FUNCTIONAL BIOGEOGRAPHY: EVALUATING COMMUNITY ASSEMBLAGE PATTERNS AND ECOSYSTEM FUNCTIONING IN INTERTIDAL SYSTEMS USING TRAIT-BASED APPROACHES

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ABSTRACT

Analyses of taxonomic diversity patterns within coastal systems has been critical in the development of the theory of biogeography. Increasing evidence, however, shows that the variety of functions that species perform in ecosystems (rather than their taxonomic identity) is a better predictor of the influence of the environment on the species. This information has been useful in predictive ecology leading to the development of trait-based approaches (TBA). Until the late 1970s, however, limited effort (particularly in marine systems) was channeled towards patterns in functional species traits and how they may be affected by changes in environmental gradients. Here, I mapped the functional biogeography of the South African coastline based on a suite of species' reproduction and development traits. Because species composition is one of the key tools used by zoogeographers to map species distribution patterns, I expected lower variability in trait composition within main biogeographic regions than in intervening transition zones based on the habitat templet theory and following the biomass ratio and limiting similarity hypotheses. In brief, the habitat templet theory proposes that "the habitat provides a templet upon which evolution forges species characteristics", while the biomass ratio hypothesis assumes that the most abundant species traits determine ecosystem functioning. The limiting similarity hypothesis also sometimes referred to as the niche complementarity hypothesis, however, predicts that species can coexist if their niches complement one another. In light of the habitat being an evolutionary templet, abiotic and biotic habitat patterns were measured as nearshore SST and chlorophyll-*a* gradients, respectively. I expected the SST gradient to act as the stronger key filter of trait diversification because temperature is often considered the most influential environmental factor affecting species survival with seasonality of SST affecting the timing of spawning and along with food availability, possibly influencing fecundity.

Functional trait data were thus compiled for macroinvertebrate species collected from fifty-two rocky shore sites from three main bioregions (east, south, and west) and two transition zones (south-west and south-east). Biological trait analysis and functional diversity indices were used to evaluate how traits related to species development and reproduction respond to temperature and chlorophyll-*a* (used as a proxy for food availability) gradients along the coastline. GLMM and hierarchical cluster analyses showed distinct patterns/shifts in SST and chlorophyll-*a* gradients across bioregions, with two main breaks in SST separating the east and south-east overlap (SEO) bioregions from the south, south-west overlap (SWO) and west bioregions. In contrast, chlorophyll-*a* exhibited three major breaks with the east, SEO–south–SWO, and west clustering independently of each other. The RLQ analysis (a type of co-inertia analysis) which simultaneously ordinates 3-matrix datasets [i.e., (environment × site[R]), (species × site[L]) and (species × traits [Q])] showed that the higher SST gradient on the east and SEO promoted higher abundance and biomass of simultaneous hermaphrodites while higher chlorophyll-*a* gradients on the SWO and west coasts strongly promoted reproductive maturity at larger-sizes. The combined fourth-corner analyses showed that the modalities within the development trait domain responding to chlorophyll-*a* gradients primarily included filter feeders, sessile and swimming species

and also species living on the infratidal zone. In addition, the reproduction trait domain showed higher sensitivity and association to differences in chlorophyll-*a* and SST gradients than development traits. Overall, SST and chlorophyll-*a* gradients influenced the distribution of the most dominant traits as indicated by shifts in community-weighted mean trait values across bioregions. This suggests the importance of habitat filtering on coastal species reproduction.

A separate study evaluating the influence of large-scale biogeographic effects *vs* the micro-scale biogenic habitat structure offered by coralline seaweeds across 24 sites revealed some notable effects of both factors on the diversity and abundance of macroalgal epifauna. There was a notable biogeographic influence on epifauna, with the SEO recording the highest epifaunal species richness and abundance, followed by the south coast, then the SWO and lastly the west coast. In addition, the total biomass gradient of the corallines followed a similar trend. The epifauna however, showed no host-specificity, illustrating that epifauna may not be species–centric as commonly assumed, and the higher diversity of epifaunal diversity may well be simply because those corallines are the available habitat within the sampled part of the coastline.

Lastly, macroinvertebrate trait distribution on the South African coastline confirms that the habitat, particularly the biotic filter (in this case chl-*a*) provides a templet upon which evolution forges species traits. However, since temperature is a proxy for nutrient availability (cold upwelling brings nutrients), then temperature drives chlorophyll-*a*. Subsequently this means the abiotic component indirectly drives trait distribution by influencing the biotic environment (chl-*a*). For epifauna species, also, the coralline diversity and composition can also be regarded as a biotic filter influencing the epifaunal abundances and composition across different bioregions. Moreover, since temperature is regarded as a conservative trait in seaweeds, temperature tolerance defines the biogeographical boundaries of seaweeds, therefore temperature may be indirectly affecting epifauna abundances through coralline species diversity and biomass.

In summary, considering the deterministic processes governing ecosystem functioning and community assemblage, the mass ratio and limiting similarity hypotheses showed complementary effects. Different bioregions provided variable support for these two hypotheses, but overall, the mass ratio hypothesis (weighted by species biomass) received stronger support and may be more meaningful to the interpretation of ecosystem functioning and persistence within rocky shore systems. Lastly, although, the SWO showed some of the characteristics of a subtraction zone based on the relatively low abundance, diversity, and biomass measures. Nonetheless, there was evidence of high functional redundancy across all other four bioregions. This suggests that in the context of development and reproduction traits, the rocky shore ecosystem along the SA coastline may be functionally stable at this stage.

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DEDICATION

To my beloved mother (Sibongile),
dad (David), and little sister (Sharon),
Twenty-two years later, the pain of losing you still lingers on, and I miss you ever so deeply. Although you are not physically present to share the joys and victories of life,
I know you are and have been by my side every step of the way.
This is the "last one" for the team!!
And I celebrate this achievement with you.
I hold you in my heart, till I can hold you again in heaven.

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CHAPTER 1

GENERAL INTRODUCTION AND THESIS OVERVIEW

The crucial first step to survival in all organisms is habitat selection. If you get to the right place, everything else is likely to be easier. Edward O. Wilson, Biophilia, 1984

General Introduction and Thesis Overview

1.1. Species distribution and biodiversity patterns

Macroscopic analyses of emergent patterns of species abundance, distribution, diversity, and functioning over large geographic scales have huge potential for testing the generality of the underlying mechanisms that structure the natural world (e.g., Currie & Fritz 1993; Lawton, 1999; Ricciardi & Bourget, 1999). Establishing the mechanisms driving biogeographic patterns is an essential prerequisite for understanding and predicting species responses to environmental changes. Such predictions have also been motivated by the impact of human activities on natural ecosystems such as coastal habitats and the implications for the goods and services they deliver (Cardinale et al., 2012; Hautier et al., 2015; Mensens et al., 2017). Species within coastal areas are under the influence of natural and anthropogenic stressors that can affect the functioning of ecosystems (Micheli et al., 2016) and can compromise their capacity to sustain ecosystem services (Worm et al., 2006; Halpern & Floeter, 2008; Naeem et al., 2012; Tilman et al., 2014; De Laender et al., 2016).

Considering the species themselves, a taxon's geographical distribution results from a combination of historical, regional, and local processes, ecological interactions, and accidental or planned species introductions (Knox, 1980; Lindberg, 1991; Ruiz et al., 1997). Some ecologists have suggested that community organisation depends on the phylogenetic relatedness of its interacting members (Anderson et al., 2004). Phylogenetic assembly results from constraints due to long-term historical patterns of speciation, extinction, and biogeographic migration. It is distinguished from ecological assembly rules, driven by dispersal (both active and passive), abiotic and biotic processes (Belyea & Lancaster, 1999; Lortie et al., 2004; Götzenberger et al., 2012). The functioning of an ecosystem is, however, not governed by the phylogenetic content of its biota but by the functional traits of individuals, the distribution and abundance of these individuals, and their biological activities (Naeem & Wright, 2003). Species diversity is expected to affect ecosystem processes because the number and kinds of species present determine the specific traits represented in an ecosystem (Symstad et al., 2003). At intermediate spatial scales, environmental and habitat conditions may act to filter out species with unsuitable traits while facilitating the co-occurrence of functionally similar species (Gallien & Carboni, 2017). At small spatial scales, species interactions are expected to drive community patterns of distribution and abundance (Tilman, 1982; Schoener, 1983; Silvertown et al., 1999). Thus, species diversity within an ecosystem can be determined by these ecological and community assembly concepts, which are the focus of this thesis and are discussed in greater detail in the following pages.

1.2. Community assembly rules: Deterministic and/or stochastic theories

A theoretical debate has arisen over whether community assembly rules govern communities. Beta diversity, generally defined as species compositional difference among communities, is a central concept to understanding theories and mechanisms of community assembly (Fukami & Nakajima, 2011). There is a wide selection of mechanistic hypotheses explaining community assembly. These include dispersal limitation, deterministic processes such as habitat filtering and stochastic processes generating ecological drift, or larger-scale processes that create differences in the sizes of species. The two broad concepts concerning community assembly that are the focus of this thesis are stochastic and deterministic theories (with greater emphasis on the latter). The fundamental differences between these two lie in species demographic characteristics (Sommer et al., 2014). Stochastic theories (Connor & Simberloff, 1979) assume that all species are ecologically similar and coexist because of random demographics, neutral performance of individuals, and or ecological drift (Hubbell, 2001). On the other hand, deterministic theories are niche-based theories that explain variations in community structure through interspecific trade-offs and spin-offs among species that impede or facilitate co-existence (Chase, 2003). These are usually referred to as assembly rules.

Two concepts can further explain deterministic processes: habitat filtering and limiting similarity (MacArthur & Levins, 1967; Weiher & Keddy, 1995). The assembly of species within a community is thought to result from a hierarchical process in which species must pass a set of abiotic and biotic filters acting at various spatio-temporal scales (Zobel, 1997), selecting the species best adapted to local conditions. While the understanding that the abiotic environment shapes the distribution of species across the landscape predates much of the modern study of ecology (Humbolt & Bonpland, 1805 in Kraft et al., 2014), the current use of the environmental filtering concept has its roots in the study of plant community assembly and dynamics in the late 1970's and early 1980's (Bazzaz, 1991; Woodward & Diament, 1991). These foundational studies described the environment as a metaphorical 'sieve' or 'filter' that only permits species with particular traits or phenotypes to establish and persist, excluding all others. The concept has considerably grown in usage since this time, playing an essential role in many studies of community assembly, succession, invasion biology, and biogeography (e.g., Weiher et al., 1998; Richardson et al., 2000; Webb, 2000; Cornwell & Ackerly, 2009; Swenson et al., 2012; Whitfeld et al., 2012).

At this stage, it is worth noting that most authors use the terms 'environmental filtering', 'abiotic filtering' and 'habitat filtering' interchangeably to refer to the role of the abiotic environment. However, recently some authors have distinguished these terms, using 'habitat filtering' as a more inclusive term to refer to the combination of both biotic and abiotic factors (e.g., Maire et al., 2012). On the other hand, the environmental filtering concept focuses on the relationship between an organism and the abiotic environment, recognising that not all organisms will successfully establish and persist under all abiotic conditions. From this perspective, the environment is seen as a selective force, culling species unable to tolerate conditions at a particular location. Consequently, I use 'habitat filtering' throughout this thesis to reduce ambiguity and emphasise my focus on both biotic and abiotic factors, while minimally applying 'environmental filtering' to specific concepts involving only the abiotic parameters.

While it is increasingly recognised that deterministic and stochastic processes co-occur, their relative influence continues to fuel contemporary debate (Chase & Myers, 2011; Botta-Dukát & Czúcz, 2016). This question is particularly pertinent to ecosystems at the transition of biogeographical zones, as they often have characteristics relevant to both processes. Populations in transition environments typically differ in demographic characteristics from those in main habitats. They tend to be smaller, fragmented and have lower reproductive success, leading to demographic and genetic connectivity that is different from those in main habitats (Sommer et al., 2014). These attributes render marginal populations more vulnerable to drift processes, environmental fluctuations, Allee effects, demographic stochasticity, and local extinction (Kawecki, 2008), which can make it more difficult to detect the signature of niche-based processes (Chase & Myers, 2011) and ecosystem functioning patterns.

Describing or measuring ecosystem functioning is difficult, especially when considering the differences of opinion among the scientific community regarding what the concept means, with various definitions quoted in the literature or, sometimes, no precise definition given at all (Jax, 2005). Ecosystem functioning is a prominent and multi-dimensional concept in ecology that refers to the performance of an ecosystem (Jax, 2005). As it encompasses several phenomena (Hooper et al., 2005), the overall functioning of an ecosystem is complex and involves many factors relating to the system's chemical, physical, and biological components. No one individual parameter can be used to fully describe the functioning or performance of entire ecosystems (Giller et al., 2004), so consideration of multiple variables may be the most appropriate way to shed light on the concept (Duffy & Stachowicz, 2006). Thus, an ecosystem's performance or "functioning" can be assessed or evaluated across different dimensions. These include: (i) ecosystem processes (for example, biomass production or nutrient cycling), (ii) ecosystem services (e.g., climate regulation and resource provision), and (iii) analysing the persistence of the processes and services across space and time (Linden, 2016). As alluded to earlier, ecosystem functioning is primarily affected by an ecosystem's abiotic (chemical and physical) and biotic components (Jax, 2005; Bremner, 2008). However, of the two, biotic components, i.e., the role of biological organisms in the ecosystem, have been regarded as the most influential (Cardinale, 2012; van Linden, 2016). Moreover, because it is difficult to assess all the concepts of ecosystem functioning, for this study, I therefore use the term ecosystem functioning to refer to an estimate of the production output of intertidal species in terms of the total biomass produced by individual species across communities. In essence, total biomass was used as a proxy to estimate the production of the rocky shore system, where higher biomass was assumed to relate to a more stable system as suggested by Bell et al. (2014).

1.3. The ambiguity of traits

In its broadest English sense, a trait is any distinguishing characteristic or feature. In ecology, a functional trait is any trait that affects fitness indirectly via its effects on survival, growth, and reproduction (Violle et al., 2007). Nevertheless, in ecological usage, the term 'trait' is ambiguous, and its true meaning has consistently been debated (Lavorel & Garnier, 2002; Chown et al., 2004; Costello et al., 2015). Some authors split the term into different facets. The main facets include species functional/biological traits, taxonomic traits, and ecological traits. Functional or biological traits can be further broken down into two: response and effect traits. However, the terms taxonomic and ecological traits will be avoided in this thesis to minimise ambiguity and will simply be referred to as taxonomic diversity and ecological variables, respectively.

1.3.1. Species functional traits

Species functional traits are behavioural, morphological, physiological, or phenological characteristics of individuals that influence their response to the environment and/or their effect on ecosystem properties and/or services (Díaz et al., 2013; Beauchard et al., 2017). Functional traits hold the promise of more predictive ecology that goes beyond case studies of species or taxonomic groups (McGill et al., 2006). In addition, they reflect adaptive strategies and underlying physiological trade-offs. For example, in vascular plants, functional trait variation primarily reflects competitive dominance (plant size) and the leaf economics spectrum, which emerges from physiological trade-offs between structural integrity and growth potential (Díaz et al., 2016).

1.3.1.1. Response traits

Response traits are phenotypic components that determine the species' fitness, and performance in response to an environmental change. For example, a combination of reproduction traits or development mechanisms can translate to the ability of a species to disperse across geographical barriers (Beauchard et al., 2017). Response traits document size, motility, trophic position, and reproduction and thus indirectly characterize growth, survival, and reproduction at the species level; these, in turn, influence the observed site or habitat occupancy patterns and species distributions (Violle et al., 2007). Therefore, response traits often offer *a priori* explanations of community assemblages and species distributions. For example, in the face of predation or a temporal change, traits associated with reproductive frequency can be increased or lowered as a response to the pending threat. Due to rapid species loss and deterioration of ecosystems, ecologists urgently need to understand how changes in the environment alter community structure and assembly and how these changes, in turn, influence ecosystem functioning. Such information helps predict possible consequences of environmental change and allow decision-makers and stakeholders to initiate target-oriented protection and restoration actions.

1.3.1.2. Effect traits

The effect traits of an organism are qualitative characteristics that affect an organism's performance or behaviour (Lavorel & Garnier, 2002) and contribute to the function being measured. Examples include organism size (which may affect biomass), water retention capacity in bryophytes (regulating ecosystem hydrology), and burrowing behaviour (altering soil structure), or gut digestive features that influence nutrient turnover in animals (Diaz et al., 2013). In addition, if bioturbation is the ecosystem function of interest, then traits associated with behaviour, feeding and sediment reworking represent effect traits.

1.3.2. Other forms of traits

1.3.2.1. Taxonomic traits

The most common and widely used trait classification concerns taxonomic traits, which refers to the phenotypic characteristics of any organism from genus level to phylum. Taxonomic identity has been shaped over time through a myriad of processes such as evolution, speciation, or competition (Bell, 1967; Beauchard et al., 2017). Here, I refer to this aspect as taxonomic diversity.

1.3.2.2. Ecological traits

Ecological traits are also referred to as environmental requirements. They are used to highlight the differences and tolerances among biological strategies across spatial and temporal variation in environmental conditions (Beauchard et al., 2017). These traits play vital roles in the structuring and functioning of the ecosystems and include habitat preference, mobility type and body size. The difference in habitat preference among species affects species interactions through habitat filtering (Sato et al., 2020). In practice, however, it is assumed that ecological traits are not relevant in causally explaining species occurrences because they are measured where species are found (Beauchard et al.,2017). This assumption is based on the premise that species biology is rooted in evolutionary adaptations to environments that experience spatio-temporal variability in biotic and abiotic components. Therefore, other traits responding to this variability are expected to be more critical. As stated, I refer to as ecological traits as ecological variables.

Lastly, it is essential to note that response and effect are used here to refer to functional traits and should not be confused with other usages, such as the response to or effect of a perturbation on ecosystem functioning or the response to or effect of a biotic factor on a population. Response–effect trait frameworks have proven powerful predictors of ecosystem functioning since response traits often correspond to effect traits (see e.g., Larsen, Williams & Kremen, 2005; Pakeman, 2011; Díaz et al., 2013; Karp, Moeller & Frishkoff, 2013; Heuner et al., 2015). Conversely, the insurance effect (Naeem & Li, 1997) is at work if response traits are uncorrelated to effect traits as this buffer ecosystem functioning under environmental change (Eklöf et al., 2012). Empirical tests of the response–effect trait frameworks are, however, rare (Klumpp & Soussana, 2009) due to limited knowledge on the traits of biota other than terrestrial plants (Lavorel et al., 2013), which restrains our capacity to predict ecosystem functioning for different types of communities.

1.4. Application of functional traits

By providing a more mechanistic point of view than the use of species identities alone, species functional trait approaches help to test hypotheses about the existence of assembly processes (Cornwell & Ackerly, 2009; Mason et al., 2012; Spasojevic & Suding, 2012), to predict the abundance of species (Shipley et al., 2006; Laughlin et al., 2012) and to understand the influence of organisms on ecosystem functioning (Díaz & Cabido, 2001; Lavorel & Garnier, 2002). Ecological processes, including biodiversity-ecosystem functioning relationships, cannot be understood without accounting for trait variation across biological scales of organization, including at fine scales. Although trait variation underlies our understanding of the patterns and importance of biodiversity, there is a poor understanding of how variation in trait composition at different levels of biological organisation structures communities and ecosystems. Species functional traits can determine changes in species densities under environmental change and the species' contribution to ecosystem functioning (Lavorel & Garnier, 2002; Baird & Van den Brink, 2007; Mensens et al., 2017). This evaluation of ecosystem functioning under environmental change has been achieved by relating traits predicting species densities (response traits) to traits driving the contribution to functioning (effect traits, Suding et al., 2008; Hillebrand & Matthiessen, 2009). This approach, also termed the trait-based approach (TBA), has provided a useful approach to exploring the mechanisms underpinning the non-random assembly of communities. The foundation of TBA lies in theoretical ecology, particularly the habitat templet theory (Southwood, 1977), mass ratio and niche complementarity hypotheses (García-Palacios et al., 2017). These hypotheses provide a mechanistic understanding of the underlying drivers that influence species habitat use, distribution, composition, and overall biodiversity-ecosystem functioning (BEF).

TBA ignores the fact that individuals belong to species but instead describes individuals by a few taxon-transcending properties: their key traits. A combination of many traits characterises an individual, and the key traits are the few properties that capture the most of its Darwinian fitness. TBA aims to describe how the structure and function of ecological communities emerge from properties of the individual organisms and to enable the description of the dynamics of ecosystem functioning (Mason et al., 2012) as a response to habitat filtering and/or limiting similarity. Moreover, there has been increasing realisation that species-environment as well as intra- and interspecific species interactions to ecosystem functions such as climate regulation have significant cascading effects on ecosystem structure, health, and functioning (Byers et al., 2017).

Further, the use of traits to understand natural community assembly patterns is becoming standard practice, as is its use to support management tools in ecosystems undergoing adverse anthropogenic effects (de Bello et al., 2010; Resh & Rosenberg, 2010; Statzner & Bêche, 2010; van der Linden et al., 2017). Increased biological knowledge has triggered the development of trait-based frameworks that have since been used in theoretical studies (Statzner et al., 2010). These are currently used for practical ecosystem management and conservation and understanding the effects of the environment on community structure (Johnson et al., 2006; Dolédec & Statzner, 2008; van der Linden et. al., 2017).

As with taxonomic-based approaches, trait-based approaches include multivariate methods based on a community's functional structure. The two main analytical approaches in trait-based analyses are (i) functional diversity (FD) measures and (ii) biological trait analyses (BTA). Certain components of an organism's biology affect ecosystem functioning (Petchey & Gaston, 2006) and FD is the value, variation, and range of these functional traits. The origins of FD as a tool for understanding community functional composition is integrated into two hypotheses. These are the functional identity or commonly referred to as the mass ratio hypothesis and the functional complementarity hypothesis (Dolbeth et al., 2015). The former assumes that the abundance or biomass of the dominant traits will determine ecosystem functioning. This means the importance of a species to ecosystem functioning is proportional to its relative proportion within the community. On the other hand, the functional complementarity hypothesis assumes that ecosystem functioning is improved by the dissimilarity of traits within the system. The functional complementarity hypothesis considers the presence or absence of traits and the diversity of multiple traits within a community. These two hypotheses have yielded two (sometimes complementary) methods of measuring trait composition within communities. The first calculates the average community trait values i.e., the community-weighted mean (CWM), while the second calculates the variation of trait values among species using functional diversity indices (FDIs). CWM is based on the dominant trait categories within a community. The former assumes that, as the environment acts as a bottleneck, an increase in the abundance of optimally adapted species will improve ecosystem functionality. On the other hand, FDIs calculate the variation of trait values among species (Petchey & Gaston, 2006). FDIs describe two broad aspects of functional diversity: (i) how much of the functional niche space is filled by the existing species (functional richness) and (ii) the variability in how this space is filled (functional evenness, functional divergence, functional dispersion) (Schleuter et al., 2010; Villéger et al., 2008; Degen et al., 2018).

BTA is another analytical approach developed to measure ecosystem functioning. The approach describes multiple aspects of functioning based on features of the biological ecosystem component (Bremner et al., 2008). It explores potential relationships between individual species or communities and environmental characteristics, the latter including the effects of human activities. BTA is based on the habitat templet theory, which states that species' characteristics evolve due to habitat constraints (Southwood, 1977). The incorporation of biological traits in community ecology was initially used in terrestrial and freshwater research (Bonada et al.,2006; Statzner & Bêche, 2010); however, there is a growing recognition of the benefits of a biological trait approach within marine systems (Linden, 2016). This growing success of biological BTA has given a new impetus to marine community ecology. The initial stages of BTA involve the identification of key aspects of functioning in the ecosystem under consideration and the selection of suitable indicator traits. Traits are classified and assigned at species level and the most relevant to large spatial scale community ecology include life-history strategies, reproduction, morphology, and resource acquisition. This trait classification can be used to understand why different taxonomic entities (e.g., species, genera) occur in similar habitats (Dolédec et al., 1996; Legendre et al.,1997; Dray & Legendre, 2008) as organism performances can result from common adaptations to environmental forces (Greenslade, 1983; Southwood, 1988). BTA distinguishes the roles of species within a community and highlights the potential for functional redundancy. It uses multivariate ordination to describe patterns of biological trait composition over entire assemblages (i.e., the types of traits present in assemblages and the relative frequency with which they occur) (Bremner et al.,2006). Lastly, a more informative and nuanced way of using BTA is to group functional traits into trait domains or strategies. This is because species comprise multiple interacting traits (Verberk et al., 2008)

1.5. Integrating taxonomic- and trait-based approaches

Much of the study of the relation of biodiversity to the environment and species distribution patterns (e.g., Hawksworth 1995; Johns et al., 2013; Martin et al., 2013) does not concern itself with ecosystem functioning or functional traits (Mitwally, 2022). Instead, its emphasis has been on taxonomic diversity (TD), i.e., the richness (number of species) and evenness (relative species abundances) of assemblages (Parker et al., 2001; Lepofsky et al., 2005; McKie et al., 2008;), based on abundance, biomass and/or the presence/absence of species. Traditional ecological diversity indices focus on the relative abundances of species within a community while ignoring the degree of difference between species (Zoltan, 2017). The primary assumption is that species occurrence is random. Despite analytical techniques being sufficiently sophisticated to detect multiple gradients in ecosystems (Gauch, 1982; Dolédec & Chessel, 1991), correlations between species distributions and habitat characteristics have limited potential for a mechanistic understanding of ecological patterns since analyses based on taxonomic grounds alone do not confirm assembly rules independent of species biology (Resh et al., 1994; Fleishman et al., 2006).

