

Using numerical modelling to investigate temperature and wave exposure as drivers of macroalgal characteristics

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Introduction

Kelps are a group of large seaweeds of the order Laminariales (Ochrophyta), which despite their relatively low taxonomic diversity of species in genera (Bolton 2010), nevertheless form the basis of one of the most productive ecosystems globally (Mann 1973). Kelps generally have a dependence on cool, temperate and arctic seawater temperatures (Bolton 2010; Mohring et al. 2014; Cavanaugh et al. 2011; Dayton 1985), and dominate the nearshore biomass within the rocky shallow coasts in both hemispheres (Steneck et al. 2002). Their size and complex morphology provide a heterogeneous habitat structure (Steneck et al. 2002) that accommodate a multitude of turf and subcanopy seaweed species, and diverse assemblages of sessile and mobile invertebrates and vertebrates (Mann 1973; Steneck et al. 2002), each depending on a wide suite of ecological services provided by the kelp forests (Gaines and Roughgarden 1987; Paul and Steneck 1993; Levin 1994; Willis and Anderson 2003; Anderson et al. 1997; Dayton 1985). Wave exposure and temperature are regarded as important environmental drivers of kelp forests, and play a role in the distribution (Gorman et al. 2013), abundance (Cavanaugh et al. 2011; Dayton et al. 1998), diversity (Wing et al. 2007; Wernberg and Goldberg 2008), composition (Leliaert et al. 2000; Dayton 1985; Norderhaug et al. 2012; Harley et al. 2012), growth (Cousens 1982) and productivity (Pedersen and Nejrup 2012; Dayton et al. 1998; Krumhansl and Scheibling 2012) of kelps.

Temperature and wave exposure have been shown to play a role in driving kelp morphology. For example, a study by Serisawa et al. (2002) compared the morphology of *Ecklonia cava* Kjellman growing in warm temperate and cool temperate morphologies. The results showed that wrinkles in the blade and reduced size to be a characteristic of warm temperate regions. However this study did not take into account the interaction with other environmental variables such as wave exposure. Wave exposure has also been shown to be the main drivers of morphological adaptation across various kelp species. Past research has shown that in highly wave exposed areas kelp morphology tends to take on characteristics which reduce drag, increase strength and increase flexibility (Mark Denny and Gaylord 2002; Hurd 2000; Fowler-Walker, Connell, and Gillanders 2005, @Thomsen2004–yd). For example, a study by Wernberg and Thomsen (2005) examined the consistency of wave exposure as a driver of *Ecklonia radiata* (C. Agardh) J. Agardh across a broad geographic range, and showed trends towards drag-reducing (small size, narrow laterals and blades, low spinosity) and increased strength (large holdfast, thick stipe and thick blades and lamina) at high wave exposure sites. The morphological adaptation to wave exposure must be kept in balance with other important processes, such as nutrient assimilation and light absorption, which are dependent on the amount of surface area of the blades. Therefore, there is a trade-off between reducing overall drag and maintaining nutrient and photosynthetic ability. The morphological adaptability of kelps is driven by a combination of environmental factors that in turn do not act independently of one another. A study by Wernberg et al. (2003) investigated the morphology of *E. radiata* in order to quantify the morphological variation and whether it was dependent on spatial differences along the Australasian coast. They found no correlation between spatial distance and morphological similarity and rather the morphology of kelps was representative of multiple environmental forcings on different morphological characters at different spatial scales (Wernberg et al. 2003). Due to the complex effects of environmental drivers on kelp morphology, one can also expect differences in morphology between deep and shallow water populations of the same species. Wave exposure may be greater in shallower environments, or it may be reduced through damping effects of kelp and other subtidal species (Kobayashi, Raichle, and Asano 1993; Mia2013; Dubi and Tørum 1995). Shallower environments are exposed to higher irradiance levels which increases temperatures (Dellatorre et al. 2012; Dunne and Brown 2001) as well as an altered hydrodynamic environment which effect vertical mixing in the shallow nearshore.

The kelps *Laminaria pallida* and *Ecklonia maxima* (Osbeck) Papenfuss are important habitat forming seaweeds that exist around the coast of South Africa and offer a unique opportunity to investigate the

drivers of macroalgal morphological characteristics between canopy and sub-canopy species, as well as between deep and shallow water environments. Although both these species exist in the subtidal, *L. pallida* dominates deeper waters while *E. maxima* forms dense surface canopies in from the subtidal to shallower waters. Therefore, *E. maxima* is exposed to variations in wind drive surface waves, swell and temperature, while *L. pallida* is exposed to variations in swell and temperature. Molloy and Bolton (1996) investigated the effect of depth and wave exposure on *L. pallida* at different depths and wave exposure and showed that depth had a greater effect than wave exposure when considering all the morphological characteristics (wave exposure alters with depth); when considering individual characteristics, however, wave exposure had the most significant effect on blade thickness. Another study by Rothman et al. (2017) investigated the changes in morphology in shallow populations of *L. pallida* and *E. maxima* along the South African coastline and into Namibia; *E. maxima* exhibited no morphological changes along the coast but the stipes of *L. pallida* become increasingly hollow further north along the coastline. They suggested that turbidity was the environmental driver responsible for this change.

Measures of wave exposure in ecological studies often incorporate integrative measures of hydrodynamic conditions at a particular site which are based on cartographical models of wave exposure. Cartographical models of wave exposure are regarded as ‘fetch-based-models’ which measure the length of open water associated with a particular site in a straight line, and are regarded as simple measures of wave exposure. Advances in numerical modelling based on physical/linear wave theory incorporate more complexity (wind forcing, wave-wave interactions, wave breaking, diffraction and variation in wave direction) into the models and allow for a quantitative, reproducible approach for measuring wave exposure. Currently, no ecological studies investigating macroalgal morphological characteristics in relation to the wave environment have incorporated 3D spectral numerical modelling. Previous research investigating drivers of kelp morphological characteristics have often used qualitative estimates of wave exposure and did not consider other morphological characteristics. Furthermore, wind is an important component of surface gravity waves (Holthuijsen 2010) and previous work has not differentiated between surface gravity waves and swell waves, which the current work will aim to achieve. Other considerations such as possible differences in morphology between sub-canopy and canopy species, shallow and deep water populations have not been considered in previous research which ignores the effects of wave damping. The aim of this study is, therefore, to understand how temperature and wave exposure can influence the morphology in two species of kelps around South Africa, as well as between deep and shallow populations of the same species. This will be achieved by initially understanding the variation in temperature and waves using an advanced numerical model. The numerical model will then be used as a basis for investigating the consequences for morphological characteristics of *E. maxima* and *L. pallida* using multiple statistical tools.

Materials and methods

Site selection

Sites were chosen to represent an array of environmental gradients, as indicated in figure 1. St. Helena Bay and Betty’s Bay constituted the north western and south eastern boundary sites, respectively. These sites are roughly 300 km apart, and lie within separate marine provinces and cover a cline in wave exposure and temperature. Study sites span across the majority of the south-west coast, in varying thermal and wave energy regimes. The region is dominated by kelp communities that persist in contrasting abiotic environments. The west coast region has been termed as a cool temperate region, which is defined as a region where mean monthly temperatures are always above 10°C and always below 15°C (Smit et al. 2013). East of Cape Point marks the beginning of an overlap or transition area, which is also referred to as the Benguela-Agulhas Transition Zone (Smit et al. 2013). The Agulhas Marine Province is characterised by a wide temperature range of up to 7°C difference between mean monthly temperatures between summer and winter and is classified as warm temperate region (Smit et al. 2013).

Due to the Cape Peninsula temperate latitude, winter months bring an increased frequency of frontal depressions that originate from the Southern Ocean (Reason, Landman, and Tennant 2006). These low pressures are joined by large swells with increased wave energy. The nearshore environment, with the accompanied biota, therefore experiences high wave energy events, with increased frequency in winter (Veitch et al. 2019). The large peninsula acts as an obstruction for large south westerly swells, providing decreased wave energy along the west side of False Bay (Shipley 1964). Conversely, the west coast of

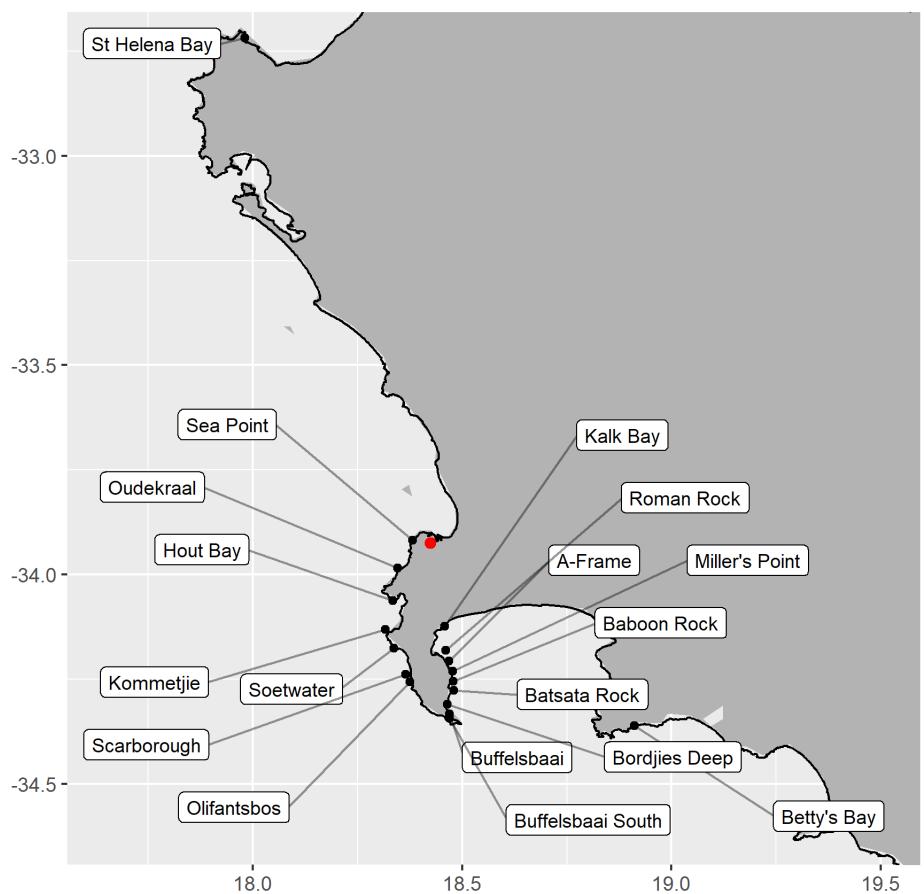


Figure 1: Map of the study area and sampling sites. The red dot indicates the position of Cape Town for sake of reference.

