patterns in seagrass morphometrics and epiphyte biomass (Table 3.3).

Table 3.2

Abiotic variables recorded over 12 months at five sites in Langebaan Lagoon. Means ± 1 standard error, minimum and maximum values are presented. Small letters represent homogenous means between sites that are not significantly different when compared using Tukey HSD testing.

	Centre Banks	Klein Oesterval	Oesterval	Bottelary	Geelbek
Water temperature (ºC)	15.86^{a} ± 0.46	18.64^{abc} ± 0.75	17.89^{ab} ± 0.65	20.74^{bc} ± 0.93	21.42^{c} ± 0.92
	12.68	13.62	13.07	14.68	15.01
	20.15	25.53	23.78	27.68	28.49
Salinity	34.26^{a} ± 0.21	34.40^{a} ±0.21	34.71^{a} ± 0.20	34.86^{a} ±0.29	35.76^{b} ±0.55
	32.38	32.40	32.80	32.30	31.87
	35.80	36.30	36.13	37.32	40.65
Ph	7.78^{a} ± 0.19	7.88^{bc} ± 0.13	7.86^{c} ± 0.14	7.98^{ab} ± 0.13	8.21^{a} ± 0.13
	6.88	7.09	7.06	7.08	7.31
	9.67	9.48	9.48	9.32	9.28
Turbidity (nephelometric turbidity units)	6.99^{a} ± 0.58	5.73^{a} ± 0.39	6.66^{a} ± 0.45	8.57^{a} ± 0.69	23.79^{b} ± 3.07
	4.40	3.60	4.30	5.10	7.70
	16.10	12.90	14.00	18.00	73.30
Oxygen (mg/litre)	7.52^{a} ± 0.16	8.66^{ab} ± 0.26	8.26^{ab} ± 0.70	8.83^{b} ± 0.27	11.76^{c} ± 1.92
	6.17	6.84	6.24	7.32	7.32
	8.40	16.40	9.60	10.65	26.44
Chlorophyll a (mg/litre)	2.10^{a} ± 0.21	1.46^{a} ± 0.11	1.71^{a} ± 0.10	2.01^{a} ± 0.16	5.63^{b} ± 0.69
	1.00	0.70	1.00	0.90	1.70
	7.30	3.40	3.60	4.10	15.50
Exposure/shore height (m)	Low shore	Low/mid/high shore	Mid/low shore	High shore	High shore

Table 3.3
Results of distance-based multiple regression modelling (DistLM) used to estimate the proportion of variation explained by continuous and categorical environmental variables on seagrass morphometrics and epiphyte biomass. Overall, five best model solutions are presented ranked by fit based on AIC values. *P* values are significant at < 0.05 and in bold.

Marginal Tests			
Variable	**Pseudo-F**	***p***	**Proportion of variation**
Temperature	4.16	**0.009**	4.11%
Salinity	8.78	**< 0.001**	8.30%
Turbidity	13.86	**< 0.001**	12.51%
Oxygen	13.72	**< 0.001**	12.39%
Chlorophyll *a*	6.29	**< 0.001**	6.09%
Exposure	19.21	**< 0.001**	16.53%
Overall best solutions			
AIC	**R^2**	**Number of variables**	**Selections**
6.26	0.36	6	Temperature, Salinity, Turbidity, O_2, Chl *a*, Exposure
7.76	0.34	5	Temperature, Salinity, Turbidity, Chl *a*, Exposure
9.31	0.32	5	Temperature, Turbidity, O_2, Chl *a*, Exposure
9.59	0.32	5	Temperature, Salinity, Turbidity, O_2, Exposure
10.16	0.31	4	Temperature, Salinity, Turbidity, Exposure

Results from generalized additive mixed modelling (GAMMs) showed patterns in seagrass densities in Langebaan Lagoon to be largely (> 80%) predicted by water temperature, turbidity, oxygen, salinity and exposure (Table 3.4). High seagrass densities were not supported in low and midshore positions, while densities were predicted to decline in water temperatures above 22^{o}C (Fig. 3.4).

Warmer water temperature and higher salinity is predicted to have a significant negative effect on leaf length, a response similarly observed for turbidity (Table 3.4). This is supported by observations of longer leaves at cooler temperatures closer to the mouth, and shorter leaves in more turbid conditions at the end of the lagoon. Leaf width on the other hand, is predicted to decrease with increasing levels of chlorophyll *a* but increase with higher levels of dissolved oxygen. Increasing salinity is also predicted to produce narrower leaves (Fig. 3.4), while low and mid shore heights are predicted to support longer/wider leaves (Table 3.4).

Water temperature, oxygen and salinity were the principal factors influencing aboveground biomass accounting for 69% of variation (Table 3.4). Exposure was not a significant predictor of aboveground biomass, whereas warmer temperature and higher oxygen is expected to negatively influence seagrass biomass (Fig. 3.4).

Four environmental factors were significant in predicting patterns in epiphyte biomass (Table 3.4). Warmer temperature is predicted to favour epiphyte growth along with increasing levels of chl *a* (Fig. 3.4), which will be supported in low shore stands. In contrast, decreasing water clarity and salinity are expected to negatively influence epiphyte growth. These variables explained only 29% of variation implying that other factors, possibly biotic and abiotic, are better predictors of epiphyte growth.

Table 3.4

Summaries of generalized additive mixed models for top performing models predicting the responses of five seagrass metrics and epiphyte biomass to one categorical and five continuous environmental predictors. Estimates (Est) and standard errors (SE) of parametric coefficients are presented, along with approximate significance of thin plate regression spline smoother (s) terms and estimated degrees of freedom (Edf) for predictor variables. All variables are significant at $p < 0.05$.