Moreover, most biogeographers have focused on single taxon distributions to demarcate biogeographic boundaries. This then becomes more challenging when multiple taxa and trophic levels are considered in one study. However, recent studies have shown that assessing the variation of communities may capture patterns that cannot be revealed by single taxon analyses. For example, in South Africa, Sink et al. (2005) found several species co-occurring in both the subtropical Natal and tropical Maputaland rocky intertidal despite the vastly different environmental properties of these biogeographic units. These findings were only revealed through the examination of community abundance variation. Species characteristic of Maputaland have tropical affinities and it is proposed that this region forms part of the tropical Indo-West Pacific Province. On the other hand, subtropical Natal appears sufficiently distinctive to be recognised as a subtropical biogeographic province different from Maputaland (Sink et al., 2005). Similarly, Blanchette et al. (2008) analysed rocky intertidal communities of the Pacific coast of North America and, while they corroborate previous descriptions of biogeographic units, they demonstrated regional variations in community patterns. The analysis of rocky intertidal community patterns appears to function better when using multiple species, rather than single taxa to delimit biogeographic zonation as more trophic levels will capture more environmental variation (e.g., wave stress and temperature gradients) and ecological interactions (e.g., biological invasion, predation, and competition for space), providing improved resolution of spatial patterns (Dolbeth et al., 2003; Schiel, 2011).

Nonetheless, research has expanded to include the diversity of functions performed by the species as of paramount importance in the structure, stability and functioning of a plethora of systems

(Cadotte et al., 2011; Swenson, 2011; Zhou et al., 2016). For example, the turf morphological structure of some seaweed species has been associated with influencing the species diversity, abundance and in some instances the functional composition of some epifaunal assemblages. Further, contrary to traditional species abundance diversity, functional diversity and its effects does not automatically increase when species richness increases. Thus, taxonomic diversity in isolation is not always a good surrogate for functional diversity. The integration of both approaches is, however, assumed to provide significant ecological information. Functional diversity is a good estimator of ecosystem health and the vulnerability of an ecosystem as it implicitly contains information about how many species with similar traits may compensate for the loss of one another in an ecosystem through functional redundancy (Petchey et al., 2009). This essentially means functional trait-based methods cannot work in isolation but will rely on species identity and particularly presence/absence, abundance and or biomass data. The use of abundance and biomass has gained more attention among ecologists, with the former being widely used than biomass. While both ecologically meaningful, it is important to realise that biomass and abundance shed light on different processes. Abundance is essentially relevant in the analyses of demography, intrinsic and extrinsic population growth while biomass is more useful in investigations of resource allocation (Fontrodona-Eslave et al., 2021). These two metrics are nonetheless not completely independent of each other and are related through their link with body size. In assemblages such as fish communities, abundance is expected to decrease with body size as the larger taxa typically have lower numbers. On the other hand, biomass often scales positively with body size resulting in an inverse relationship between the two (i.e., biomass and abundance). However, if for any reason the relationship is not entirely symmetrical, then biomass and abundance are expected to have consequences on the evaluations of functional diversity and ecosystem functioning. It is on this logic that both biomass and abundance measurements were considered in this study on evaluating community assemblage patterns in intertidal systems using trait-based approaches.

1.6. Thesis Objectives and Overview

Reich et al. (2003) define a functional trait as a characteristic that may notably impact the ability of an individual to survive in an environment and understanding these may provide important insights into mechanisms of community assembly (McGill et al., 2006; Kraft et al., 2008; Mayfield & Levine, 2010; Paine et al., 2011; Katabuchi et al., 2012; Shipley et al., 2012) and ecosystem functioning. Given the unique ecological characteristics of rocky shore assemblages, it is crucial to simultaneously investigate how their functional traits vary along a biogeographical gradient and to disentangle the relative effects of biogeographical and environmental drivers on these patterns.

Thus, I used a trait-based approach to: (i) evaluate the distribution of reproduction and development traits along the biogeographic gradient of the coastline of South Africa, and (ii) evaluate how deterministic processes (habitat filtering *vs* limiting similarity) influence rocky shore community assemblages and production. I hypothesise that, because taxonomic diversity is only one component of biodiversity, species' names provide minimal information about their contribution to ecosystem functioning or how they respond to the environment. Studies using functional traits to test the strength of different processes of community assembly also often find that habitat filtering plays a key role in community formation of various ecosystems (Paine et al., 2011; Shipley et al., 2012). Therefore, I suggest that the inclusion of functional trait diversity in rocky shore systems may provide stronger inferences regarding community assembly and distribution patterns in response to two environmental factors: sea surface temperature and phytoplankton food availability as measured by chlorophyll-*a.*

The main objective of this thesis was to explore the effects of environmental conditions (sea surface temperature and chlorophyll-*a*) on functional structure in rocky shore communities and their subsequent consequences for ecosystem functioning with an emphasis on the transition regions between major biogeographic provinces. The study, therefore, aims to contribute towards the current understanding of species assemblages, particularly focusing on the role of the environment and species biological traits while recognising that identifying all the underlying mechanisms goes beyond the scope of this thesis. **Chapter 1** is the General Introduction which sets the context of the study objective. I have briefly reviewed some topics and hypotheses linked to our understanding of community assemblages and ecosystem functioning. **Chapter 2** considers the effects, responses, spin-offs, and trade-offs among rocky shore species functional traits in response to changes in nearshore oceanographic conditions and spatial gradients. This chapter primarily uses biological trait analysis approaches. I examine assembly mechanisms within and across biogeographic provinces. Firstly, I investigate spatial variation in abundance and biomass patterns along a biogeographical gradient (i) among species, (ii) among functional characteristics, and subsequently, (iii) I compare observed patterns against null models of random assembly. Specifically, I test whether species distribution patterns along the biogeographic gradient are more similar than expected if they were random and compare measures of co-occurrence and the ecological similarity of species to determine whether a common response to the environment causes the observed patterns. I test the hypotheses that environmental conditions impose a deterministic filter on community assembly and that community structure varies systematically along the biogeographic gradient. Consistent with the trait-based hypothesis of habitat filtering in harsh environments, I predicted that co-occurring species are more similar in their functional characteristics than would be expected by chance. In combination, these approaches reveal how biogeographic and functional patterns influence community organisation along an environmental gradient to elucidate assembly processes at biogeographic transition zones. The aim of **Chapter 3** was to understand community functional structure, that is the relationship between species functional traits and ecosystem functioning. The chapter was focused on mapping beta species diversity relative to functional traits as a response to environment filters or biogeography. This chapter was based on functional diversity indices e.g., community weighted means, functional richness, functional evenness, functional divergence, and Rao's quadratic entropy. These indices elucidate functional diversity and provide insights into the productivity potential of the site or coastal region. I considered functional diversity as the diversity in distribution and range of expressed functional traits, with the latter reflecting characteristics of organisms that influence ecosystem processes. This chapter also compared whether taxon-based indices and functional diversity indices reveal concurring species distribution patterns. Lastly, a number of rocky shore macroinvertebrates such as mussels and barnacles, have been identified as habitat-forming species or ecosystem engineers. However, for the coast of South Africa, there has been relatively limited work on seaweeds at multi-species and/or community level and biogeographic effects on epifaunal assemblages. Previous studies have shown that seaweeds ameliorate environmental conditions by attenuating temperature and water loss, and this depends on the density and morphology of the seaweeds present. Therefore, the aim of **Chapter 4**, was to identify and assess any possible interactions between the turf morphological structure of geniculate coralline seaweed species and epifaunal assemblages and how biogeographic effects may influence both. For this, I compared epifaunal diversity within seaweeds at the species and community levels, and across the four biogeographic provinces identified for seaweeds. It is important to note that, depending on the organism of interest, there is a slight difference in the number of bioregions identified on the coast of South Africa. For macroinvertebrates, there are five bioregions identified i.e., east, south-east overlap (SEO), south, south-west overlap (SWO) and west. On the other hand, for seaweeds, the east and SEO are identified as a single region referred to as the SEO, giving a total of just four bioregions (SEO, south, SWO and west). A general synthesis of the overall findings in the context of the existing literature is provided in **Chapter 5.**

CHAPTER 2

SPECIES ASSEMBLY IN COASTAL MARINE SYSTEMS: THE INTERACTION OF BIOGEOGRAPHY AND FUNCTIONAL TRAITS

The habitat provides the templet on which evolution forges characteristic life-history strategies
(Southwood, 1977)

Species assembly in coastal marine systems: The interaction of biogeography and functional traits

2.1. Coastal systems as bio-indicators of drivers of biogeographic patterns

An interplay of simple and complex ecological mechanisms, including environmental factors, habitat diversity, dispersal, disturbance, and interactions among species, contribute to biodiversity patterns and distribution (Kneitel et al., 2003; Krasnov et al., 2015; Berdugo et al., 2019). Establishing the mechanisms behind these factors and interactions is crucial for understanding and predicting species distribution and responses to environmental changes. For example, the abiotic factor environmental temperature is one of the most fundamental determinants of biological patterns and processes (Kordas et al., 2011). Since biochemical and physiological rates translate into organismal survival, growth, and reproduction, environmental temperature plays a significant role in determining when and where species (particularly ectothermic species) can survive and thrive (Hochachka & Somero, 2002). In addition, the broad-brush effects of temperature changes are already observable across a wide variety of systems and taxa, with shifts in the distribution and abundance of species and the timing of life-history events occurring as one would predict over spatial (e.g., latitudinal, and altitudinal) and temporal (e.g., seasonal) thermal gradients (Southward et al., 2005; Helmuth et al., 2006; Mieszkowska et al., 2007).

Not every species has responded as predicted (e.g., Hawkins et al., 2009), and it is widely acknowledged that temperature is not the sole driver of species persistence. For example, some distributional patterns across thermal gradients depend more on interactions among species than upon the direct effects of temperature (MacArthur, 1984). On this premise, several ideas have evolved to explain species distribution patterns. One of these ideas suggests that a species' response to spatial or temporal variation in temperature will depend both on direct effects on the individual- and population-level attributes of that species and/or on indirect effects mediated by changes in the distribution, abundance, and behaviour of competitors, predators, or conspecifics. Thus, although general patterns of change in species distribution may be robust and predictable (e.g., Parmesan & Yohe, 2003), accurate predictions regarding the consequences of temperature shifts for particular species or ecosystems of interest often remain elusive and are context-specific. It is also because of this idea that more universal approaches such as species functional traits have received extra attention to understand the composition of communities beyond the taxonomic identity of their component species.

The functional traits of species within intertidal ecosystems reflect the survival strategies of species under the long-term (and/short-term) effects of natural selection or stress factors, which are an evolutionary result (Vannote & Sweeney, 1980; Yoshimura et al., 2006). Of course, difficulties exist for in-field surveys; for instance, as ecosystems change over time, abiotic factors may also vary and thus becoming confounding factors for biodiversity and ecosystem functions. Hence the causes or the consequences of changes in biodiversity and ecosystem functions are unclear. For example, biodiversity can drive ecosystem functions, while ecosystem functions can limit or improve biodiversity development. Similarly, biodiversity and ecosystem functions can change abiotic properties, while abiotic changes may cause variation in biodiversity and/or ecosystem functions (Cardinale et al., 2012). However, a direct link has been shown between functional diversity and ecosystem functioning, indicating that shifts in ecosystem processes and services result from functional diversity instead of taxonomic losses *per se* (Berke et al., 2014). This link has yielded a line of study focused on biodiversity and ecosystem functioning known as biodiversity-ecosystem functioning (BEF) studies.

BEF research has proliferated following concerns that biodiversity loss would negatively affect the ecosystem functions, processes, and ecosystem services it underpins. However, despite evidence that biodiversity strongly affects ecosystem functioning, the effects are often context-specific in dynamic habitats such as coastal systems. The BEF approach debates the disadvantages of neglecting species functional identity. Therefore, there has been the suggestion to integrate traditional BEF studies and in-field investigations when studying the relationship between biodiversity and ecosystem functions. Such studies should: (i) consider more trophic levels (such as in-field invertebrate and microorganism communities) and expand to large scale experiments; (ii) consider multiple traits which can then be grouped into life-history strategies or trait domains e.g., reproduction, dispersal, synchronisation, and development mechanisms (Verberk et al., 2008). The reproduction trait domain involves the reproductive investment of a species e.g., egg size, egg number and brood care. Dispersal trait domain entails how species colonise habitats and is constrained by body plan. For example, species with planktotrophic larvae have larger dispersal ranges than direct developers. Further, the synchronisation trait domain concerns the timing of reproduction, development or dispersal and is thus intimately linked to other species traits in these other domains. Lastly, species traits related to the development trait domain include development time, growth rate, body size and adaptive morphology and physiology.

Looking at the rocky shore ecosystem of South Africa, an overall pattern of biogeographic distribution and zonation patterns possibly linked with species functional traits is observed. At a macroscopic scale, the coast is primarily divided into three biogeographical provinces comprising approximately 1300 km of rocky shores and 1700km of sandy beaches. Existing studies on the biogeography of the South African coastline fit into two categories (Scott et al., 2012). On one hand, the first category demarcates biogeographic provinces based on distribution patterns and affinities of selected species, e.g., octocorals (Williams, 1992), coastal fishes (Turpie et al., 2000), seaweeds (Bolton & Stegenga, 2002). This creates differences based on taxa being investigated (Stephenson & Stephenson, 1972; Emanuel et al., 1992; Scott et al., 2012). On the other hand, some biogeographers determine boundaries at the community level and focus on how oceanographic affinities (e.g., temperature gradients) define communities. Regional differences caused by past and present differences in climatic changes primarily driven by upwelling and downwelling episodes are predicted to cause differences and shifts in chlorophyll-*a* and temperature gradients. It is this latter category that will be adopted in this study. The basis of this category is attributed to nearshore oceanographic properties primarily the influence on water temperature and nutrients of two major large marine ecosystems (LME's): the Benguela upwelling system dominates the west coast while the south-flowing Agulhas Current influences the east and south coasts (Thomas et al., 2001, Lutjeharms, 2006). It is worth noting, however, that species differences (instead of the two primary LMEs) have contributed to the division of the coastline into the west, east, and south coasts (Fig.2.1) and also two transition zones (south-east and south-west) overlaps.

Although there are confounding factors associated with the approach of using oceanographic affinities, one of the main benefits of this approach is that it can reveal subtle changes brought about by habitat filtering. For instance, differences in water temperature along the flow of the Agulhas current are assumed to bring strong influences on the biogeography of the subtropical east coast and the warm temperate south coast provinces (Stephenson & Stephenson, 1972). Despite this, the transition zones or overlapping region between these two coasts is deemed one of the most difficult to define (Emanuel et al., 1992; Sink et al., 2005). Some studies resort to defining these regions in terms of changes in species composition. A general consensus among zoogeographers, however, is that the SEO extends from Port St Johns (PSJ) to East London (EL)- Fig.2.1. In contrast, the western overlap (i.e., south-west overlap) is more definitive and extends from Cape Agulhas to around Cape Point (Fig.2.1). Some work has also identified species breaks as located at Cape Point, East London, and Durban (Emanuel et al., 1992), also see Fig.2.1.

Based on the assumptions of the habitat filtering concept, the aim of this study was to investigate how benthic intertidal species and communities respond to shifts and differences in nearshore oceanographic parameters in this case temperature and chl-*a*. Although long-term mean temperatures are relatively similar between coasts, South Africa is more strongly pulsed over shorter timescales (Wieters et al., 2009). These small-scale differences in SST are assumed to directly affect the feeding of benthic species through its influence on metabolic rates (Wieters et al., 2009), reproduction frequency, reproductive type, growth rates, and mobility.

On the other hand, chl-*a* has considerable impacts on resource availability and will influence species development mechanism, size, and habitat. However, although these environmental stresses may not completely filter/determine all functional roles, they will significantly influence the diversity of species within functional trait combinations (Valdivia et al., 2017). This is because the environment and within-species interactions are thought to have interdependent selective effects on trait combinations and overall functional diversity (Valdivia et al., 2017).

On this premise, I sought to examine the relationship between multiple functional traits and biogeography. Therefore, I grouped the traits to represent two main suites/domains, which in essence are also referred to as life-history strategies in the literature (Verberk et al., 2008). This life-history strategy approach acknowledges species as comprising a suite of traits instead of just single traits. For example, trophic level and body size are traditionally viewed as important aspects of the biology of a species that can have profound impacts across multiple scales of organisation, from the individual to the ecosystem level (Gaston et al., 2000; Verberk et al., 2008). In isolation, however, trophic level and body size are not explicitly decisive in assigning species to a strategy and only gain relevance when placed within the context of the other species traits. This then sets limits to development rates, ultimately shaping a strategy indirectly through relations with other traits such as adult life span. Based on Verberk et al. (2008), I will refer to each strategy as a suite of traits or a trait domain to minimise ambiguity.

I selected a suite of traits associated with development and reproduction trait domains or life-history strategies because of their well-known significance in driving species abundance and biomass, distribution, and ecosystem functioning. Under the development trait domain, I selected body mass or size, fragility, and mobility as some of the traits because they directly affect the structure and dynamics of ecological networks and indicate the stability of the environment. On the other hand, for the reproduction trait domain I included traits associated with reproductive type and frequency, development mechanism, and size at reproductive maturity. The reproduction traits were selected to resemble those from the trait categories suggested by Verberk et al. (2008), which include brood care, egg number and reproductive investment (see Table 2.1), however egg size could not be measured in this study. I hypothesised that an increase in species with low *per capita* investment in reproduction would dominate transitional regions (i.e., SEO and SWO). At the same time, within the main bioregions (where the environmental parameters are expected to be more stable), high *per capita* reproductive investment species such as direct developers, longer development rates, and protracted reproductive frequency are expected to dominate community assemblages. Lastly, assessing trait responses to environmental gradients requires the simultaneous analysis of data contained in three matrices, also known as an RLQ or co-inertia analysis. This is an exploratory analysis used to evaluate the relationships among the environment (R), species abundance/biomass (L), and traits (Q) (Legendre et al., 1997). Further testing and estimating the direct association between traits and environmental variables (also known as the fourth corner method (Doledec et al., 1996)). However, Legendre et al. (1997) combined these two methods in what is termed as the combined fourth corner method. Based on this combined method, I assessed how specific traits within the two trait domains respond to gradients in temperature and chlorophyll-*a* and whether the results obtained can be used to predict the spatial patterns and distributions of abundances and biomass of intertidal rocky shore species across and within bioregions and transition zones. In summary, although species diversity and abundance metrics for the bioregions of South Africa are relatively well understood, the main aim of this study was to (i) assess the influence of functional traits of species to rocky shore ecosystem functioning and (ii) test for trait responses to changes in temperature and chl-*a* gradients within these bioregions and transition. I expected that biological traits of species would influence or explain the observable differences and shifts in species composition within and across bioregions.

Table 2.1. Trait categories used in this study derived from work by Verberk et al., 2008

Trait domain	Verberk's trait categories	Trait categories used herein
Reproduction	• Brood care	• Development mechanism
	• Egg number	• Reproductive frequency
	• Reproductive investment	• Size at reproductive maturity and reproductive frequency
		• Reproductive type
Development		
	• Adaptive morphology and physiology	• Feeding mode
		• Mobility
		• Fragility
		• Habitat preference
	• Body size	• Adult size

2.2. Materials and Methods

2.2.1. Study Area

A total of fifty-two rocky shore sites were sampled from the three main biogeographic provinces (west, south, and east) and two transition zones (south-west [SWO] and south-east [SEO]) and along the coastline of South Africa (Fig.2.1). These sites were spread over an area of 3025 km of the coast from Mabibi in the furthest on the east to Port Nolloth furthest on the west coast (Fig.2.1). On the east 10 sites were sampled, while 11 sites were each sampled for the south-east and west coasts. The south coast had 12 sites while the south-west had 8 sites. The variation in sites sampled was to cater for the variability in total estimated distance across each bioregion or transitioning zone. For example, the SWO has the least number of sites because it has the shortest coastal distance than other bioregions. Based on past surveys and the literature, all sites were relatively wave-exposed. Samples for macroinvertebrates were collected between October and December 2018.

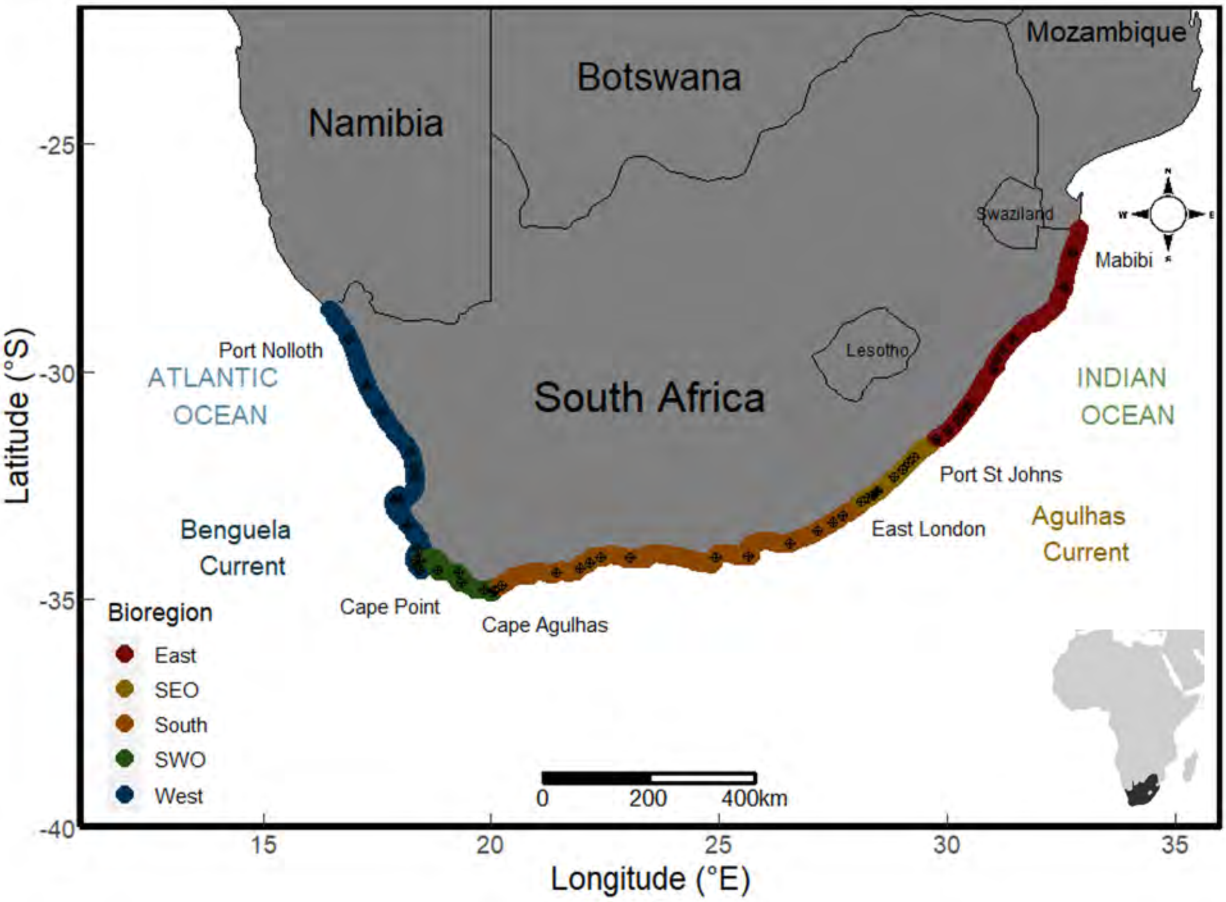


Fig.2.1. A map showing sampled sites along the coast of South Africa. Different colour codes represent the bioregions and transition zones. Insert showing the map of Africa and location of South Africa. Mabibi, the furthest site sampled on the east coast, Port St Johns and East London are the range limits of the east and SEO regions, Cape Agulhas and Cape Point are the range limits of the south and SWO, respectively while Port Nolloth is the furthest site sampled on the west coast. Site names, codes, and coordinates listed in Table 2.2.