Cape Point is battered by these large swells. Multiple sites, therefore, exist where kelps grow in diverse temperature and wave energy climates, in close proximity. The topography and elevation along the Cape Peninsula channel and shield winds along False Bay. This is however absent in winter, where strong northerly winds are prevalent from St. Helena Bay to Betty's Bay (Field et al. 1980; Jury, Kamstra, and Taunton-Clark 1985; Andrews and Hutchings 1980; Jury 1980). Patterns are also evident in the wave data. Seasonal variations in significant wave height (H_s), peak period and wave direction are also present. The direction of the dominant swell changes to the south west in winter, generated by strong low pressures that originate from the southern ocean (Reason, Landman, and Tennant 2006), which False Bay is sheltered from (Shipley 1964; Atkins 1970; Dufois and Rouault 2012). In summer, these swells rotate anticlockwise and are able to enter False Bay, providing an increased variability of H_s and T_p in this region. It should be noted that what is classified as sheltered around the South African coastline (a high energy coastline) might be classified as exposed in other regions of the world (Norderhaug et al. 2012; Leliaert et al. 2000). It is due to the near consistent south-westerly swell and the complex orography around the peninsula that the wave energy distribution around the Cape Peninsula varies significantly over a small geographical area.

Abiotic environment

In order to compare abiotic variables for sites around the coast, large historical databases for temperature, wave energy and wind were accessed.

Temperature

Shallow water temperatures were sourced from The South African Coastal Temperature Network (SACTN) website (<https://github.com/ajsmit/SACTN>). In terms of nearshore temperature, *in situ* data are preferred over satellite SST, which have shown to exhibit large biases (Smit et al. 2013). Linear interpolated SST were calculated for sites where *in situ* recorders were absent. These data were used to group sites into 'Cool temperate' and 'Warm temperate' categorisations to investigate the possible affect of thermal regime on kelp morphological characteristics.

Wave environment

Wave model variable data formed part of the South African Coastal Vulnerability Assessment, presented to the Department of Environmental Affairs (DEA) and produced by the Council for Scientific and Industrial Research (CSIR) (Rautenbach 2015). The South African wave climate was modeled via 20 spectral numerical wave models that simulated the offshore wave climate to the nearshore. The boundary conditions of these models were obtained by using the NOAA Wave Watch III (WWIII) model output, distributed via the National Centers for Environmental Prediction (NCEP) product (Office of the Director 2000; Environmental Modeling Center / Marine Modeling Branch 2005). The particular hindcast product utilised during the DEA-CSIR study spans 1994-2013 at a 3-hour resolution. These data were then used to model swell propagation into the coastal models while wind waves (seas) were generated via stationary computations in the Simulating Waves in the Nearshore SWAN model (Booij, Holthuijsen, and Ris 1997). The assumption of stationary computations are acceptable as the model domains were small enough so the temporal variation of the model boundary were slower than the time it takes for that boundary condition to propagate to the coast. SWAN allows one to extract wave variables from specific gridded locations in the nearshore. For False Bay, a resolution of 200 meters was modelled and output produced at both the 7 meter and 15 meter isobaths. A 200 meter resolution was used as the False Bay computational grid was nested within a larger grid (1 kilometer resolution). This allowed for a computational effective wave resolution of increasing resolution, from the NCEP, low resolution output to nested, high resolution coastal output. For Table Bay and east of Cape Hangklip the resolution was 500 meters and also had output at the 7 meters and 15 meter isobaths. These contour outputs were chosen in the original study by the CSIR as most engineering run-up calculations require wave parameter information at these contour depths and were the main focus of the original study. For this study the 7 meter contours were used. These data were then used to calculate over all wave power (kW/m) as this was considered the best measure of overall wave exposure. Annual wave power was plotted and categorised into different wave exposure categories which ranged from fully sheltered to extremely exposed.

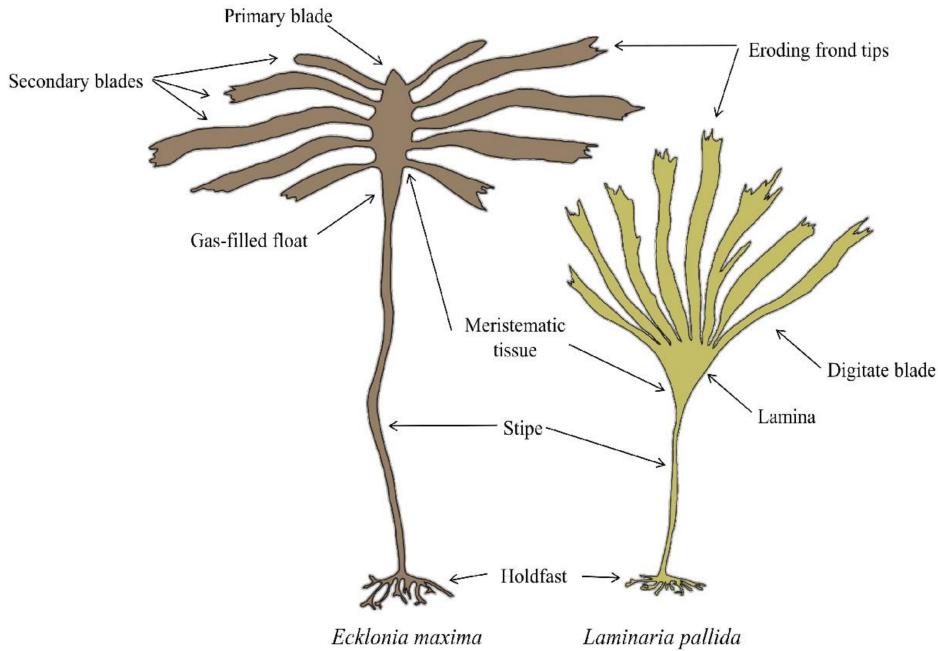


Figure 2: Schematic of *L. pallida* and *E. maxima* morphology (Dyer 2018).

Collection of kelp morphological characteristics

The morphological characteristics of both species are presented in figure 2. *Laminaria pallida* is characterised by a single smooth blade which is divided longitudinally into sections, and develops from a single meristematic region located at the junction between the blade and the stipe (Dyer 2018). This species has a solid stipe but develops a hollow stipe along the west coast northward and into Namibia (Rothman et al. 2017). *Ecklonia maxima* consists of a single primary blade which develops above a gas-filled float and a hollow stipe below. Secondary blades are produced laterally from the primary blade from several meristematic regions along the margins of the primary blade, known as digits (Dyer 2018). Both species are held to the substrate by finger-like haptera, collectively known as the holdfast.

Morphological measurements of *L. pallida* and *E. maxima* were collected at 18 sites along the Western Cape coast of South Africa (Fig. 1) between October 2014 and April 2015. In each instance only the largest individuals were sampled to ensure that only mature and fully grown sporophytes were measured. Thirteen samples were collected for each species at each of the sites. The morphological traits named in Tables 1 and 2 were measured for comparison between sites. Because the macroalgae differ in morphological features, species-specific morphological characteristics were included. This allowed comparison between adjacent and non-adjacent sites around the peninsula. Between February 2017 and November 2018, morphological measurements for *E. maxima* individuals in shallow water (<1m) at

seven sites along the Western Cape coast of South Africa were also collected. The same morphological characteristic measurements were taken as for the deeper *E. maxima*, and this allowed comparison between morphological characteristics between deep and shallow individuals within sites. Measurements were not collected for *L. pallida* in the shallow depths, as this species is largely absent from the shallow in this portion of the South African coastline.

Statistical analyses

Summary statistics were calculated for each site and regions for each of the environmental variables considered in this study. The summary statistics calculated for temperature, waves and wind variables were minimum, maximum, mean, range and standard deviation for annual timescales. In addition, annual median wave and wind direction were also calculated; all summary data and their respective abbreviation are presented in Table 3. The median was calculated for wind and wave direction, as issues arise when calculating the mean and standard deviation for compass metrics. Dot and whisker plots were used to present the summary statistics for both temperature and wave variables. Summary statistics for wind was not plotted and instead are discussed, as the data was coarse relative to the other environmental variables considered in this study.

Characterisation of morphological characteristics in relation to temperature and wave exposure non-parametric statistical methods were used. Morphological characteristics were categorised according to temperature regime and wave exposure category for each each species and population of kelp in this study. Significant differences between temperatret regime and wave exposure categories were tested with wilcox tests. Notched boxplots allowed comparison between individual categories of wave exposure. In order to investigate specific drivers of morphological characteristics a distance-based redundancy analysis was performed using the *rda* function in the *vegan* software package (Oksanen et al. 2015) in R (R Core Team, 2019). The abiotic data covered all study sites for both species of kelp. Both morphology and abiotic data (temperature, waves and wind) were standardised using the *decostand* function in the *vegan* software package; morphology data were used as response variables and the abiotic data as explanatory variables. To determine the explanatory variables that best describe patterns in the response data, a full RDA was performed using a complete set of explanatory variables. Forward selection was then used to reduce the number of explanatory variables as well as prevent the inflation of overall type I error. To further improve the model, pairwise coefficients and Variance Inflation Factor (VIF) were calculated to identify variables with high multicollinearity. The computation of the parsimonious RDA was followed by permutation tests of the adjusted *R*² to assess significance of constraints.

Results

Abiotic environment

Temperature

The mean annual coastal water temperature for the study sites located on the western side of the peninsula ranged from 14.5 ± 0.9 °C (mean \pm SD) at St. Helena Bay, the most northern site on the western side of the peninsula, to 14.6 ± 0.3 °C at Olifantsbos, the most southern site on the western side of the peninsula (see figure 3A). For sites located on the eastern side of the peninsula (within False Bay), the annual mean coastal water temperatures ranged from 15.5 ± 0.9 °C at Buffelsbaai to 15.0 ± 0.9 °C at Betty's Bay, the most eastern site on the coastline in this study (see figure 3A). Oudekraal had the lowest annual mean coastal water temperature of 12.3 ± 0.9 . Annual maximum coastal temperatures for study sites located on the western side of the peninsula ranged from 16.3 °C at St. Helena Bay to 15.1 °C at Olifantsbos. For sites located east of the peninsula, annual maximum coastal water temperatures ranged from 16 °C at Buffelsbaai to 16.5 °C at Betty's Bay. Amongst all sites, Kalk Bay had the highest annual maximum temperature of 19 °C. Annual minimum coastal water temperatures for the study sites on the western side of the peninsula ranged from 12.9 °C at St. Helena Bay to 14.1 °C at Olifantsbos, and on the western side of the peninsula ranged from 15.0 °C at Buffelsbaai to 13.6 °C at Betty's Bay. The annual range in temperature on the western side on the peninsula was 3.4 at St. Helena Bay to 0.9 at Olifantsbos, and on the eastern side on of the peninsula was 1.0 at Buffelsbaai to 2.9 at Betty's Bay. As can be seen in