	Parametric coefficients				**Non-parametric smooth terms**			
	Est	**SE**	***t***	***p***	**Predictor**	**Edf**	***F***	***p***
Shoot density (R^2 = 83%)								
Intercept	6.28	0.06	107.19	0.00	s(Temperature)	3.59	6.75	0.00
Exposure Low	-0.66	0.10	-6.95	0.00	s(Turbidity)	3.60	13.41	0.00
Exposure Mid	-0.64	0.10	-6.17	0.00	s(Oxygen)	1.88	8.41	0.00
					s(Salinity)	2.90	17.97	0.00
Leaf density (R^2 = 83%)								
Intercept	5.13	0.06	87.44	0.00	s(Temperature)	3.48	6.72	0.00
Exposure Low	-0.64	0.09	-6.93	0.00	s(Turbidity)	3.62	12.98	0.00
Exposure Mid	-0.62	0.08	-6.13	0.00	s(Oxygen)	1.64	8.36	0.00
					s(Salinity)	2.78	18.01	0.00
Leaf length (R^2 = 76%)								
Intercept	4.82	0.08	61.92	0.00	s(Temperature)	1.00	11.69	0.00
Exposure Low	0.32	0.08	3.92	0.00	s(Turbidity)	2.55	5.85	0.00
Exposure Mid	0.21	0.08	2.60	0.01	s(Salinity)	1.00	11.07	0.00
Leaf width (R^2 = 71%)								
Intercept	0.27	0.04	6.32	0.00	s(Chl *a*)	1.00	9.73	0.00
Exposure Low	0.27	0.04	6.13	0.00	s(Oxygen)	1.00	5.62	0.02
Exposure Mid	0.20	0.04	4.69	0.00	s(Salinity)	1.00	12.05	0.00
Aboveground biomass (R^2 = 69%)								
Intercept	-0.72	0.07	-9.72	0.00	s(Temperature)	1.00	22.78	0.00
					s(Oxygen)	1.80	6.92	0.00
					s(Salinity)	2.18	5.29	0.00

	Parametric coefficients				Non-parametric smooth terms			
	Est	**SE**	***t***	***p***	**Predictor**	**Edf**	***F***	***p***
Algal epiphyte biomass (R^2 = 29%)								
Intercept	0.07	0.03	2.49	0.02	s(Temperature)	1.00	7.32	0.01
Exposure Low	0.11	0.05	2.42	0.02	s(Chl *a*)	1.80	4.14	0.01
					s(Turbidity)	1.00	11.74	0.01
					s(Salinity)	2.90	3.55	0.02

4. Discussion

In Langebaan Lagoon, seagrass growth factors showed marked variation across sites and seasons, owing mostly to differences between stands closer to the mouth (Centre Banks, Klein Oesterval, and Oesterval) and those at the lagoon's far end (Bottelary and Geelbek). Environmental conditions were significantly different between these sites, but not consistently between seasons, indicating a greater influence of the local environment on seagrass patterns than seasonal forcing. These findings imply that small-scale influences on seagrasses are as significant if not more important, than large-scale global and climatic factors. As a result, increased research and management at smaller scales may have a bigger positive influence on seagrass habitats.

4.1. Temporal Patterns in Seagrass Metrics

The densest stands of *Zostera capensis* in Langebaan Lagoon were measured in early summer (October), with densities dropping to the lowest by the end of summer, illustrating the effects of supra-optimal temperature and light conditions on seagrass growth. These observations are consistent with the typical growth cycle of temperate seagrasses, which exhibits substantial seasonal changes and is related to extensive temperature and light variations that occur throughout the year (C. Duarte 1989). Seasonal environmental fluctuations influence seagrass productivity and growth, particularly in temperate regions where shoot formation rates are slower during winter due to cold and low light levels, while growth increases in early summer due to increasing temperature and irradiance (Qiu et al. 2017; Delgado-Serrano and Tuya 2023).

In this study, populations of *Z. capensis* were considerably reduced by the end of summer, particularly at Centre Banks and Geelbek, and then increased again with lower temperatures in late autumn and winter. Other studies on temperate seagrasses have shown that densities and biomass are at their peak in spring and early summer (Duarte 1989; Olesen and Sand-Jensen 1994; Ito et al. 2021). These high densities are subsequently followed by a rapid reduction in cover, most likely caused by heat stress, resulting in the loss of shoots and leaves (Bergmann et al. 2010). Following heat stress and desiccation, rapid leaf growth in *Z. capensis* was observed experimentally (Adams and Bate 1994), demonstrating its ability to

recover when temperatures are favorable. This flexibility in seagrasses is a key feature of their capacity to acclimate under a range of environmental conditions (Duarte et al. 2006; Lee et al. 2007; McDonald et al. 2016).

The seagrass population at Centre Banks had the longest leaves, the highest biomass, especially in autumn, and the lowest shoot density. Due to its location in the lagoon's center, the sand bank is the first to be submerged by the incoming tide, allowing plants to experience a shorter emergence period during spring tides and remain submerged during neap tides (Day 1959, pers. observation). In addition, this site does not appear to drain fully during low tide, but rather retains a layer of water at the base of the plants and throughout much of the bed. Water temperatures at Centre Banks were lower on average throughout the year than at other sites, ranging from 13 to 20^{o}C. Temperature ranges at other sites were higher (13–29°C), significantly so at Bottelary and Geelbek. Edgcumbe (1980) measured optimal temperatures for *Zostera capensis* reproductive and vegetative growth in the laboratory to be between 15–20°C and observed lower growth rates when plants were continuously exposed to < 10^{o}C and > 26^{o}C. This is comparable with the optimum temperature range proposed for *Z. marina*, where growth was limited above 20^{o}C (K. S. Lee et al. 2007; Nejrup and Pedersen 2008; Beca-Carretero et al. 2018). Water temperatures above optimum levels increase leaf respiration and reduce photosynthesis in seagrasses, which is a limiting growth factor for some species during summer (Kim et al. 2012; Rasmusson et al. 2020), and plays a key role in influencing seagrass growth in Langebaan Lagoon.