Table 2.2. List of sampled sites and site codes

Bioregion	Sites	Site Code	Latitude	Longitude	Bioregion	Sites	Site Code	Latitude	Longitude
East	Mabibi	E1	-27.384893	32.732282	South	Brenton on Sea	S6	-34.078636	23.035597
East	Cape Vidal	E2	-28.143895	32.556132	South	Harrold's Bay	S7	-34.056321	22.400024
East	Nkwazi	E3	-29.289334	31.439553	South	Mosselbaai	S8	-34.185329	22.160444
East	Pebble Beach	E4	-29.515336	31.23137	South	Vleesbaai	S9	-34.299152	21.944789
East	Umhlanga	E5	-29.724985	31.090042	South	Stillbaai	S10	-34.390389	21.429284
East	Brighton	E6	-29.937799	31.008814	South	Arniston	S11	-34.690758	20.235701
East	Port Shepstone	E7	-30.741439	30.459697	South	Struisbaai	S12	-34.804419	20.064884
East	Margate	E8	-30.864049	30.371875	SWO	Cape Agulhas	SWO1	-34.826844	20.016461
East	Port Edward	E9	-31.047917	30.230134	SWO	Cape of Good Hope	SWO2	-34.335671	18.438255
East	Mkambati	E10	-31.277926	30.023722	SWO	Olifantbos	SWO3	-34.256542	18.382292
SEO	Port St Johns	SEO1	-31.462852	29.744413	SWO	Aasfontein	SWO4	-34.768207	19.846946
SEO	Presley Bay	SEO2	-31.88123	29.263916	SWO	Van Dyk's Bay	SWO5	-34.623353	19.351266
SEO	Coffee Bay	SEO3	-31.986907	29.154026	SWO	Hermanus	SWO6	-34.408978	19.270733
SEO	Dwesa	SEO4	-32.309727	28.829375	SWO	Pringlebaai	SWO7	-34.351591	18.813216
SEO	Folokwe	SEO5	-32.141231	29.013227	SWO	Fish Hoek	SWO8	-34.143593	18.436926
SEO	Jacaranda	SEO6	-32.619469	28.474327	West	Kommertjie	W1	-34.126854	18.33815
SEO	Seagulls	SEO7	-32.638734	28.429553	West	Mouille Point	W2	-33.899604	18.401759
SEO	Kei Mouth	SEO8	-32.693346	28.374456	West	Yzerfontein	W3	-33.36542	18.160092
SEO	Haga Haga	SEO9	-32.763474	28.25282	West	Paternoster	W4	-32.804501	17.882421
SEO	Cintsa West	SEO10	-32.840203	28.117258	West	St Helana Bay	W5	-32.750636	18.016397
SEO	Kidd's Beach	SEO11	-33.152581	27.700416	West	Elandsbaai	W6	-32.314814	18.329889
South	Hamburg	S1	-33.292571	27.480758	West	Lambertsbaai	W7	-32.09953	18.302242
South	Old Women's River	S2	-33.479259	27.154651	West	Strandfontein	W8	-31.755405	18.224454
South	Cannon Rocks	S3	-33.751198	26.546549	West	Groenriviermond	W9	-30.861712	17.577007
South	Schoenmakerskop	S4	-34.046233	25.6346	West	Hondeklip	W10	-30.310719	17.269207
South	Jeffrey's Bay	S5	-34.060294	24.928108	West	Port Nolloth	W11	-29.286945	16.878452

2.2.2. Environmental data

Satellite data were downloaded for 7 years for each of the 52 sites to assess the effects of the environment as a habitat filter for species distribution. This was a compromise as some species, such as whelks and barnacles, can live for 10 years and 6–20 years, respectively. The average life span of most common limpets is highly variable across taxa with some tropical species having short lifespans of ~1 year (Liu, 1994) than temperate species grow more slowly and reach larger maximum size and therefore have longer lifespans (Sousa et al., 2017). In addition, the life span of most mussel species (including *Perna perna* and *Mytilus galloprovincialis*) is from 2 to 5 years (Berry, 1978; Abada-Boudjema & Dauvin, 1995)

2.2.2.1. Sea surface temperature (SST)

Nearshore satellite-derived sea surface temperatures (SST) were obtained from the Multi-Scale Ultra High-Resolution SST from 2002 to present-day gridded dataset (jplMURSST41) approximately 5–10 km offshore. Small differences between satellite and *in-situ* data may exist. However, satellite data were the only available descriptors of both SST and chl-*a* for this large-scale study. The SST data for this study were extracted for the years January 2014 to December 2020. A Group for High-Resolution Sea Surface Temperature (GHRSST) Level 4 sea surface temperature analysis produced as a retrospective dataset (four-day latency) and near-real-time dataset (one-day latency) at the JPL Physical Oceanography DAAC using wavelets as basis functions in an optimal interpolation approach on a global 0.01° grid. The version 4 Multiscale Ultrahigh Resolution (MUR) L4 analysis is based upon nighttime GHRSST L2P skin and subskin SST observations from several instruments, including the NASA Advanced Microwave Scanning Radiometer-EOS (AMSR-E), the JAXA Advanced Microwave Scanning Radiometer 2 on GCOM-W1, the Moderate Resolution Imaging Spectroradiometers (MODIS) on the NASA Aqua and Terra platforms, the US Navy microwave WindSat radiometer, the Advanced Very High-Resolution Radiometer (AVHRR) on several NOAA satellites, and *in situ* SST observations from the NOAA iQuam project.

The Open-source Project for a Network Data Access Protocol (OPeNDAP) facility was used to download SST data via the Environmental Research Division's Data Access Program (ERDDAP) data server using the rerddap (Chamberlain, 2021), akima (Akima & Gebhardt, 2020), and ncdf4 (Pierce, 2019) packages in R. Data were downloaded as grids via the griddap function via a specially formed Uniform Resource Locator (URL)- (https://upwell.pfeg.noaa.gov.erddap). Subsequently, the daily SST products were averaged into monthly minima, mean, and maxima SST products. Air temperature data would have been desirable to characterise better the environmental conditions to which intertidal organisms are exposed. However, these data were not available for my entire study area.

2.2.2.2 Nearshore chlorophyll-*a*

Monthly minimum, mean and maximum satellite chlorophyll-*a* measurements were obtained from the gridded dataset (erdMH1chla8day), which is an 8-day composite of global chlorophyll-a, from the MODIS (Moderate-resolution Imaging Spectroradiometer) NPP, L3SMI, Global, 4km, Science Quality, starting from 2003 to present day (monthly composite).The chl-*a* data were extracted at a monthly temporal resolution of 0.05° (approximately 4 km) spatial resolution for the years January 2014 to December 2020. Data were processed in R statistical software package using the same packages as those cited for SST.

2.3. Field sampling and data processing

The intertidal system of the South African rocky shore habitat can be divided into vertical zones primarily based on the species composition and tide levels. My study encompassed the sublittoral fringe to upper balanoid zones or low spring tide to high neap tide levels (Branch et al., 2016) with tidal heights or zones classified following Branch & Branch (2018). It is critical to note that these zones are usually not clearly defined and may be influenced by the angle of the rock ledge, rock type, and how the wave breaks onto the rock ledge. Consequently, the number of replicates slightly varied across sites to obtain good coverage of the communities present. For example, the infratidal and the low shore limpet-dominated zone characterised by *Scutellastra cochlear* zones were combined into one zone (lower fringe zone) across many sites. In addition, because the subtidal fringe zone which usually comprises the invasive ascidians (*Pyura spp*), was excluded from my study. I did not sample the high intertidal zone (the Littorina zone) due to time constraints and because it primarily comprised bare rock. The sampling design, however, included the tidal heights at which the greatest diversity and abundance of sessile and mobile organisms are encountered. Approximately 80% of the sites had 3 zones. In addition, to assess the species and functional trait interactions across zones, I also sampled the "transitioning zones" (i.e., where I observed an overlap of species from distinct heights on the shores). Specimen were collected under the research permits (Res2018/16 and Res/2019/30). For collections from 2 sites (Dwesa and Mkambati) within marine protected areas, I used the research permit (RA 0269).

The sampling method I used involved the stratified random sampling technique using quadrats. Bare rock was avoided, and quadrat placement was pre-selected to capture maximum diversity.

Quadrat placements were restricted to flat or gently sloping surfaces avoiding tide pools or deep crevices. Samples were collected from 4 replicate transects approximately 50m (Llanos et al., 2020) wide, parallel to the water line across the four different shore heights. Before sample collection, digital photographs of species assemblages were captured from quadrats (25×25cm (625cm^2); n = 4 per shore height) placed on flat surfaces along each transect within each shore height. Scrapers and chisels were used to collect species from the rock substratum. Samples were bagged in Ziploc bags and labelled by transect, shore height, and site name. Macroinvertebrate samples were preserved in 70% ethanol, while seaweed samples were preserved in 5% formalin. Mobile organisms (e.g., the mussel worm *Pseudonereis podocirra* were collected before collecting sessile species such as mussels. All sampling was performed during spring low tides. The diversity and abundance of highly mobile species such as amphipods could not be accurately represented in this study due to the limitations of the sampling technique used. In addition, because the abundance of encrusting poriferans was not quantified, they were also excluded from the study.

All macroinvertebrate samples were identified to species level (Day, 1974, Kilburn & Ripley, 1982; Branch et al., 1991). Species names and authorities were checked on the World Register of Marine Species (WoRMS). Because organisms were initially preserved in ethanol, all specimens were blotted with a paper towel and briefly set to air dry under a fume hood for approximately 2 hours before taking any weight measurements. Using digital calipers or graduated string, all species were hand-counted, and size classed by length and diameter (to the nearest 0.1 mm). As the biological trait analysis (BTA) can be assessed using either abundance or biomass data, wet and dry biomass data were also measured and calculated since these allow a better estimate of production measurements (TerHorst et al., 2008; Bolam & Eggleton, 2014).

Total wet weight (TWW) and shell-free wet weight (SFWW) were also measured and recorded for each species. TWW was the weight of a species whether shelled or not. Secondly, shelled species were de-shelled to obtain SFWW. Dry shell free weight (DSFW) was obtained after drying the organisms to constant weight in an oven (60°C, ~72h). Ash free dry weight (AFDW) which is weight of organic material was further obtained by subtracting sample ash weight from DSFW after incineration in a muffle furnace (500°C, ~6-8h). In addition, to obtain individual weights (i.e., TWW, SFWW, DSFW, AFDW) for any species of a particular size, the total weight was divided by species counts within its size class.

2.4. Trait selection and the fuzzy coding technique

Macroinvertebrate species were defined and categorised based on 9 main trait categories with 39 within-trait differences hereafter referred to as trait modalities (Table 2.3). These traits were selected as fundamental for studying species life-history strategies that drive production and ecosystem persistence and were not species-centric. The trait categories were further partitioned into either the development or reproduction trait domain (MarLin, 2006; Verberk et al., 2008). Trait information was obtained from various websites (including SeaLifeBase, WoRMS and BIOTIC–Biological Traits Information Catalogue), published literature, and personal observations. Wherever information was unavailable for a particular species, trait information from the closest taxonomic relative was used. The number of traits to include in functional diversity studies is critical as using fewer traits can detect functional redundancy. On the other hand, in this case where too many traits are used, the estimation of functional diversity starts to resemble species richness. The selected traits in this study had minimal redundancy and overlap.

Table 2.3. List of selected traits for this study, their relevance, functions, and processes.

Biological Functional trait	Trait relevance, functions, and processes	Trait code
Feeding type	Highlights food acquisition; organism's adaptation to the environment; trophic position- relates to energy flow within an ecosystem; relates to the position in the food web, influence on the abundance of other species, and adaptations to habitat.	F-Filter-feeder F-Grazer/Herbivore F-Deposit Feeder F- Carnivore/Predator/Omnivore F-Scavenger
Reproductive frequency	Reflects the investment in reproduction. Continuous reproduction may support demographic resilience in unstable conditions. Species with annual protracted frequencies increase their chances of survival in unstable environments. In contrast, semelparous species concentrate their energy to produce the fittest offspring.	RF-Annual protracted RF-Annual episodic RF-Continuous RF-Semelparous
Reproductive type	Suggests the species' potential to recover after a disturbance	RT-Asexual/Spores RT-Gonochoric RT-Sequential hermaphrodite RT-Simultaneous hermaphrodite
Developmental mechanism	Recruitment succession; Juvenile survival; Population sustainability It also reflects the ability of organisms to spread over temporal and spatial scales and influences nutrient cycling (Degen et al., 2018).	DM-Direct Developer DM-Planktotrophic DM-Lecithotrophic
Mobility/ adult life habitat	Foraging mode: Ability to escape predation promoting species persistence. May reflect species adaptation to the habitat/environment.	M-Sessile (Adherent to substratum >95% of adult time) M-Sedentary M-Crawler M-Swimmer M-Burrower

Continued…Table 2.3. List of selected traits for this study, their relevance, functions, and processes.

Biological Functional trait	Trait relevance, functions, and processes	Trait code
Adult size: body length/shell diameter	Represents community stability, e.g., long-lived species indicate a mature community that has not been disturbed in a long time. Small-bodied organisms can mean unstable systems. Body size is also correlated with other biological attributes of species. Reflects position in the food web, species abundance, metabolic rates, dispersal ability, mobility, and home range	AS-Extra small <10mm AS-Small 10-30mm AS-Medium 30-50mm AS-Large 50-70mm AS-Extra Large >70mm
Fragility	Represents the protective mechanism a species possesses that enables it to withstand or avoid predation. It also highlights persistence and longevity.	F-Fragile/Soft F-Intermediate F-Robust/Hard-shelled
Living location/environmental position/Preferred habitat	Highlights species' tolerance levels to abiotic stresses	HBT-Fringe HBT-Low-shore HBT-Mid-shore HBT-High-shore HBT-Pools
Size at reproductive maturity	Highlights the rate of potential turnover; suggests demographic resilience under adverse conditions.	SRM-XS (<10mm) SRM-S (10-30mm) SRM-M (30-50mm) SRM-L (50-70mm) SRM-XL (>70mm)

The trait information of all collected species was captured via the fuzzy coding technique (Table S2.1.1). The method aims to address challenges associated with the direct assignment of a taxon to a single trait attribute, as this can lead to an inaccurate organism profile (Mondy et al., 2014). The fuzzy coding technique compensates for the different confidence levels of trait information obtained from the literature (Chevene et al., 1994). I used a scale of 0 to 3 to describe the affinity of a species to different modalities of a given trait (Chevene et al., 1994), accounting for phenotypic, spatial, or temporal differences within taxa (Statzner & Bêche, 2010). Although some literature extends the scale from 0 to 5, the fuzzy coding approach of 0 to 3 is the original approach and is consistently preferred for marine systems (e.g., Bremner et al., 2003; Vinagre et al., 2019; Liu et al., 2019). A fuzzy code of 0 means a complete lack of affinity with a particular trait. A fuzzy code of 1 means low affinity to a particular trait. While a code of 2 means taxon has a higher affinity for a particular trait category, it also exhibits similar or partial affinity for another. Lastly, a fuzzy code score of 3 means the taxon has an exclusive affinity for a particular trait. As a standard procedure of the RLQ analysis, I standardised each trait separately using the "prep. fuzzy" function in the ade4 package (Dray et al., 2007) to transform the fuzzy codes into proportions with a sum of modalities per trait = 1.

2.5. Data analysis

2.5.1. Differences in environmental parameters across bioregions, sites, and years

A Generalised Linear Mixed Model (GLMM) was used to evaluate the differences in SST and chlorophyll-*a* values across bioregions, sites, and years. Bioregion was treated as a fixed factor. Year and Site (nested in Bioregion) were treated random factors. The GLMM was performed in R using the packages lme4 (Bates et al., 2015), MuMIn (Barton, 2020). Model selection was based on the lowest Akaike Information Criterion (AIC). The package multcomp (Hothorn et al., 2008) was used for *post hoc* analysis. Homogeneity of variances was checked using Levene's test.

In addition, I used the agglomerative hierarchical clustering algorithm (with the Ward linkage method) to present dendrograms which summarised separately the similarity in temperature and chl-*a* variables among sites and bioregions. Hierarchical cluster analysis comprises algorithms that group similar objects into clusters. The distance matrix was calculated using the Euclidean distance metric. All analyses were performed in R version 4.1.0.

Lastly, to visualise the data across seasons and bioregions, the monthly mean values for temperature and chl-*a* across all the years are presented as bar plots. The data were further divided into the following four seasons; December to February (summer), March to May (autumn), June to August (winter) and September to November (spring) based on the definitions of Brown (1992).

2.5.2. The RLQ approach for biological trait analysis

The core idea of the BTA approach is to fit a predictive model for species abundance or biomass as a function of environmental parameters, species traits, and their interaction. The BTA approach uses a multivariate stepwise ordination to describe patterns of biological trait composition over entire assemblages, i.e., the types of traits present in assemblages and the relative frequencies with which they occur (Bremner et al., 2006). This approach requires multiple data taking the form of three input matrices (R, L, and Q) and computes species traits– environment correlations in a fourth matrix, also referred to as the fourth corner. The matrix, *L (species x site)* –can be computed into 3 different versions (i.e., presence/absence or abundance or biomass). Because these data yield different results, separate RLQ analyses were performed for each suite of traits using abundance (Figs.2.6.1 & 2.6.2) and biomass data (Figs.2.6.3 & 2.6.4). During the exploratory phase, analyses were performed with both non-transformed and log-transformed (log x+1) with no significant differences in the results. In this thesis, however, I present results from the transformed data.

For computing the RLQ analysis, first, a correspondence analysis (CA) was performed to measure the ecological distances among species across sites. Next, a Hill-Smith analysis was performed on the second matrix *R (environment × site)*, which links the ecological distance of species to the environmental data by using the sample score results obtained from the *L* matrix as row-weights. Lastly, the third matrix *Q (species × traits)*– contained fuzzy coded trait information for species from all sites. The fuzzy coded data were weighted by abundance and biomass and analysed in separate analyses. The matrix *Q* and log (x+1) transformed *L*-matrix were multiplied to obtain a *site × trait* array (matrix *QL*). From this *Q* matrix, the Hill-Smith analysis was performed. This analysis links the trait data to taxon data using the taxon score results of the CA as row weights. The final RLQ analysis simultaneously conducts ordinations on the three separate result tables.

2.5.3. An extension to RLQ: The combined fourth corner analysis and test of random assembly

While RLQ analysis provides a summary of a 3-matrix multivariate ordination among species, traits, and the environment, it still fails to identify the critical environmental variables underlying the observed trait distributions or the extent of the association between the traits and the environment leading to what is known as the fourth corner problem. In addition, since the fourth-corner method considers variables measured on different statistical units (species traits and the environment), appropriate randomisation procedures need to be performed to obtain an adequate testing procedure (Dray & Legendre, 2008). The two new proposed methods combine two permutation models, also known as model 2 and model 4. Model 2 (i.e., RLQ analysis, 999 permutations) permutes the *n* samples (i.e., rows of matrix *R* or *L*) to test the null hypothesis that the environmental conditions do not influence the distribution of species. In other words, the null hypothesis assumes no relationship between *R* and *L*. On the other hand, model 4 (fourth-corner analysis, 4999 permutations; $alpha = 0.05$) tests the null hypothesis that the species traits do not drive the species composition or abundances. Thus, by using the combined fourth-corner method, the output from the Monte Carlo permutation tests (also known as Model 6), the significance of the RLQ models or this fourth corner problem is addressed (Dray et al., 2014). The permutation Model 6 allows the evaluation of correlations between specific trait attributes and environmental variables (i.e., one single trait and one single environmental variable at a time). The combination of the RLQ and fourth corner methods has been considered the most powerful method for BTA as it combines the graphical interpretation of the RLQ and inferential statistics (Beauchard et al., 2017).

2.6. Results

2.6.1. Inter- and intra-annual variability in nearshore sea-surface temperature across bioregions

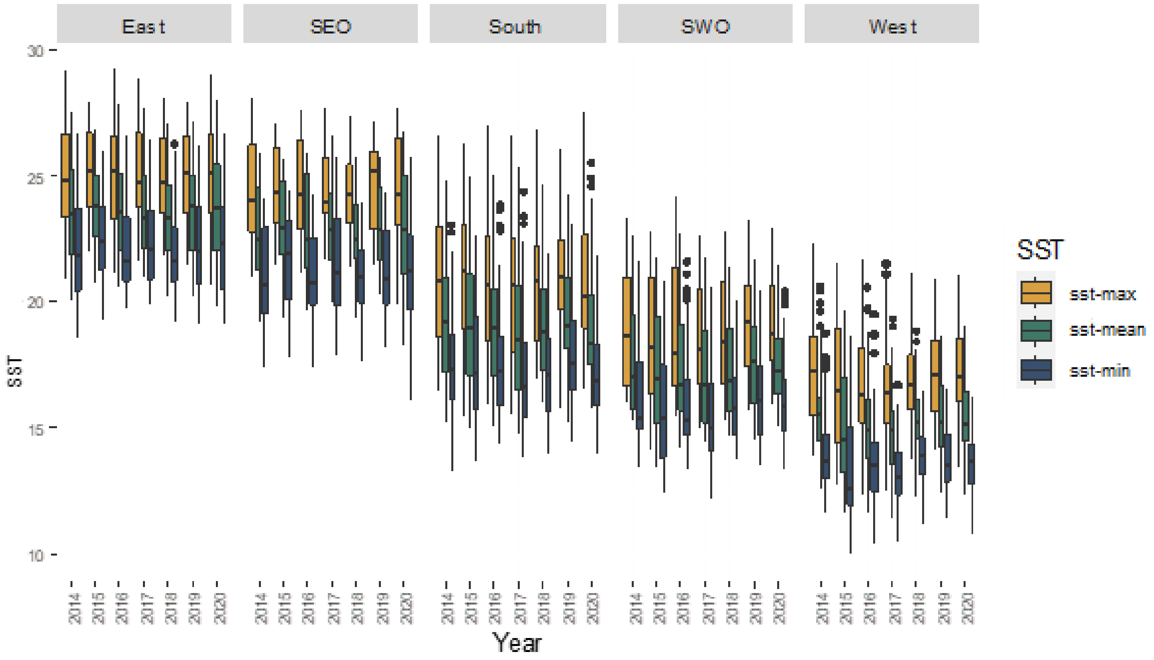


Fig.2.2. Yearly minimum, mean, and maximum nearshore SST variability across bioregions between 2014-2020.

Prior to conducting the RLQ and combined fourth corner analyses, both the temperature and chl-*a* data were analysed separately (Fig.2.2, Table 2.4 and Fig.2.4, Table 2.5, respectively) to test for differences across bioregions, sites, and years. Fig.2.2 highlights the variability in minimum, mean, and maximum SST concentration across a period of the 7 years considered in this study. The *post hoc* tests showed no significant differences between the east and SEO for all three estimates i.e., minimum, mean, and maximum. Of all the bioregions, the two bioregions were also not significantly different from each other (Table 2.4). Overall, for all the years, the east coast had the highest readings for SST with a gentle decline towards the west coast (Fig.2.2). A graphical presentation of these data for all the years across seasons at site level also showed a gradual decrease in SST with bioregion from east to west (Fig.S2.1a-d). The first 2 sites i.e., Mabibi and Cape Vidal which are the furthest on the east coast i.e., close to the Mozambican border (Fig.2.1), exhibited the highest SST across all sites (Fig.S2.1a-d). All bioregions exhibited minimal seasonal variability across the years as indicated by the almost similar standard deviations.

Table 2.4. GLMM results and Tukey *post hoc* showing contrasts of sea-surface temperature between bioregions

Mean SST

Fixed effects	Estimate	Standard Error	t value	*p* value
(Intercept)	0.04241	0.001143	37.105	**<0.0001**
East-SEO	0.00112	0.001499	0.745	0.456
East-South	0.01024	0.001437	7.124	**<0.0001**
East-SWO	0.01525	0.001409	10.827	**<0.0001**
East-West	0.0235	0.001355	17.351	**<0.0001**

Random effects

Groups	Name	Variance	Standard Deviation
Site	(Intercept)	1.39E-06	0.00118
Year	(Intercept)	4.86E-08	0.00022
Residual	8.85E-03	0.094053	
Number of observations	4366		
Site	52		
Year	7		
DF residuals	4358		

Contrasts	*p* value
East - SEO	0.94531
East - South	**<0.0001**
East - SWO	**<0.0001**
East - West	**<0.0001**
SEO - South	**<0.0001**
SEO - SWO	**<0.0001**
SEO - West	**<0.0001**
South - SWO	**<0.0001**
South - West	**<0.0001**
SWO - West	**<0.0001**

The full model comprising Bioregion as a fixed factor and Sites and Years as random factors (with no interactions) had the lowest AIC value. The GLMM showed similar significant differences in minimum, mean and maximum SST across bioregions ($p<0.0001$). Tukey *post hoc* tests performed using the multcomp package (Horthorn et al., 2008) indicated differences between specific bioregions. The east coast was not statistically different from the SEO. These two bioregions however differed from the other bioregions i.e., the south, SWO and west coasts (Table 2.4). Further, this is corroborated by the cluster dendrogram (Fig.2.3) which revealed two main groups in SST: the east (east and SEO coasts) and west (the south, SWO and west coasts) with the exception of S1 and S2 which are the most easterly south coast sites (i.e., closest to the SEO).