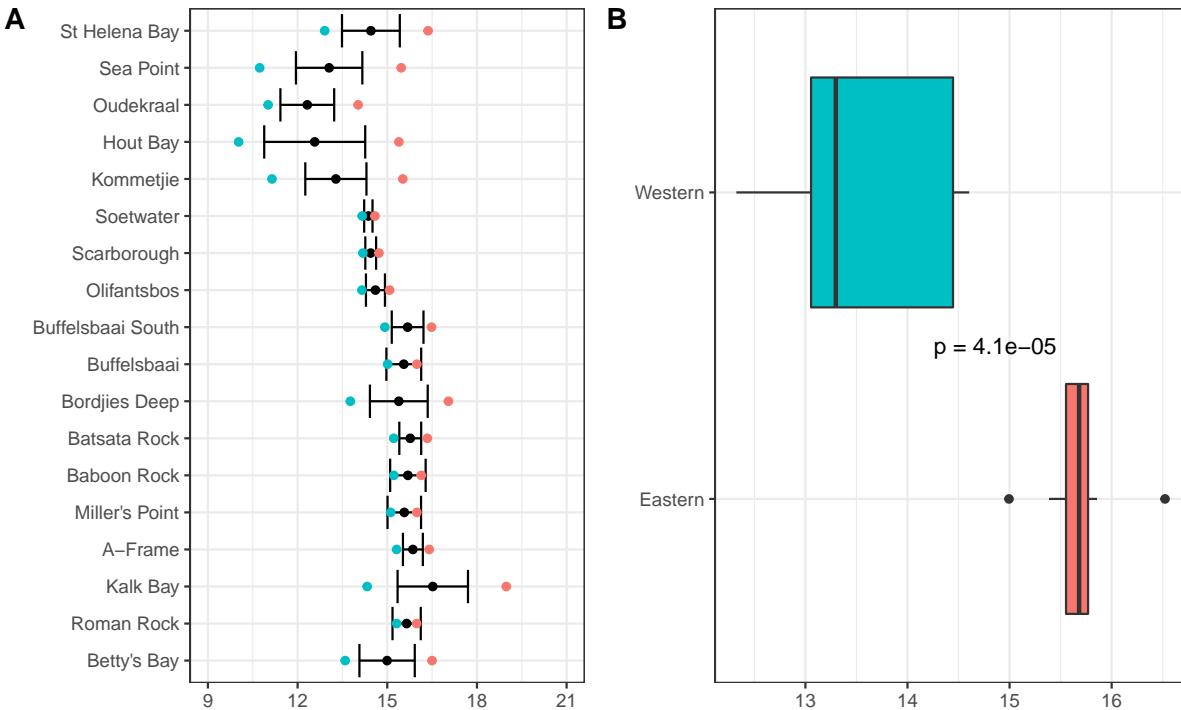


Figure 3: Temperature variables at the collection sites around the Cape Peninsula are represented in plot A. Temperature variables include minimum represented by blue dots, mean represented by black dots, maximum by red dots and whiskers standard deviation. Summary of temperature data for sites grouped by region are represented in plot B. See appendix for significance level guide.

figure 3A, the trend in the range of temperature decreases from St. Helena Bay to Miller's point and then increases from Kalk Bay to Betty's Bay. Also, annual range in temperatures within False Bay are larger in winter (August) compared to summer (February).

Wave environment

Our data show the western side of the peninsula experiences higher significant wave heights and variation in wave heights compared to the eastern side of the peninsula on both an annual and seasonal scale (see figure 4). Mean significant wave height ranged from 0.5 ± 0.2 m (mean \pm SD) at St. Helena Bay to 2.3 ± 0.7 m at Olifantsbos on the western side of the peninsula, and on the eastern side of the peninsula it ranged from 0.9 ± 0.4 m at Buffelsbaai to 1.9 ± 0.6 m at Betty's Bay (see figure 4A). The maximum significant wave height ranged from 1.4 m at St. Helena Bay to 4.7 m at Olifantsbos on the western side of the peninsula, and on the eastern side ranged from 2.6 m at Buffelsbaai to 4.2 m at Betty's Bay. Mean peak period for sites on the western side of the peninsula ranged from 10.3 ± 3.5 s at St. Helena Bay to 11.0 ± 2.0 s at Olifantsbos, and ranged from 10.6 ± 3.0 s at Buffelsbaai to 10.8 ± 2.2 s at Betty's Bay (see figure 4B). The data shows no trend in mean peak period for the coastline. These data show that the western side of the peninsula has a lower variation (SD) compared to the eastern side of the peninsula, with Miller's point showing the highest variation across timescales. Maximum peak period ranged from 18.9 s at St. Helena Bay to 18.4 s at Olifantsbos for the western side of the peninsula, and ranged from 18.0 s at Buffelsbaai to 18.0 s at Betty's Bay on the eastern side of the peninsula. When wave variables were grouped by region significant differences were found for both mean significant swell height and mean peak period. The western region experiences a significantly higher mean significant swell height ($p < 0.05$; see figure 4C) and mean peak period ($p < 0.05$; see figure 4D). These wave heights and their variability are modulated by the relative sheltering against the predominant south-westerly swell direction and the size of the fetch for local wave generation.

Data for median wave direction showed no trend across timescales; however the variation (SD) in wave direction is lower on the western side of the peninsula compared to the eastern side both annually and for

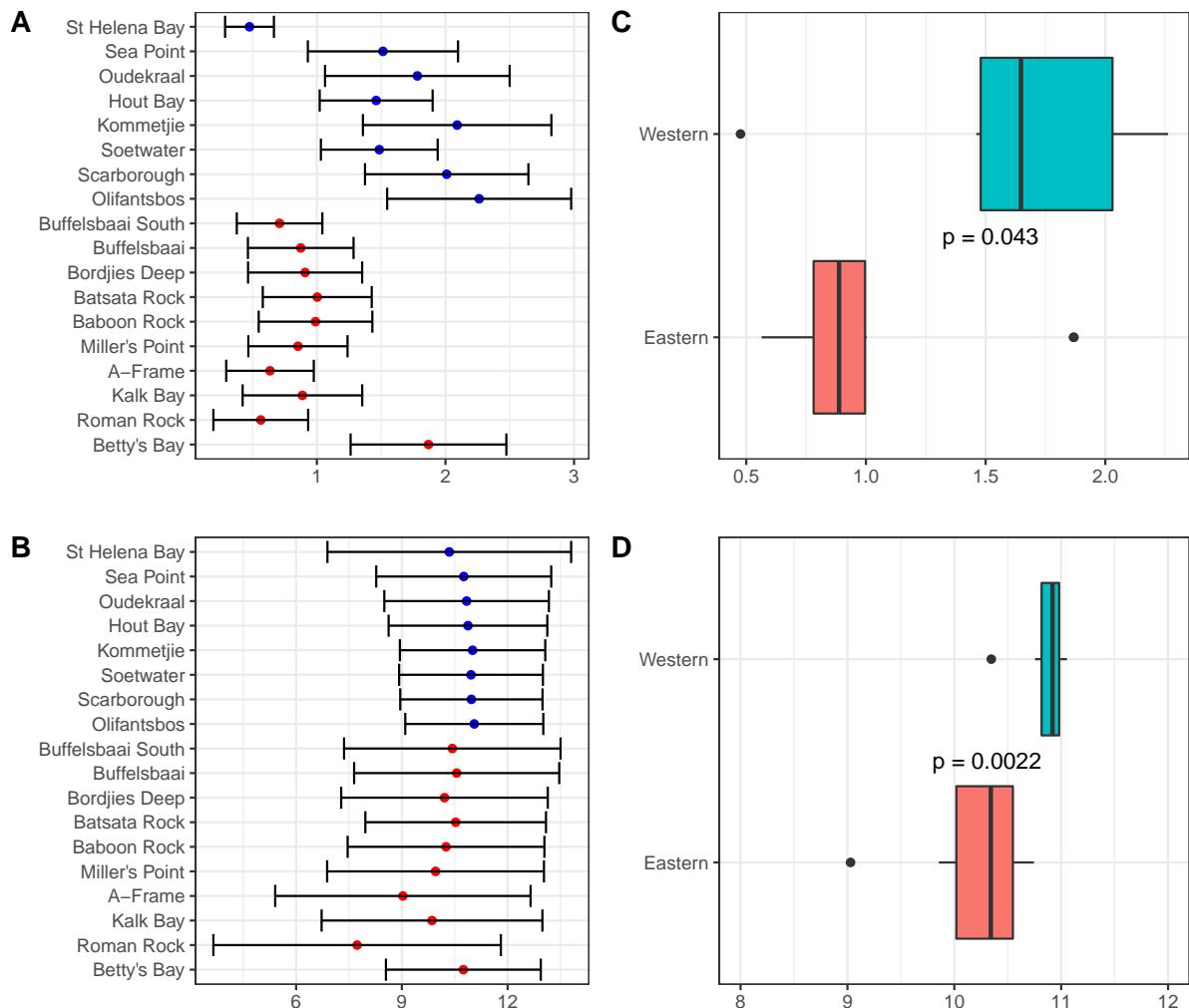


Figure 4: In plot A1 and A2 wave variables at each collection site around the Western Cape coast are presented. Mean variables are represented by dots and standard deviation by whiskers. Blue dots represent sites grouped to the western category and red dots represent sites grouped to the eastern category.

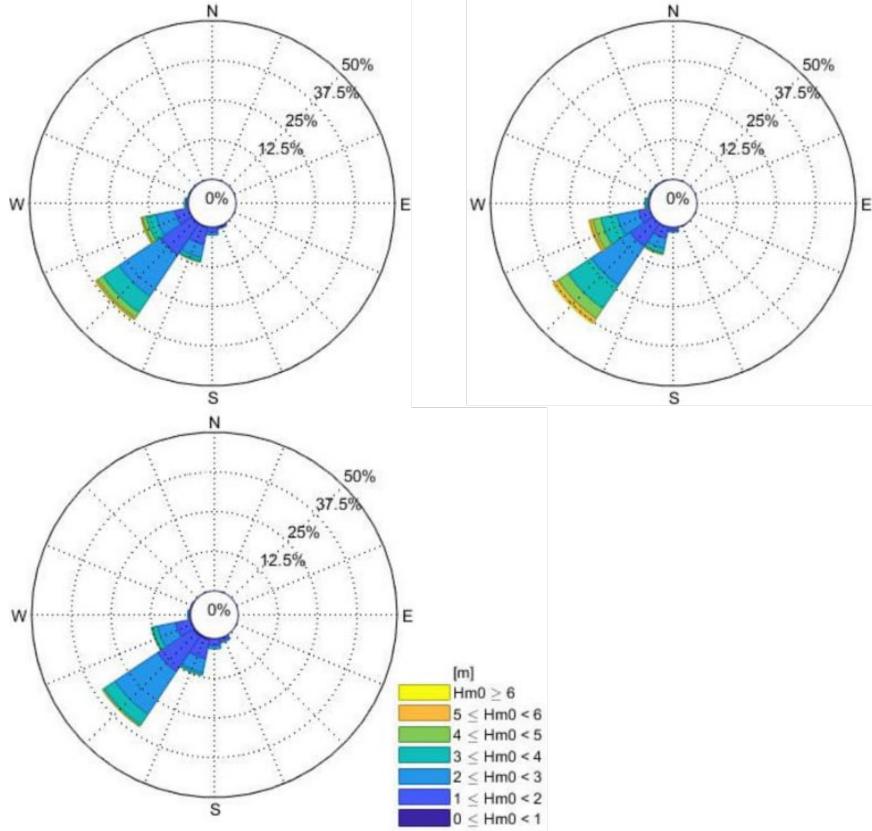


Figure 5: Wave rose figure

winter. Summer data were the exception and showed lower variation for the eastern side of the peninsula (see figure 5). Wave variables divided into Annual (top), Austral summer (middle) and Austral winter (bottom) respectively. This phenomenon can be explained by the sheltering effect of the Cape Peninsula, resulting in a wave climate with a narrower directional spreading on the eastern side of the peninsula (refer to Fig. 7).