All sites had low water column pH in winter and higher pH in summer, which is a common trend in estuaries and nearshore environments (Daniel et al. 2013; Fietzke et al. 2015) because lower pH enhances seagrass photosynthesis which increases under higher light and temperature conditions (Koch et al. 2013, Cox et al. 2015, Borum et al. 2016). Given the strong negative correlation between plant biomass and water column pH in this study, it is predicted that lower pH will improve seagrass performance in Langebaan. Ecosystem engineers such as seagrasses, corals and macroalgae can influence water column pH at local scales (meters to kilometers) via CO_2 exchange during photosynthesis, respiration (autotrophs) (Hofmann et al. 2011; C. M. Duarte et al. 2013), and shell formation (calcifying organisms) (Mucci 1983; Hurd et al. 2009). As a result, the range and frequency of pH fluctuations may vary significantly across temporal and spatial scales (Hofmann et al. 2011, Saderne et al. 2013), concealing the local and global consequences of acidification on coastal ecosystems (Duarte et al. 2013). A fundamental necessity for understanding these impacts is long-term, high-resolution pH measurements *in situ*.

Similar to pH, oxygen levels can vary daily at small spatial scales (Felisberto et al. 2015) and while seagrass size and biomass were lower at Geelbek, dissolved oxygen (DO) levels were generally greater compared to sites closer to the mouth. At Geelbek, a combination of biological and abiotic variables was likely more influential than oxygen. Despite being the third most important contributor to seagrass variation (after exposure and turbidity), DO was identified as a strong predictor of seagrass density and biomass in the GAMMs. DO levels are presumably controlled by photosynthetic rates (Silva et al. 2009) and land-based runoff enriched by organic matter from surrounding salt marshes at Geelbek and

Bottelary (Whitfield 2005). Furthermore, the greater concentration of particle matter in the water column at Geelbek is most likely related to phytoplankton, which might impact respiratorily and photosynthetically driven DO levels (Clavier et al. 2011).

Geelbek had the highest temperature, salinity, turbidity, oxygen, and chlorophyll a levels across all seasons, which, coupled with the long period of emergence, generated distinct local conditions that favoured a particular seagrass morphotype (i.e., shorter leaves and lower biomass). During high tide, it was also the shallowest location, with seagrasses localized at the upper intertidal and rarely spreading into mid or lower shore sections. Tidal flow patterns at the southern end of the lagoon resulted in increased suspended particles (highest average turbidity: 23.79 3.07 NTU), reducing light levels in the water column, while light reaching seagrass beds closer to the mouth was likely similar given the comparable depths at which these populations occur (Flemming 1977). The decreased irradiance during submergence could explain the establishment of narrow fringing beds at Geelbek, as the limiting light environment confines plants to this shore height. Light variation and exposure were important factors impacting differences in seagrass growth between sites, as seen by the biggest variation being attributed to exposure and turbidity (Table 3.3), both of which were significant predictors of all seagrass metrics (Fig. 3.4). Suspended sediment has been shown to have a direct impact on seagrasses by a combination of light reduction, burial (smothering), or affects to the physico-chemistry of the rhizosphere, resulting in loss and changes in seagrass community structure (Zabarte-Maeztu et al. 2021). The migration of *Zostera capensis* and many other seagrass species to upper shoreline positions where they are exposed to supra-optimal air temperatures for extended periods, suggests that these plants are better able to cope with high UV and desiccation but not low irradiance in the water column (Björk et al. 1999; Kim et al. 2020).

4.2. Environmental Influences on Seagrasses

Environmental variables contributed 66% to the observed variation in seagrass parameters, with exposure as a consequence of shore height contributing the highest (19.21%) spatial variability. Many seagrass species, including *Zostera capensis*, exhibit morphological acclimation in the form of downsizing in the upper intertidal zone. Smaller shoots and narrower leaves, such as those found at Geelbek and Bottelary, are a characteristic feature associated with tolerance to desiccation in intertidal seagrasses, since a general reduction in size reduces rates of water loss (Tanaka and Nakaoka 2004; Shafer et al. 2007; Cabaço et al. 2009). Small narrow leaves indicate phenotypic plasticity because damage to photosynthetic tissue is decreased in shorter leaves (Tanaka and Nakaoka 2004, Shafer et al. 2007). Björk et al. (1999) observed that *Halophila ovalis* from Zanzibar, East Africa, coped with desiccation in the upper intertidal by flexing down their thin, malleable leaves to flatten out on the sediment surface during low tide, and remain moistened by sediment pore-water and inflow from upper levels of the shore. In the same tidal zone, *Halodule wrightii* formed dense stands allowing leaves to overlap during emersion and avoid drying out when not in direct contact with the moist sediment (Björk et al. 1999). Both these strategies were observed for *Z. capensis* in upper intertidal sites in Langebaan.

