

# Structural and Environmental Influences on Seagrass Epifaunal Communities: Seasonal Effects and Implications for Ecosystem Health

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## Abstract

Seagrass ecosystems play a vital role in marine environments, providing essential services, and supporting a diversity of fauna and algae that are critical components in marine trophic structures. However, global and local seagrass declines due to various influences raise concerns about the health of these ecosystems. This study investigated the structural and environmental drivers influencing epifaunal communities associated with the dwarf eelgrass (*Zostera capensis*), in a temperate lagoon ecosystem. Variation in epifaunal patterns across phenotypically distinct seagrass populations were observed. Large-leaved morphotypes in deeper intertidal stands near the lagoon mouth exhibited higher species diversity and richness. Conversely, small-leaved populations in higher shore stands supported greater species abundances, notably, two desiccation-resistant gastropods, *Assiminea* sp. and *Siphonaria compressa*. Seasonal differences in epifauna were significant, with higher abundances observed during spring and summer, while diversity and richness peaked in autumn and winter. Several key factors influencing epifaunal abundances were identified. The results of structural equation modelling showed seagrass shoot densities and leaf width to have positive direct effects, with light (turbidity) and oxygen levels also playing important roles. Temperature, pH, and exposure indirectly affected epifaunal abundances, however, temperature had a direct effect on seagrass structure and significantly influenced five out of six seagrass metrics measured. Ongoing assessments of seagrass distribution in the lagoon indicate more significant declines in populations near to the lagoon mouth, suggesting a simultaneous reduction in associated epifaunal communities reliant on large-leaved seagrass beds. As climate change-induced warming continues, further declines in seagrass populations are anticipated, particularly in large-leaved varieties. This trend is likely to have adverse consequences for the associated epifaunal communities and other trophic levels within the ecosystem. Given the significance of seagrass habitats for food provision and sustaining livelihoods, the loss of these ecosystems could have far-reaching consequences. Preserving seagrass ecosystems is therefore crucial to ensuring the continued provision of these ecosystem services.

## Structural and Environmental Influences on Seagrass Epifaunal Communities: Seasonal Effects and Implications for Ecosystem Health

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Seagrass ecosystems play a vital role in marine environments, providing essential services, and supporting a diversity of fauna and algae that are critical components in marine trophic structures. However,

global and local seagrass declines due to various influences raise concerns about the health of these ecosystems. This study investigated the structural and environmental drivers influencing epifaunal communities associated with the dwarf eelgrass (*Zostera capensis*), in a temperate lagoon ecosystem. Variation in epifaunal patterns across phenotypically distinct seagrass populations were observed. Large-leaved morphotypes in deeper intertidal stands near the lagoon mouth exhibited higher species diversity and richness. Conversely, small-leaved populations in higher shore stands supported greater species abundances, notably, two desiccation-resistant gastropods, *Assimineia* sp. and *Siphonaria compressa*. Seasonal differences in epifauna were significant, with higher abundances observed during spring and summer, while diversity and richness peaked in autumn and winter. Several key factors influencing epifaunal abundances were identified. The results of structural equation modelling showed seagrass shoot densities and leaf width to have positive direct effects, with light (turbidity) and oxygen levels also playing important roles. Temperature, pH, and exposure indirectly affected epifaunal abundances, however, temperature had a direct effect on seagrass structure and significantly influenced five out of six seagrass metrics measured. Ongoing assessments of seagrass distribution in the lagoon indicate more significant declines in populations near to the lagoon mouth, suggesting a simultaneous reduction in associated epifaunal communities reliant on large-leaved seagrass beds. As climate change-induced warming continues, further declines in seagrass populations are anticipated, particularly in large-leaved varieties. This trend is likely to have adverse consequences for the associated epifaunal communities and other trophic levels within the ecosystem. Given the significance of seagrass habitats for food provision and sustaining livelihoods, the loss of these ecosystems could have far-reaching consequences. Preserving seagrass ecosystems is therefore crucial to ensuring the continued provision of these ecosystem services.

**Keywords:** Macrofauna, *Zostera*, phenotypic plasticity, structural equation modelling, temperate lagoon, Langebaan Lagoon.

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## 1. Introduction

Preserving and perpetuating biological diversity is grounded in the understanding that a decline in biodiversity could disrupt ecosystem functioning and thereby jeopardize the array of vital ecosystem services benefiting society (Costanza et al., 1997; Hooper et al., 2012; McCann, 2000). A diverse ecosystem inherently entails functional redundancy, where multiple species can perform specific roles. This redundancy ensures that functional ecosystems persist even if one species faces stressors like disease or over-exploitation. Species sharing similar functions might exhibit varied responses to stressors, bolstering ecosystem resilience. This, in turn, sustains ecosystem stability and enhances the probability of recovery from stress or disturbances (Elmqvist et al., 2003).

The preservation of biodiversity is indispensable for enhancing the capacity of intricate systems to navigate change and to diminish susceptibility to species loss. The higher the stability of an ecosystem, the more significant its role in supplying critical services to society, including carbon dioxide recycling, oxygen production, and the maintenance of productive fisheries (Balvanera et al., 2006; Cardinale et al., 2012; Ghilarov, 2000; Hooper et al., 2005). Examining the diversity of fauna within marine or terrestrial systems holds significance as it enables the exploration of various hypotheses related to the mechanisms underlying species distributions and the preservation of biodiversity (de Juan et al., 2013; Virta et al., 2021).

Benthic macrofauna in coastal ecosystems are primarily composed of molluscs, amphipods, decapods and polychaetes which often play a key role as the trophic link between primary producers and pelagic consumers (Heck et al., 2008). In a typical seagrass food web, the main components include seagrass plants, periphyton, algal epiphytes, detritivores, invertebrate grazers, vertebrate grazers, meso-predators, piscivorous predators and humans (Duffy, 2006). Seagrass structure supports macrofaunal communities that predominantly occur as epifauna (living on seagrass blades), and infauna (dwelling in or on sediment surfaces) (Bologna & Heck, 1999; Klumpp & Kwak, 2005; Leopardas et al., 2014). Macrofauna serve as a vital link in the food chain, connecting primary producers with intermediate and larger predators, both directly and indirectly associated with seagrass habitats (Baden et al., 2010; Heck et al., 2008).