In Figure 5 the total coastal wave exposure of the Cape Peninsula is given in terms of wave energy (kW per meter wave crest length). The classification from fully sheltered to extremely exposed is based on the total wave energy upper and lower limits. The western periphery of the Cape peninsula is almost continuously exposed to high wave exposures while the eastern periphery of the peninsula (western coastline of False Bay) revealed sheltered wave exposures (see figure ??). There the marked seasonality, with higher energy waves during winter, may be clearly observed once more.

To clarify the averaged wave exposure maps presented, the propagation of a typical offshore wave spectrum as produced from a single time-step in SWAN is presented in figure ???. Tracing the wave height contours into False Bay its clear why this bay's western periphery is predominantly sheltered. It should be mentioned that some of the annual winter frontal depression systems pass the Cape Peninsula from the west to east, resulting in wave propagating towards the continent from much more southerly directions. This results in positive and negative wave exposure anomalies all around the peninsula.

Drivers of kelp morphological characteristics

Significant differences were found between cool temperate and warm temperate regimes for most *L. pallida* morphological characteristics with lamina length, number of digits and thallus mass the exceptions (see figure 6). Certain morphological characteristics such as stipe mass, stipe length, total length and stipe diameter had significantly higher means for kelps in cool temperate regimes when compared to kelps for the warm temperate regime. Conversely, lamina weight and lamina thickness had significantly lower means for kelps in the cool temperate regime compared to kelps in the warm temperate regime. When

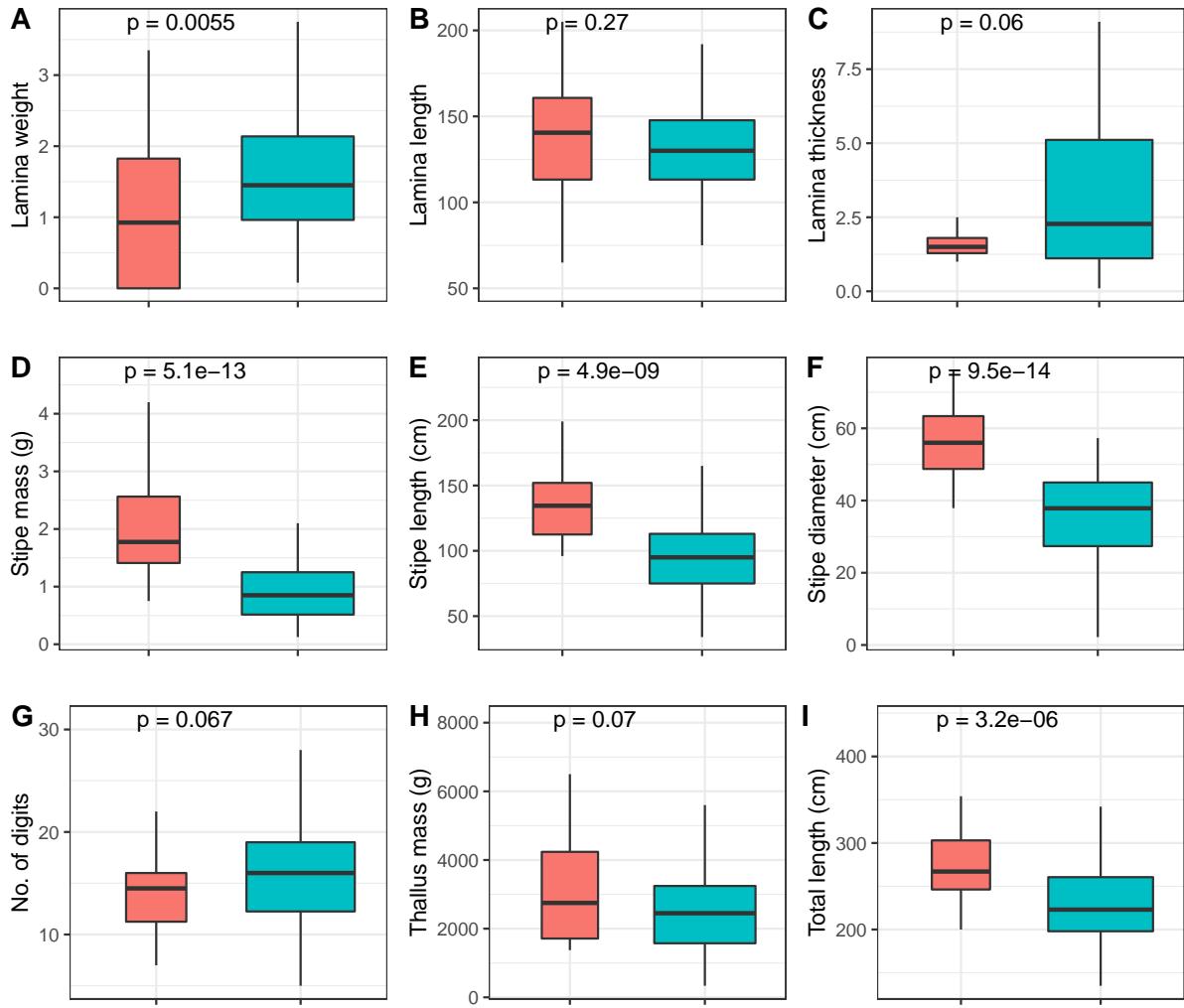


Figure 6: Boxplots of *L. pallida* morphological characteristics group by temperature regime.

L. pallida morphological characteristics were grouped to wave exposure categories kruskal-wallis tests revealed significant differences amongst categories for most morphological characteristics with lamina length, number of digits and thallus mass the exceptions. The morphological characteristics that were significantly different amongst sites exhibited similar patterns, with increasing mean values from the full sheltered to extremely sheltered categories and a decrease in mean values for the remainder of the categories. Two morphological characteristics, namely lamina thickness and stipe diameter, both exhibit higher variations for the exposed categories compared to other morphological characteristics.

Six out of the ten deep *E. maxima* morphological characteristics showed differences between cool temperate and warm temperate regime except for frond mass, frond length, stipe mass and epiphyte length. Mean values for primary length, primary width and stipe circumference were significantly higher for kelps from cool temperate regions than for kelps from warm temperate regions (see figure 7. The remaining morphological characteristics, stipe length, number of tufts and total length had significantly lower values for kelps from cool temperate compared to kelps from the warm temperate regime. Significant differences amongst wave exposure categories were found for all morphological characteristics of deep *E. maxima* populations. Certain morphological characteristics showed a gradual increase in value with increasing degree of wave exposure. The remaining morphological characteristics exhibited decreased values for only the higher wave exposure categories and then a sharp increase in value for the highest wave exposure category.

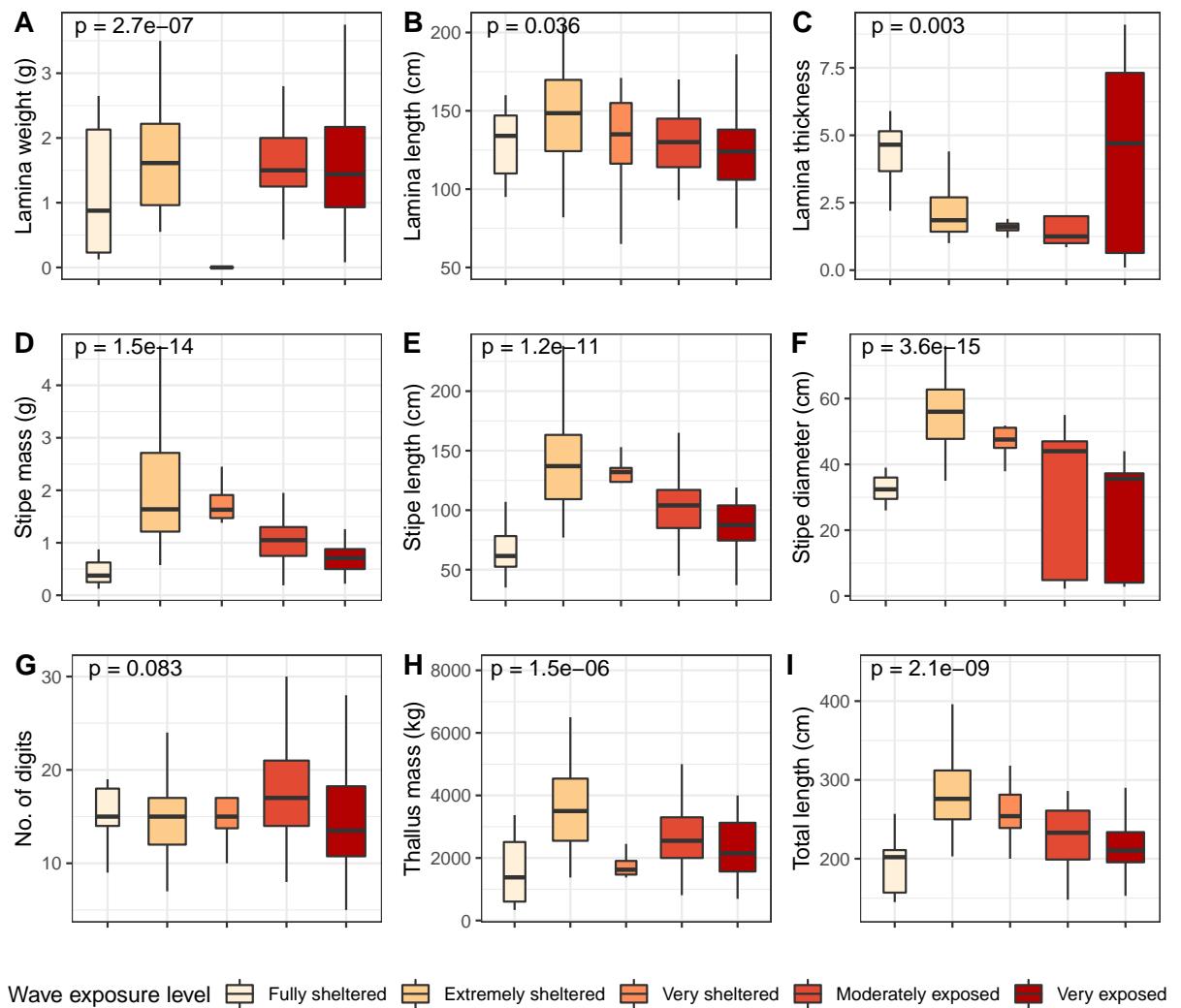


Figure 7: Boxplots of *L. pallida* morphological characteristics group by wave exposure category.