In seagrass populations around the world, phenotypic plasticity has been documented, demonstrating an immediate response to environmental conditions in a single generation. Intertidal populations of *Zostera japonica*, *Z. noltei* and *Z. marina*, for example, produce shorter, narrower leaves compared to subtidal populations (Peralta et al. 2000; Cabaço et al. 2009), indicating a key acclimation strategy that demonstrates resilience and an ability to survive in sub-optimal conditions. In other cases, reductions in shoot size from subtidal to intertidal zones have been observed in *inter alia Z. capricorni, Halodule uninervis* and *Halophila ovalis* in Australia (Dawson and Dennison 1996), *H. wrightii* in Florida (Phillips 1967), *Cymodocea rotundata* and *Thalassia hemprichii* in Japan (Tanaka and Nakaoka 2004) and *H. ovalis* in Thailand (Kaewsrikhaw et al. 2016). Similar acclimations were seen in *H. wrightii* and *H. ovalis* by Den Hartog (1970). Large, upright leaves of low intertidal, and subtidal populations are difficult to flex downwards onto the sediment, making them more vulnerable to desiccation, as was seen in *C. rotundata* and *T. hemprichii* populations in East Africa, which resulted in die-offs when exposed during extremely low tides (Bjork et al. 1999).

Seagrass populations in Langebaan Lagoon are likely clonally distributed with low genomic diversity suggesting high connectivity and gene flow (Phair et al. 2019). Gene flow is mostly vegetative with occasional seed dispersal and observed differences between high (Oesterval) and low (Geelbek) shore populations are attributed to phenotypic responses to environmental conditions rather than genetic variations. In addition, the two morphotypes were not observed to co-occur within the same site i.e., average leaf length/widths were consistently greater at sites closer to the mouth and smaller in high shore sites further away (Fig. 3.2). As a result, there was no indication that morphological expressions were not solely because of prevailing environmental conditions. Similarly, the genetic basis for environmental acclimation in three paired populations of *Zostera marina* suggested relatively high gene flow and low genetic differentiation among submerged and exposed populations in the Wadden Sea, Germany (Oetjen and Reusch 2007). In that study, a possible functional link with environmental characteristics that explained divergences for some populations, was a locus responsible for channelling water across cell membranes (Oetjen and Reusch 2007). Daily changes in respiratory and physiological responses in *Posidonia oceanica* in Revellata Bay, Mediterranean Sea, were found to be unparalleled expressions of related genes in high and low shore plants as a consequence of variation in light conditions (Procaccini et al. 2017). Shallow plants displayed more efficient energy use through photochemical channels because of the elevated light available, requiring higher synthesis of proteins for protection and recovery from photodamage compared to submerged plants. These genetic distinctions indicate the prevalence of locally adapted genotypes to varying light environments in exposed and submerged meadows (Procaccini et al. 2017). Similar genetic expressions that suppress or stimulate loci to adapt to local environmental conditions, are likely responsible for differences in high and low shore populations of *Z. capensis* and require further investigation.

While specialised acclimations to reduce rates of water loss during air exposure are not apparent in leaf tissue of upper intertidal seagrasses (Björk et al. 1999, Tanaka and Nakaoka 2004), the ability to tolerate desiccation is certainly key to their survival. *Zostera capensis* has a thin leaf cuticle that is perforated and fragile in places potentially lacking a physiological barrier to desiccation (Barnabas et al. 1977). Previous

studies of responses of *Z. capensis* to desiccation stress found that recovery was primarily attributable to new leaf growth rather than rehydration of desiccated leaves (Adams and Bate 1994). Faster leaf turnover rates have been observed in smaller compared to larger seagrass plants (Marbà et al. 2006), further evidenced in the average lifespan of individual leaves of the small *Z. japonica* which is > 10 days less than that of larger leaves of *Z. marina* (Lee et al. 2006). High leaf turnover appears to be a strategy in small-leaved populations to offset energy costs of leaf production compared to repairing desiccation damage (Shafer et al. 2007). Higher leaf production also results in denser meadows with overlapping leaves, which buffers water loss and compensates for the absence of a robust cuticle layer (Barnabas et al. 1977, Adams and Bate 1994).

The observed disparities in leaf form and biomass across Langebaan Lagoon might be explained by environmental variables at the site scale. Other environmental factors, such as flow rate, wave energy, and water retention time, as well as nutrient levels in the sediment and water column, can differ at small (tens of meters) spatial scales (Cardoso et al. 2004; Borg et al. 2005; Delgard et al. 2016) and are likely to influence seagrass growth in addition to seasonal variability (Alcoverro et al. 1995; Duarte et al. 2006). Investigations of *Zostera marina* beds in San Diego Bay, USA, for example, revealed that sites within the bay differed from those closer to the mouth in density and biomass (Moore and Hovel 2010), as observed in Langebaan. This is most likely due to environmental gradients from the mouth to the head which influence parameters including salinity, nutrient delivery, and water retention time (Largier et al. 1997). Furthermore, the hydrodynamics of a system including flow velocity and wave action have been demonstrated to influence gas exchange and nutrient uptake in seagrass plants (Schanz and Asmus 2003; Cornelisen and Thomas 2006). In Puget Sound, USA, wave energy was found to be the primary factor influencing the distribution of *Z. marina* accounting for 86% of variability in seagrass percent cover (Stevens and Lacy 2012). Similarly, meadows of *Posidonia oceanica* in Malta, revealed less overall cover, more complex patch morphologies, and lower within-patch structural complexity throughout a low to high gradient of wave exposure (Pace et al. 2017).

Barr et al. (2008) discovered that at saturating light levels, wave surge enhanced wet mass while bulk flow rates boosted nutrient access in the macroalga *Ulva australis*. Mainstream velocity of seawater influences rates of nutrient uptake in macroalgae and is a critical component in defining macroalgae productivity, structure and physiology (Hurd 2000; Barr et al. 2008), extending also to seagrass systems (Weitzman et al. 2013; Gillis et al. 2017; El-Hacen et al. 2019). This lends support to the presence of larger plants towards the mouth of Langebaan Lagoon, where water velocity and flow rates are likely to be higher than at the lagoon's far end.