Seagrass habitats support a remarkable diversity of fauna and algae, even though the seagrass plants themselves have relatively limited species diversity. For instance, Orth et al. (1984) compared faunal community densities between seagrass meadows and unvegetated areas from several studies and discovered that seagrass meadows consistently supported a richer assemblage of fauna compared to nearby unvegetated areas in both tropical and temperate ecosystems. These patterns have been observed in other studies primarily attributed to the structural complexity of seagrass habitats, the abundance of food found within them, and the greater stability of sediment in comparison to bare sandflats (Bos et al., 2007; Carr et al., 2016; McCloskey & Unsworth, 2015). However, there are exceptions to this general paradigm.

Disturbances by organisms like callianassids can influence faunal assemblages by favoring burrowing infauna, but when seagrasses are present, epifauna and seagrass-specific burrowers can replace them. This ecological shift can sometimes mask differences in species diversity indices between callianassid-dominated sandflats and seagrass habitats (Barnes & Barnes, 2012). However, in cases where locations lacking callianassid bioturbators were studied, specifically in the Knysna Estuary, South Africa, seagrass habitats were found to support fewer individuals compared to bare sandflats. While seagrasses did support more species, primarily due to the presence of epifauna, the numerical differences in individuals were statistically insignificant (Barnes & Barnes, 2014). Unvegetated sandflats typically harbour a distinct suite of species (Casares & Creed, 2008). Despite often having lower species diversity compared to vegetated areas, these unvegetated sandflats make a significant contribution to overall diversity in nearshore coastal environments.

The abundance of many macrofaunal species has been found to have a positive correlation with the structure of seagrass, including biomass, canopy and the root-rhizome system (Ávila et al., 2015; Edgar, 1990; S. Y. Lee et al., 2001). In *Zostera capensis* (Setchell) beds in Mozambique, macrofaunal patterns were attributed to the enhanced habitat complexity created by the standing crop and biomass of seagrasses (Paula et al. 2001). This pattern is also observed in smaller seagrasses with lower structural complexity, such as *Halophila decipiens*. In Guanabara Bay, Brazil, *H. decipiens* was found to support significantly greater macrofaunal diversity, richness, and density in seagrass habitats compared to bare sand (Casares and Creed 2008).

Seagrass stems and leaves provide a substrate for the attachment of epiphytes, periphyton and encrusting algae. Epiphytes include both micro- and macroalgae, while periphyton is a mucus-like layer that coats seagrass blades comprising largely of diatoms, blue green, red, and filamentous algae, as well as particulate material, bacteria and microfauna (van Montfrans et al. 1984, Klumpp et al. 1992). Algae and periphyton are highly nutritious and easily digested by grazing invertebrates which find both food and shelter in seagrass beds (Schneider and Mann 1991, Edgar 1992, McNeely et al. 2001). Furthermore, the structural substrate provided by seagrasses for photosynthesizing epiphytes significantly enhances primary productivity in seagrass ecosystems (Borowitzka et al., 2006; Smit et al., 2005). However, an excess of algal epiphytes can become problematic for seagrasses.

Coastal water eutrophication, primarily resulting from land-use practices and effluent discharges, has been associated with seagrass loss (Burkholder et al., 2007; Cardoso et al., 2004; Ruiz & Romero, 2003). While toxic effluent can be lethal to seagrasses (Govers et al., 2014; Koch & Erskine, 2001; Macinnis-Ng & Ralph, 2004; Negri et al., 2015), an excess of nutrients in the water can promote the growth of planktonic and benthic algae, which compete with seagrasses for nutrients and reduce light penetration in the water column, further inhibiting seagrass photosynthesis (Short et al., 1995). In addition, excessive epiphytic algal growth can

smother seagrasses (Nelson & Lee, 2001; Walker & McComb, 1992) and disrupt the balance of dissolved carbon dioxide and oxygen (Raun & Borum, 2013). In some cases, long-lived epiphytes can weigh down seagrass leaves, leading to breakage (van Montfrans et al., 1984). Climate warming, coupled with increased coastal eutrophication, is predicted to promote algal growth, adding further stress to seagrass ecosystems.

The influence of environmental factors, especially temperature, light (irradiance), and salinity, on seagrass growth and distribution has been extensively studied (Lawrence, 2023 *in review* ; K. S. Lee et al., 2007). Typically, seagrass growth exhibits a noticeable seasonal pattern characterized by increased growth during the spring and summer months, followed by a decline in autumn and winter (Dunton, 1990; Huong et al., 2003; Vermaat et al., 1987). This seasonal pattern is primarily attributed to the individual or interactive impacts of temperature and light (Clausen et al., 2014; Nejrup & Pedersen, 2008; Pérez-Estrada et al., 2021).

Salinity plays a key role in influencing the distribution, biomass, and productivity of macrofauna in estuarine and lagoon ecosystems (Al-Wedaei et al., 2011; Vuorinen et al., 2015; Whitfield, 1992). This influence is evident in the way species are distributed along a salinity gradient, ranging from seawater levels at the estuary mouth, to brackish conditions in the middle reaches, and ultimately encountering freshwater sources in the upper reaches (Allanson & Baird, 1999; Barnes & Ellwood, 2012). For instance, research conducted in 28 coastal water bodies, including estuaries, shallow bays, and lagoons in Sussex, England, identified seawater-derived salinity as the primary environmental factor driving the distribution of taxa across freshwater and saline assemblages (Joyce et al., 2005). Similarly, in the Celestun coastal lagoon in Mexico, benthic community structure was found to be spatially influenced by salinity along a gradient, while sediment characteristics had a temporal impact on species diversity without affecting abundance (Pech et al., 2007). These patterns are largely attributed to the ionic composition of the water body, which, in turn, is influenced by the salt composition of the soil and minerals introduced from runoff or seepage waters (Pérez-Ruzafa et al., 2011).

Changes in salinity levels resulting from processes such as evaporation, flooding, water abstraction, pollution, and reduced water flow have significant implications for the structure and abundance of macrofaunal communities (Allanson & Baird, 1999; Van Niekerk et al., 2013). For instance, in the Swartkops estuary in South Africa, where salinity levels are typically similar to seawater, sediment characteristics played a more prominent role in influencing macrobenthos (Mclachlan & Grindley, 1974). Following a flood event in this system, a substantial decrease in salinity occurred, leading to alterations in the distribution of macrobenthic organisms. These changes persisted for at least two years following the flood (Mclachlan & Grindley, 1974).