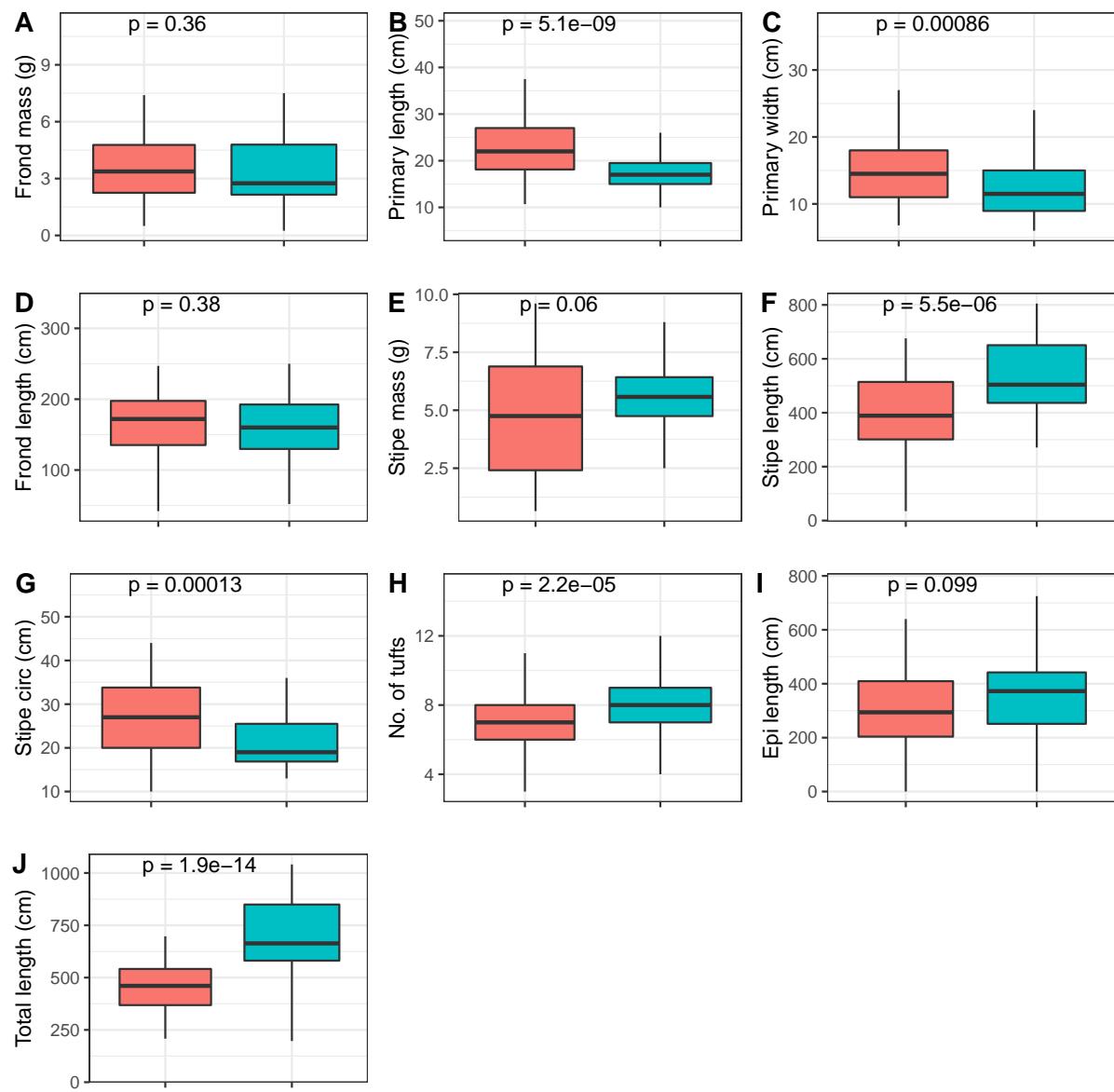


Figure 8: Boxplot of morphological characteristics for deep population *E. maxima* grouped by temperature.

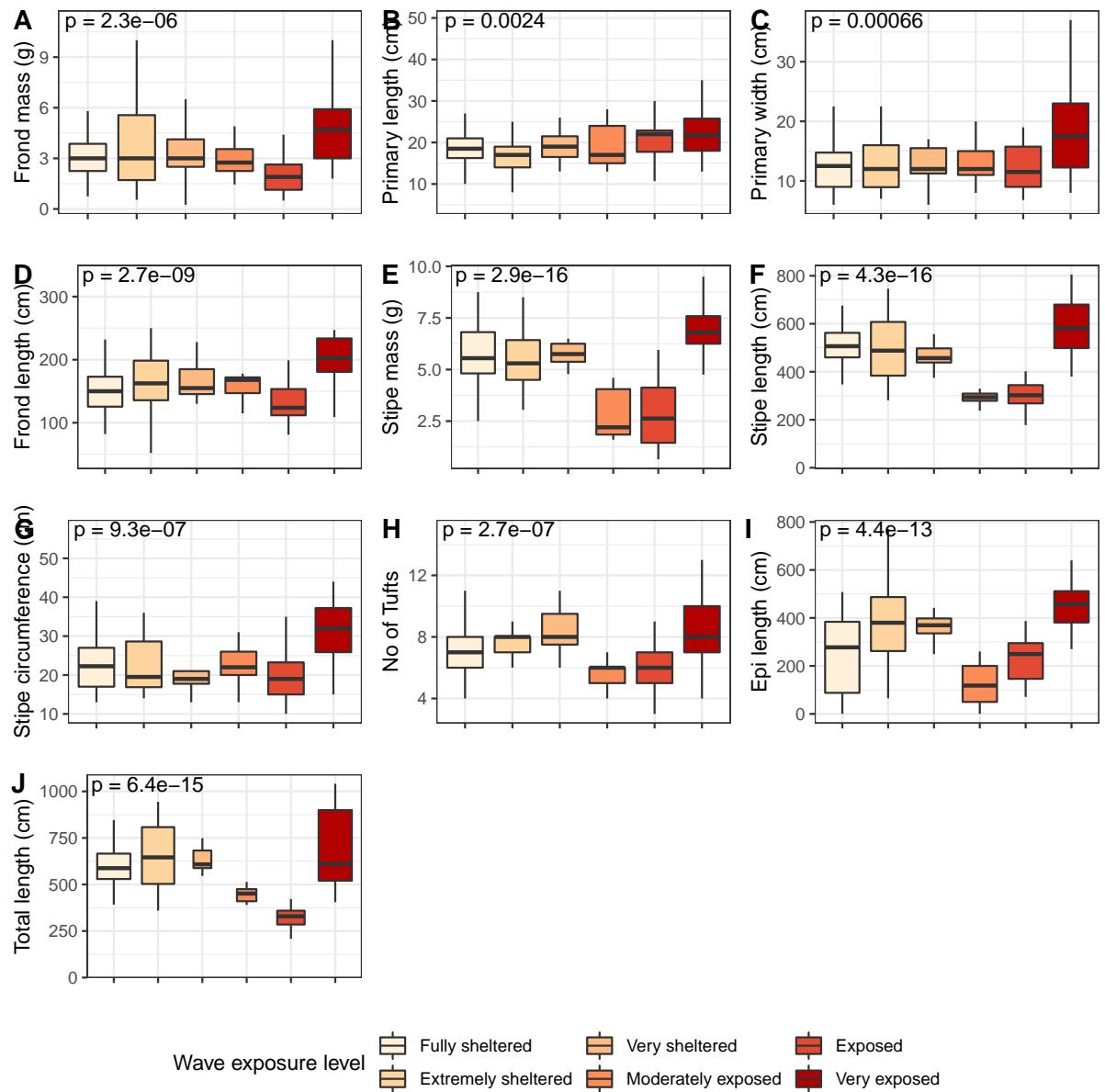


Figure 9: Boxplot of morphological characteristics for deep population *E. maxima* grouped by wave exposure.

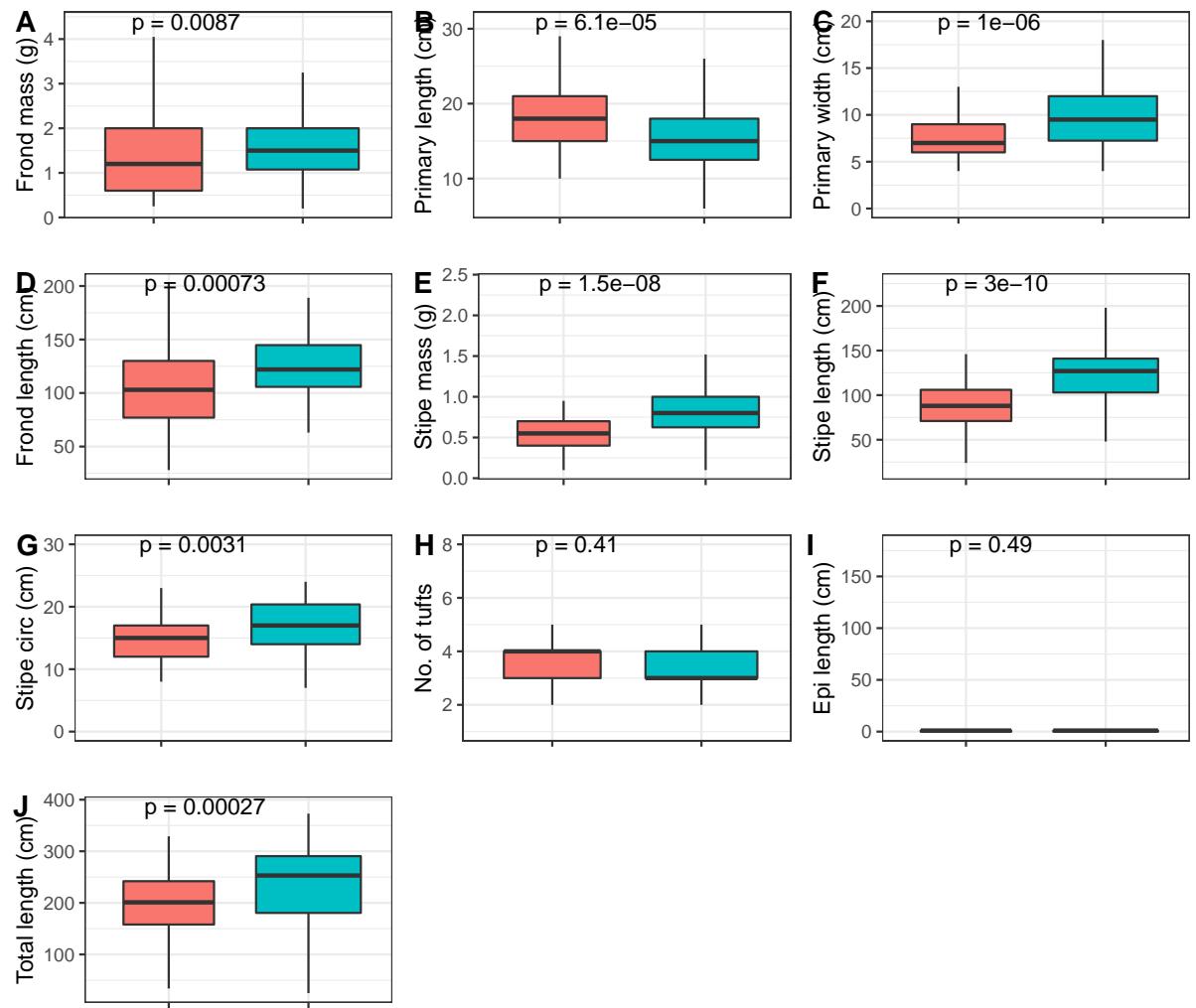


Figure 10: Boxplot of morphological characteristics for shallow population *E. maxima* grouped by temperature regime.