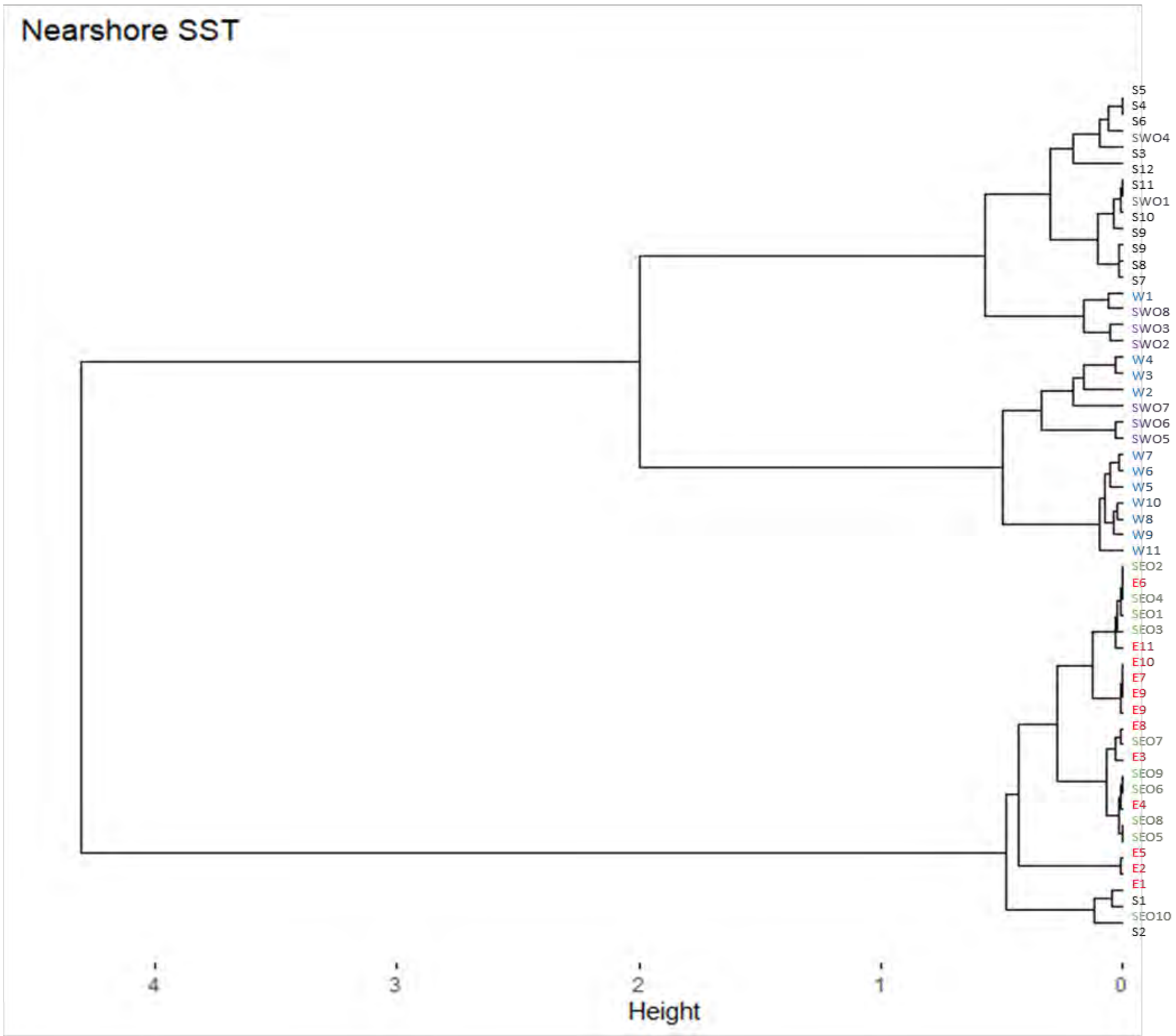


Fig.2.3. Dendrogram output of hierarchical cluster analysis showing clustering of sites based on mean SST values. Height =represents the ecological distance metric at which the clusters are formed. Sites are colour coded by bioregion. The west coast is represented by blue e.g., W1, W2, W3. The SWO = purple, the south coast=black, the SEO =green and east coast=red.

2.6.2. Inter- and intra-annual variability in nearshore chlorophyll-*a* across bioregions

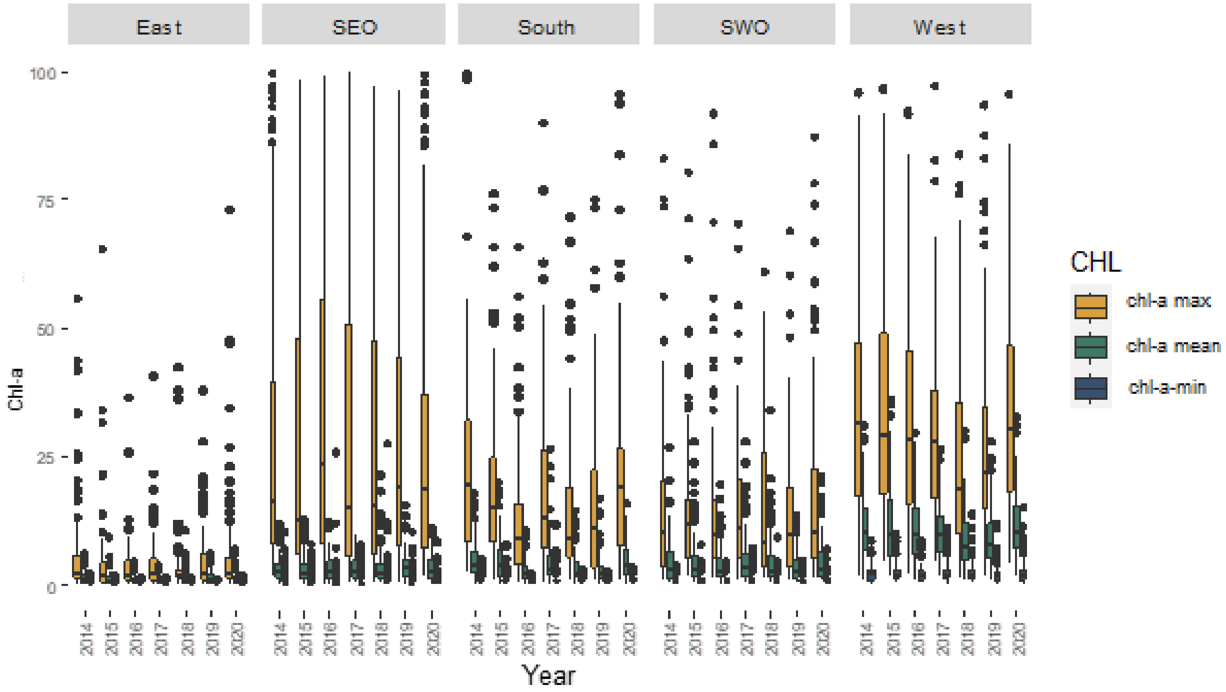


Fig.2.4. Yearly minimum, mean, and maximum nearshore chlorophyll-*a* variability across bioregions between 2014-2020.

The SEO and west coast showed highest concentrations in maximum chl-*a* in comparison to other bioregions (Fig.2.4). The GLMM showed variable significant differences among bioregions among the minimum, mean and maximum nearshore chl-*a* estimates (Table 2.5). The minimum chl-*a*, for the SEO was significantly different from the SWO and west coasts only. On the other hand, the mean and maximum chl-*a*, for the east coast were significantly different from all other bioregions while all other bioregions did not differ from each other (see Table 2.5). The east coast showed the lowest gradient (Fig.2.4).

Table 2.5. GLMM results and Tukey *post hoc* showing contrasts of chl-*a* between bioregions

Mean Chl-*a*

Fixed effects	Estimate	Standard Error	t value	*p* value
(Intercept)	1.38	0.1781	7.749	**<0.0001**
East-SEO	-1.0408	0.2462	-4.228	**<0.0001**
East-South	-0.8584	0.2431	-3.531	**<0.0001**
East-SWO	-1.106	0.2438	-4.537	**<0.0001**
East-West	-1.2643	0.2463	-5.133	**<0.0001**

Random effects

Groups	Name	Variance	Standard Deviation
Site	(Intercept)	0.16552	0.40684
Year	(Intercept)	0.00011	0.01027
Residual	0.5187403	0.72024	
Number of observations	4366		
Site	52		
Year	7		
DF residuals	4358		

Contrasts	min	Max	mean
East - SEO	0.8899	**0.0002**	**<0.0001**
East - South	0.9961	**0.0038**	**<0.0001**
East - SWO	0.4076	**0.0001**	**<0.0001**
East - West	0.2257	**0.0001**	**<0.0001**
SEO - South	0.6612	0.94	0.99831
SEO - SWO	**0.0458**	0.9988	0.99938
SEO - West	**0.0176**	0.8858	0.99876
South - SWO	0.4511	0.7824	0.99999
South - West	0.3609	0.4299	0.97796
SWO - West	0.9938	0.9637	0.98606

The dendrogram plot for chl-*a* showed three major clustering patterns (Fig.2.5). The sites on the east, west coasts, and a combination of the SEO, south, and SWO clustered separately.

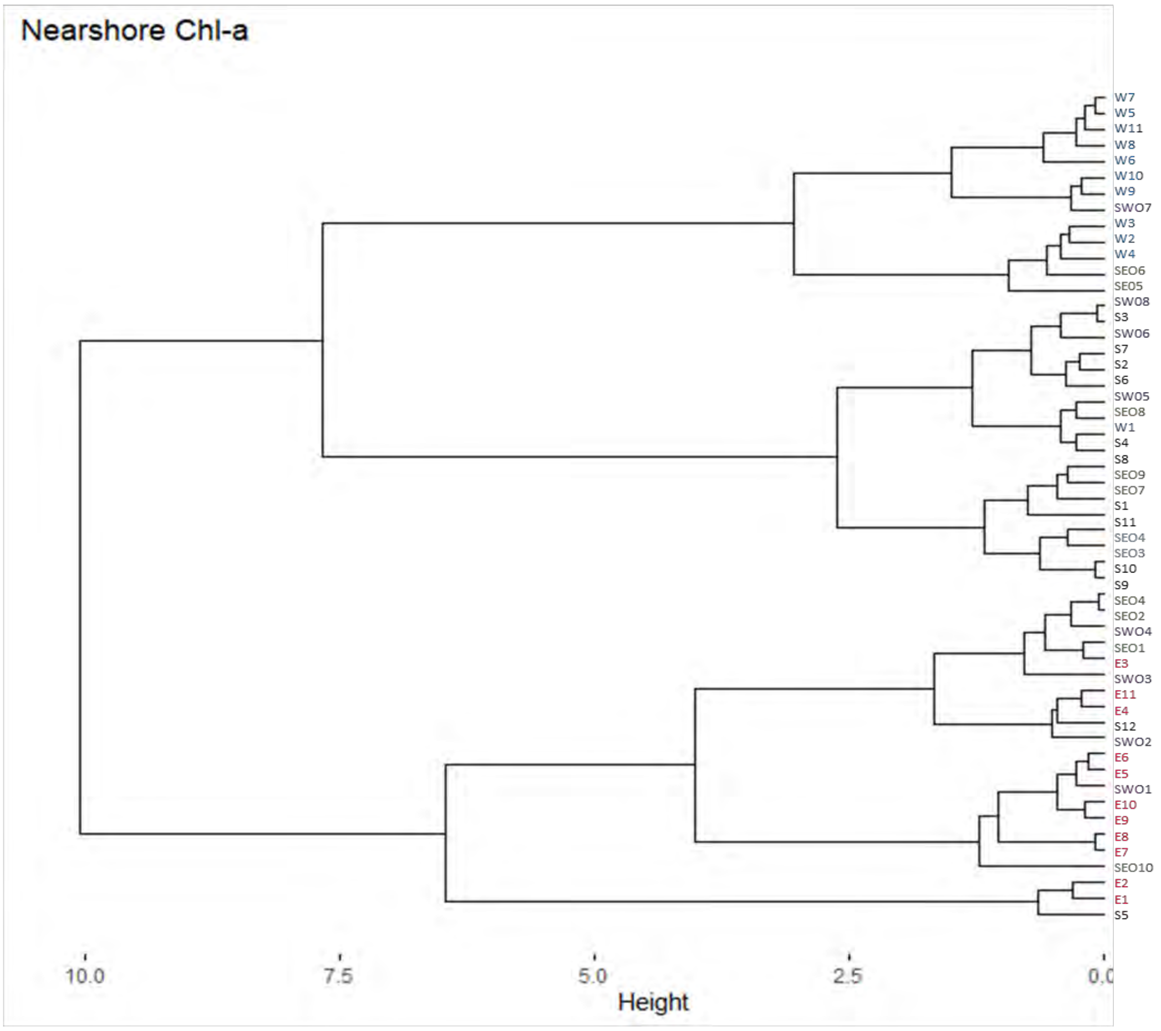


Fig.2.5. Dendrogram output of hierarchical cluster analysis showing clustering of sites based on mean chl-*a* values. Height =represents the ecological distance metric at which the clusters are formed. Sites are colour coded by bioregion. The west coast is represented by blue e.g., W1, W2, W3. The SWO = purple, the south coast=black, the SEO =green and east coast=red.

Lastly, graphical presentations of these data were partitioned by seasons showed a gradual increase in *chl-a* as bioregion changed from east to west (Fig.S2.2a-d). Across all seasons, all sites on the east coast exhibited the least inter-annual variability in chl-*a* (Fig.S2.2a-d) while there was also greater intra-annual variability within bioregions e.g., sites within the SWO (Fig.S2.2a-d) as indicated by the higher standard deviations (Fig.S2.2a-d). Site 25 i.e., Schoenmakerskop (-34.046233, 25.6346), exhibited the lowest values for both chl-*a* and SST than surrounding sites across all seasons.

2.6.3. Correlating trait attributes, species abundance, and environmental parameters

The first 2 axes of the RLQ analysis for the suite of development traits (axes 1 and 2) explained 93.57% and 5.98% of total variance, respectively (Table 2.6). These results suggest the strong influence of temperature and chl-*a* on the suite of traits associated with species development. The ordination plots of the RLQ analysis for development traits indicated that the distribution of trait modalities in the feeding (t1) and mobility (t3) trait categories were most influenced by chl-*a* concentration (Fig.2.6.1). Both trait categories had an average of 4 out of 5 trait modalities responding to the chl-*a* gradient. Examples of species possessing some of these traits include the Natal lightfoot crab (*Grapsus tenuicrustatus*), the long-siphoned whelk (*Lugubrilaria lugubris*), rotund burnupena (*Burnupena rotunda*), the furry-ridged triton (*Cabestana africana*), the three-antennaed worm (*Lysidice natalensis*), the knobbly dogwhelk (*Mancinella capensis*), the polychaetes (*Arabella iricolor*), *Syllidae spp*, and *Sedentaria spp*, multicoloured topshell (*Gibbula cicer*) and the rock snail (*Tylothais savignyi*). The remaining trait categories i.e., adult size, habitat preference and fragility had at least one trait modality within each category influenced by the chl-*a* gradient.

Table 2.6. Properties of multivariate RLQ ordination (weighted by abundance data) showing the percentage variations, eigenvalues, covariance, and correlation explained by the first two axes (1 and 2), covariance, correlation.

	DEVELOPMENT		REPRODUCTION	
RLQ Properties	**Axis 1**	**Axis 2**	**Axis 1**	**Axis 2**
Variance (RLQ) %	93.57	5.98	97.84	1.74
Eigenvalue	12.06	0.77	16.3	0.29
Covariance	3.47	0.87	4.03	0.53
Correlation	0.56	0.34	0.33	0.60

Further, the habitat preference (low shore; t4.2 and pools; t4.5) and fragility (particularly soft/exposed/brittle – t5.1) and adult size (t2.2 and t2.5) trait categories were correlated with the temperature gradient. These 3 trait categories had an average of at least one trait modality responding to SST. Examples of species possessing some of these traits include the brown mussel (*Perna perna*), zoanthids species such as *Zoanthus durbanensis*, *Palythoa natalensis* and the anemones

(*Actinia ebhayiensis* and *Bunodactis reynaudi*). Lastly, the majority of sites influenced by the chl-*a* environmental filter were in the western bioregions (West, South and SWO), while the temperature filter influenced species within the east and south-east transition zones (Fig.2.6.1).

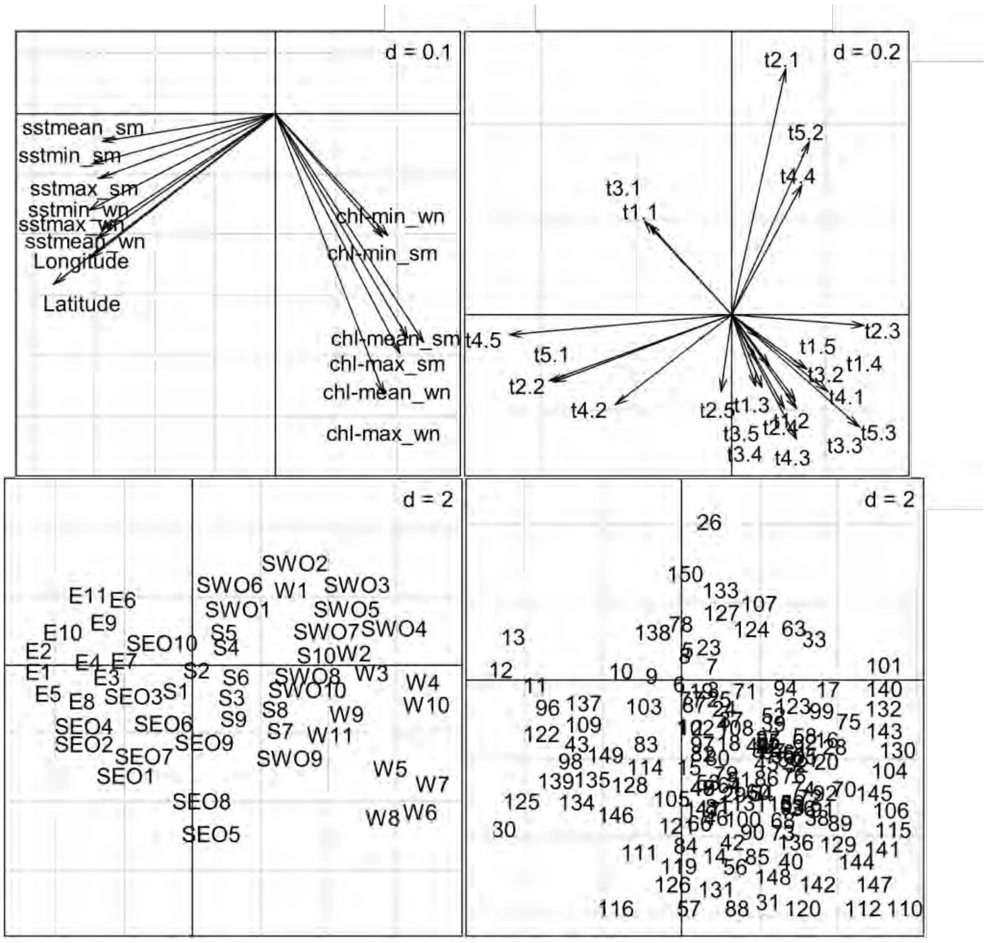


Fig.2.6.1. RLQ ordination plot indicates the correlation between development traits, sites, and species abundance. The top left panel represents the environmental variables assessed. The top right represents the (coded) development traits selected in this study, while the bottom left shows the distribution of sites and, lastly, the bottom right panel shows the ordination of all species collected. Refer to Tables 2.2, 2.7, and S2.1.1 for sites, traits, and species names, respectively. The d value in the upper right corner is the scale of the graph given by a grid.

A second RLQ analysis for reproduction traits weighted by abundance projected variances of 97.84% and 1.74% on axis 1 and 2, respectively (Table 2.6; Fig.2.6.2). Chl-*a* concentration was positively correlated with reproduction traits that characterised macroinvertebrate species described by modalities including reproductive type (apart from simultaneous hermaphrodites-t7.4), size at reproductive maturity (except sizes <10mm), and these traits were predominantly found at sites on the west coast. On the other hand, sites in the east and south-east transition zones were positively correlated with temperature and were characterised by species with asexual reproduction (t7.1) and direct developers (t8.1). In addition, species with a gonochoristic reproductive type (t7.2) were negatively correlated with temperature while positively correlated with chl-*a*. Further, species with a continuous reproductive frequency (t6.3) were negatively correlated with the chl-*a* gradient, while species with planktotrophic larval development (t8.2) were positively correlated with chl-*a*. Latitudinal gradients positively correlated with direct developers (t8.1) and species that reproduce asexually (t7.1).

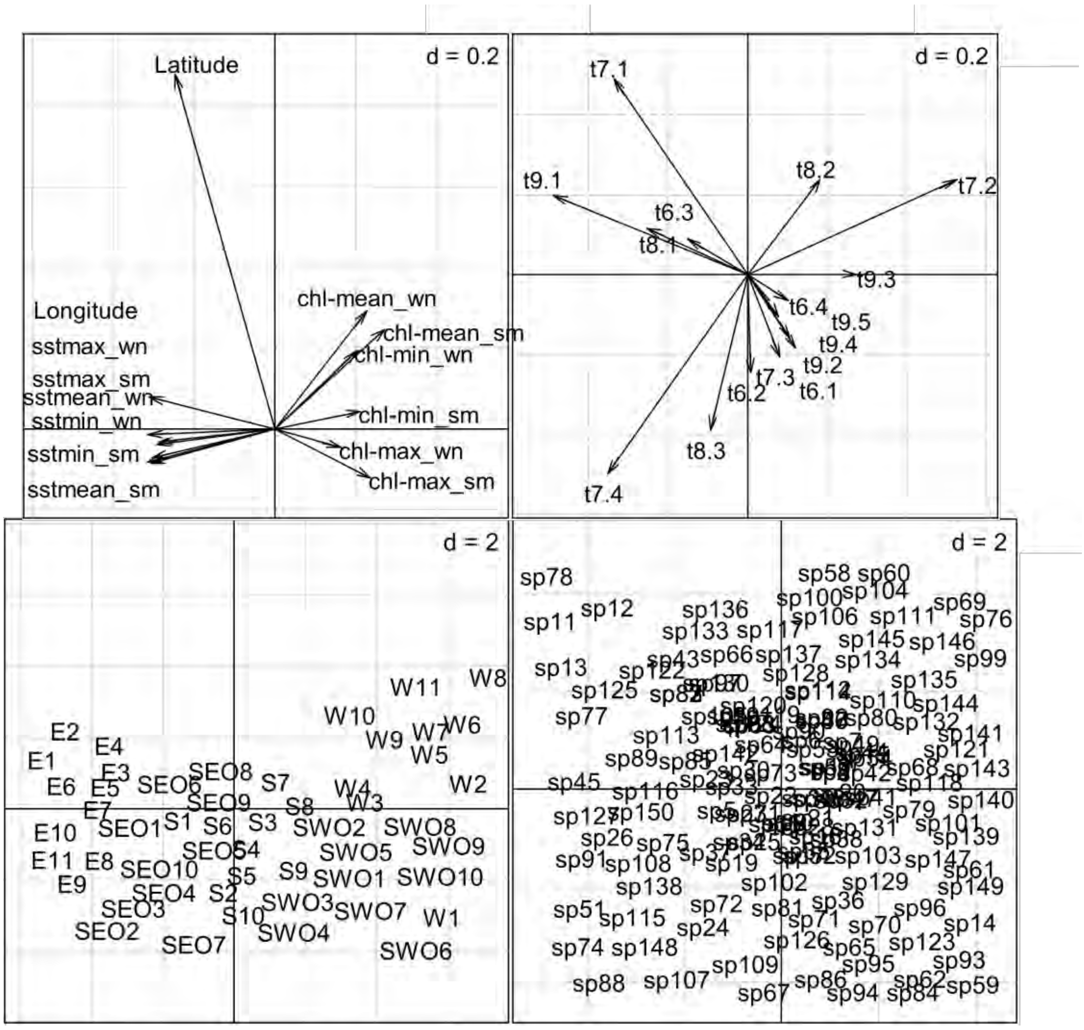


Fig.2.6.2. RLQ ordination plot indicates the correlation between reproduction traits, sites, and species abundance. The top left panel represents the environmental variables assessed. The top right represents the (coded) reproduction traits selected in this study. The bottom left shows the distribution of sites, and lastly, the bottom right panel highlights the ordination of species. Refer to Tables 2.2, 2.7, and S2.1.1 for sites, traits, and species names, respectively. The d value in the upper right corner is the scale of the graph given by a grid.