Teske and Wooldridge (2003) observed that endemic mud and sand fauna in estuaries in the Eastern Cape, South Africa, were primarily influenced by substrate characteristics, while salinity played a role in limiting species from marine and freshwater habitats. Langebaan Lagoon shares similarities with estuaries, despite the absence of direct freshwater input. It is believed that groundwater seepage, supported by the presence of freshwater-associated plants like *Phragmites australis* and *Typha capensis* on the southeastern banks of the lagoon, contributes to its unique conditions (Allanson & Baird, 1999; Christie, 1981). The lagoon's enclosed nature creates a relatively stable tidal environment, with water residence times exceeding 30 days observed in the inner basin (Largier et al., 1997). Salinity levels in Langebaan Lagoon vary from the mouth to the head (Lawrence, 2023 *in review* ), and while no effect of freshwater input was detected, increased salinities at locations like Bottelary and Geelbek are likely due to evaporation resulting from diurnal heating (Lawrence, 2023 *in review* ) as well as in the salt marsh creeks at the head of the lagoon (Day, 1959; Flemming, 1977).

In non-quantitative surveys of *Zostera capensis* beds, Day (1959) noted that macrofauna in Langebaan Lagoon exhibited a distribution pattern along a salinity gradient, ranging from marine species (mainly found in Saldanha Bay) to estuarine species (predominantly occurring in the lagoon). He attributed this pattern to the shelter provided by reduced wave action and its indirect impact on the substrate, rather than temperature or salinity. Day also observed that faunal community characteristics in Langebaan were similar to those in other estuaries in the Western Cape, South Africa (Day, 1959). However, specific detailed descriptions of macrofauna associated with seagrass habitats in Langebaan, both in terms of spatial and temporal dynamics, as well as the influence of environmental variables, are currently lacking. Such information is crucial for enhancing our understanding of macrofaunal diversity in this ecosystem.

The decline of seagrasses in Langebaan Lagoon has prompted an investigation into the role of algal epiphytes and the distribution of grazing epifauna. In this study, a specific group of macro-epifauna was examined using visual counts, which differs from traditional techniques used to quantify infauna. Traditional methods are more suitable for assessing a broader range of fauna associated with both seagrass and unvegetated habitats (Raz-Guzman & Grizzle, 2001). Visual counts, conducted during daylight hours, provide estimates of faunal composition that mainly represent non-cryptic, diurnal, and sessile species (Edgar et al., 2001). However, sampling during low tide can lead to an underrepresentation of potentially important ecological species (Pearman et al., 2016). Conversely, traditional coring methods may also miss cryptic components and patterns in species distribution influenced by succession and colonization, especially among sessile and motile epibenthic communities (Moura et al., 2008). As a result, both approaches categorize a subset of the overall faunal assemblage.

This study focuses on understanding the differences in epifaunal species composition among seagrass populations in vegetated areas only. To achieve this, a subset of species primarily involved in grazing on seagrasses and epiphytes was examined. Visual assessment was considered a suitable method to gauge the extent of epibenthic diversity supported by different seagrass morphologies. Visual techniques for assessing a subset of macrofauna in their natural habitat have been successfully employed in previous studies (Källén et al., 2012; Q. Lee et al., 2012; Poulos et al., 2013; Vonk et al., 2008) to address specific research questions and uncover meaningful patterns in diversity and species composition (Kuenen & Debrot, 1995; Vellend et al., 2008). Additionally, studies in other ecosystems like coral reefs and kelp forests have primarily focused on surface fauna, as assessing infauna, while enhancing overall diversity understanding, often involves significant habitat destruction and is generally avoided. Consequently, there exists a much larger body of literature on surface fauna in these ecosystems.

The objective of this study was to assess the spatial and temporal variations in macro-epifaunal community structure, including abundance, richness, and diversity, within *Zostera capensis* populations in Langebaan Lagoon. The primary factors that contribute to these variations were determined, including seagrass structural elements (such as biomass, leaf characteristics, density, and epiphyte biomass) and environmental factors (i.e., temperature, salinity, pH, turbidity, oxygen levels, and chlorophyll a concentration). This research provides a foundational understanding for further investigations into trophic interactions, specifically grazing, as well as the impacts of temperature on *Z. capensis* (Lawrence & Bolton, 2023).

## 2. Methods

### 2.1. Study Site and Sampling

Epifauna (hereafter referred to as epifauna) were assessed in intertidal *Zostera capensis* beds in Langebaan Lagoon on the west coast of South Africa (Map 1; 18°03'E, 33°08'S). Part of the West Coast National Park and designated a RAMSAR site for its ecological and conservation significance, the lagoon is an important wetland and layover for migratory birds (Christie, 1981; Compton, 2001; Day, 1959). It is approximately 15 km long and 4 km wide and opens into a bay with a mouth to the sea in the north. There is no freshwater inflow from rivers, instead freshwater input occurs through groundwater seepage during the rainy season (Whitfield, 2005). The lagoon experiences a spring tidal range of 1.8 m at the mouth to 1.5 m at the head (Day, 1959). The benthic substrate of the lagoon mainly consists of sandy sediment. In addition to *Zostera capensis*, various algal species and salt marsh grass (*Spartina* sp.) comprise the vegetation within and around the lagoon edge (Schils et al., 2001).

Sub-populations of seagrasses from five sites: Centre Banks, Klein Oesterval and Oesterval (closer to the lagoon mouth), Bottelary and Geelbek (further away from the mouth) were sampled in this study (Fig. 1). The sites were selected based on *a priori* knowledge of their position in the lagoon that displayed consistent and high seasonal and interannual *Z. capensis* coverage (Lawrence, 2023, *in review*).

### 2.2. Seagrass Metrics

At each site, five randomly selected cores ( $\emptyset = 10$  cm, 15 cm deep) were collected within *Zostera* beds across

four austral seasons (spring, summer, autumn and winter). Core samples were rinsed with seawater on-site then stored in labelled bags for transportation. In the laboratory, shoot and leaf densities and average leaf lengths and widths of the tallest 20% of shoots, were recorded. Roots/rhizomes were then separated from leaves, and epiphytes gently scraped off all leaves. Dry mass was estimated for seagrass leaves and epiphytes (60°C, 14 hrs).

### 2.3. Epifauna Sampling

To assess the influence of plant structure on epifaunal diversity and determine if different morphologically distinct seagrass populations supported varied epibenthic diversities, invertebrate fauna present in both the seagrass canopy and sediment surface was estimated. A visual census method was employed to quantify the densities of epifauna within quadrats (50 cm x 100 cm) targeting a size fraction >3 mm. The surveys were conducted during spring low tide when the seagrass beds were fully exposed. This method allowed for the quantification of a subset of seagrass-associated fauna, primarily focusing on invertebrates that graze on seagrass leaves and epiphyton and differs from traditional techniques used to quantify infauna i.e., digging and sieving sediments (Edgar et al., 2001). Traditional methods are more suitable for evaluating a general suite of fauna associated with both seagrasses and unvegetated habitats, which even if sampled collectively is often analysed separately to answer specific questions ((Rodil et al., 2021).