Environmental forcing alone may not be responsible for seagrass development but may include species-specific traits that influence plant physiological responses to exposure, depth, temperature and light limitations (Tanaka and Nakaoka 2004; Staehr and Borum 2011; Park et al. 2016; Park et al. 2021; Peralta et al. 2021). Intrinsic factors such as the ability to store and use resources as well as partition resources for growth (e.g., rhizome internodes, leaf growth or reproduction) may also contribute to patterns in seagrass morphological responses to environmental conditions, and further explain the temporal and

spatial patterns in *Zostera capensis* in Langebaan Lagoon (Lawrence and Bolton 2023). *Z. capensis* exhibits intraspecific acclimation to environmental contexts through the expression of specific morphological characteristics (Lawrence and Bolton 2023).

Rising global temperatures are predicted to have a significant impact on the growth of intertidal seagrasses (Rasheed and Unsworth 2011; Hammer et al. 2018), particularly at sites that are exposed for longer periods (Valle et al. 2014) and where ambient water temperatures are likely to exceed thermal optima for growth and photosynthesis, such as at Geelbek. Temperature influences plant growth and metabolism in a variety of ways. These include metabolic rate reductions at low temperatures due to limitations on enzyme activity, light capture, and nutrient uptake, which gradually disappear with increasing temperatures, causing metabolic rates to rise along with a heightened demand for nutrients, resulting in nutrient limitation (Staehr and Borum 2011). Beyond optimum temperatures, metabolic rates are lowered due to a restriction in enzyme capacity, whereas supra-optimal temperatures eventually exhaust metabolic functioning through incapacitation or protein denaturing (Atkin and Tjoelker 2003) limiting productivity. The capacity for acclimation was found to be limited in three tropical seagrass species (*Z. muelleri*, *Halodule uninervis* and *Cymodocea serrulata*) studied over a latitudinal range of > 1,500 km, despite optimal temperatures and maximum photosynthesis (Catherine J. Collier et al. 2017). However, thermal optima can be useful in clarifying a species vulnerability to ocean warming in both present and future scenarios (Collier et al. 2017).

The considerable variation in seagrass morphological metrics between locations in Langebaan Lagoon, particularly between Centre Banks and Geelbek, provides insight into intraspecific acclimation strategies in *Zostera capensis* to cope with effects of temperature and exposure. The consequences of rising temperatures at Langebaan could include further population changes where small-leaved morphotypes replace large-leaved ones, resulting in lower biomass and reduced structural and habitat complexity. Warming may drive small-leaved populations to their ecological limits, resulting in population decline and overall loss of seagrasses in the system.