Table 2.7. List of traits names and codes according to trait domain used in RLQ ordination plots

Trait Code	Development trait domain	Trait Code	Reproduction trait domains
t1.1	Feeding group-Filter-feeders	t6.1	Reproductive frequency-Annual protracted
t1.2	Feeding group-Grazers/Herbivores	t6.2	Reproductive frequency-Annual episodic
t1.3	Feeding group-Deposit feeders	t6.3	Reproductive frequency-Continuous
t1.4	Feeding group-Carnivores/Predators/Omnivores	t6.4	Reproductive frequency-Semelparous
t1.5	Feeding group-Scavengers	t7.1	Reproductive type-Spores/Asexual
t2.1	Adult size-Extra Small	t7.2	Reproductive type-Gonochoristic
t2.2	Adult size-Small	t7.3	Reproductive type-Sequential hermaphrodites
t2.3	Adult size-Medium	t7.4	Reproductive type-Simultaneous hermaphrodites
t2.4	Adult size-Large	t8.1	Development mechanism-Direct developer
t2.5	Adult size-Extra Large	t8.2	Development mechanism-Planktotrophic
t3.1	Mobility-Sessile	t8.3	Development mechanism-Lecithotrophic
t3.2	Mobility-Sedentary	t9.1	Size at reproductive maturity-Extra small
t3.3	Mobility –Crawlers	t9.2	Size at reproductive maturity-Small
t3.4	Mobility-Swimmer	t9.3	Size at reproductive maturity-Medium
t3.5	Mobility-Burrower	t9.4	Size at reproductive maturity -Large
t4.1	Preferred habitat position_Infratidal	t9.5	Size at reproductive maturity-Extra large
t4.2	Preferred habitat position_Low		
t4.3	Preferred habitat position_Mid		
t4.4	Preferred habitat position_High		
t4.5	Preferred habitat position_Pools		
t5.1	Fragility-Soft/Exposed/Brittle		
t5.2	Fragility-Intermediate		
t5.3	Fragility-Robust		

2.6.4. Correlating trait attributes, biomass, and environmental parameters

The first 2 axes of the RLQ analysis for the suite of development traits (axes 1 and 2) projected a total variance of 67.19% and 31.97%, respectively (Table 2.8) when weighted with biomass data. These results suggest a strong influence of temperature and chl-*a* on the suite of traits associated with species development.

Table 2.8. Properties of multivariate RLQ ordination (weighted by species biomass) showing the percentage variations, eigenvalues, covariance, and correlation explained by the first two axes (1 and 2), covariance, correlation.

	DEVELOPMENT		**REPRODUCTION**	
RLQ Properties	**Axis 1**	**Axis 2**	**Axis 1**	**Axis 2**
Variance (RLQ) %	67.19	31.97	60.40	38.37
Eigenvalue	5.94	2.82	2.69	1.71
Covariance	2.43	1.68	1.64	1.30
Correlation	0.50	0.63	0.46	0.59

The ordination plots of the RLQ analysis for development traits indicated the biomass of species living in the infratidal zone (t4.1), robust/complex body form (t5.3), medium to large-sized species (t2.2, t2.3), sedentary species (t3.2) were dominantly in the west and SWO regions and were influenced by shifts in chl-*a* concentration (Fig.2.6.3). Species with these traits included the large limpets; *Scutellastra argenvillei* and *Cymbula granatina.* In contrast, the temperature gradient drove the biomass of species that preferred mid-shores (t4.3), species with intermediate body fragility (t5.2), species attaining adulthood at small sizes (t2.1) with these species (including all the zoanthids) were predominantly recorded on the east and SEO regions (Fig.2.6.3).

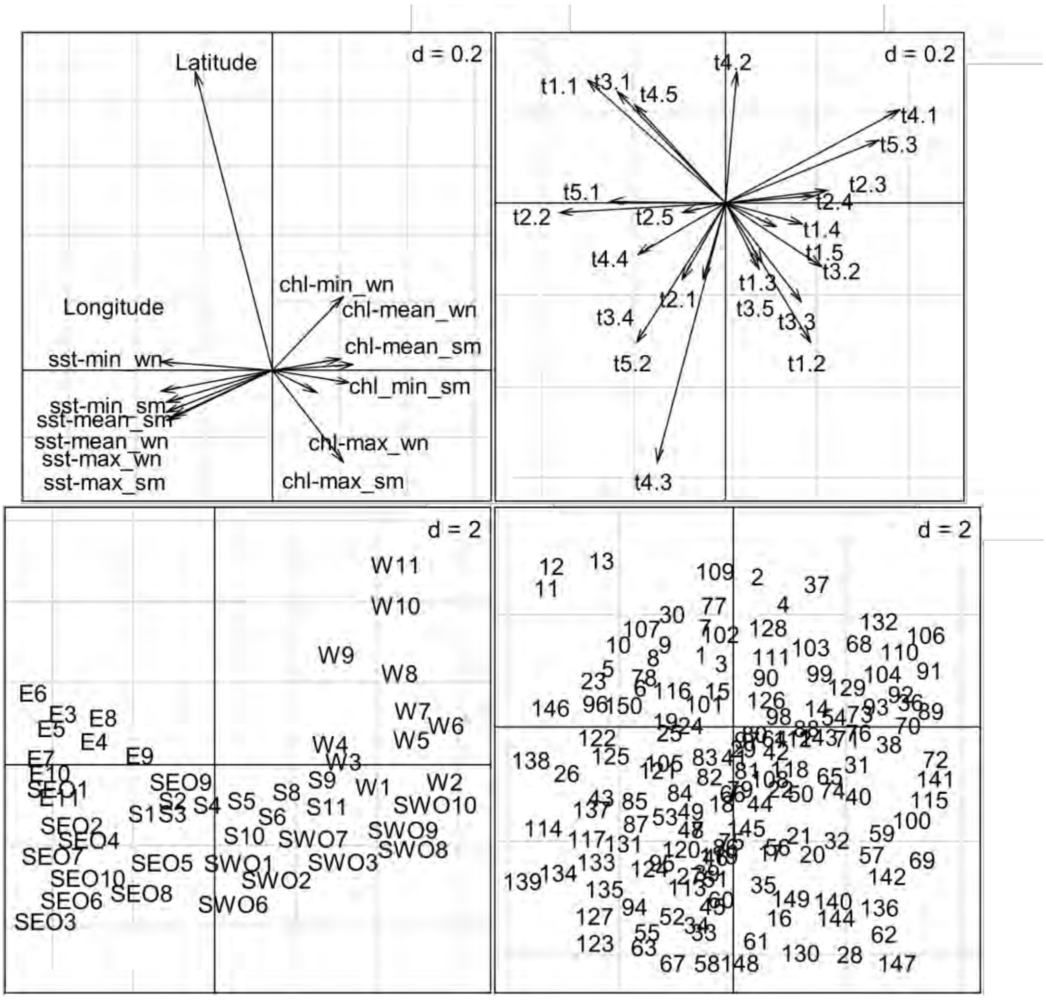


Fig.2.6.3. RLQ ordination plot indicating the correlation among development traits, environment, sites, and species biomass. The top left panel represents the environmental variables assessed. The top right represents the (coded) development traits selected in this study. The bottom left shows the distribution of sites, and lastly, the bottom right panel highlights the species distribution. Refer to Tables 2.2, 2.7, and S2.1.1 for sites, traits, and species names, respectively. The d value in the upper right corner is the scale of the graph given by a grid.

Now looking at the suite of reproduction traits, the first 2 axes of the RLQ analysis (axes 1 and 2) projected an inertia of 60.40 % and 38.37%, respectively (Table 2.8) when weighted with biomass data. The ordination plots of the RLQ analysis (Fig.2.6.4) indicated the biomass of gonochoristic reproductive type (t7.2) and species with planktotrophic development mechanism (t8.2) were predominantly in the west coast and were correlated with chl-*a* concentration (Fig.2.6.4). Sedentary (t3.2), grazers or herbivorous (t1.2) species were dominant in the south and SWO regions. On the other hand, temperature and latitudinal gradient drove the biomass of species with simultaneous hermaphroditism (t7.4), those which attained sexual reproduction at very small sizes (t2.1) and those with asexual reproduction types (t7.1). These traits were predominantly in the east and SEO regions (Fig.2.6.4). Some of these species include zoanthids, sponges and sea anemones.

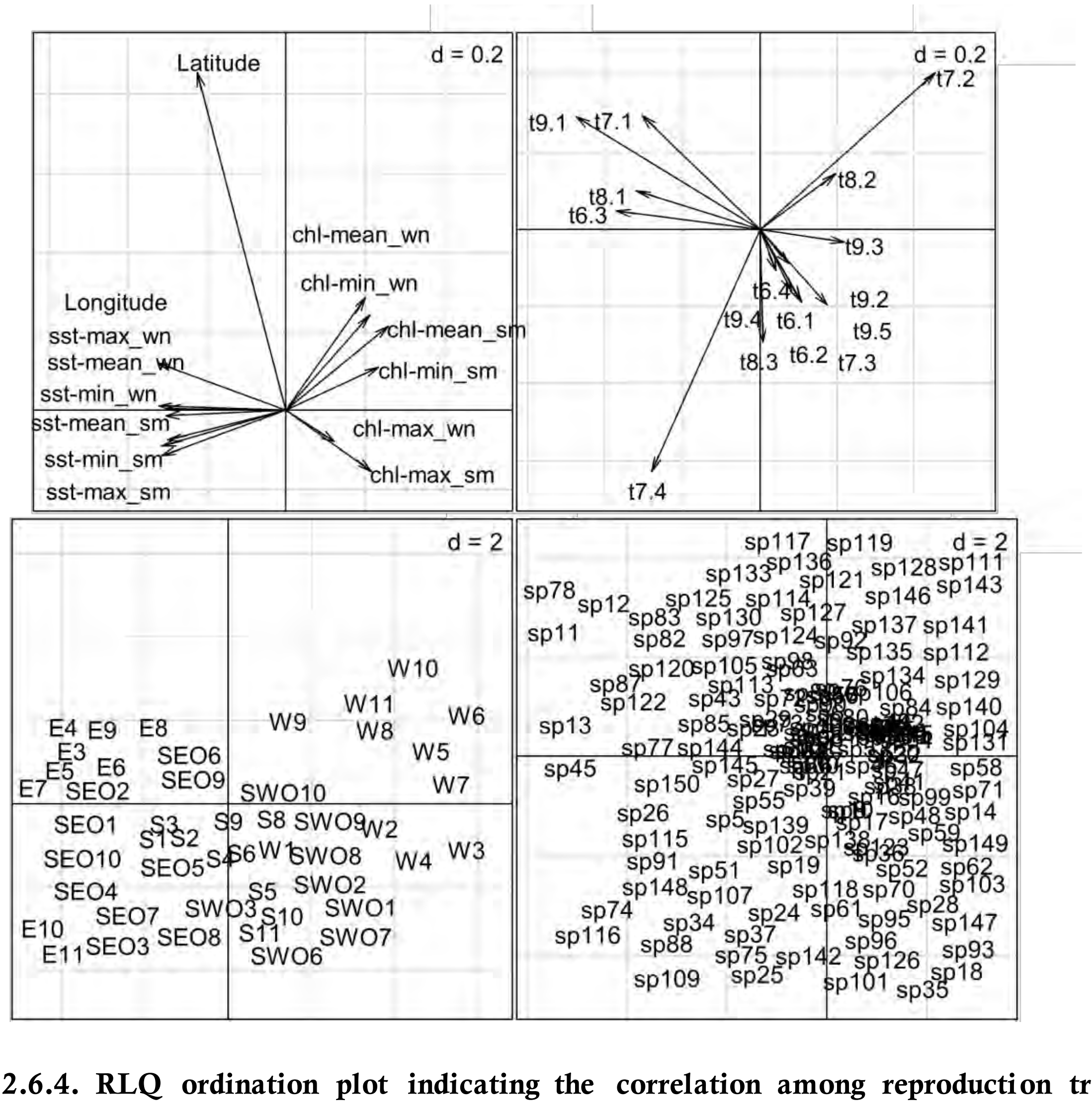


Fig.2.6.4. RLQ ordination plot indicating the correlation among reproduction traits, environment, sites, and species biomass. The top left panel represents the environmental variables assessed. The top right represents the (coded) reproduction traits selected in this study. The bottom left shows the distribution of sites, and lastly, the bottom right panel highlights the species distribution. Refer to Tables 2.2, 2.7, and S2.1.1 for sites, traits, and species names, respectively. The d value in the upper right corner is the scale of the graph given by a grid.

2.6.5. A summary of the RLQ analysis results

A comparison of the RLQ analyses using biomass and abundance weighted data for both the development trait domain and the reproduction trait domain show that chl-*a* influenced more similar trait combinations for both abundance and biomass weighted data than SST. For instance, there was a slightly higher number of the total trait modalities associated with chl-*a* than SST (i.e., 10 *vs* 6).

For the development trait domain, the RLQ ordination plots for biomass show almost similar trait modality distributions (i.e., in response to the chl-*a* gradient) to ordination plot using abundance data. In contrast, for the same trait domain, the distribution of trait modalities for the SST gradient is notably different between abundance *vs* biomass weighted data. For biomass, 3 out of 5 trait modalities for adult size and habitat preference, 2 out of 3 trait modalities for fragility, 2 out of 5 for mobility and 1 out of 5 trait modalities for feeding were correlated to SST. For abundance data, however, 2 out of 5 trait modalities for habitat preference, 1 out of 3 trait modalities for fragility and 2 out 5 trait modalities for adult size were correlated to SST.

Now considering the reproduction trait domain, abundance and biomass showed broadly similar patterns in the distribution of trait modalities for both SST and chl-*a*. For example, 2 out 4 similar trait modalities (i.e., t7.1 and t7.4), 1 out of 4 also similar trait modalities (i.e., t6.3) and 1 out of 5 also similar trait modalities (i.e., t9.1) responded to SST. Trait modality distribution in response to the chl-*a* gradient also showed similar patterns for both abundance and biomass weighted data. For both metrics, 3 out 4 similar trait modalities for reproductive frequency (t6.1, t6.2 and t6.4), 1 out of 3 similar trait modalities for development mechanism (i.e., t8.2) and 4 out of 5 similar trait modalities for adult size (i.e., t9.2, t9.3, t9.4 and t9.5). In summary, for the reproduction trait domain there were many overlaps in the trait modalities associated with both parameters. In contrast, the development trait showed more distinct differences in the trait modalities associated with each environmental parameter.

Overall, the main patterns in site distribution and grouping of the environmental parameters observed were almost similar for both RLQ analyses whether weighted by the biomass or the abundance metric. Sites grouped in line with the influence of the two main currents, i.e., sites influenced by the Benguela grouped together and likewise for those influenced by the Agulhas. However, the major differences between the two metrics were among the distribution of trait combinations particularly within the reproduction trait domain.

2.6.6. Tests of random assembly of intertidal species abundances and traits

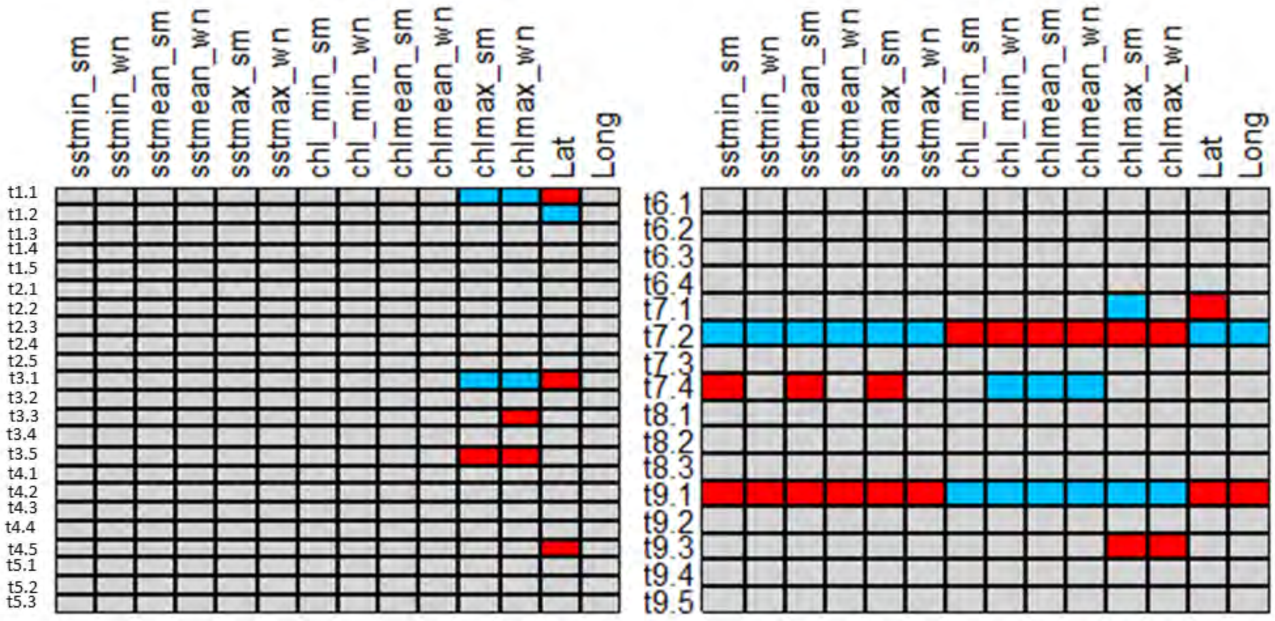


Fig.2.7.1. Combined fourth corner output showing specific trait responses (weighted by abundance) to environmental parameters. Red indicates significant positive ($p<0.05$) associations, while blue indicates significant negative associations. The *y*-axes (t1.1– t9.5) represent trait modalities while the *x*-axis labels represent the environmental parameters e.g., sstmin_sm represents the minimum SST in summer, sstmin_wn represents minimum SST in winter. Lat= latitude, Long = longitude.

The graphical output from Monte-Carlo random tests performed on Model 6 (Fig.2.7.1) revealed a significant correlation between the environmental parameters (temperature and chl-*a*) and species abundance (i.e., taxonomic identity) (Model 2; p = 0.01) but showed no correlation between the environmental parameters and development traits (Model 4; p = 0.37). On the other hand, there was a significant correlation between environmental parameters and the patterns observed in species abundances (Model 2; $p<0.0001$) and between the parameters (temperature and chl-*a*) and reproduction traits (Model 4; $p<0.001$). Further, the trait data weighted by abundance showed positive and negative correlations between trait modalities within the reproduction trait domain, particularly for species with a gonochoristic reproductive type (t7.2) and temperature, location, and chl-*a*, respectively (Fig.2.7.1, t7.2). Simultaneous hermaphrodites (t7.4) were positively and negatively associated with higher temperature and lower chl-*a*, respectively (Fig.2.7.1).

In addition, size at reproductive maturity, particularly species that attain reproductive maturity at extra small sizes (>10mm), were positively influenced by temperature and location (lat & lon) while negatively associated with chl-*a* concentrations (Fig.2.7.1, t9.1). These results were consistent with the fourth corner output when weighted by abundance. Unexpectedly filter-feeders (t1.1) were negatively correlated with maximum chl-*a*, while positively associated with latitude (Fig.2.7.1). On the other hand, grazers and herbivores were negatively associated with latitudinal gradients (Fig.2.7.1, t1.2). Sessile species were negatively correlated to maximum chl-*a* and positively correlated to latitude (Fig.2.7.1, t3.1). Crawler (t3.3) and burrowing (t3.5) species were positively correlated to chl-*a* (Fig.2.7.1).

2.6.7. Tests of random assembly of intertidal species biomass and traits

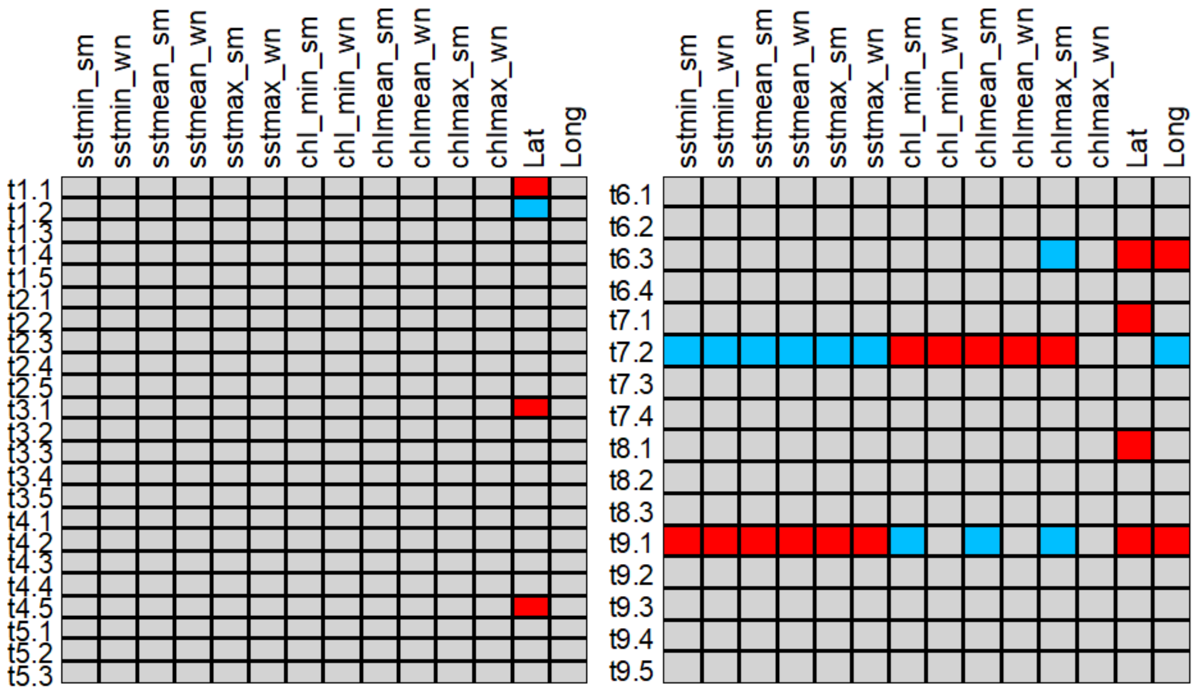


Fig.2.7.2. Combined fourth corner output showing specific trait responses weighted by biomass to environmental parameters. Red indicates significant positive correlations, while blue indicates negative correlations ($p<0.05$). The y-axes (t1.1–t9.5) represent trait modalities while the x-axis labels represent the environmental parameters e.g., chl_max_sm represents the maximum chl-a in summer, chlmax_wn represents the maximum chl-a in winter. Lat= latitude, Long = longitude.

Fig.2.7.2 revealed a significant correlation between the environmental parameters (temperature and chl-*a*) and species biomass (i.e., secondary production) (Model 2; $p = 0.001$) but showed no correlation between the environmental parameters and development traits (Model 4; $p = 0.32$). On the other hand, there was a significant correlation between environmental parameters and the patterns observed in species abundances (Model 2; $p<0.0001$) and between the parameters (temperature and chl-*a*) and reproduction traits (Model 4; $p<0.001$). Using trait data weighted by biomass, specific reproduction traits, including continuous reproductive frequency (t6.3), were negatively correlated and sensitive to chl-*a* in summer and positively correlated with location (i.e., lat & lon, see Fig.2.7.2, t6.3). In addition, species with asexual reproduction (t7.1) and gonochoristic reproductive (t7.2) were also sensitive to temperature and latitudinal gradient, while direct-developing species were correlated to both temperature and chl-*a* (Fig.2.7.2, t7.1 & t7.2). Size at reproductive maturity, particularly species that attain reproductive maturity at extra small sizes (>10mm), were positively influenced by temperature and location (latitude & longitude, Fig.2.7b) while negatively associated with chl-*a* concentrations (Fig.2.7.2, t9.1). Lastly, filter-feeders (t1.1), sessile species (t3.1) and those that use rock pools as the primary habitat (t4.5) were positively correlated to latitude under the development trait domain, while there was a negative correlation between the same parameter and grazers/herbivores (t1.2).

2.7. Discussion

Satellite-derived environmental data have revealed high physiographic heterogeneity across space and time (Li et al., 2013). This has subsequently been associated with changes and differences in species diversity across ecosystems. Orton (1920) was amongst the first authors to suggest that change in sea temperature is a critical factor influencing reproduction in marine invertebrates. Emanuel et al. (1992), showed how mesoscale differences in habitats have a stronger influence on community composition than macroscale changes in latitude. Hochachka & Somero, (2002), also added that environmental temperature influences various organismal processes in ectotherms, including growth, reproduction, and survival. Parameters such as growth, reproduction, and mortality are dependent on a complex array of selective forces and are important to understanding the distribution and abundance of a species.

With these various effects attributed to environmental parameters, I, therefore, examined whether there was a biotic response (functional traits and subsequently shifts in species abundances and biomass) to environmental gradients across bioregions. I assumed that if the effects of the environment can be evident based on the taxonomic composition of the biota, it holds that the environment may be indirectly affecting that which constrains the species (in this case, a suite/combination of traits). Although Emanuel et al. (1992) highlighted the fact that macroscale zoogeographic patterns reflected the distributional range of species, the relative abundances of species and the composition of communities can alter markedly over short distances in response to differences in physical conditions such as wind and ocean current patterns. It is my assumption that such responses to these factors may be related or driven by species functional traits. For example, most marine invertebrates have an obligate developmental period during which they are incapable of settling. During this pre-competency phase, changes in physical conditions can influence the ability and survival of certain organisms. None-the-less, if these species possess continuous and protracted reproductive frequency traits, they may persist in that environment suggesting a trait-based advantage over the environment.