Five quadrats were randomly placed within each seagrass bed at each of the five sites across four seasons ( $n = 420$ ). Within each quadrat, all visible fauna present on, among, and below the seagrass leaves were identified and counted. If any specimen could not be identified on-site, they were collected for later identification. Species were then categorised into phyla and functional groups using guidebooks (e.g. (Branch, 2017) and the World Register of Marine Species ([www.marinespecies.org](http://www.marinespecies.org)).

### 2.4. Environmental Variables

To investigate the influence of environmental variables on epifaunal community structure, temperature, pH, turbidity, salinity, oxygen and chlorophyll *a* were recorded monthly at each site using a handheld CTD (Conductivity Temperature Depth profiler (YSI 6820 V2-2V)). The average of three readings taken approximately 10m apart constituted one measurement.

### 2.5. Epifauna diversity indices

Epifaunal community structure was described using the diversity indices related to the number and abundance of species recorded. Abundance was determined as the total number of individuals ( $N$ ) recorded across all sites and seasons. Species richness was defined using the Margalef index ( $d$ ) that calculates the average number of species per unit number of organisms collected (Margalef, 1989). Species diversity was first determined after the Shannon-Wiener index ( $H'$ ) (Shannon 1963), and thereafter converted to “effective number of species” by calculating the exponential ( $\exp(H)$ ) of each diversity value after Hill (1973). This transforms the non-linear  $H'$  to a linear form that permits statistical comparisons that are intuitive, while the unit “number of species” allows for diversity comparisons across metrics (Jost et al. 2006, Jost et al. 2010).

### 2.6. Statistical Analyses

Distribution of seagrass and environmental variables were explored using multi-panel scatterplots and rank correlations to evaluate outliers, correlations, and skewness. Strong co-linearity ( $\pm 0.7 - 0.9$ ) was identified between shoot and leaf densities, leaf length and width, and temperature and pH. These variables were excluded from multivariate analyses to avoid confounding the true degree of variability (Lipovetsky and Conklin 2001).

Diversity indices were assessed visually using histograms and q-q plots. Variances in the data were tested for normality (Shapiro-Wilk’s test) and homogeneity (Levene’s Test) and natural log transformed where necessary to meet assumptions for parametric analyses. Two-way factorial ANOVAs were used to test for main and interactive effects of site (random factor: five levels) and season (fixed factor: four levels) on each

index: abundance ( $N$ ), richness ( $d$ ) and diversity ( $H'$ ) followed by Tukey's HSD tests. Univariate analyses were performed using Sigma Stat (IBM SPSS Statistics 29).

Species abundance across seasons (fixed) and sites (random factor nested within season) was compared using multivariate data testing in PRIMER 6 (Clarke & Gorley, 2006). Abundance was considered an adequate metric on which to assess the effects of seagrass structure, epiphyte biomass and environmental factors since epifauna were largely comprised of grazers whose densities were important in controlling epiphytes (Hovel et al., 2002; Vonk et al., 2010). Data were 4<sup>th</sup>-root transformed to down-weight the influence of large variances. Visual assessments of relationships between variables in ordination space were made using non-metric multidimensional scaling (MDS) and cluster dendrograms based on Bray-Curtis similarity matrices. Non-parametric multivariate analyses of variance were explored using PERMANOVA (Permutational Multivariate Analysis of Variance) (Anderson et al. 2008). Within group differences as well as comparisons of species composition between groups (i.e., beta diversity, Anderson et al. 2006) were tested using Permutational Analysis of Multivariate Dispersions (PERMDISP (9999 permutations)). The relative contribution of individual taxa to the similarity among sites across seasons was evaluated using SIMPER (similarity percentage breakdown).

To determine the environmental factors (temperature, salinity, turbidity, pH, oxygen, chlorophyll  $a$  and exposure) and seagrass metrics (shoot density, leaf length, aboveground biomass, algal epiphyte biomass) that best explained epifaunal variability, a distance-based linear model (DistLM, selection procedure 'best' and criteria 'AIC') was used. DistLM calculates the proportion of variability contributed by each factor using multiple regression modelling to partition variation according to selected predictor variables (Anderson et al. 2008). After all possible model combinations were explored, the five best models that explain variability based on smallest AIC values and adjusted  $R^2$  derivatives are presented.

To partition the net effects of environmental variables (exogenous) and seagrass structure (endogenous) on epifaunal abundance (endogenous) into direct and indirect effects, maximum-likelihood estimated structural equation models (SEM) were created in AMOS (IBM SPSS Amos version 26 Graphics). Structural equation modelling is a multivariate analysis framework that encompasses techniques derived from factor and path analyses (Grace, 2009). This framework enables the examination of both direct and indirect relationships between observed and unobserved (latent) variables. These relationships are represented by paths that indicate the statistical dependency, and the associated parameters specify the magnitude of the effect (direct or indirect) of independent variables on dependent variables (observed or latent).

A full model was specified based on theory and hypothesised relationships that (i) exogenous environmental variables: temperature, salinity, pH and oxygen would positively or negatively influence endogenous variables: seagrass biomass, leaf length/width, shoot density, epiphyte biomass, chlorophyll  $a$  (chl  $a$ ) and epifaunal abundance; while (ii) turbidity and exposure would negatively influence all endogenous variables; and (iii) seagrass density, leaf length/width, epiphytes and chl  $a$  would positively influence epifaunal abundance. Stepwise model selection was performed in which variables with non-significant paths i.e. regression coefficients  $p > 0.05$  were removed until all remaining paths were significant ( $p < 0.05$ ) (Grace, 2009). Model fit was assessed using the chi-square value and the root mean square error of approximation (RMSEA) as measures of goodness-of-fit and evaluated by ensuring observed and predicted covariance matrices were aligned. Models were then adjusted to produce a low chi-square value with a corresponding  $p$  value  $> 0.05$  denoting observed and fitted models were not significantly different, and an RMSEA  $< 0.08$  indicating acceptable fit (Grace, 2009). The final model output presents standardized coefficients to compare the strength of direct and indirect effects.