Declarations

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Figures

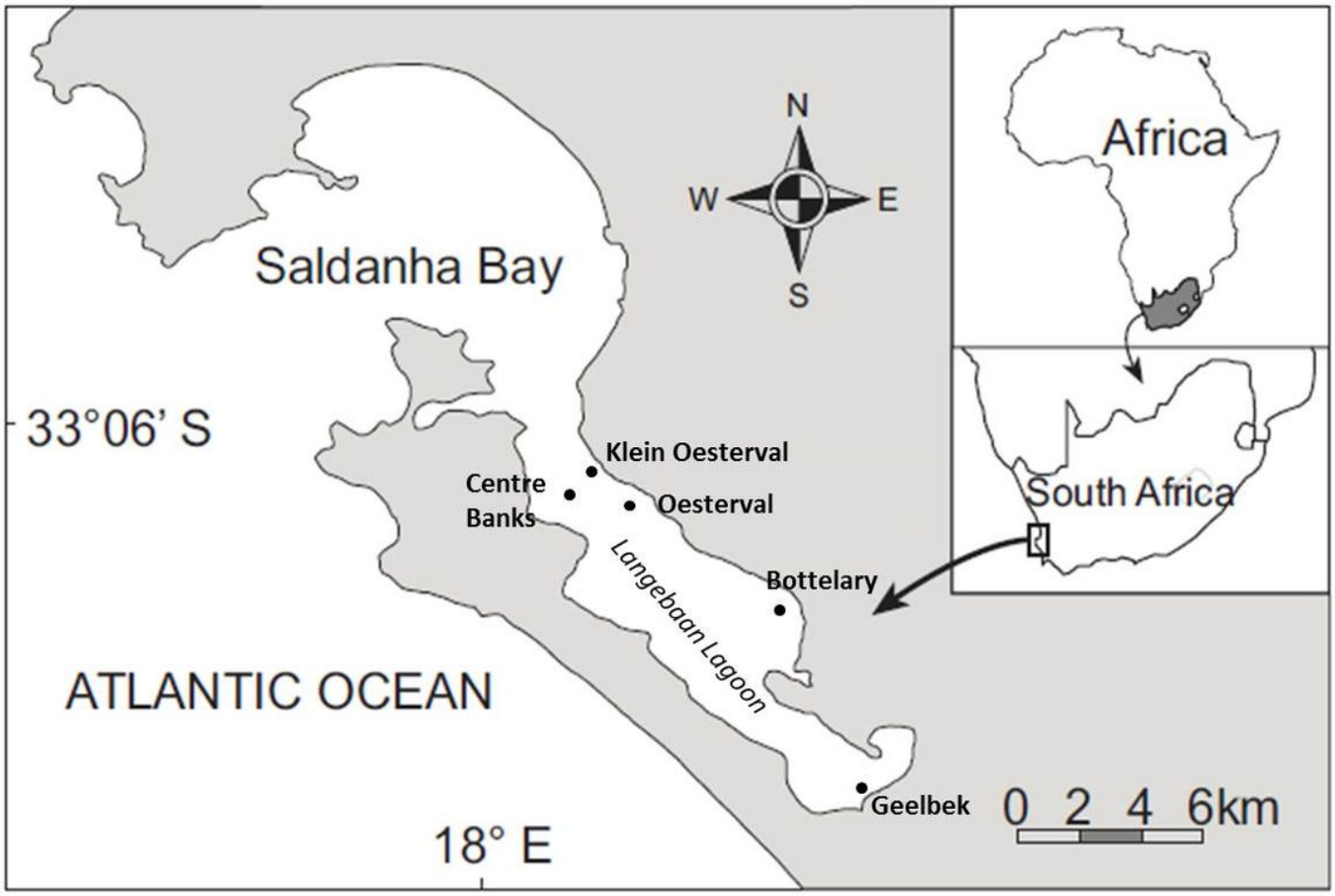

Figure 1

Langebaan Lagoon on the west coast of South Africa indicating the five major *Zostera capensis* populations sampled in this study.

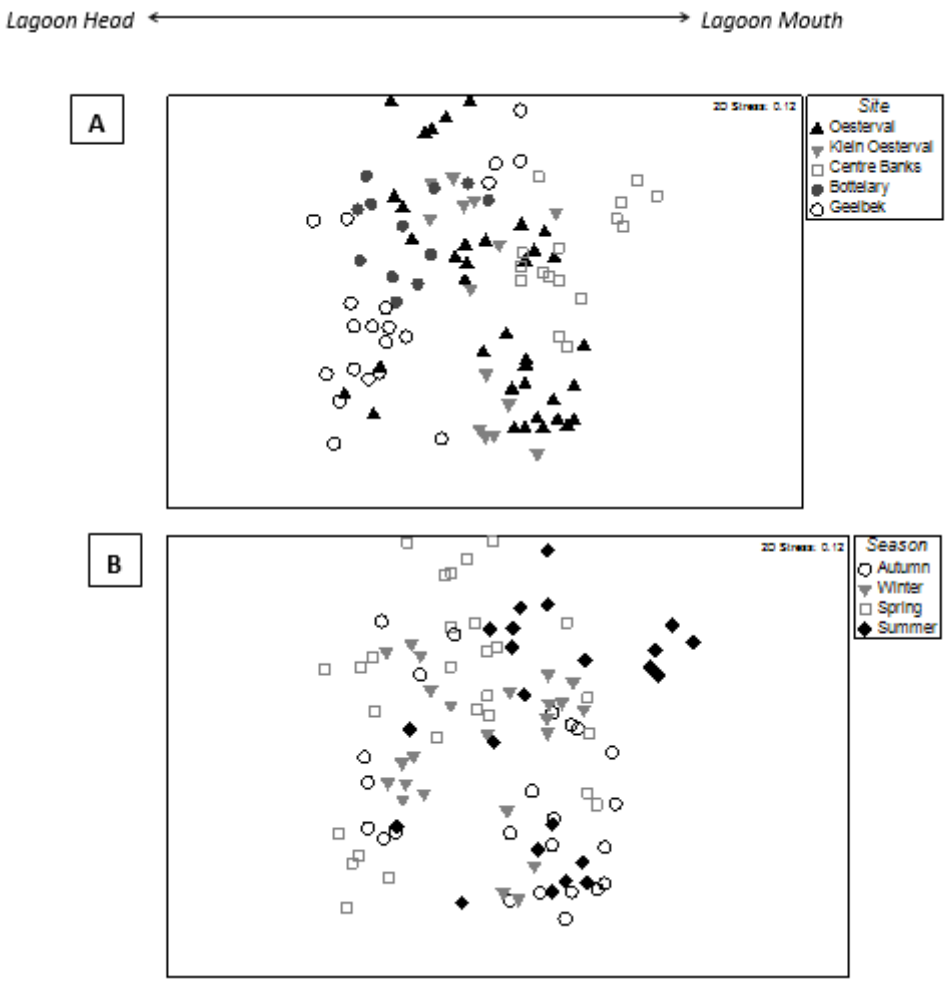

Figure 2

Fig. 3.1: Multi-dimensional scaling ordination of distances among centroids based on Euclidean distances for site (A) nested within season (B) distributions of morphometrics and associated epiphyte biomass of *Zostera capensis* in Langebaan Lagoon.