2.7.1. The habitat templet theory and species assemblages

2.7.1.1. The abiotic templet: Temperature influence on species- and trait distribution

The habitat templet theory (HTT) of Southwood (1977) states that there is a match between overall species traits and environmental conditions (Townsend & Hildrew, 1994). The HTT is a key concept in explaining differences in species assemblages between locations or periods. Based on this idea, species' traits are expected to provide an increased mechanistic understanding of species-environment relationships and the drivers of species' distributions. Linking traits to environmental conditions is, however, not straightforward, as traits are interconnected within species, and each species comprises a suite of traits or life-history strategies where some may be more important or more responsive to environmental pressures than others (Townsend & Hildrew, 1994; Verberk et al., 2008). This is to say, species traits of all domains together shape one or more life-history strategies, with certain species traits being more pronounced, and therefore more defining for any given strategy. Thus, this study aimed to evaluate the variability of these traits and some of their interactions in order to understand how the environment, particularly temperature and chl-*a*, drives rocky shore macroinvertebrate trait distributions through species abundances and biomass. The inclusion of biomass in this study also established the link between biomass estimates and food availability. Schnack (1998) suggested that biomass presents a more accurate proxy of the food available to macrofaunal communities and ecosystem functioning over a long period than species abundance. This suggestion is based on the biomass-ratio hypothesis proposed by Grime (1998). This hypothesis postulates that the extent to which the traits of a species affect ecosystem function is likely to be related to the contribution of the species to the total biomass of the community. According to this hypothesis, the functioning of ecosystems is determined to a large extent by the traits of the dominant species. Several studies have tested this hypothesis for different ecosystem functions such as primary production (Díaz & Cabido, 1997; Lavorel & Garnier, 2002; Garnier et al., 2004; Vile et al., 2006), nitrification (Laughlin, 2011), and litter decomposition (Tardif et al., 2015). The overall challenge highlighted in these studies is in identifying the key functional traits of the dominant species that subsequently have important effects on ecosystem functioning.

Empirical evidence suggests that for most species across all biogeographic provinces on the South African coastline, gametogenesis occurs as sea-surface temperatures rise, and the breeding season occurs when water temperatures are at or about their warmest. This close relationship between monthly changes in the average surface water temperature and gonad development of South African marine invertebrates has led many authors to speculate on a link between temperature and the overall reproductive attributes of species (e.g., Brown, 1971; Branch, 1974; Thum & Allen, 1976; Laudien et al., 2001; Schleyer et al., 2004). In addition, previous work on rocky shores, in South Africa and elsewhere, has found that shifts in seawater temperature (Branch, 1974; Bowman & Lewis, 1986), latitude and temperature (Helmuth et al., 2006), and climate change (Moore et al., 2011) can deeply influence the reproductive biology and phenology of patellid limpets. Such reproductive patterns are usually associated with latitudinal variation in temperature, photoperiod, or insolation. Although it is well known that species from lower latitudes tend to grow more rapidly than species from higher latitudes, it is not yet clarified whether physiological constraints, changes in growing seasons, or a combination of both might be the cause of these different growth rates

(Henriques et al., 2017). According to Hodgson (2010), for organisms that extend from the more temperate south coast of South Africa well into the east coast, the breeding season of populations becomes more protracted at lower latitudes, which is regarded as the general trend for marine invertebrates. For example, on the warm-temperate south coast, the sea cucumber *Pseudocnella sykion* breeds in summer (Foster & Hodgson, 1995), while on the east coast it has been shown that it breeds all year-round (Khonjwayo, 1996).

Another species likely influenced by environmental properties is the barnacle *Balanus glandula*. Physical transport processes, such as the formation of eddies (Archambault et al., 1999), downwelling (Jenkins et al., 2000), and countercurrents influence the abundance of *B. glandula* along the coast, presumably through their effects on the transport of barnacle larvae to rocky shores. The precise temperature limits of *B. glandula* distribution are unknown, but the warmer waters of the south coast may be outside its optimal temperature range. Some indication of its preferred temperature range can be gleaned from its global distribution. The annual mean temperature at the southern limit of its native range on the Pacific coast of North America is around 17 °C (Kado, 2003), whereas long-term temperature means over the distributional range of introduced *B. glandula* in Japan are between 10 °C and 15 °C (Kado, 2003). Similarly, Rico et al. (2006) gives a temperature range from 7.9 °C to 17.9 °C (Elias & Vallarino, 2001) for an invaded site in Mar del Plate, in South American. This suggests that *B. glandula* is a cool-temperate species that is unlikely to extend its distribution eastwards beyond its current temperature range along the west coast of South Africa to temperatures exceeding 17 °C east of Cape Point (Laird & Griffiths, 2008). In addition, its small adult size, small size at reproductive maturity, and fast reproduction frequency established from my study may be a spin-off to its rate of spread indirectly being limited by ideal temperatures. On one hand, this is to say, its range limits are allowing the species to full colonise the region with the most ideal abiotic parameters. On the other hand, what this shows is the critical influence of the abiotic habitat filter acting as a bottleneck to the spread in the distribution of this invasive species. This situation could also suggest and illustrate response and effect traits at work. A further investigation into the traits related to thermal tolerance may further elaborate on this.

For most benthic invertebrates, it is also generally assumed that the presence of pelagic larvae ensures that most populations are 'open' and recruitment is independent of local habitat drivers (but see Caley et al., 1996). However, recent work has suggested that local retention of larvae may be more common than is generally acknowledged (Jones et al., 1999; Swearer et al., 2002), suggesting some role of the habitat in driving species persistence or mechanisms within the species themselves. This evidence comes from various sources, including population genetics, the occurrence of endemic species, and the persistence of introduced and/or invasive species (Jenkins, 2005). In some species, however, the relationship between the breeding cycle and temperature is equivocal. Joska & Branch (1983) could see no link between temperature and the reproductive cycle of the gastropod, *Oxystele variegata* in False Bay on the west coast of South Africa. The observed similarities in the reproductive cycles of the warm-temperate south coast and cool-temperate west coast populations of the patellogastropods *Helcion pruinosus* and *H. pectunculus.* suggested that factors other than temperature are more important (Henninger & Hodgson, 2001; Gray & Hodgson, 2003). For example, for some molluscs, latitude, and therefore photoperiod may be an influencing factor (Lasiak 1987b; Gray & Hodgson, 2003).

Longitude, in addition to correlating with a gradient in SST, was associated with the distribution of development traits such as adult size, habitat choice, and body form, feeding type, and mobility (Fig.2.6.1). Examples of species within these trait categories that responded to the latitude and SST gradient included the chiton (*Ischnochiton textilis*), the isopod (*Cirolana venusticauda*) and the flatworm (*Planocera gilchristi*). Although, there were species with extra-large sizes (t2.5), smaller adult size modalities (particularly extra-small (<10mm, t2.1) and small (10-30mm, t2.2)) were primarily found on the eastern parts of the coastline in the east and SEO regions (Fig.2.6.1). On the other hand, the medium to large-sized species (i.e., 30-50mm, t2.3 and 50-70mm, t2.4) were more common on the colder western parts on the coastline. This shift in size range may be an effect of unique evolutionary histories or unique habitat preferences of these species on this part on the coastline and not necessarily an effect of the temperature gradient. For example, some of the most common species in the east and SEO regions are the zoanthids (*Zoanthus* and *Palythoa* spp), the pea and coral crabs (*Pinnotheres* and *Tetralia* spp), which are relatively very small (<30mm), and rock oysters (*Saccostrea* sp) and brown mussels (*Perna perna*) which are very large (>70mm).

Lastly, with regards to invasive species, as the size of a physical or biological system changes, different components are expected to adjust so that the organism can continue functioning. For example, in the case of the mussel, *Mytilus galloprovincialis,* its anatomical and physiological attributes and thermal tolerances may change or increase with habitats (new abiotic environment) and interaction with native species (Somero, 2010). This finding supports the conjecture of Stachowicz et al. (2002) suggesting that global warming could be a boon for invasive species in marine ecosystems. Locally, since its establishment on the coast of South Africa, *M. galloprovincialis* has notably spread towards the SEO bioregion which is on the warmer eastern parts of the coastline. In summary, these results corroborate those of Tittensor et al. (2010) who found that, overall, temperature has a consistent and dominant role in structuring broad-scale marine diversity patterns, particularly for ectothermic species, with habitat selection and functional traits (based on this study) being important for coastal taxa.

The preceding discussion attempts to decouple the effects and influences of SST on benthic species traits along the coast of South Africa. There is no doubt that predicting temperature-driven change on this coastline is further complicated by the number of different climatic zones found along a relatively short coastline and the contrasting changes expected within each zone. Looking at the latest trends of the two LME's driving coastal dynamics on the coast of South Africa, recent studies have shown that surface waters along South Africa's subtropical east coast are warming significantly (Goyal et al., 2021) and creating a more turbulent Agulhas Current at mesoscales (van Niekerk et al., 2022). A more turbulent Agulhas Current may be associated with an increase in the occurrence of offshore cyclonic meanders (known as "Natal Pulses") and the formation of Agulhas Rings. These rings link the Indian and South Atlantic as they spin off into the Atlantic at the Agulhas Retroflection (Stramma & Peterson, 1990; Lutjeharms, 2006). This mechanism drives heat exchange and dispersal of marine organisms along the east coast waters, also the Indian and South Atlantic oceans (Lutjeharms & van Ballegooyen, 1988; van Leeuwen et al., 2000; Le Gouvello et al., 2020, Silva et al., 2021). It is assumed that changes in the strength and turbulence of the Agulhas Current will influence dynamically driven coastal and shelf-edge upwelling and cross shelf exchange processes between the deep ocean and the coastal regions (Rouault et al., 2010; Backeberg et al., 2012). In contrast, sections of the country's south and west coast are cooling seasonally as winds that favour upwelling increase. The Benguela Current is the strongest wind-driven coastal upwelling system known. In the southern Benguela, seasonal shifts in the latitudinal location of the South Atlantic High along a north-west axis often leads to strong seasonal variations in wind intensity, with increased upwelling during the summer season (van Niekerk et al., 2022). On its offshore boundary, the dynamics of the Benguela Current circulation are modulated by the intermittent passing of warm Agulhas Rings and eddies (Veitch et al., 2018). Negative annual average temperature trends have been reported along the southern and western South African coastline over the last four decades (Rouault et al., 2010; Duncan et al., 2019).

2.7.1.2. The biotic templet: the influence of chlorophyll-*a* on species- and trait distribution

The GLMM model highlighted that for mean and maximum chlorophyll-*a*, the east coast was significantly different from all other bioregions while for minimum chl-*a*, the SEO region was only significantly different from the SWO and west coasts (Fig.2.4, Table 2.5). Overall, the mean and maximum chl-*a* values for the east coast were significantly lower than for all other bioregions, as expected, with the west exhibiting the highest mean values. Bustamante et al. (1995) highlighted that chl-*a* concentrations off the south-east coast are lower than those off the northwest coast. They (Bustamante et al., 1995) also recorded that autumn-winter peaks on the south coast and little seasonality on the east coast have also been recorded in previous studies. It is commonly acknowledged that south-easterly winds promote the upwelling of nutrient-rich deep waters, promoting high productivity on the west coast of South Africa (Carr, 2001), and there are notable summer-spring peaks on the west coast. The latter could be among the reasons for high variability in chl-*a* across sites on the west coast in comparison to SWO sites (Fig.S2.2a-d). For example, across all seasons, the most- eastern sites of the SWO, e.g., from site 37 moving east to site 32, exhibited less variability in chl-*a* than sites 38 to 42 (Fig.S2.2a-d).

On the other hand, the properties of the Agulhas Current have been widely studied (refer to 2.7.1.1). The current flows along the east coast towards the south coast of South Africa before moving offshore and broadening of the continental shelf west of East London near latitude 34° S (Fig.2.1); along the south coast, the Agulhas Current is further from shore and turns back east between Cape Agulhas and Cape Point (Branch et al., 2002). Its flow creates coastal dynamic upwelling in the vicinity of Port Alfred and Port Elizabeth on the south coast, bringing nutrient rich cold water to the surface and small-scale changes in nearshore chl-*a*. This further makes the south coast cooler than the east coast and these temperature gradients correspond to gradients in coastal zone productivity. This may also explain the sudden drop in SST from sites 23-25 (Fig.S2.1a-d) which are within the range of the upwelling cell.

Undoubtedly, biotic factors are assumed to exert greater control over reproductive periodicity for some macroinvertebrates. Linking this chl-*a* biotic filter to reproduction traits, Griffiths (1977) examined the reproductive cycle of two intermittent spawner indigenous mussel species, *Choromytilus meridionalis* and *Aulacomya atra* from the west and south coast populations. It was found that, because these species do not have large food reserves, food availability may be of greater importance for maturation of the gonad than temperature, which differs considerably between the two coasts. Lasiak (1990) also suggested that the asynchronous continuous reproductive cycle at the population level seen in the grazing limpet *Cellana capensis* may reflect food availability to individual limpets.

Based on the outputs of the RLQ analyses of the reproduction trait domain, using both abundance and biomass weighted data, this study showed that, higher chl-*a* as indicated by chl-max (Figs.2.6.2 & 2.6.4), had a stronger association with trait categories 6,7 and 9. These categories represent reproductive frequency, reproductive type, and size at reproductive maturity, respectively. Under reproductive frequency, annually episodic and annually protracted species were the most closely associated with chl-*a*. These species primarily occurred on the west and SWO bioregions. In addition, most species within the western part of the coastline attained reproductive maturity at larger sizes. Gonochoristic and sequential hermaphroditic species also exhibited a stronger association with chl-*a*.

For the developmental trait domain, the RLQ plots (Fig.2.6.1 & 2.6.3), with the exception of filter feeders (t1.1), grazer and herbivore species (t1.2), showed a stronger association with higher chl-*a* than deposit feeders (t1.3), carnivores, predators, and carnivores (t1.4) and scavengers (t1.5). In addition, sedentary species (t3.2), and crawlers (t3.3) were more strongly affected by higher chl-*a* values in comparison to burrowers (t3.5). Overall based on the combined fourth corner output, for the development trait domain, higher chl-*a* values showed more positive associations with feeding type (t1) and mobility (t3) trait categories (Figs.2.7.1 & 2.7.2).

A study of South African rocky shores by Bustamante et al. (1995) found that the biomass of grazers was correlated with intertidal benthic algal production. Ricciardi & Bourget (1999), on the other hand, ascertained that mean annual water temperature is a significant predictor of total macroinvertebrate biomass and the best single predictor of grazer biomass. Since most sedentary organisms recorded from the warm temperate regions are grazers e.g., the limpets *Cellana capensis* and *Scutellastra granularis* and the topshell *Oxystele tabularis* and periwinkles *Afrolittorina knsynaensis* and *Afrolittorina africana*, it is reasonable to assume an effect of the interaction between benthic algal production and temperature on grazer biomass. The warm temperate regions of the coast of South Africa are dominated by turf seaweed species such as *Gelidium pristoides* and geniculate coralline species, their turf matrix traps many food particles, subsequently increasing and explaining the abundance of deposit feeders and grazers in the region. Therefore, broad access to diverse food sources, combined with the relatively low energetic cost of food capture for sedentary organisms, suggests that the success of benthic feeders is related, at least in part, to optimal feeding (Riisgard & Larsen, 1995; Gili & Coma, 1998).

2.7.2. Integrating single traits into suites of traits to predict community assemblages

Species traits are connected between and within trait categories through trade-offs that are often driven by an interplay of habitat properties. In addition, species comprise various traits that come together to influence the survival of that species within any given environment. Therefore, traits cannot be viewed separately and instead should be combined as a 'suite' or life-history strategy (Verberk et al., 2008). Species possess life-history traits that buffer them against adverse physical environmental conditions, such as the simultaneous negative effects of competitors and poor environmental conditions. Other traits amplify the effects of unfavourable conditions of events (Chesson & Huntly, 1988). That said, the suite of reproduction traits is one of the four most important interrelated domains of traits influencing life-history strategies (Siepel, 1994), the other three domains being: development, dispersal, and synchronisation. Although development and dispersal trait domains are deemed separate by Verberk et al. (2008), when applied to intertidal systems, there appears to be a great deal of overlap between the strategies within the trait domains.

Further, because trait-based approaches are sensitive to the number of traits and trait modalities and thus to reduced redundancy and/or numerical noise (Beauchard et al., 2017), the dispersal trait domain was found to be nested in the development domain. At this point, it is crucial to keep in mind some of the limitations of borrowing concepts initially designed for specific systems (in this case, freshwater habitats). Some of these limitations are explained in greater deal in the following paragraphs.

2.7.3. Reproduction trait strategies and biogeography

I used the combined fourth corner analysis to examine the association between trait modalities within each trait domain and the environmental parameters (temperature and chl-*a*). The results revealed that trait modalities within the reproduction trait domain (RT) correlate more closely to both temperature and chl-*a* gradients than do the suite of development traits. There were some specific positive and negative correlations between reproduction trait modalities and both temperature and chl-*a*. Most of the results from the combined fourth corner results were supported by the 4 reproduction strategies suggested by Verberk et al. (2008), i.e., strategies R1, R2, R3, and R4. However, R2 was significantly nested in R4 and is explained within the same context. It is also important to note that, however, the reproduction strategies by Verberk et al. (2008) do not include the trade-offs and/or spin-offs among reproductive type effects such as differences between simultaneous and sequential hermaphrodism. These have been discussed as some limitations of the current reproduction strategy approach. Although the results from this study do not perfectly or uniformly fit into these specific strategies as they were initially developed for freshwater systems, however, the unifying factor is that they were made for macroinvertebrate species and also the dominant trait modalities for each strategy mentioned is corroborated by the observations made from this study.

2.7.3.1. Strategy R1: Sequential reproduction and active dispersal

Strategy R1 involves sequential reproduction. The main characteristic traits of species within this strategy have rapid juvenile development, long-lived adults, active dispersal, and a protracted reproductive period. My results showed development mechanism (either planktotrophic, direct development or lecithotrophic development), when coupled with small size at reproductive maturity and continuous reproduction trait modalities, is often correlated with a rapid juvenile development strategy. These trait modalities were sensitive to temperature and chl-*a*. Examples of such species include the simultaneous/permanently hermaphroditic barnacles, e.g., *Chthamalus dentatus* and *Balanus glandula.* These two species were the second most abundant species across the whole coast after zoanthids. These barnacle species are short-lived but have larvae in the water column all year round, meaning that, although larvae might be washed offshore, they can recruit any time when the winds and currents are onshore, suggesting, that although they may not exhibit persistence, they have the potential for it.

In addition, most marine macroinvertebrate species are regarded as long lived and biphasic i.e., having highly dispersive planktotrophic larval development and sedentary adults. Along the South African coastline, such species include mussels (e.g., *Mytilus galloprovincialis, Choromytilus meridionalis, Semimytilus patagonicus,* and *Aulacomya atra*), barnacles (*Octomeris angulosus*), some limpets (*Eoacmaea albonotata*), and segmented worms (e.g., *Pseudonereis podocirra*, *Platynereis dumerilii, Perinereis vallata*), and the sea anemone (*Actinia ebhayiensis*). These species have prolonged spawning linked with temperature and chl-*a* gradients. The South African coastline is assumed to favour this existence of pelagic planktonic larvae for most species (Scott, 2009), and this may be due to the various localised upwelling cells along the South African coastline. By spreading the reproductive effort over a longer period and larger spatial scales, species with this reproduction strategy minimise the probability of total reproductive failure. Broadcast spawning minimises offspring competition with parents for space or resources, as the young are swept into the water column and carried away. These findings suggest that reproductive patterns are controlled by stimuli that could be endogenous or exogenous in origin (Dahan & Benayahu, 1997). Further, the stimulus for synchronous spawning may also be triggered by a change in water temperature, increased wave action, the tides in particular seasons, lunar rhythms, or chl-*a* concentration.

2.7.3.2. Strategy R2: Sequential reproduction with many small eggs and no active dispersal

In this strategy, species are suggested to sequentially produce batches of eggs with low investment in adult longevity. They invest in a large clutch size rather than large eggs, which results in a longer development time, precluding offspring from reproducing in the same season. In marine macroinvertebrates this is equated to species with protracted and continuous reproductive frequency with direct development of offspring. These species include zoanthids such as *Zoanthus natalensis, Zoanthus durbanensis,* and *Palythoa natalensis.*

2.7.3.3. Strategy R3: Sequential reproduction with parental care and no active dispersal

The third strategy (R3) that showed positive and negative correlation with reproduction traits and the environmental parameters involves sequential reproduction with parental care, no active flight, or dispersal. This was equated to species with direct development and small size at reproductive maturity. According to Verberk et al. (2008), species with this strategy are expected to spread reproductive effort over a long period with no dispersal, and many have a short adult life span. Such species invest in egg size rather than clutch size. The higher *per capita* investment in offspring development can be combined with parental care and allows more rapid development. Examples of species with this strategy include patellid limpets and predatory whelks such as *Nucella dubia* and *Trochia cingulata.* As direct developing species, the juveniles have limited dispersal and often live within the same habitats as the adults. My results indicate that such species were limited to the warmer regions, particularly the east and south-east regions, suggesting that the habitat constrain or filter these species to these particular locations.

2.7.3.4. Strategy R4: Early age at first reproduction, no active flight or dispersal

This strategy (R4) entails early age at first reproduction with no dispersal, while R2 involves sequential reproduction with many small eggs and no dispersal. Species with the R4 strategy attain a high rate of increase through the early onset of reproduction, sometimes with asexual reproduction. Early reproduction and several reproductive cycles compensate for the limited dispersal to deal with adverse environmental conditions. Over a long period, this strategy could also equate to many eggs, thus linking it to R2 reproduction strategy. Examples of species I found from my study that can fit into these 2 strategies include zoanthids (*Zoanthus natalensis, Zoanthus durbanensis, Palythoa natalensis*), barnacles (*Chthamalus dentatus*), and worms (*Sedentaria spp*). Because these species are more common on the east coast than other bioregions, I speculate their persistence may be a compromise or trade-off within this R4 strategy and the 'unfavourable' environmental filter (in this case, low chl-*a* concentration). Therefore, to allow for population persistence, these species possess these trait spin-offs, including early age at first reproduction, continuous reproduction, limited to no mobility, are filter-feeders, and have small adult sizes. These strategies translate to low *per capita* investment.

In conclusion, the reproduction trait domain showed a distinct separation in trait categories between the easterly sites and westerly sites. For example, for reproductive frequency (t6), the trait modalities for species with annual episodic (t6.2) and annual protracted (t6.1) reproductive episodes and also most species which attain reproductive maturity (t9) at larger sizes (t9.2, t9.3, t9.4, and t9.5) were closely associated with the colder and nutrient rich waters of the west and SWO coast. On the other hand, asexual (t7.1) and simultaneous hermaphroditic (t7.4) reproductive types, direct developer species (t8.1), lecithotrophic species (t8.3) and species attaining reproductive maturity at extra-small sizes (<10mm, t9.1) where the most common trait modalities on the eastern sites of the coast.

2.7.4. Limitations with the current reproduction trait strategy approach

One missing crucial aspect with the reproduction strategy proposed by Verberk et al. (2008) is the failure to include a strategy which involves the trade-offs among different reproductive types such as gonochoristic, asexual, or hermaphroditic. For example, the presence of hermaphroditism (both simultaneous and sequential) which is a critical spin-off is linked to population persistence. My results indicated that simultaneous hermaphroditic species were overall positively and negatively associated with higher temperature and lower chl-*a* concentration respectively. This reproduction strategy translates to a selective advantage for a species by increasing its reproductive potential and survival. Some common limpet species possessing simultaneous hermaphroditism along the coast of South Africa include limpets such as *Siphonaria capensis, Siphonaria serrata* (Pal & Hodgson, 2005), *Helcion penctunculus*, and *Cymbula oculus* (Branch, 2010) and various barnacle species, including *Octomeris angulosa, Chthamalus dentatus*, *Austramegabalanus cylindricus*, *Amphibalanus venustus*, *Tetraclita serrata,* and *Tetraclita squamosa,* and the bisexual mussel S*emimytilus patagonicus*.

There were also many sequential hermaphroditic species, including the mussels (*Brachidontes variabilis, Striarca symmetrica,* and *Barbatia obliquata*), limpets (*Siphonaria anneae, Cymbula oculus, Siphonaria concinna, Siphonaria oculus, Scutellastra aphanes, Dendrofissurella scutellum, Crepidula porcellana,* and *Cymbula sanguinans*), oysters (*Striostrea margaritacea,* and *Ostrea atherstonei*) and barnacles (*Tetraclita serrata* and *Octomeris angulosa*). The main advantage of sequential hermaphroditism is that it allows for a selective advantage to an individual by increasing its reproductive potential relative to other gonochoristic or non-transforming members of the community. This is largely because age-specific fecundity in many populations is not distributed in the same way for males and females. By functioning as that sex with the higher fecundity in a particular age span, an organism could increase its reproductive potential relative to lifetime males or females. The extent of the benefit that comes from such sex changes depends on both the population demography and the species' spawning habits (Warner et al., 1975).