### 3. Results

#### 3.1. Epifaunal Community Structure

Grazing invertebrates comprised 53%  $m^{-2}$  of total epifauna recorded in seagrass beds in Langebaan Lagoon (Table 3.1). This group was dominated by the generalist microgastropod *Assimineia globulus* (31.45%  $m^{-2}$ ) and the pulmonate limpet *Siphonaria compressa* (16.12%  $m^{-2}$ ). The keyhole limpet *Fissurella mutabilis* was only found in beds in the low shore zone comprising 3.26%  $m^{-2}$  of total epifaunal abundance (Table 3.1).

Seagrass beds also supported 43.45% m<sup>-2</sup> of predatory species, mainly the non-native anemone, *Sargartia ornata* (43.38% m<sup>-2</sup>). Dominant at sites closer to the lagoon mouth, this species was generally found in spring and autumn. In its native habitat (Mediterranean and Western Europe), *S. ornata* attaches to kelps and rocky shores, however in Langebaan Lagoon it is found among *Zostera* shoots attached to loose rocks and feeds mainly on amphipods and polychaetes (Robinson & Swart, 2015).

The hermit crab, *Diogenes brevisrostris* had a dual function as grazer and deposit feeder and comprised 2.67% of total abundance. A small percentage (0.83%) of suspension feeding organisms was also encountered, the most abundant being a solitary ascidian, *Pyura stolonifera* (0.4%), found mainly growing in sediment between seagrass shoots (Table 3.1).

### 3.1.1. Abundance

Epifaunal abundances exhibited a distinct gradient of increase from the mouth to the head of the lagoon (Fig. 3.1A). Bottelary displayed the highest abundances across all seasons (136.68 m<sup>-2</sup>) followed by Geelbek (83.78 m<sup>-2</sup>). This was due to elevated densities of *Assimineia globulus* and *Siphonaria compressa*. Oesterval exhibited an average species abundance of 79.14 m<sup>-2</sup>, while Centre Banks registered a slightly lower average abundance of 68.84 m<sup>-2</sup>. In contrast, Klein Oesterval recorded the lowest abundance among the surveyed sites (23.66 m<sup>-2</sup>). These sites were dominated by *Sargartia ornata*. Centre Banks supported the greatest average abundance of *Fissurella mutabilis* (26.55 m<sup>-2</sup>), while the hermit crab, *Diogenes brevisrostris* was most abundant at Klein Oesterval (36.74 m<sup>-2</sup>). *A. globulus* was also prevalent at high shore sites at Oesterval while *F. mutabilis* was exclusively found at sites closer to the mouth and absent at Bottelary or Geelbek. Similarly, *A. globulus* was not detected at Centre Banks and an average of 1.26 individuals was recorded at Klein Oesterval in winter.

Differences in abundance were significant across sites ( $F = 10.80, p < 0.001$ , Fig. 3.1A). Mean abundances at Centre Banks and Klein Oesterval were similar while Oesterval, Bottelary and Geelbek displayed homogenous means (Tukey HSD,  $p < 0.05$ , Fig. 3.1A). Despite the high abundance (252.93) of individuals at Centre Banks in autumn there were no significant seasonal differences in abundance between sites ( $F = 2.66$ , NS), however, the interaction between site and season proved significant ( $F = 6.68, p < 0.001$ ).

### 3.1.2. Richness

In contrast to abundance, epifaunal species richness exhibited a distinct trend, with higher values observed in proximity to the lagoon mouth and lower values towards the lagoon head (Fig. 3.1B). Centre Banks displayed the highest average species richness (1.48) across all seasons, followed by Klein Oesterval (1.27) and Oesterval (1.13). In contrast, the number of species recorded at Bottelary and Geelbek was comparatively lower (0.53 and 0.55 respectively). These differences were significant across sites ( $F = 8.01, p < 0.001$ ), seasons ( $F = 3.64, p = 0.02$ ) and their interaction ( $F = 3.09, p = 0.001$ ). Post hoc analysis revealed significant mean differences in means between each of the sites located closer to the mouth and the two sites at the lagoon head (Tukey HSD,  $p < 0.05$ , Fig. 3.1B). Seasonal variation in species richness was primarily driven by a significant difference observed between summer and autumn (Tukey HSD,  $p = 0.04$ ).

### 3.1.3. Diversity

Species diversity had a similar pattern to richness with higher values observed closer to the lagoon mouth and lower values at the lagoon head (Fig. 3.1C). Klein Oesterval exhibited the highest species diversity (2.40) followed by Centre Banks (2.28), Oesterval (2.05), and Geelbek (1.81) – diversity was lowest at Bottelary (1.47). These differences were significant across sites ( $F = 4.20, p = 0.004$ ) attributed mainly to differences in mean diversity between Bottelary and Centre Banks, and Bottelary and Klein Oesterval (Tukey HSD,  $p = 0.006$ ). Seasonal differences in diversity were also significant ( $F = 6.54, p = 0.001$ ) as well as the interaction between site and season ( $F = 2.70, p = 0.004$ ) indicating variations in diversity between warmer and cooler months (Tukey HSD,  $p < 0.05$ ).

## 3.2. Spatiotemporal Variations in Epifaunal Communities

Both site and season were found to have significant influence on variation in epifaunal abundance within *Zostera capensis* habitats in Langebaan Lagoon (PERMANOVA,  $p < 0.001$ ; Table 3.2). Site differences accounted for the largest proportion (36.83%) of the observed variation, which was more than twice the contribution of seasonal differences (17.28%). A significant portion of variation (21.33%) was attributed to the interaction between site and season, while 24.56% of epifaunal variation remained unexplained (Table 3.2). Site differences were evident in the clear spatial separation of epifaunal abundance in the dendrogram and MDS plot showing a 60% dissimilarity in two groupings (Fig. 3.2 A&B). One cluster comprised Centre Banks, Klein Oesterval and Oesterval (closer to the mouth), and the other Bottelary and Geelbek (closer to the head of the lagoon).

Beta-diversity differed between sites (PERMDISP:  $F = 17.8, p < 0.01$ ), with pairwise comparisons confirming differences in abundances between sites at the mouth and those at the lagoon head (pairwise PERMDISP  $t = 2.48, p < 0.04$ ). The species *Siphonaria compressa* and *Assimineia globulus* contributed largely to the observed dissimilarity contributing as much as 91% to the observed variation (Table 3.3). *Fissurella mutabilis*, *Parvulastra exigua*, *Diogenes brevisrostris* and *Pyura stolonifera* were the main species accounting for >60% of observed patterns at Centre Banks, Klein Oesterval and Oesterval (Table 3.3).