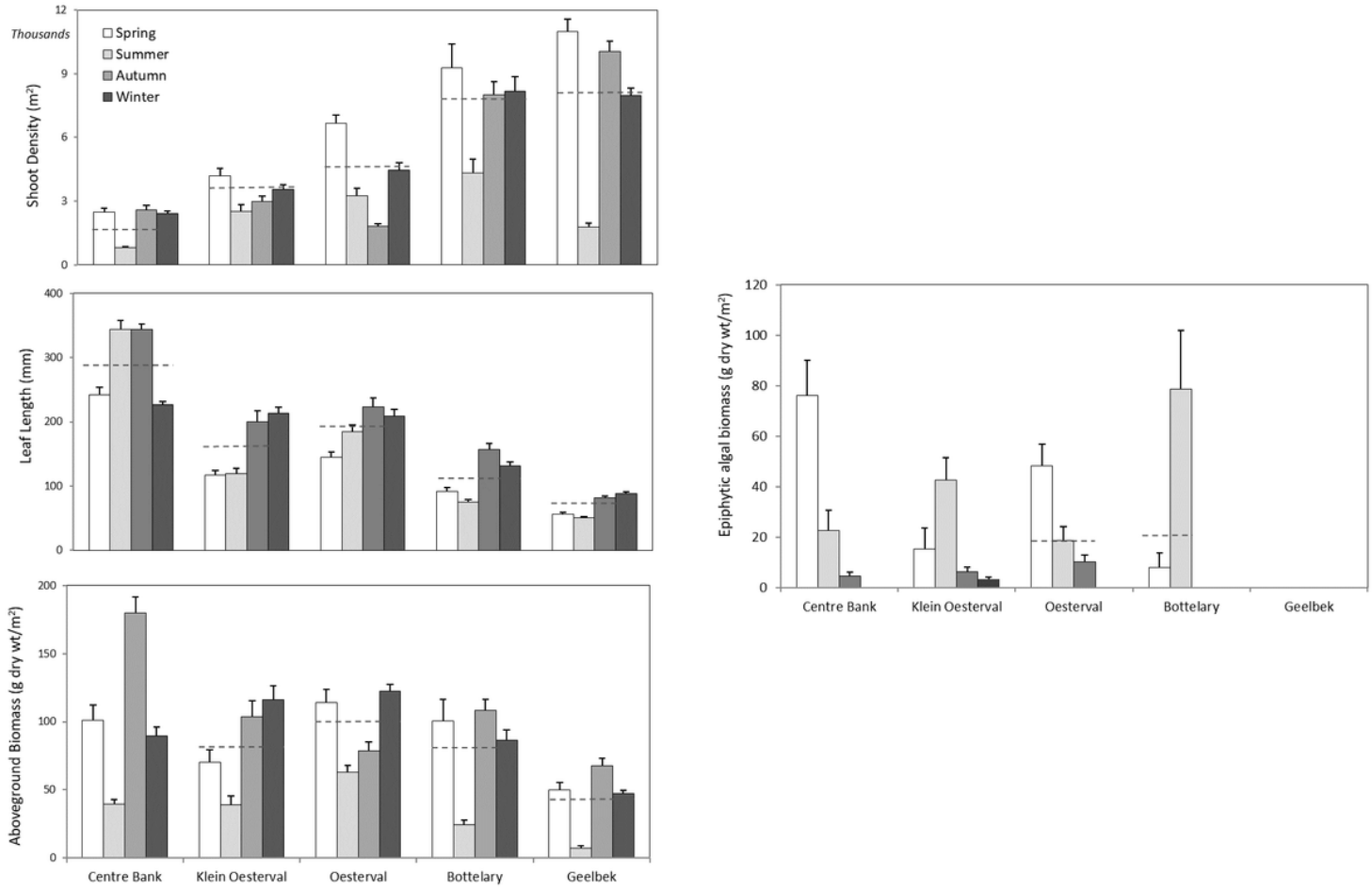

Figure 3

Fig. 3.2. Mean shoot density (A), leaf length (B), aboveground biomass (C), and epiphytic algal biomass (D) of *Zostera capensis*at four sites across four seasons. No epiphytes were recorded at Geelbek. Small letters indicate similar means (dotted lines), not significantly different when compared using an *a posteriori* Tukey HSD test. Error bars represent +1SE.