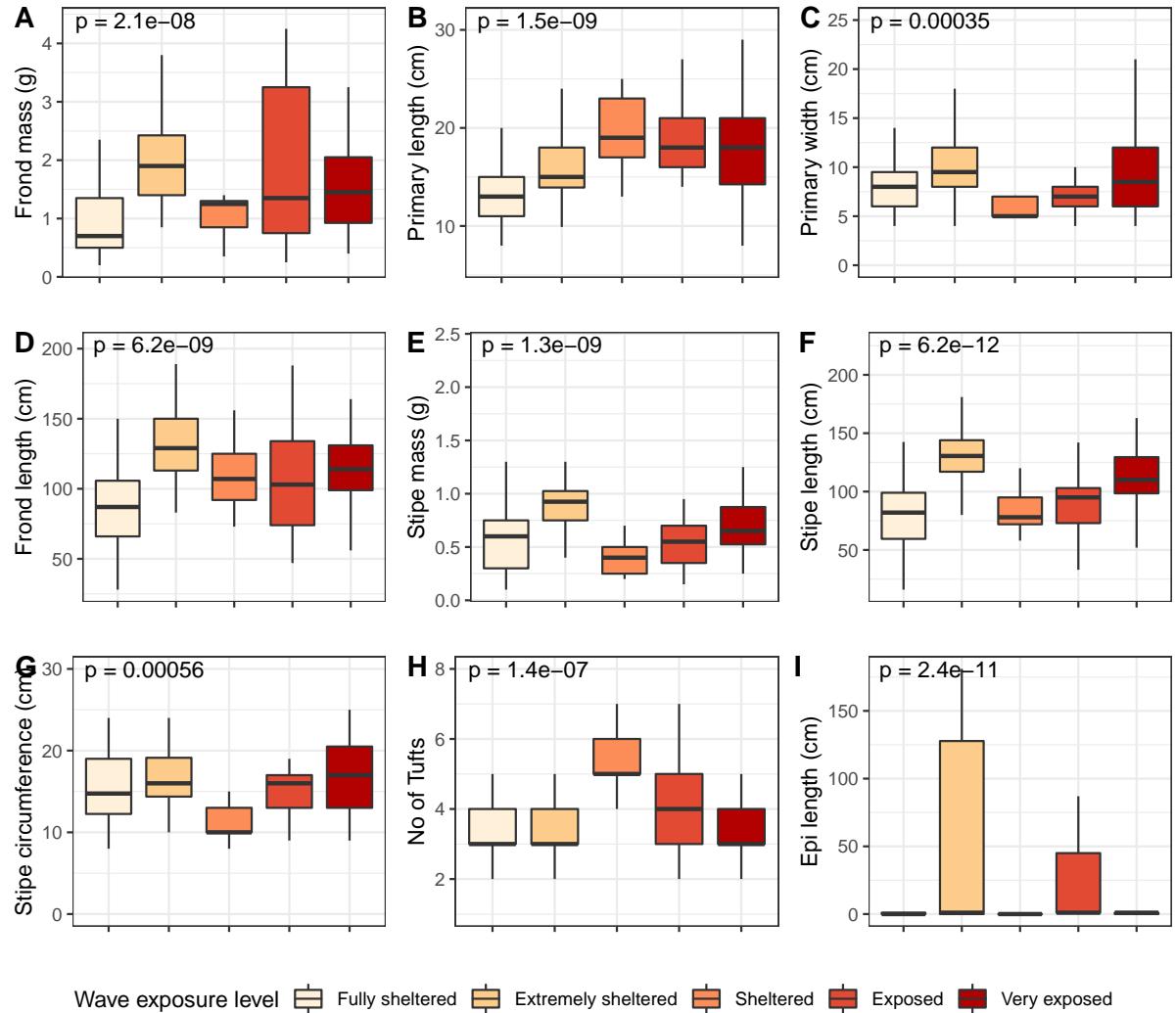


Figure 11: Boxplot of morphological characteristics for shallow population *E. maxima* grouped by wave exposure.

Abiotic drivers of *L. pallida* morphological characteristics

Forward selection, assessment of VIF and an examination of pairwise Pearson correlation coefficients allowed us to retain the most parsimonious descriptors of *L. pallida* morphological characteristics with an adjusted R^2 of 0.49, explaining 72% of the variation (global permutation test on final model: d.f = 1, $F = 8.51$, $p = 0.008$). RDA1 was the only significant axis in the model and explained 48% of the variation while RDA2 was not significant and explained 63% of the variation. Total length, stipe length, stipe diameter and stipe mass were positively influenced (i.e., increased size corresponding with the environmental driver) by *hs_mean* and *dir_median* for kelps mostly from the western region and negatively influenced (i.e., decreased size corresponding with the environmental driver) by *tp_sd* and *mean_temp* for kelps from the eastern region. Although sites from the western region did not cluster as closely as eastern region study sites, grouping according to region was still evident.

Abiotic drivers of *E. maxima* morphological characteristics

Forward selection, assessment of VIF and Pearson correlation coefficients allowed us to retain the most parsimonious descriptors of deep *E. maxima* morphological characteristics with an adjusted R^2 of 0.39, explaining 67% of the variation (global permutation test on final model: d.f = 5, $F = 2.4$, $p = 0.026$). RDA1 was the only significant axis in the model ($p = 0.03$) and explained 72% of the variation. The non-significant axis for the model explained 17% of the variation. Primary length, primary width and stipe circumference were positively influenced by *hs_mean*, *tp_mean* and *dir_median* for kelps from the western region. The remaining morphological characteristics were positively influenced by *min_temp* and negatively influenced by *tp_sd* for kelps from the eastern region.

Forward selection, assessment of VIF and Pearson correlation coefficients allowed us to retain the most parsimonious descriptors of shallow *E. maxima* morphological characteristics with an adjusted R^2 of 0.36, explaining 61% of the variation (global permutation test on final model: d.f = 4, $F = 2.41$, $p = 0.013$). The model consisted of one significant axis, RDA1 ($p = 0.02$) and explained 62% of the variation. Stipe length, stipe mass and stipe circumference were positively influenced by *max_temp* and *mean_temp* along RDA1, and explained 50% and 55% of the variation respectively. The remaining morphological characteristics were positively influenced by *tp_max* and negatively influenced by *dirw_median* along RDA2 and explained 86% and 94% of the variation respectively. There was overlapping of clusters according to region with no clear patterns in sites evident.

Discussion

This study considered important drivers of kelp morphology that have been identified in previous research (Fowler-Walker, Wernberg, and Connell 2006; Miller, Hurd, and Wing 2011; Fowler-Walker, Connell, and Gillanders 2005; Stewart et al. 2009; Wing et al. 2007; Molloy and Bolton 1996; Pedersen and Nejrup 2012; Wernberg and Thomsen 2005; Thomsen, Wernberg, and Kendrick 2004), namely temperature and wave exposure, around the Cape Peninsula on two prolific kelp species. The complex geomorphology of the western Cape coastline creates an ideal natural laboratory for studies of kelps in interaction with their environment. Unlike previous research, this study used a numerical model to provide the various variables of wave exposure. We also considered wind in addition to temperature and wave variables, since wind is an important component of wind-driven surface gravity waves (Holthuijsen 2010). The results show that specific variables of wave exposure are the main drivers of kelp morphology with temperature only playing a minor role. Furthermore, the investigation of differences in morphological characteristics between shallow and deep populations of *E. maxima* suggests that in low wave exposure environments the role of temperature as a morphological driver increases, such as in False Bay.

The annual and seasonal patterns in both wind influence the thermal regime around the coastline by inducing upwelling. Upwelling brings deep, cool nutrient rich water to coastal areas and therefore induces a decrease in temperature (Field et al. 1980; Andrews and Hutchings 1980; Gill and Clarke 1974; Cram 1970; Rouault, Pohl, and Penven 2010; Blanke et al. 2002). The wind speed and wind direction help drive upwelling in summer on the western side of the Cape peninsula, where southerly winds blow parallel to the coast and trigger upwelling (Field et al. 1980; Rouault, Pohl, and Penven 2010). This is not the case for False Bay which is shielded from the dominating wind and swell the Cape Peninsula is subject