Although spatially distinct seasonal patterns were not clearly evident, the assessment of individual sites revealed seasonal groupings with varying degrees of similarity, ranging from 25 to 75% (Fig. 3.3). MDS plots separated species abundances in spring from summer, autumn and winter at Centre Banks and Klein Oesterval. In the case of Oesterval, abundances were separated into two groups: spring and summer, and autumn and winter (Fig. 3.3). No distinct seasonal grouping was observed for Bottelary, while at Geelbek, the abundance in autumn appeared to be different from the other seasons (Fig. 3.3). Generally, there was no significant seasonal effect observed in beta-diversity (PERMDISP:  $F = 3.24, p = 0.09$ ), however pairwise comparisons revealed significant differences between epifaunal abundances in autumn and winter (pairwise PERMDISP  $t = 3.31, p < 0.01$ ) and winter and summer (pairwise PERMDISP  $t = 3.19, p < 0.01$ ).

### 3.3. Influence of Environment and Seagrass Structure on Epifaunal Abundance

All seagrass variables including epiphytic algal biomass were significant in explaining variation in epifaunal abundance (PERMANOVA: DistLM,  $p < 0.01$ , Table 3.4). Initially, distance-based linear models were run without including leaf width due to its strong correlation with leaf length. However, a better fit was achieved when leaf width was included. Among the seagrass variables, leaf width contributed the highest proportion of variation in epifaunal abundance, followed by leaf length, density, biomass, and epiphyte biomass (Table 3.4). All seagrass variables were selected in the first model that best explained variability in epifaunal abundance determined by lowest AIC and highest  $R^2$  values. The second best model which included four variables (density, leaf width, epiphyte and seagrass biomasses), and had an AIC value < 2 levels from the first model, also adequately explained the observed variation (Table 3.4).

Environmental variables assessed independently in a DistLM marginal test, found exposure to contribute the highest proportion of variation followed by chl *a* and turbidity (Table 3.5). Temperature, salinity, and oxygen accounted for smaller proportions of variation (Table 3.5). All environmental variable contributions were significant ( $p < 0.001$ ). The top two models based on AIC and  $R^2$  parameters, that best explained variation in epifaunal abundance selected five (all) and four (excluding turbidity) environmental variables respectively (Table 3.5).

The final structural equation model (SEM) employed to explore the influence of environmental variables and seagrass metrics on epifaunal abundance revealed several noteworthy findings. The direct effects of temperature, salinity, pH, and exposure on abundance were found to be non-significant (chi-square = 90.66,  $df = 45, p = 0.35, RMSEA = 0.083$ ; Fig. 3.4B). However, turbidity exhibited a strong negative direct effect (-0.85), while oxygen displayed a positive direct effect (1.09). Indirectly, temperature, pH, exposure, and oxygen had negative effects on epifaunal abundance, whereas turbidity had a positive indirect effect (Table 3.6). Although all environmental variables directly influenced leaf length, this did not translate into indirect effects on abundance. In contrast, leaf width was negatively influenced by temperature and turbidity, and

positively influenced by pH and exposure. It exerted a positive direct effect, explaining 65% of the variation in abundance (Fig. 3.4B, Table 3.6). Similarly, shoot density had a positive direct effect on abundance, accounting for 65% of variation (Fig 3.4B). Shoot densities were negatively influenced by pH, oxygen and exposure and positively affected by turbidity (Table 3.6). No other seagrass metrics emerged to directly influence epifaunal abundances.

#### 4. Discussion

Epifaunal biodiversity in *Zostera capensis* beds in Langebaan Lagoon, as reflected by species diversity and richness, exhibited a pattern of higher values nearer the lagoon mouth and in beds situated below mean low water levels. In contrast, a decline in these measures was evident upstream and in high shore beds. Species abundances displayed a divergent trend, with lower counts observed at the mouth and higher counts in upstream locations. Spatial and temporal disparities significantly impacted epifaunal species abundance, primarily driven by two species among the total of 24 recorded. Notably, these differences were pronounced and linked to specific locations and seasons. Environmental factors played a more substantial role, both directly and indirectly, in explaining the observed variation than the structural attributes of the seagrass beds.

##### 4.1. Richness, Abundance and Diversity of Seagrass Epifauna

Despite fairly stable salinities in the lagoon, species richness and diversity displayed a similar pattern of decline from the mouth as observed in typical estuaries where variation in faunal communities are largely influenced by a salinity gradient (Allanson & Baird, 1999; Barnes, 2010; Heymans & Baird, 1995). However, unlike typical estuaries, salinity levels in the lagoon increased with distance from the mouth likely due to evaporation and the lack of distinct inflow of freshwater. Variation in epifaunal community structure is not necessarily attributed directly to salinity but could be an indirect effect since salinity is often correlated with other environmental variables (Yamada et al., 2007). Factors such as current velocity, wave intensity, competition, and predation, which were not assessed in this study, could account for the unexplained variation in community structure.

In a similar enclosed bay with no freshwater input and a relatively high salinity range (22 - 35) in Arcachon, France, macrofauna in beds of another dwarf-eelgrass, *Zostera noltei* showed similar patterns to that observed for Langebaan Lagoon (Blanchet et al., 2004). Species richness was lowest in assemblages furthest from the mouth and at higher tidal levels while abundances were highest at these places. In that study, distance from oceanic waters (km) was used as an environmental factor and was the main attributor of differences between assemblage groups along with tidal range (Blanchet et al., 2004). Similarly, Barnes and Ellwood (2012) found richness and diversity to be highest in *Z. capensis* beds below mean low water levels in the marine-dominated section of the Knysna estuary, South Africa. In that large estuarine system species richness did not display the classic decline with distance from the mouth, but instead had a stable fauna separated by abrupt changes in areas where salinity levels fell below 30 (Barnes & Ellwood, 2012). In Arcachon, species occurring in areas of relatively low salinities were not distinct but rather a subset of those present at the mouth, which was not the case at Langebaan. Several species were found only at sites closer to the mouth and not at Bottelary and Geelbek. In contrast, a stable faunal composition was observed at Knysna despite the wide range in salinity (<5–35). While the observed variation in Knysna was supposedly due to changes in relative abundance of dominant species, or the lack of marine species in upstream localities and upper boundaries of seagrass beds (Barnes & Ellwood, 2012), species variation in Langebaan was more likely a result of exposure and tolerance to desiccation (this study), availability of seagrass habitat (Angel et al., 2006) as well as the ability to survive under periods of exposure to sun and wind during low tide (Day, 1959).