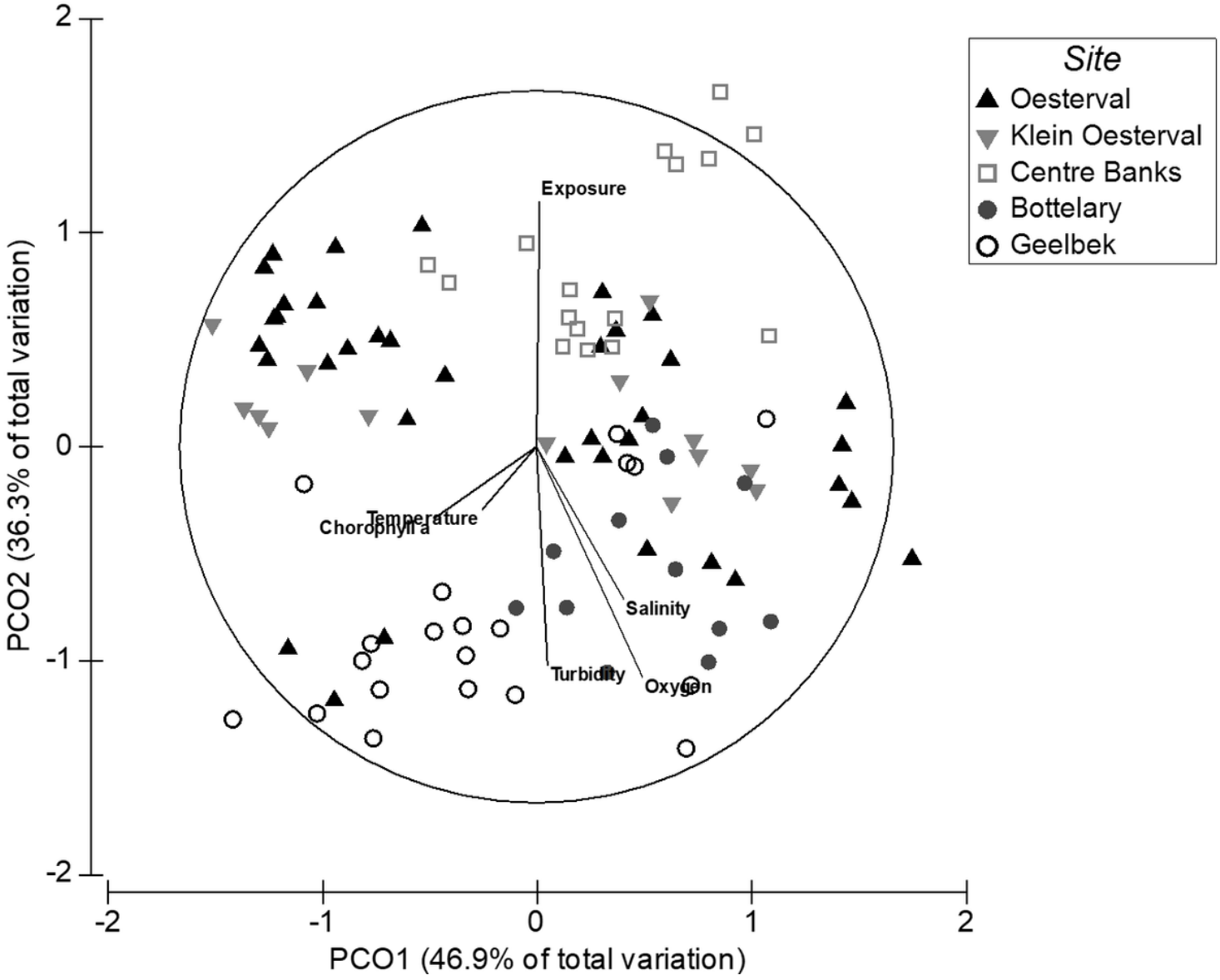

Figure 4

Fig. 3.3. PCO of seagrass metrics and epiphyte biomass from five sites in Langebaan Lagoon partitioned based on Euclidean distances between group centroids. Six environmental vectors are overlain, and lengths and direction of trajectories indicate the correlative strength of the relationship between environmental variables and the PCO axes.

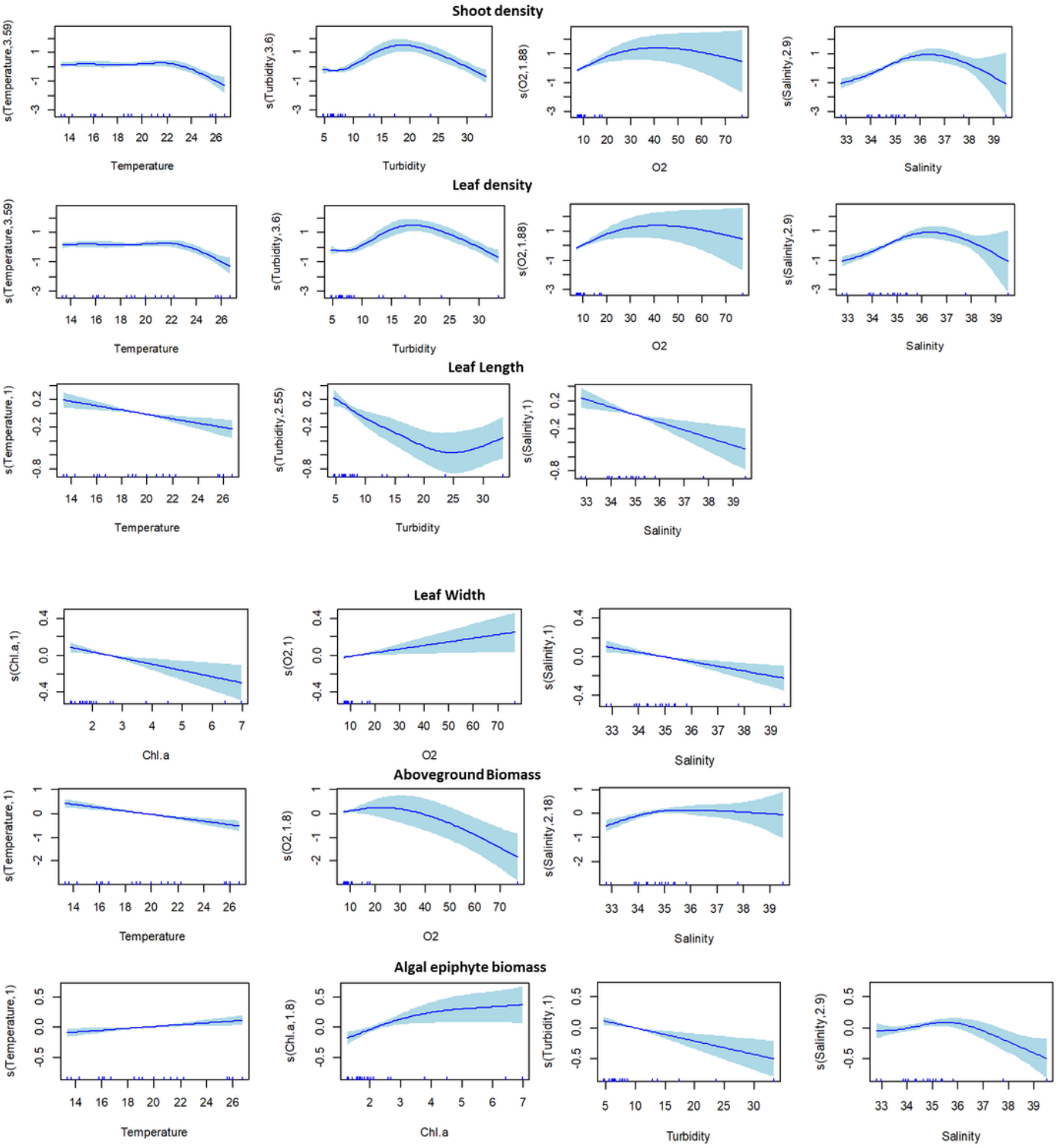

Figure 5

Fig. 3.4: Plots of significant environmental predictors with fitted smooth terms showing linear and non-linear relationships with six seagrass metrics from five sites in Langebaan Lagoon. Smoothed curves are represented by solid lines shaded by 95% confidence intervals. Short vertical lines (rug) on the x-axis indicate actual observations for each variable forming the basis of the model's response.The y-axis indicates the "component smooth" centred on zero representing partial residuals from the model fit.