The RLQ analyses plots (Fig.2.6.2 & 2.6.4) also showed that these hermaphroditic species are subtropical and warm-temperate species and were more abundant on the eastern parts of the coastline, which are primarily influenced by the warm Agulhas Current than on the west coast, which is influenced by the cold Benguela Current. In addition, the majority of these species produce relatively large egg masses. These findings lead one to speculate on whether there is a correlation between sequential hermaphrodism and the environment. According to McClain et al. (2014), the frequency of hermaphroditism is expected to increase under low food availability as population density (and hence mate availability) decreases. In addition, abiotic factors, such as temperature, may have important influences on physiological, biochemical, and reproductive attributes of oysters (Zapata-Restrepo et al., 2019), but see Newell & Branch (1980). I speculate that, the occurrence and/or evolution of sequential hermaphroditic species may be a response trait (see Chapter 1) to the warmer temperatures. For the oysters (*Striostrea margaritacea* and *Ostrea atherstonei*), which are warm season spawners, temperature changes in combination with hormonal control may be linked to the control of their sex ratio (Teaniniuraitemoana et al., 2016) and subsequently the occurrence of sequential hermaphrodism in species. For example, in another oyster species (*Ostrea edulis*), gametogenesis and sex determination were observed to be predominantly affected by temperature. In their research, Zapata-Restrepo et al. (2019) found that shifts in sea water temperatures and warmer condition through the year could cause accelerated gametogenesis and skewed sex ratios in natural populations of the oyster *Ostrea edulis*. Female mussels of the family Mytilidae are understood to undergo sex inversion and in some instances hermaphroditism, in response to food availability, temperature, genetics, and pollutants (Chelyadina et al., 2018).

In addition, the synchronisation strategies proposed by Verberk et al. (2008) fall short in accounting for some occurrences within the marine system, for example episodic reproductive frequency. Several authors have revealed that the episodic reproductive frequency among molluscs in different habitats including sandy beaches on the coast of South Africa is variable. For example, the south and south-east coasts species reproduce in spring/summer (McGwynne & van der Horst, 1985; Lasiak, 1986, 1987; Pal & Hodgson et al., 2005), whereas those on the west coast are autumn and/or winter breeders (Branch, 1974; Griffiths, 1977). I conclude that this could be influenced by seasonal food availability (compare Fig.S2.2a-d). In a study by Bustamante et al. (2005), the maximum body size of the common limpet, *Scutellastra granularis*, was also positively correlated with level of *in situ* primary production. This corroborates some environmentally induced intra-trait variability among species and the impact of seasonal biotic habitat filtering. For the latter, invertebrate productivity has been directly linked to inshore seasonal productivity patterns reported for phytoplankton by Brown (1992).

Also, limpets from warm temperate waters either have biannual spawning periodicity, with the main reproductive period occurring in summer, or protracted spawning compared to the single spawning period for species on the cool temperate west coast (Gray & Hodgson, 2003). More interestingly, investigations of the reproductive seasonality of 30 species from the subtropical bioregion showed no single reproductive pattern as being more dominant than others (Hodgson, 2010). Emmerson, (1994), found a substantial number of species with continuous or all year-round spawning. Considering that temperature easily affects reproduction activity, this continuous reproductive frequency among many species may be an insurance for high abundance of species such as the brown mussel *Perna perna* in these warm temperate waters.

In conclusion, although it is evident that not all species, e.g., the mussel species listed on the above list, have the same trait modalities that explicitly qualify them to fit into a specific reproduction strategy e.g., one that includes both hermaphroditism and planktotrophic development, the combined fourth corner analytical approach highlights some potential trade-offs within the trait domain for these mussel species. More specifically, the mussel species show how hermaphroditism seems more sensitive to temperature than planktotrophic development (evidenced by the grey boxes in Fig.2.7.1 & 2.7.2). This can explain why investment in one trait may constrain investment in another as concluded by Verberk et al. (2008).

2.7.5. Development trait strategies and biogeography

Most of the trait modalities within the development trait domain exhibited little to no correlation to the environmental parameters. This was expected because all species within any habitat or that have successfully colonised a habitat possess or have evolved an adaptive set of traits or a baseline of traits that afford them the ability to persist in that habitat. This can be said for endemic species with limited geographic ranges. For example, there is high endemicity of echinoderms, opisthobranchs gastropods, and polychaetes along the south coast (Awad et al., 2002). In their study, they (Awad et al., 2002), attributed the geographical location of the south coast further away from political boundaries and to some extent sampling bias as some of the leading causes behind these high endemicity patterns observed. There are also invasive species that possess the traits required to colonise and survive in a broad range of habitats. This means both groups of species already possess the basic traits which allow them to persist in either specific habitats or broad habitat ranges.

2.7.5.1. Body size

Although the RLQ analysis suggested that different size classes were associated with specific bioregions, such as larger species on the west than the east coast, a test of random assembly showed no significant correlation between overall adult size and bioregion. This is contrary to the findings of Roy et al. (2001), who considered body size to be amongst the top biological factors that may influence species distribution patterns. It is assumed that a select number of species with larger bodies will spread faster in contrast to smaller-sized ones, presumably because of the correlation with body size and the ability of adults to disperse efficiently. However, these size/region correlations are not to be generalised for all species (Scott et al., 2012). In my study, larger body sizes showed no correlation with either temperature or chl-*a*, despite the widespread understanding that the west coast supports low diversity, but high biomass in comparison to the east coast. A possible reason why few developmental traits were affected by either temperature or chl-*a* is associated with the evolutionary strategies developed by species to cope with intertidal conditions, which, as the interface between land and sea, are notoriously stressful. Thus, because body temperature is often a strong correlate of fitness (Huey & Berrigan, 2001), organisms have evolved various strategies for regulating their body temperatures. Following periods of thermal stress associated with tropical and temperate shores worldwide, limpet mortality has been reported (Garrity, 1981; Williams et al., 2005). Therefore, to cope with the high temperatures experienced during low tide, limpets have evolved various behavioural, physiological, and morphological strategies explained below.

2.7.5.2. Adaptive morphology and physiology

For most gastropods, maintaining shore position and mobility requires keeping the foot in adhesive contact with the substratum (Smith & Morin, 2002). However, in addition to serving as an adhesive appendage, the foot also forms a large conductive surface between the substratum and the snail's body, tending to bring the two closer to the same temperature, a potentially harmful situation on hot days (Denny & Harley, 2006). Other morphological adaptations that have been recorded for gastropods to lower body temperature on hot days are (i) high-spired shells and (ii) architectural features such as bumps and ridges (Vermeij, 1973). It is evident that both these mechanisms operate, but only one offers some protection from extreme body temperatures and, in some cases, predation. For example, in South Africa, during microcosm experiments, clingfish were observed to select smoother-shelled limpet species (Lechanteur & Prochazka, 2001). This highlights some evolutionary mechanisms that species have adopted to cope with various and often stressful physical habitat conditions. Limpets may also lift the shell and portions of the foot away from the substratum, reducing the contact area of the foot and increasing the area available for evaporative cooling (Williams et al., 2005). In Hong Kong, *Cellana grata* migrates up to one vertical meter with the advance and retreat of the tide, thus remaining within the swash zone for a greater proportion of the day (Williams & Morritt, 1995). Also, from field observations, many limpets tend to occupy crevices and vertical substrata, which remain cooler than flat, gently sloping surfaces. In some instances, when stranded at low tide in an unfavourable thermal microhabitat, some limpets will ‘mushroom’ by raising the margin of their shell off the substratum and exposing their soft tissues to the air. This behaviour is thought to be an emergency attempt at evaporative cooling.

On the other hand, my results corroborated those of Branch & Steffani (2004), that the west coast supports high densities and biomasses of two large limpets (i.e., shell length sizes of >70mm) *Cymbula granatina* and *Scutellastra argenvillei*. These large species of limpets inhibit recruitment of other species, probably by bulldozing them off the rock face leading to notable consequences on the presence and diversity of other species. This could be a size advantage trade-off, i.e., high *per capita* investment in offspring reproduction while forgoing high abundances. Of note, this low species richness is one of the community properties leading to empty niches, and this is suggested as a plausible reason for the increase in invasion by fast-growing non-native species (Mack et al., 2000) within the west coast.

Numerous authors have also pointed out that littorinid snails, as a group, have gone the furthest towards reducing contact with the substratum. Rocky shore, estuarine, and mangrove species of littorinids around the world glue the lip of the shell to the substratum and withdraw the foot into the shell, sealing the opening of the shell with the horny operculum (Miller, 2008). This behaviour minimises desiccation (McMahon, 1990) and can lower body temperature by reducing body contact with the hot substratum (McQuaid & Scherman, 1988). The snails typically do not re-emerge from the shell until they have been wetted by water, which usually produces a vigorous extension of the foot and quick contact between the foot and the substratum.

In summary, all these examples seek to highlight how different species have adapted to various morphological, behavioural, and physiological traits to cope with abiotic stresses, particularly temperature. All the mentioned strategies evolve over a long time, thus causing these intertidal species to be eurythermal. These findings may also mean that water temperature and chl-*a* may not have significant or observable interspecific trait changes that can be observed within the scope of this study. Therefore, I would recommend the analysis of intra-trait variability among species.

2.8. A brief evaluation of other trait domains

Verberk et al. (2008) listed four main trait domains. Two of them were adopted in this study, the other two being dispersal and synchronisation. These two domains were not actively considered because the traits that fit within them are highly redundant with the other two trait domains already considered in this study. However, I briefly explain their relevance in this study and highlight their linkages to the reproductive and development trait domains already considered here.

2.8.1. Dispersal trait strategies

Dispersal plays an important role in marine biogeography, meaning no organism could occupy an extensive geographic range without some dispersal mechanism. However, the eventual size of a geographic range may often be more strongly mediated by a suite of other factors (Gaston, 2003), perhaps operating at much larger spatial and temporal scales than the average dispersal distance.

2.8.1.1. Strategy D1: Short development time and strong dispersal

Species possessing this strategy invest in rapid development and high dispersal. This constrains body size and reproductive capacity. To circumvent this trade-off, species have long-lived adults and high *per capita* investment. This trade-off can be observed in some false limpets such as *Siphonaria capensis*. Other species within this strategy (excluding the trade-off) include the invasive barnacle, *Balanus glandula*, on the south-west overlap and west coasts of South Africa.

2.8.1.2. Strategy D2: Large clutch size and strong dispersal

Species with this strategy have large clutch sizes and strong dispersal. Many eggs mean low *per capita* investment and low investment in adult longevity. Within this strategy, Verberk et al. (2008) highlighted that in fresh-water habitats there is often a trade-off between low adult longevity and high dispersal which is suspected to lead to challenges associated with a low density, such as finding a mate. However, within the intertidal ecosystem, invasive species like *Mytilus galloprovincialis*, do not exhibit this trade-off or rather are not hindered by this trade-off as they occur at high densities and don't have to search for mates because they have external fertilisation. The dispersal and effects of invasion by *M. galloprovincialis* have been widely studied (Robinson et al., 2007; Zardi et al., 2008; Ma et al., 2021). Studies have revealed that mussel larvae are dispersed like passive particles matching the speed and direction of surface currents generated by wind. Wind-driven dispersal of larvae is thus held to be responsible for the spread of *M. galloprovincialis* (McQuaid & Philips, 2000; Branch & Steffani, 2004).

There are other interactions pertaining to dispersal including concepts of dispersal and larval supply addressed by hypotheses concerning pre-recruitment and post-recruitment effects that could not be investigated in this study. Some common species which conform to the predictions of these hypotheses include barnacles (which were amongst the highest in abundance and biomass in this study). Boland (1997) showed that, bioregion had a significant effect on the abundances of barnacle species, with *Octomeris angulosa* and *Tetraclita serrata* occurring at higher abundances on the south coast than the west coast where the barnacle *Balanus glandula* is most abundant. Some of the reasons ascribed to this occurrence include pre-recruitment (abundance of larvae, settlers, and juveniles) and post-recruitment (abundance of larger organisms that compete for space) due to environmental stressors such as wind direction. More recent theoretical and empirical work also found that larval duration in the water column increases with decreasing temperature (O'Connor et al., 2007; McClain et al., 2014). Therefore, because all 3 barnacles have a pelagic larval stage, this extended period in the water column may increase its vulnerability to predation, subsequently lowering its successful recruitment on the cold west coast. For *B. glandula*, one spin-off that makes the species persistent is possibly directly due to the fact that it has successfully colonised this colder system.

In addition, along the west coast, low pre-recruitment is not surprising given the persistent upwelling on the west coast, perhaps making it difficult for barnacle larvae to return to shore. There are also fish within the kelp forests that prey on barnacle larvae. On the other hand, post-recruitment can be affected by smothering by intertidal algae, kelp wrack, thermal stress, and predation by large limpets on the west coast (Boland, 1997b). The pre-recruitment hypothesis can explain the west and south coast anomalies within barnacle densities (Boland, 1997a), except for

Balanus glandula. Larval supply has been used to explain patterns of adult abundances in other areas (Raimondi, 1990) and is thought to affect the coastline of South Africa as well. Because most intertidal species depend on nearshore hydrographic conditions and have pelagic larval stages, the functional traits and interspecific interactions that possibly influence pre-recruitment and post-settlement survival strategies may be worth testing at the community level while comparing larval densities.

2.8.1.3. Strategy D3: Early age at first reproduction and strong dispersal

Species possessing the D3 strategy have strong dispersal and a high intrinsic increase primarily achieved through multivoltinism or continuous reproduction rather than a large clutch size. Rapid juvenile development is a spin-off achieved at the cost of reduced body size, adult longevity, and reproduction investment. Rapid development and low adult longevity decrease the age at first reproduction. Species in this strategy may exhibit poor synchronisation in breeding. Common species with this strategy include barnacles including *Chthamalus dentatus, Balanus glandula,* and amphipods such as *Jassa spp.* Although amphipods lack a larval stage, their dispersal could be limited compared with taxa possessing planktonic larvae (Franz & Mohamed, 1989). Nevertheless, many marine invertebrates with direct development have a wide geographical distribution due to what is termed rafting (Castilla & Guiňez, 2000; Thiel, 2003). Rafting (by seaweed, e.g., kelp) is an alternative dispersal mechanism potentially available for species without or with reduced larval development time, which has been proposed as more effective (l00s to 1,000s of km) than planktonic larval development (Johannesson, 1988).

2.8.2. Synchronisation trait strategies

Synchronisation strategies encompass reproductive timing, development, and dispersal mechanisms to achieve maximum population persistence. The strategies in this domain include S1, which entails 'slow growth and synchronised emergence', S2, i.e., short growth period and resistant stages', S3: short synchronised juvenile development time, and S4: high per capita investment with no dispersal. I found S1, S2, and S3 not particularly relevant for intertidal species. Thus, I briefly explain strategy S4 in relation to my study species.

2.8.2.1. Strategy S4: High per capita investment, no active flight

Species with this strategy have limited dispersal capabilities, increasing the importance of local persistence. In the marine environment, these species include the large limpets, which are mostly direct developers. These species include *Cymbula granatina*, *Scutellastra granularis, Siphonaria serrata,* and *Scutellastra longicosta* are gonochoristic and spawn once annually. Around Cape Point, *S.*

granularis and *Cymbula granatina* spawn in the summer, while *S. longicosta* spawns in the winter. More specifically, synchronised development has also been observed from the south coast populations of *S. granularis*, where gametogenic activity has coincidentally increased at the same time that microalgal biomass on intertidal rocks increased (Vat, 2000).

2.9. Trait plasticity and other influences on community assemblages and distribution patterns

One aspect that cannot be ignored in trait-based approaches is plasticity. Phenotypic plasticity is a common response of organisms to environmental variation and an important source of diversity within and across populations (Hirsch et al., 2014). This is one of the challenges in trait-based approaches that the fuzzy coding system used in this study seeks to address. However, some of this plasticity is still difficult to incorporate when the plasticity is externally driven. This includes predator-induced morphological plasticity observed in blue mussels (*Mytilus edulis*) (Reimer & Tedengren, 1996; Reimer & Harms-Ringdahl, 2001). These mussels are more sensitive to predators particularly shore crabs (*Carcinus maenas*) and sea stars (*Asterias rubens*) and when food is scarce. Mussels sense their predators in at least two ways, according to a study on zebra mussels, a freshwater species (Hirsch et al., 2014). One way is by smelling the presence of the predators (olfactory stimuli through water-borne scents); these cues are called kairomones. The other way is by sensing alarm cues from attacked conspecifics, and then they develop inducible defences such as reducing their filtration activity through valve closure (Reimer et al., 1995). It has been shown that blue mussels accelerate their gonad development and/or increase their reproductive effort in the presence of predators (Reimer, 1999).

For suspension feeders, trait plasticity is in the form of the use of a wide variety of methods to capture food items from the fluid in which they live. In many cases, some form of filter, net, or sieve-like structure is employed to intercept particles as they pass by the organism, such as the baleen of whales (Sanderson & Wassersug, 1993), gill rakers in fish (Lauder, 1983), modified mouthparts of invertebrates (Zhang, 2006), or other modified body parts such as legs and tube feet (LaBarbera, 1978). Trapping food particles in flowing water can place unique constraints on the form and function of feeding structures in suspension feeders. The size and form of the filtering apparatus must balance particle capture efficiency against mechanical constraints such as the drag created by fluids passing through and around the filter (Cheer & Koehl, 1987). While many suspension feeders (e.g., filter-feeding vertebrates, or animals that actively pump water: Lauder, 1983; Sanderson & Wassersug, 1993) dictate the rate of flow through their feeding apparatus, the subset of suspension feeders that extend the feeding apparatus into flowing fluids is somewhat at the mercy of the surrounding flow conditions.

Phenotypic plasticity can also result as a response to wave exposure (Kaandorp, 1999; Okamura & Partridge, 1999; Marchinko, 2003; von Dassow, 2005). For instance, barnacle cirral morphology varies plastically among habitats along a flow-speed gradient and has been correlated with maximum flow speeds experienced at sites over several weeks (Marchinko & Palmer, 2003; Chan & Hung, 2005). Barnacles growing in wave-protected waters grow longer, thinner cirri than conspecifics growing at wave-exposed sites, and these cirral traits can be altered between moults in response to changing flow patterns (Marchinko, 2003), leading to the structure of the cirri hypothesis. Li & Denny (2004) found a correlation between cirral morphology and maximum water velocity. In laboratory experiments, Field & McFarlane (1968) found that *Octomeris angulosa* and *Tetraclita serrata* protruded their cirri at different current speeds, with *O. angulosa* feeding at high current speeds while *Tetraclita serrata* feeding at low speeds. From this study and others (see Branch & Branch, 1981), it was therefore concluded that *T. serrata* has a more fragile cirrus and therefore may struggle to survive in areas of strong currents and wave action. Arsenault et al. (2001) found that leg length of the barnacle *B. glandula* declines with increasing wave exposure.

Along the west and south coasts of South Africa, the two most abundant barnacle species in the intertidal zone are *Octomeris angulosa* and *Tetraclita serrata*. These two species have similar vertical ranges but appear to be segregated along a horizontal gradient of wave exposure (Branch & Branch, 1981; Delafontaine & Flemming, 1989). The relative abundances of *T. serrata* and *O. angulosa* were expected to vary in space and time according to changes in wave action and temperatures during the low tides (Boland, 1997a). However, it is assumed that barnacles have adapted morphologically to facilitate conductive heat exchange adaptations by having a roughly conical shape and having large areas of attachment to the substratum. *O. angulosa* forms a single-layered matrix in which individuals are interlocked and cemented together. Each individual is firmly glued to the substratum and its neighbours, thereby making a matrix structure resistant to wave damage. *O. angulosa* individuals are long-lived, and spaces in the matrix are rare. When there is a space present, larvae recruit to the base of the animals on the perimeter of the space and shore-up the exposed adults. On the other hand, *T. serrata* has several characteristics that allow it to withstand severe heat-loading and desiccation stress. For example, the small aperture may increase the amount of extra-viscera water for evaporative cooling (Suzuki & Mori, 1963), decrease water loss (Achituv & Borut, 1975), while the thick walls and ribbing on the shell is all thought to work together in reducing heat-loading (Newell, 1976).

Lastly, another important factor which can have dramatic effects on the intertidal landscape affecting east coast littoral communities is the human exploitation of fish, invertebrates and macroalgae. This continuous removal of the large gastropods by locals has undoubtedly altered the intensity of predation across the region, but its consequences on regional patterns of the landscape still need to be assessed through experimental manipulations.

In conclusion, as alluded to earlier, although species behavioural traits and persistence interact with the environment, more on these interactions go beyond the scope of this study, including the effects of prevailing winds, current direction, an abundance of predators that threaten larval stages in the water column and predators on the shore where the adults attach. These lead to varying spin-offs and trade-offs among various species. Therefore, co-occurring species within a habitat are not expected to belong to the same life-history strategy, or conversely, not all species with the same life-history strategy are limited to the same habitat.

2.10. Conclusion

Some prominent trait–environment relationships were evident in macroinvertebrate assemblages around the coast of South Africa. The trait-based approach revealed some linkages between species traits and the environment and their trade-offs and spin-offs. Past research along the coastline of South Africa suggests that one of the critical biological drivers of species distribution patterns is life-history patterns, which is represented by reproduction strategies in this study. The combined fourth corner method results showed reproduction traits as more responsive to temperature and chlorophyll-*a* gradients ($p<0.05$) than developmental traits. Although the combined fourth-corner analysis showed how single trait modalities responded to the environment, partitioning the traits into suites or trait domains following Verberk et al. (2008) condensed the trait information into more meaningful strata, and this approach may therefore constitute a promising tool for explaining differences in species assemblages between locations or time periods. This is because the use of trait suites or domains increases the signal-to-noise ratio, often reducing very complex, biodiverse assemblages into a few meaningful, easily interpretable relationships. My results corroborate the importance of considering multiple rather than single traits when linking macroinvertebrates to environmental variables, including the potential information conveyed by evolutionary history. This multiple-species approach highlights the utility of comparing results from species with differing ecological characteristics so as to formulate hypotheses about underlying mechanisms when the large-scale nature of the study precludes an experimental approach. As such, it may have wide applications ranging from fundamental to applied ecological research, including biomonitoring.

In conclusion, the major breaks in trait distribution coincided with the oceanographic regimes of the two large marine ecosystems or LMEs (i.e., the Agulhas Current on the east and south and the

Benguela Current on the west) dominating the coast of South Africa. These LMEs are predominantly associated with the observed changes in temperature and nutrients in this study measured through chl-*a* patterns. For chl-*a*, the coast was primarily separated into three regions: (i) the east coast, (ii) the SEO, south and SWO and (iii) west coast with the east coast significantly different from all other bioregions. On the other hand, the SST showed major breaks, i.e., the east and SEO *vs* the south, SWO and west bioregions. Looking at the premise of the habitat templet theory, the influence of the chl-*a* gradient was clear across all trait analyses and across the 7-year time period considered in this study. On one hand, the results confirm that the habitat, particularly the biotic filter (in this case chl-*a* used as a proxy for food availability) provides a templet upon which evolution forges species traits. On the other hand, since temperature is a proxy for nutrient availability (where cold upwelling brings nutrients), then temperature drives chlorophyll-*a* and this subsequently means the abiotic component indirectly drives trait distribution through its influence on the biotic environment (chlorophyll-*a*).