In Langebaan Lagoon, epifaunal community structure was dominated by grazers i.e., *Siphonaria compressa*, *Fissurella mutabilis* and *Assiminea globulus*. *A. globulus* was the main species recorded at Bottelary and Geelbek and occurred in lower abundances in high shore beds at Oesterval and Klein Oesterval, although high abundances were previously observed at Oesterval in both seagrass and saltmarsh vegetation in the high shore (Day, 1959). Regarded as a broad niche generalist and capable of adapting to a range of environmental

conditions, this mud snail feeds mainly on bacteria and diatoms found on sediment surfaces and occasionally on epiphytic periphyton and is strongly averse to prolonged periods of submergence (Angel et al., 2006). Gastropods have been documented to dominate many estuarine systems (Allanson & Baird, 1999) and Barnes (2013) recorded a dominance of gastropods including 125 times greater average densities of *Assiminea* in upper-estuarine and enclosed sites compared to elsewhere in the Knysna estuary. In Arcachon, seagrass beds at high shore sites and sites further from the mouth were dominated by a single gastropod, *Peringia ulvae* (Blanchet et al., 2004). The prevalence of gastropods in high shore areas is likely attributed to their ability to resist desiccation supported by the upward expansion of habitat provided by seagrass and saltmarsh vegetation.

High shore sites in Langebaan were also dominated by the pulmonate limpet *Siphonaria compressa* which has been identified as South Africa's most threatened marine invertebrate. Classified as Critically Endangered by the IUCN (Kilburn, 1996), this limpet has an extremely narrow habitat range and grows only in *Zostera capensis* meadows in Langebaan Lagoon and the Knysna estuary (Allanson & Herbert, 2005). In this study, densities of 100 m<sup>-2</sup> were recorded at Geelbek and Bottelary and <5 m<sup>-2</sup> at Oesterval. None were found at Klein Oesterval and Centre Banks, however, Angel et al (2006) found densities between 40-80 individuals per m<sup>2</sup> at the lower edge of seagrass beds at Klein Oesterval over a 30 year period. Analyses of faecal pellets revealed that *S. compressa* primarily feeds on bacteria, diatoms and filamentous algae found on seagrass leaves (Allanson & Herbert, 2005).

High abundances of the two dominant grazers *Assiminea globulus* and *Siphonaria compressa* at the same sites suggest a lack of competition and the exploitation of different niches. This hypothesis was explored by Angel et al. (2006) who assessed the interaction between *A. globulus*, *S. compressa* and *Zostera capensis* cover in relation to low tide exposure at Langebaan. They found that *S. compressa* thrived on the lower edge of seagrass beds subjected to shorter periods of exposure and suggested that the virtual absence of the limpet from the upper zone was largely the result of avoiding physiological stress from desiccation - a consequence of its small size and thin shell. Experimental transplants of seagrass into sandbanks saw a proliferation of *S. compressa* and concluded that confinement of the limpet to beds in the high shore was suboptimal and essentially due to the restriction of the seagrass beds themselves to expand further into the low shore due to sediment disturbance by the burrowing sand prawn, *Kraussillichirus kraussi* (Angel et al., 2006). The conclusions of that experiment do not explain the absence of *S. compressa* from low shore beds at Oesterval and Centre Banks in this study. Here, a likely reason is competition with grazing gastropods (Orth et al., 1984) such as *Fissurella mutabilis*, which is less tolerant to desiccation and occurred in high abundances at low shore sites close to the mouth and but not at high shore sites i.e., Geelbek and Bottelary.

In contrast, Angel et al. (2006) recorded high and low densities of *Assiminea globulus* on the upper and lower edges of seagrass beds respectively and noted a positive correlation with exposure. Once again, this was attributed to disturbance of sediment and reduction of diatoms due to bioturbation, however these snails also appeared to prefer exposure rather than submergence (Angel et al., 2006). This species' preference for more exposed parts of seagrass beds is likely related to the availability of food in the form of sand-dwelling diatoms that are abundant in the high shore zone (G.M. Branch, unpublished data), and therefore occupies a different niche to that of *Siphonaria compressa*. Given that *S. compressa* likely feeds essentially on periphyton on seagrass leaves (Allanson & Herbert, 2005), there was no evidence to indicate that abundance or zonation of these two species had been influenced by competition.

Environmental conditions such as a longer tidal emergence period at Bottelary and Geelbek correspond to a higher susceptibility of species to desiccation. This explains the lower species richness at these sites, and the high abundances of the desiccation resistant *A. globulus* and attests to the resilience of *S. compressa* to persist in suboptimal conditions. The cushion star *Parvulastra exigua* and keyhole limpet *F. mutabilis* were previously reported to have completely declined at Klein Oesterval (Pillay et al., 2010) but was subsequently recorded in this study. In addition, *Pyura stolonifera*, *Sargartia ornata* and *Oxysteles antoni* not documented in that survey, were also found. These findings underscore the considerable variability inherent in seagrass ecosystems. The elevated abundances of grazers further emphasize the important trophic role of grazing

within both seagrass and intertidal ecosystems more broadly (Asmus & Asmus, 1985; van Der Heijden et al., 2020).

Species richness and densities recorded in this study were comparable to the survey of macrofauna within seagrass and un-vegetated sandflats at Klein Oesterval using the traditional method of digging and sieving (Pillay et al. 2010). That study yielded a total 27 species and while infauna ( $n = 15$ ) was not targeted in this study, a total 13 species were documented at Klein Oesterval - nine species were recorded in both surveys, and an additional four were recorded in this study only. These patterns allude to the strengths and weaknesses in sampling techniques, many of which fail to capture various components within faunal assemblages influenced by processes such as life history stages, succession and colonization (Moura et al., 2008) as well as temporal restrictions related to tidal regime, season and day/night sampling. While traditional methods are considered comprehensive in providing estimates of biodiversity, alternative methods including the use of a selection of indicator species in single or multimetric indices, can be useful to assess the ecological status of benthos in marine and estuarine environments (Borja et al., 2011; Dauvin et al., 2016) particularly when resources are limited. Using a subset of species has been found to provide meaningful descriptions on faunal community structure (Kuenen & Debrot, 1995; Vellend et al., 2008). Importance should therefore be placed on consistency of methods used as well as regularity of surveys to provide informative results to address research and management objectives (Magurran et al., 2010).

#### 4.2. Influence of Seagrass Structure and Environmental Variables on Epifaunal Abundance

Significant variability stemming from both site and season was evident along with a seasonal pattern in epifaunal abundance (Figure 3.1). Abundances were observed to be at its highest during summer, but generally decreased in cooler months. Highest abundances of epifauna were found in denser seagrass beds at Bottelary and Geelbek, while beds with longer leaves near the lagoon mouth supported a richer suite of species compared to short-leaved populations, albeit in lower densities. Despite the absence of positive and significant correlations between epifaunal abundance and seagrass metrics, all the assessed seagrass variables were selected as important in elucidating the variation in epifaunal populations. Among these variables, leaf width and length emerged as the most influential contributors to the observed variation, accounting for 29.78% and 24.39% respectively.