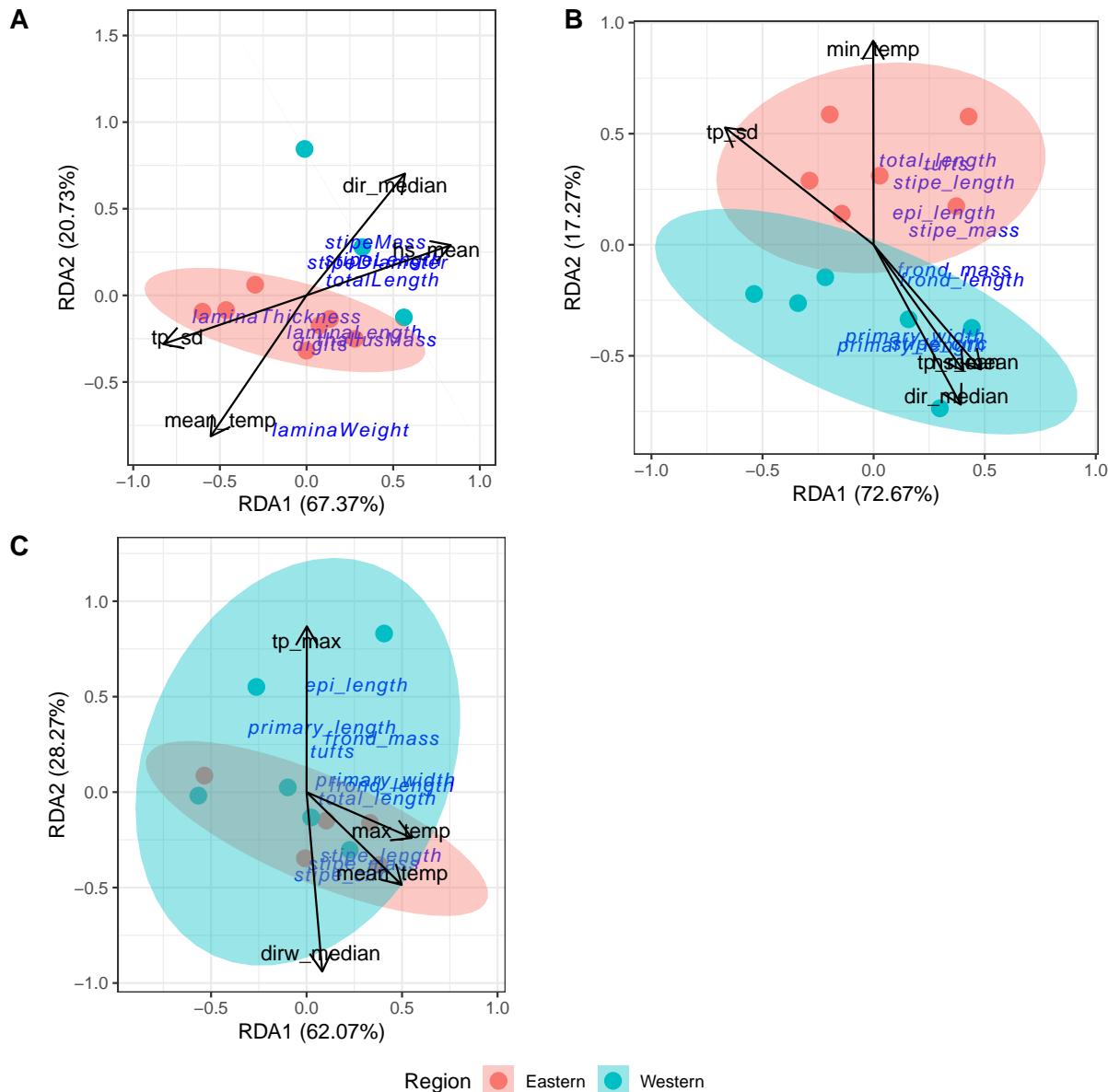


Figure 12: RDA output for *L. pallida* (A), deep *E. maxima* (B) and shallow *E. maxima* (C).

to, with the exception being the winter months where upwelling becomes more favourable for the region due to the change in swell and wind direction, causing lower temperatures to dominate during this time (Rouault, Pohl, and Penven 2010; Andrews and Hutchings 1980). The directional sheltering effect of the Cape Peninsula, against the dominant swell direction is clearly observed in the wave exposures presented in figure ???. Increased wind speed at sites along the west side of the peninsula in a southerly direction trigger upwelling events along the western side of the peninsula (Rouault, Pohl, and Penven 2010; Field et al. 1980). In general, the western side of the peninsula is more exposed than the eastern side (False Bay) and experiences significantly higher significant swell height and significant peak period. This was also reflected in the wave exposure categories which show a trend of decreasing wave exposure (wave power) around the peninsula and into False Bay. There are also differences between the types of waves that each side of the peninsula experiences. The ???? analysis shows the western side of the peninsula is not only more exposed but the hydrodynamics are largely swell driven, while on the eastern side most of the wave energy is driven by a combination of swell and wind with the latter being the predominant driver.

We provide strong support that variations in the environmental variables, particularly wave exposure variables, are driving kelp morphological characteristics around the Cape Peninsula. Morphological adaptation due to water motion may manifest in a number of ways in high wave energy environments. For instance, reduction of blade thickness, blade elongation, increase of stipe length, increase in stipe circumference and force of attachment (Fowler-Walker, Wernberg, and Connell 2006; Wernberg and Thomsen 2005; Friedland and Denny 1995; Mark Denny and Roberson 2002; Bekkby et al. 2014; Denny, Gaylord, and Cowen 1997; Mark Denny and Gaylord 2002) have been identified in previous studies. Although this study did not measure force of attachment, other morphological responses to temperature and wave variables were evident. Species-specific responses are evident in both wave exposure and temperature. In cool-temperate environments *L. pallida* tended to show increases in certain morphological characteristics (stipe mass, stipe length and stipe diameter) while in the warm-temperate environments these were significantly lower. This was also true for deep *E. maxima* populations, which had longer, thinner stipes for kelp in the warm-temperate compared to kelp in the cool-temperate. Reduction in certain morphological characteristics has been attributed to temperature by Serisawa et al. (2002) in the kelp *E. cava*, which was smaller and shorter in warmer sites compared to cooler sites. The reduction in size of adult may be a response to low nutrient conditions, which has been shown to reduce growth rate and overall morphology (Simonson, Scheibling, and Metaxas 2015). Warmer temperatures are associated with low nutrient concentrations (Waldron and Probyn 1992) and the low frequency of upwelling conditions in False Bay (low nutrient supply) coupled with warmer temperatures may be a contributing factor. It should be noted however, that from these analyses that in general the cool-temperate region is more exposed to waves than that of the warm-temperate region. Therefore, the significantly larger morphological characteristics for kelp from the cool-temperate region may overlap with responses to wave exposure which was exhibited strongly in both species. When grouped by wave exposure category, *L. pallida* characteristics showed a significant increase in length for the ‘Extremely sheltered’ category (6-10 kW/m; figure ??) compared to the fully sheltered category (<5 kW/m; see figure ??), which maybe a ‘go-with-the-flow’ tactic. Kelp are able to increase flexibility by increasing stipe length which increases the extension capabilities of kelp to a passing wave (Mark Denny and Gaylord 2002; Hurd 2000). However, increasing stipe length is only beneficial under lower exposure levels as a long stipe actually increases overall drag on the plant under higher exposure levels (Mark Denny and Gaylord 2002; Denny, Gaylord, and Cowen 1997). This is reflected in Figure ?? which shows an overall reduction of *L. pallida* morphological characteristics suggesting a size reducing tactic to cope with higher levels of wave exposure. The morphological characteristics of *E. maxima* show similar patterns when grouped to wave exposure. The results suggest that deep *E. maxima* populations exhibit a different response as well as a higher wave exposure threshold. Unlike *L. pallida*, *E. maxima* exhibits a size reducing tactic with an increase in exposure level by significantly decreasing stipe mass, stipe length, stipe circumference, total length and frond length. A magnitude related reponse has been suggested by Wernberg and Vanderklift (2010) who investigated the temporal and spatial variations of various environmental drivers of the kelp *E. radiata*. The authors identified wave exposure as the most important driver of kelp morphological characteristics and that the type of response elicited is dependent on the magnitude of wave exposure.

A size reduction tactic has been shown before (Fowler-Walker, Wernberg, and Connell 2006; Mark Denny and Gaylord 2002; Hurd 2000; Fowler-Walker, Connell, and Gillanders 2005) and is regarded as strategy to reduce overall drag on the plant. However, *E. maxima* morphological characteristics changed significantly as wave exposure increases. When grouped to the higher wave exposure levels, *E. maxima* morphology exhibited a strength and flexibility increasing trait (see figure 9). Furthermore, the morphological response

of *E. maxima* to wave exposure only occurs at the ‘Moderately exposed’ (20-30 kW/m) level compared to *L. pallida* which exhibits a response at a lower wave exposure level. This suggests that *E. maxima* can tolerate higher exposure levels before having to exhibit a morphological response. The redundancy analysis performed confirms the patterns and responses observed as well as identifying specific temperature and wave variables as drivers of kelp morphology. Kelp morphology characteristics are largely wave driven for both species but differ in terms of specific temperature and wave metrics. For instance, both species morphological characteristics are determined by swell direction (*dir_median*), standard deviation in peak period (*tp_sd*) and mean significant swell height (*hs_mean*), but *L. pallida* temperature driver is mean temperature (*mean_temp*) and *E. maxima* by minimum temperature (*min_temp*). Minimum temperature as an important metric for *E. maxima* may be related to nutrient availability. Low temperatures are often associated with upwelling events which bring cool, nutrient rich water into the nearshore. False Bay has comparatively little upwelling events compared to the western side of the peninsula, and so nutrients may be a limiting factor for *E. maxima* populations within False Bay (see figure ??) and hence the identification of minimum temperature (*min_temp*) as a driver. Vertical mixing of the water column for inshore regions are driven by several abiotic processes: (1) Turbulence of breaking waves inside or outside of the surf zone (2) convective mixing through a combination of cooling and evaporation (3) wind driven currents and (4) tidal mixing (Smit et al. 2013). These abiotic processes cause effective vertical mixing of surface and deeper water stratifications which leads to a homogeneous thermal environment, which in this study may be interpreted as the mean temperature. Therefore, the homogenous thermal regime of inshore regions may be a reason why mean temperature is driver of *L. pallida* morphological characteristics. The difference in canopy type between the species may be the reason why *E. maxima* is driven by multiple wave metrics compared to *L. pallida*. Since *E. maxima* is a canopy-kelp, it is exposed to all components of a wave compared to *L. pallida* which occurs deeper in the water column. Mean temperature identified as a driver for *L. pallida* may be related to diurnal temperature fluctuations in the water column. Solar heating of the water surface in combination with wind-driven transport causes fluctuations within the water column, which can occur daily or seasonally (Kaplan et al. 2003).

Annual maximum and winter mean temperatures influence stipe length and frond length in shallow *E. maxima* individuals located at sites within False Bay; which was not the case for deeper *E. maxima* individuals as well as *L. pallida* which were largely driven by wave variables. The shallow *E. maxima* individuals may not experience the same amount of wave energy as do deeper populations. This may be due to wave dampening from deeper populations of *E. maxima*, which attenuate the wave energy entering coastal environments (Kobayashi, Raichle, and Asano 1993; Jackson 1984; Mork 1996). The morphological variations in characteristics for deep *E. maxima* populations are not seen for shallow *E. maxima* populations. The lack of variation in shallow *E. maxima* populations was also found in previous research by (Rothman et al. 2017) who showed that light was a significant driver. This influence of light may suggest photosynthetic ability and nutrient uptake as important drivers in shallow environments. Wave exposure may be reduced in shallow environments due to the wave damping effect of deep kelp and seaweed populations (Kobayashi, Raichle, and Asano 1993; Mork 1996; Jackson 1984) thereby reducing the need to adapt morphological characteristics to reduce drag. Furthermore, the reduction in differences between deep and shallow *E. maxima* at wave exposed sites on the western of the peninsula compared to sites in False Bay provides further evidence that wave exposure is not an important driver of shallow *E. maxima* populations. Increased temperatures corresponded with a reduction in stipe circumference, frond length, stipe length, total length and stipe mass resulting in slim or ‘skinny’ kelp individuals, which supports findings from previous research by (Mabin et al. 2013; Serisawa et al. 2002). These findings were confirmed by the redundancy analysis which showed the contribution of wave variables as a driver of kelp morphological characteristics was lower compared to temperature variables. The sites do cluster by region but almost overlap entirely, further indicating wave variables are not the main driver. Although wave variables were not identified as an important driver, it is important to note the wave variables identified in the RDA differ to deep *E. maxima*. The identification of median wind direction (*dirw_median*) suggests that surface gravity waves as a driver compared to swell waves (*dir_median*) identified for *L. pallida* and *E. maxima*. The identification of maximum temperature as a driver of kelp morphological characteristics may be due heating of shallow coastal waters due to solar heating.