The abiotic environment in Langebaan Lagoon significantly influenced variability in seagrass morphometric parameters (Lawrence 2023, *in press*). Notably, lower temperatures were associated with larger seagrass leaves which provide a larger surface area conducive for epiphyte colonization (Bologna & Heck, 1999; Terrados & Medina-Pons, 2011). Faunal diversity in seagrass habitats tends to increase with larger plant sizes and higher biomass, however other factors such as the ecological characteristics of fauna, can also play a role in shaping community structure (Heck & Orth, 1980; Orth et al., 1984). Given that leaves of different seagrass species differ in area per unit biomass, it has been shown that plants with greater aboveground foliar biomass provide more shelter, protection and available food than smaller plants with less surface area per biomass (Gartner et al., 2013; Hansen et al., 2010). This concept provides a plausible explanation for the observed variations in epifaunal abundances across different sites with distinct seagrass plant sizes and leaf areas within Langebaan Lagoon.

Several studies demonstrate similar patterns to that observed in Langebaan. For example, in an assessment of beds with low, medium and high densities of *Zostera marina* in the United Kingdom, infaunal diversity increased with increasing seagrass density, and significant differences in community structure between shoot density ranges were observed (Webster et al. 1998). Similarly, seagrass biomass was a key regulator of macrofaunal diversity, abundance, dominance and trophic arrangement independent of hydrodynamic and sediment properties in Apalachee Bay, Florida (Stoner 1980). Likewise, increased habitat complexity as a result of greater seagrass biomass was a key factor in regulating macrofauna in *Zostera capensis* beds in Mozambique (Paula et al. 2001). *Z. marina* shoot density exhibited a significant relationship with total faunal abundance, with varying effect magnitudes across 19 sites nested within three locations in the southwest United Kingdom (Smale et al., 2019). In that study, higher seagrass density generally corresponded to greater faunal abundance, contributing to shifts in the structure of the faunal assemblage.

In the final structural equation model, several key factors were identified to directly impact the patterns of epifaunal distribution within Langebaan Lagoon. Notably, seagrass density, leaf width, oxygen, and turbidity exhibited direct effects, while other environmental variables played a substantial indirect role (Fig. 3.4). Although there was no direct link between temperature and epifaunal abundance, and the indirect effect was relatively modest (a 1SD increase in temperature correlated with a 0.09SD decrease in epifaunal abundance), temperature displayed a direct influence on both leaf length and width (Table 3.6). It was also found to significantly predict five out of the six evaluated seagrass metrics (Lawrence 2023, *in press*). Indirect effects have been shown to influence community structure as significantly as direct effects (Wootton, 2002). Consequently, the observed decline in epifaunal abundance in the field is likely attributed to a combination of direct physiological effects of temperature and indirect impacts on the underlying seagrass ecosystem (Marbà & Duarte, 2010).

Smaller and denser morphologies of *Zostera capensis* experienced higher temperatures than their large-leaved counterparts. In seagrass beds at Bottelary and Geelbek, higher shoot and leaf densities were observed from smaller plants with narrower leaves, resulting in greater leaf area per unit biomass. The lower diversity of epifaunal species and the dominance of just two species suggest a narrow ecological niche and a high degree of adaptation to local environmental conditions at these particular sites. In a study by Edgar and Barrett (2002) conducted in Tasmania, it was determined that the primary factor influencing species richness across 48 estuaries was tidal height. Unlike seasonal variations, spatial variance played a more substantial role in influencing species richness, which is consistent with the findings in Langebaan Lagoon. Those authors also revealed a relationship between species richness, faunal biomass, and factors like salinity and seagrass biomass, particularly during low tide and shallow subtidal levels (Edgar & Barrett, 2002). Notably, physiological tolerance to environmental stress, particularly in response to exposure, has been identified as a strategy to evade the adverse impacts of predation and competition. This phenomenon is more pronounced in diverse communities within temperate seagrass ecosystems (Barnes & Ellwood, 2012).

Seagrass habitats serve as a structural foundation for epifaunal communities. Habitats characterized by structural complexity often facilitate the co-existence of a higher number of species by buffering the effects of competition and predation (Gilinsky, 1984; Menge & Sutherland, 1976; Russ, 1980). This heightened structural complexity within habitats can indirectly regulate species interactions, particularly by curbing predation. This is achieved through the provision of increased refuge options for prey species, thereby reducing capture efficacy of predators (Hammerschlag-Peyer et al., 2013; Menge & Sutherland, 1976). The presence of numerous refuges are linked to heightened prey diversity, which has been shown to balance otherwise unstable predator-prey interactions (Heck & Orth, 1980; Orth et al., 1984).

Enhanced species diversity is pivotal to the improved functioning and resilience of ecosystems (Duffy et al., 2003; Unsworth et al., 2015). While the suitability of a particular species as a food source hinges largely on its abundance, relying on rare species for sustenance is unlikely (Balvanera et al., 2006; Duarte, 2000). Consequently, the preservation and enhancement of biodiversity, encompassing both species richness and abundance, assume a critical significance in bolstering trophic structures. This, in turn, ensures the overall vitality of ecosystems and ensures the sustained provision of ecosystem services.

Epifaunal community structure in *Zostera capensis* beds was influenced directly by seagrass leaf size and density, and indirectly by environmental variables. Temperature notably shapes seagrass metrics, with warmer temperatures producing smaller, denser seagrass morphologies (Lawrence 2023, *in press*). Persistent temperature increases may prompt a shift to smaller populations with distinct faunal associations. Further warming could narrow the range of larger populations, reducing overall faunal diversity. Increasing temperatures would also mean greater levels of evaporation. Rising temperatures also enhance evaporation, potentially favoring more desiccation-tolerant species. Fluctuations in seagrass abundance could heighten the risk of the further threatened *Siphonaria compressa* limpet.

Diminished epifaunal diversity in *Zostera capensis* beds in Langebaan Lagoon suggests decreased productivity and energy flow through trophic levels, especially for fish prey. As crucial sites for recreational and industrial fisheries in the lagoon and adjacent Saldanha Bay, the loss of seagrass habitats implies a loss of food and

shelter for juvenile fish with critical consequences for these ecosystem services.

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