Conclusion

Past research shows that macroalgal morphological characteristics are largely driven by a wave exposure while others have suggested a complex interaction between various environmental variables. We confirm that wave variables are the main driver of kelp morphological characteristics in both *E. maxima* and *L. pallida* populations around the Cape Peninsula, and differences in shallow and deep populations of *E. maxima* may reflect small differences in wave and temperature variables as drivers of kelp morphological characteristics. The response of kelp morphological characteristics to wave exposure was evident and both species show a tactic based on the magnitude of wave exposure. Strength increasing traits were exhibited for lower exposure levels while a ‘go-with-the-flow’ tactic for moderate levels of wave exposure. Denny and Galord ??? showed that increased flexibility or a ‘go-with-the-flow’ tactic has a threshold value, where increased stipe length actually increase drag under high wave exposure scenarios. Therefore, under high wave exposure scenarios size reducing traits, such as reduced surface area of the overall plant should be favoured instead. This was evident in the results which showed that stipe length decreases under high wave exposure categories. This suggests that how morphological characteristics manifest themselves is dependent on the magnitude of wave exposure. Furthermore, the results suggest that in the absence of wave exposure, temperature becomes the dominant morphological driver. This is evident from the redundancy analysis for each species and deep populations of *E. maxima* which show clustering of study sites according to the region; wave variables drive morphological characteristics for kelps from the western region and temperature variables for kelps from the eastern region. Clustering of sites according to region overlapped almost completely for the RDA analysis of shallow *E. maxima* suggesting that for shallow kelp the effect of wave exposure is less variable. Temperature variables were not a significant driver of kelp morphology in this study. Although temperature plays an important role in distribution (Bolton et al. 2012; Miller et al. 2011; Rinde et al. 2014) of kelp and physiological functioning of adults and gametophytes (Mohring et al. 2014; Steneck et al. 2002; Gerard 1997; Bearham et al. 2013; Smale & Moore 2017), there is little evidence that temperature is an important driver of morphological variation. However, we suggest that temperature plays a larger role in determining kelp morphology at sites where wave energy is low enough not to elicit a response in morphological characteristics.

Conflict of Interest Statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest

Author Contributions

RC conceptualised the scope of the research reported in this paper, collected samples, undertook the majority of numerical and statistical analyses, made the first round of interpretation, and did the majority of the writing. AS and CR provided guidance in terms of writing, statistical analyses, and the final draft of the paper, as well some writing in the relevant sections. RS aided in fieldwork and statistical analyses for the temperature data. TP performed the initial analyses and interpretation of the data.

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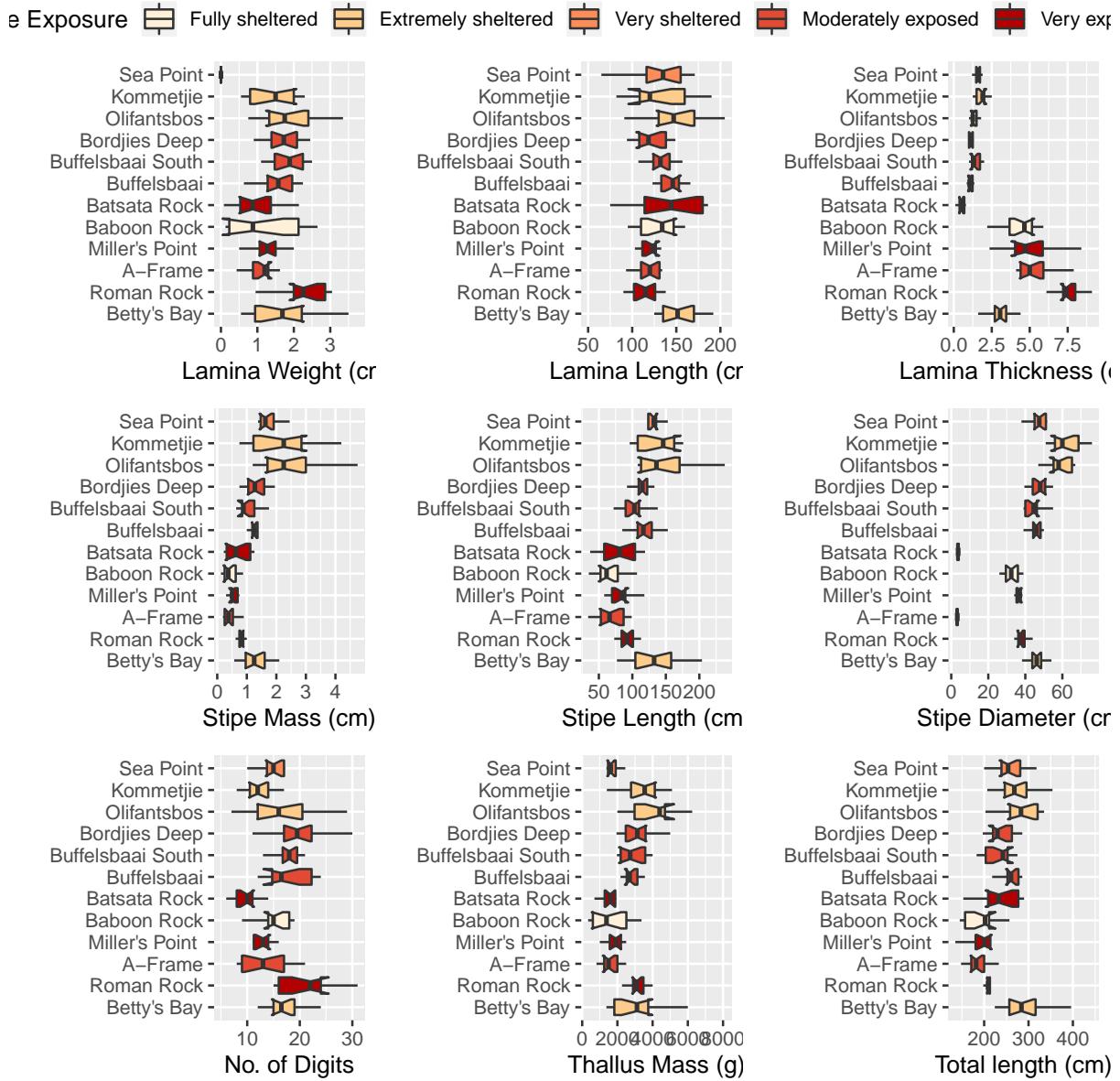
The research was funded by the South African National Research Foundation (<http://www.nrf.ac.za>) programme “Thermal characteristics of the South African nearshore: implications for biodiversity” (CPRR14072378735).

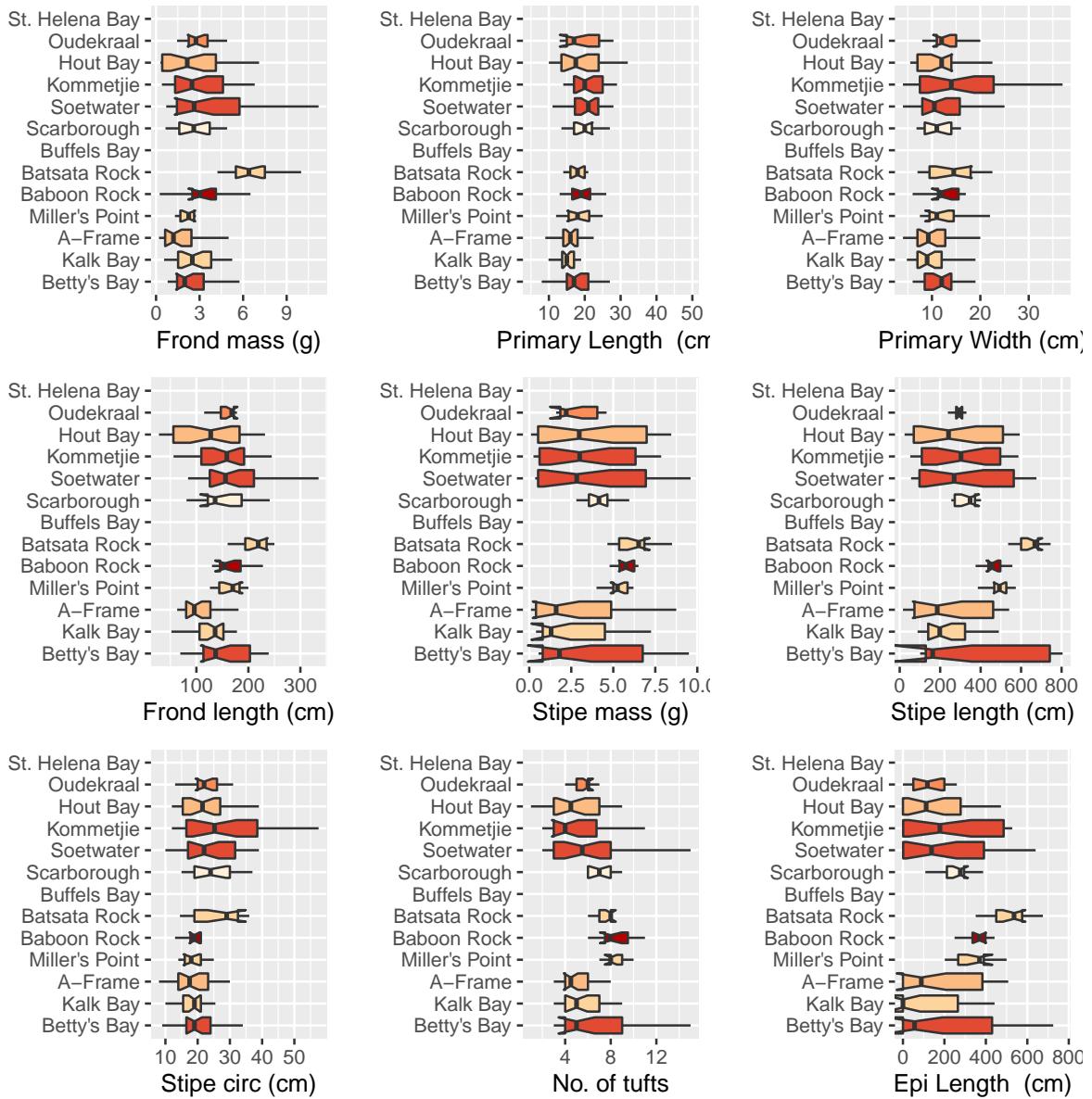
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Appendix





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