2.11. Supplementary Information

2.11.1 Fuzzy coded trait information

Table S2.1.1. Fuzzy-coded development traits for macroinvertebrates

Species Code	Species name	t1.1	t1.2	t1.3	t1.4	t1.5	t2.1	t2.2	t2.3	t2.4	t2.5	t3.1	t3.2	t3.3	t3.4	t3.5	t4.1	t4.2	t4.3	t4.4	t4.5	t5.1	t5.2	t5.3
sp1	*Perna perna*	3	0	0	0	0	0	0	0	3	3	3	0	0	0	0	0	3	2	0	0	0	0	3
sp2	*Choromytilus meridionalis*	3	0	0	0	0	0	0	0	3	3	3	0	0	0	0	2	3	0	0	0	0	0	3
sp3	*Mytilus galloprovincialis*	3	0	0	0	0	0	0	3	0	0	3	0	0	0	0	0	2	2	0	0	0	0	3
sp4	*Aulacomya atra*	3	0	0	0	0	0	0	0	3	0	3	0	0	0	0	3	2	1	0	0	0	0	3
sp5	*Semimytilus patagonicus*	3	0	0	0	0	0	0	1	3	1	3	0	0	0	0	0	3	0	0	0	0	3	1
sp6	*Gregariella petagnae*	3	0	0	0	0	0	3	0	0	0	3	0	0	0	0	3	3	2	0	0	0	3	1
sp7	*Modiolus auriculatus*	3	0	0	0	0	0	2	3	0	0	3	0	0	0	0	3	3	0	0	0	0	3	1
sp8	*Brachidontes variabilis*	3	0	0	0	0	0	3	0	0	0	3	0	0	0	0	3	1	0	0	0	0	3	1
sp9	*Striarca symmetrica*	3	0	0	0	0	0	3	1	0	0	3	0	0	0	0	3	2	0	0	0	0	3	1
sp10	*Barbatia obliquata*	3	0	0	0	0	0	3	1	0	0	3	0	0	0	0	3	2	0	0	0	0	3	1
sp11	*Zoanthus natalensis*	3	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	3	0	0	2	3	0	0
sp12	*Zoanthus durbanensis*	3	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	3	0	0	2	3	0	0
sp13	*Palythoa natalensis*	3	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	3	0	0	2	3	0	0
sp14	*Echinometra mathaei*	0	3	2	1	0	0	0	0	3	0	0	1	3	0	3	0	3	0	0	3	0	0	3
sp15	*Parvulastra dyscrita*	0	3	2	0	0	0	3	0	0	0	0	3	2	0	0	3	1	0	0	0	3	0	0
sp16	*Helcion concolor*	0	3	0	0	0	0	0	3	0	0	0	3	2	0	0	0	0	3	0	0	0	3	1
sp17	*Helcion pectunculus*	0	3	0	0	0	0	0	3	0	0	0	3	2	0	0	0	0	0	3	0	0	3	1
sp18	*Helcion dunkeri*	0	3	0	0	0	0	3	0	0	0	0	3	2	0	0	0	3	0	0	0	0	3	1
sp19	*Octomeris angulosa*	3	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	2	3	2	0	0	0	3
sp20	*Scutellastra obtecta*	0	3	0	0	0	0	0	3	0	0	0	3	1	0	0	0	0	3	2	0	0	0	3
sp21	*Scutellastra granularis*	0	3	0	0	0	0	0	0	3	0	0	3	1	0	0	0	0	2	3	0	0	0	3
sp22	*Oxystele antoni*	0	3	0	0	0	3	2	0	0	0	0	0	3	0	0	2	3	1	1	0	0	0	3
sp23	*Saccostrea cuccullata*	3	0	0	0	0	0	0	0	1	1	3	0	0	0	0	0	0	2	3	0	0	0	3
sp24	*Tetraclita serrata*	3	0	0	0	0	0	0	1	3	3	3	0	0	0	0	0	0	3	1	0	0	0	3
sp25	*Tetraclita squamosa*	3	0	0	0	0	0	0	0	3	3	3	0	0	0	0	0	0	3	2	0	0	0	3
sp26	*Chthamalus dentatus*	3	0	0	0	0	3	0	0	0	0	3	0	0	0	0	0	0	0	3	0	0	3	0
sp27	*Nucella sp 1*	0	0	0	3	0	0	3	0	0	0	0	0	3	0	1	0	0	3	2	0	0	3	2
sp28	*Cellana capensis*	0	3	0	0	0	0	0	3	0	0	0	3	2	0	0	0	0	3	0	0	0	3	2
sp29	*Roweia frauenfeldi frauenfeldi*	0	0	0	3	1	0	0	3	0	0	0	0	0	3	0	0	3	0	0	0	3	0	0
sp30	*Bunodactis reynaudi*	0	1	1	3	0	0	0	0	3	1	3	0	0	0	0	0	3	0	0	3	3	0	0

Species Code	Species name	t1.1	t1.2	t1.3	t1.4	t1.5	t2.1	t2.2	t2.3	t2.4	t2.5	t3.1	t3.2	t3.3	t3.4	t3.5	t4.1	t4.2	t4.3	t4.4	t4.5	t5.1	t5.2	t5.3
sp31	*Parechinus angulosus*	0	3	0	0	0	0	3	3	3	0	0	0	3	0	3	2	2	2	0	3	0	0	3
sp32	*Crepidula sp 1*	0	2	2	0	0	0	0	3	3	0	0	3	0	0	0	0	0	3	0	0	0	0	0
sp33	*Eoacmaea albonotata*	0	3	0	0	0	3	0	0	0	0	0	3	2	0	0	0	0	1	3	0	0	3	1
sp34	*Siphonaria serrata*	0	3	0	0	0	0	3	0	0	0	0	3	2	0	0	0	0	3	0	0	0	3	1
sp35	*Scutellastra longicosta*	0	3	0	0	0	0	0	0	3	0	0	3	1	0	0	0	2	3	0	0	0	3	1
sp36	*Scutellastra cochlear*	0	3	0	0	0	0	0	0	3	0	0	3	1	0	0	3	2	0	0	0	0	0	3
sp37	*Austramegabalanus cylindricus*	3	0	0	0	0	0	0	0	3	3	3	0	0	0	0	3	0	0	0	0	0	0	3
sp38	*Burnupena lagenaria*	0	0	0	0	3	0	0	3	0	0	0	0	3	0	1	2	3	2	0	0	0	0	3
sp39	*Scutellastra sp*	0	3	0	0	0	1	3	0	0	0	0	3	1	0	0	0	0	2	3	0	0	1	3
sp40	*Pseudonereis podocirra*	0	2	1	3	0	0	0	0	3	0	0	0	2	1	3	2	3	1	0	0	0	0	0
sp41	*Platynereis dumerilii*	0	3	0	0	0	0	2	2	0	0	1	0	0	1	3	2	3	1	0	0	3	0	0
sp42	*Perinereis vallata*	0	1	0	2	2	0	0	0	1	3	1	0	0	1	3	2	3	1	0	0	3	0	0
sp43	*Actinia ebhayiensis*	1	0	1	3	1	0	3	0	0	0	3	0	0	0	0	0	0	3	2	0	3	0	0
sp44	*Cymbula compressa*	0	3	0	0	0	0	0	0	0	3	0	3	2	0	0	0	3	0	0	0	0	3	1
sp45	*Urothoe grimaldii*	0	1	3	2	0	3	0	0	0	0	0	0	3	1	2	0	2	2	2	0	3	0	0
sp46	*Ischnochiton oniscus*	0	3	2	1	0	0	3	1	0	0	0	3	2	0	0	0	2	2	1	0	3	0	0
sp47	*Onithochiton literatus*	0	3	0	0	0	0	3	1	0	0	0	3	2	0	0	0	2	2	1	0	0	0	0
sp48	*Ischnochiton bergoti*	0	3	0	0	0	0	3	1	0	0	0	3	2	0	0	0	2	2	1	0	3	0	0
sp49	*Acanthochitona garnoti*	0	3	0	0	0	0	3	1	0	0	0	3	2	0	0	0	2	2	1	0	3	0	0
sp50	*Cymbula miniata*	0	3	0	0	0	0	0	0	0	3	0	3	2	0	0	2	2	0	0	0	0	3	1
sp51	*Siphonaria sp 1*	0	3	0	0	0	0	3	0	0	0	0	3	2	0	0	0	0	3	0	0	0	0	0
sp52	*Scutellastra natalensis*	0	3	0	0	0	0	3	0	0	0	0	3	2	0	0	0	0	2	3	0	0	3	1
sp53	*Sipunculida sp*	0	0	3	0	0	0	0	0	3	0	1	0	0	0	3	0	2	2	2	0	3	0	1
sp54	*Scutellastra argenvillei*	0	3	0	0	0	0	0	0	0	3	0	3	1	0	0	1	3	0	0	0	0	0	3
sp55	*Siphonaria capensis*	0	3	0	0	0	0	3	0	0	0	0	3	2	0	0	0	0	3	1	0	0	3	1
sp56	*Gunnarea gaimardi*	3	1	2	1	0	0	0	0	3	0	0	0	2	1	3	0	3	2	0	0	3	0	1
sp57	*Sedentaria spp*	3	1	2	1	0	0	0	0	3	0	0	0	2	0	3	0	3	2	0	0	3	0	1
sp58	*Siphonaria anneae*	0	3	0	0	0	0	3	3	0	0	0	3	2	0	0	0	0	3	2	0	0	3	1
sp59	*Cymbula oculus*	0	3	0	0	0	0	0	0	0	3	0	3	2	0	0	0	0	3	0	0	0	0	3
sp60	*Tetralia cymodose*	0	0	0	0	0	0	3	0	0	0	0	0	3	0	3	0	2	2	0	0	0	3	0

Species Code	Species name	t1.1	t1.2	t1.3	t1.4	t1.5	t2.1	t2.2	t2.3	t2.4	t2.5	t3.1	t3.2	t3.3	t3.4	t3.5	t4.1	t4.2	t4.3	t4.4	t4.5	t5.1	t5.2	t5.3
sp61	*Siphonaria concinna*	0	3	0	0	0	0	3	3	0	0	0	3	2	0	0	0	0	3	0	0	0	3	1
sp62	*Scutellastra exusta*	0	3	0	0	0	0	0	3	0	0	0	3	1	0	0	0	2	3	0	0	0	3	1
sp63	*Afrolittorina knysnaensis*	0	3	0	1	0	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	0	3	0
sp64	*Oxystele tigrina*	0	3	0	0	0	0	3	0	0	0	0	0	3	0	0	1	3	0	0	0	0	1	3
sp65	*Fissurella natalensis*	0	3	0	0	0	0	1	3	0	0	0	3	2	0	0	2	3	0	0	0	0	3	1
sp66	*Parvulastra exigua*	0	3	2	0	0	0	3	0	0	0	0	3	3	0	1	1	3	1	0	0	3	0	0
sp67	*Siphonaria oculus*	0	3	0	0	0	0	3	1	0	0	0	3	2	0	0	0	0	3	0	0	0	3	1
sp68	*Scutellastra barbara*	0	3	0	0	0	0	0	0	3	3	0	3	1	0	0	2	3	0	0	0	0	0	3
sp69	*Cymbula granatina*	0	3	0	0	0	0	0	0	0	3	0	3	2	0	0	0	0	3	0	0	0	0	3
sp70	*Burnupena pubescens*	0	0	0	3	0	0	0	3	0	0	0	0	3	0	1	3	0	0	0	0	0	1	3
sp71	*Scutellastra aphanes*	0	3	0	0	0	0	0	3	0	0	0	3	1	0	0	0	3	0	0	0	0	1	3
sp72	*Gibbula multicolor*	0	3	0	1	0	0	0	0	0	0	0	0	3	0	1	3	1	0	0	0	0	1	3
sp73	*Nucella squamosa*	0	0	0	3	0	0	3	1	0	0	0	0	3	0	1	2	2	0	0	0	0	0	3
sp74	*Vaughtia fenestrata*	0	0	0	3	0	0	0	3	0	0	0	0	3	0	1	0	2	2	0	0	0	1	3
sp75	*Siphonaria carbo*	0	3	0	0	0	0	3	0	0	0	0	3	2	0	0	0	0	1	3	0	0	1	3
sp76	*Oxystele sinensis*	0	3	0	0	0	0	0	3	0	0	0	0	3	0	0	1	3	0	0	0	0	1	3
sp77	*Botryllus sp*	3	0	0	0	0	0	3	0	0	0	3	0	0	0	0	3	0	0	0	0	0	0	3
sp78	*Isaurus tuberculatus*	3	0	0	0	0	3	0	0	0	0	3	0	0	0	0	3	0	0	0	0	3	0	0
sp79	*Fissurella mutabilis*	0	3	0	0	0	0	3	0	0	0	0	3	0	0	0	0	3	2	0	0	0	1	3
sp80	*Helcion pruinosus*	0	3	0	0	0	0	3	0	0	0	0	3	0	0	0	0	3	0	0	0	0	1	3
sp81	*Arenicola loveni*	0	0	3	0	1	0	0	0	0	3	0	0	0	0	3	2	2	1	1	0	3	0	0
sp82	*Ischyromene huttoni*	0	3	0	1	0	3	0	0	0	0	0	0	3	1	1	2	0	0	0	3	3	0	0
sp83	*Ischyromene ovalis*	0	3	0	1	0	3	0	0	0	0	0	0	3	1	1	2	0	0	0	3	3	0	0
sp84	*Listriolobus capensis*	0	0	3	0	0	0	1	3	0	0	0	3	0	1	2	0	0	0	0	2	3	0	0
sp85	*Dardanus arrosor*	0	0	0	2	3	0	0	0	2	2	0	0	3	0	0	1	1	1	1	3	2	2	0
sp86	*Nucella dubia*	0	0	0	2	2	0	3	0	0	0	0	0	3	0	0	0	1	3	2	0	0	1	3
sp87	*Parisocladus perforatus*	3	0	0	0	0	3	0	0	0	0	0	0	3	1	1	0	2	2	0	0	3	0	0
sp88	*Marphysa haemasona*	0	0	0	0	0	0	0	0	0	3	0	0	1	0	3	3	2	0	0	0	3	0	0
sp89	*Afrocominella capensis simoniana*	0	0	0	3	0	0	0	3	0	0	0	0	3	0	0	3	2	1	0	0	0	0	3
sp90	*Diodora crucifera*	0	3	0	0	0	0	3	0	0	0	0	3	1	0	0	0	3	0	0	0	0	0	3

Species Code	Species name	t1.1	t1.2	t1.3	t1.4	t1.5	t2.1	t2.2	t2.3	t2.4	t2.5	t3.1	t3.2	t3.3	t3.4	t3.5	t4.1	t4.2	t4.3	t4.4	t4.5	t5.1	t5.2	t5.3
sp91	*Burnupena cincta*	0	0	0	1	3	0	0	3	0	0	0	0	3	0	0	3	3	0	0	0	0	0	3
sp92	*Dendrofissurella scutellum*	0	3	0	0	0	0	0	3	0	0	0	3	1	0	0	3	2	0	0	0	0	0	3
sp93	*Scutellastra tabularis*	0	3	0	0	0	0	0	0	0	3	0	3	1	0	0	3	2	0	0	0	0	0	3
sp94	*Oxystele impervia*	0	3	0	0	0	3	2	0	0	0	0	0	3	0	0	0	0	2	3	0	0	1	3
sp95	*Nephyts sp*	0	2	0	3	1	0	3	0	0	0	0	0	1	1	1	0	0	2	2	0	3	0	0
sp96	*Spirobranchus kraussii*	3	0	0	0	0	0	3	0	0	0	3	0	0	0	0	3	3	3	0	0	3	2	0
sp97	*Afropinnotheres dofleini*	0	1	3	0	0	3	0	0	0	0	0	0	0	0	3	2	2	0	0	2	3	0	0
sp98	*Rathbunixa occidentalis*	0	0	0	0	0	3	0	0	0	0	0	0	0	0	3	2	2	0	0	2	3	0	0
sp99	*Burnupena catarrhacta*	0	0	0	1	3	0	1	3	0	0	0	0	3	0	0	0	3	0	0	2	0	0	3
sp100	*Trochia cingulata*	0	0	0	1	3	0	0	3	0	0	0	0	3	0	0	0	3	3	0	0	0	0	3
sp101	*Crepidula porcellana*	2	2	0	0	0	0	2	2	0	0	0	3	0	0	0	0	3	0	0	0	0	2	1
sp102	*Striostrea margaritacea*	3	0	0	0	0	0	0	0	0	3	3	0	0	0	0	2	3	2	0	0	0	0	3
sp103	*Ostrea atherstonei*	3	0	0	0	0	0	0	0	0	3	3	0	0	0	0	2	3	2	0	0	0	0	3
sp104	*Burnupena papyracea*	0	0	0	1	3	0	0	3	0	0	0	0	3	0	0	3	0	0	0	0	0	0	3
sp105	*Ligia dilatata*	0	0	0	1	3	1	3	0	0	0	0	0	3	0	0	3	3	3	3	3	3	0	0
sp106	*Burnupena rotunda*	0	0	0	1	3	0	0	3	0	0	0	0	3	0	1	3	3	0	0	0	0	0	3
sp107	*Tetraclita rufotincta*	3	0	0	0	0	0	0	1	3	3	3	0	0	0	0	0	0	0	3	0	0	0	3
sp108	*Oxystele tabularis*	0	3	0	0	0	3	2	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	3
sp109	*Amphibalanus sp1*	3	0	0	0	0	0	0	1	3	3	3	0	0	0	0	0	3	0	0	0	0	0	3
sp110	*Mancinella capensis*	0	0	0	1	3	0	0	3	0	0	0	0	3	0	0	3	2	0	0	2	0	0	3
sp111	*Pyrene flava filmerae*	0	0	0	3	0	0	3	0	0	0	0	0	3	0	0	0	3	0	0	0	0	1	3
sp112	*Lysidice natalensis*	0	3	0	2	0	0	0	0	1	3	0	0	1	0	3	2	2	0	0	0	3	0	0
sp113	*Golfingia sp*	0	0	3	0	0	0	2	2	0	0	0	0	2	1	3	0	0	2	2	0	3	0	0
sp114	*Eunice aphroditois*	0	0	0	3	0	0	0	0	0	3	0	0	0	0	3	0	0	2	2	0	3	0	0
sp115	*Onchidium sp*	0	3	0	1	0	0	0	3	0	0	0	0	3	0	0	0	3	2	0	0	0	1	3
sp116	*Planocera gilchristi*	0	0	0	3	2	0	3	1	0	0	0	0	3	0	1	0	3	0	0	0	3	0	0
sp117	*Ochetostoma formosulum*	0	0	3	0	0	0	1	0	0	3	0	0	1	0	3	0	0	3	0	0	3	0	0
sp118	*Tenguella granulata*	0	0	0	3	0	0	3	0	0	0	0	0	3	0	0	2	2	2	2	0	0	0	3
sp119	*Eurythoe complanata*	0	1	1	2	3	0	0	0	0	3	0	0	0	0	3	0	0	2	2	0	3	0	0
sp120	*Glycera tridactyla*	0	0	0	3	2	0	0	0	0	3	0	0	1	1	1	0	0	2	2	0	3	0	0

Species Code	**Species name**	**t1.1**	**t1.2**	**t1.3**	**t1.4**	**t1.5**	**t2.1**	**t2.2**	**t2.3**	**t2.4**	**t2.5**	**t3.1**	**t3.2**	**t3.3**	**t3.4**	**t3.5**	**t4.1**	**t4.2**	**t4.3**	**t4.4**	**t4.5**	**t5.1**	**t5.2**	**t5.3**
sp121	*Charybdis sp*	0	0	0	3	0	0	0	0	0	3	0	0	1	3	1	1	1	1	1	3	3	0	0
sp122	*Parisocladus stimpsoni*	0	0	0	0	0	3	0	0	0	0	0	0	3	1	1	2	2	1	0	1	3	0	0
sp123	*Scutellastra miliaris*	0	3	0	0	0	0	0	0	0	3	0	2	2	0	0	0	0	1	3	0	0	3	1
sp124	*Littorina saxatilis*	0	3	0	0	0	3	1	0	0	0	0	0	3	0	0	0	0	0	3	0	3	1	0
sp125	*Cirolana venusticauda*	0	0	0	2	2	3	0	0	0	0	0	0	3	1	1	1	1	1	1	3	3	0	0
sp126	*Heliacus variegatus*	0	0	0	3	0	0	3	0	0	0	0	0	1	0	3	0	3	0	0	0	0	0	3
sp127	*Afrolittorina africana*	0	3	0	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	3	0	3	1	0
sp128	*Diodora parviforata*	0	3	0	0	0	0	3	0	0	0	0	3	0	0	0	0	3	0	0	0	0	0	3
sp129	*Gibbula cicer*	0	3	0	0	0	0	3	0	0	0	0	0	3	0	0	2	2	0	0	0	0	0	3
sp130	*Grapsus tenuicrustatus*	0	1	3	0	1	0	0	0	0	3	0	0	3	0	0	0	0	0	3	0	1	3	0
sp131	*Arabella iricolor*	0	0	0	3	0	0	0	0	0	3	0	0	3	1	1	0	0	2	2	0	3	0	0
sp132	*Tylothais savignyi*	0	0	0	3	0	3	0	0	0	0	0	0	3	0	0	3	3	0	0	0	0	0	3
sp133	*Neorhynchoplax bovis*	0	0	0	3	0	3	0	0	0	0	0	0	1	0	3	0	0	0	0	0	2	2	0
sp134	*Acanthonyx scutellatus*	0	0	0	3	2	0	3	0	0	0	0	0	0	3	2	0	0	0	0	0	2	2	0
sp135	*Thalamita admete*	0	0	0	3	1	0	0	3	0	0	0	0	0	3	1	1	1	1	1	3	2	2	0
sp136	*Syllidae sp*	0	2	2	3	2	3	0	0	0	0	0	0	2	2	3	3	3	0	0	0	3	0	0
sp137	*Clibanarius virescens*	1	0	0	0	3	0	3	0	0	0	0	0	3	0	0	0	0	2	2	3	2	2	0
sp138	*Balanus glandula*	3	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	0	2	3	0	2	2	1
sp139	*Radsia nigrovirescens*	0	3	0	1	0	0	3	0	0	0	0	2	2	0	3	0	0	0	0	0	2	2	0
sp140	*Rhyssoplax polita*	0	3	0	1	0	0	0	3	0	0	0	2	2	0	3	0	0	0	0	0	2	2	0
sp141	*Pupillaea aperta*	3	0	0	0	0	0	0	3	0	0	0	3	2	0	0	0	3	2	0	0	0	0	3
sp142	*Argobuccinum pustulosum*	0	0	0	3	0	0	0	0	0	3	0	0	3	0	0	0	0	3	0	0	0	0	3
sp143	*Cabestana africana*	0	0	0	3	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	3
sp144	*Nucella wahlbergi*	0	0	0	3	0	0	0	3	0	0	0	0	3	0	0	0	1	3	2	0	0	0	3
sp145	*Lugubrilaria lugubris*	0	0	0	3	0	0	3	1	0	0	0	0	3	0	0	0	0	3	1	0	0	0	3
sp146	*Thyone aurea*	0	0	0	3	0	0	3	0	0	0	0	0	3	0	0	1	3	2	0	3	3	0	0
sp147	*Cymbula sanguinans*	0	3	0	0	0	0	0	1	2	3	0	3	1	0	0	0	0	3	1	0	0	0	3
sp148	*Notocomplana erythrotaenia*	0	0	0	3	0	0	3	0	0	0	0	0	3	0	1	0	0	3	1	0	3	0	0
sp149	*Ischnochiton textilis*	0	3	0	1	0	0	2	2	0	0	0	3	2	0	0	0	2	2	1	0	3	0	0
sp150	*Amphibalanus venustus*	3	0	0	0	0	3	0	0	0	0	3	0	0	0	0	1	3	0	0	0	0	3	0

Table S2.1.2. Fuzzy coded for reproduction traits for macroinvertebrates

Species Code	Species name	t6.1	t6.2	t6.3	t6.4	t7.1	t7.2	t7.3	t7.4	t8.1	t8.2	t8.3	t9.1	t9.2	t9.3	t9.4	t9.5
sp1	*Perna perna*	1	3	2	0	0	3	0	0	0	3	0	0	3	0	0	0
sp2	*Choromytilus meridionalis*	1	3	0	0	0	3	0	0	0	3	0	0	3	0	0	0
sp3	*Mytilus galloprovincialis*	1	3	0	0	0	3	0	0	0	3	0	0	3	0	0	0
sp4	*Aulacomya atra*	1	3	0	0	0	3	0	0	0	3	0	0	3	0	0	0
sp5	*Semimytilus patagonicus*	0	0	3	0	0	0	0	3	0	3	0	0	3	0	0	0
sp6	*Gregariella petagnae*	0	0	3	0	0	3	1	0	0	3	0	0	3	0	0	0
sp7	*Modiolus auriculatus*	3	0	1	0	0	3	0	0	0	3	0	0	2	2	0	0
sp8	*Brachidontes variabilis*	1	3	0	0	0	1	3	0	0	3	0	0	3	0	0	0
sp9	*Striarca symmetrica*	1	3	0	0	0	0	3	0	0	3	0	0	3	0	0	0
sp10	*Barbatia obliquata*	0	0	0	0	0	0	3	0	0	3	0	0	3	0	0	0
sp11	*Zoanthus natalensis*	0	0	3	0	3	0	0	0	3	0	0	3	0	0	0	0
sp12	*Zoanthus durbanensis*	0	0	3	0	3	0	0	0	3	0	0	3	0	0	0	0
sp13	*Palythoa natalensis*	0	0	3	0	3	0	0	0	3	0	0	3	0	0	0	0
sp14	*Echinometra mathaei*	0	3	0	0	0	3	0	0	0	3	0	0	0	3	3	3
sp15	*Parvulastra dyscrita*	3	1	0	0	0	3	1	0	0	3	0	0	2	3	0	0
sp16	*Helcion concolor*	1	3	0	0	0	2	3	0	0	0	3	0	3	0	0	0
sp17	*Helcion pectunculus*	3	0	0	0	0	2	3	0	0	0	3	0	3	0	0	0
sp18	*Helcion dunkeri*	3	0	0	0	0	2	3	0	0	0	3	0	3	0	0	0
sp19	*Octomeris angulosa*	1	3	0	0	0	0	0	3	0	3	0	0	3	0	0	0
sp20	*Scutellastra obtecta*	1	3	0	0	0	3	2	0	3	0	0	0	3	0	0	0
sp21	*Scutellastra granularis*	1	3	0	0	0	3	0	0	3	0	0	0	3	0	0	0
sp22	*Oxystele antoni*	2	0	3	0	0	3	0	0	0	0	3	0	3	0	0	0
sp23	*Saccostrea cuccullata*	3	0	0	0	0	3	1	0	0	3	0	3	0	0	0	0
sp24	*Tetraclita serrata*	1	3	0	0	0	0	0	3	0	0	3	0	3	0	0	0
sp25	*Tetraclita squamosa*	1	3	0	0	0	1	0	3	0	3	0	0	3	0	0	0
sp26	*Chthamalus dentatus*	1	3	1	0	0	1	0	3	0	3	0	3	0	0	0	0
sp27	*Nucella sp 1*	0	3	1	0	0	3	0	0	3	0	0	0	3	0	0	0
sp28	*Cellana capensis*	3	1	0	0	0	3	0	0	0	0	3	0	3	0	0	0
sp29	*Roweia frauenfeldi frauenfeldi*	1	3	0	0	0	3	0	0	3	0	0	0	3	0	0	0
sp30	*Bunodactis reynaudi*	0	3	0	0	2	2	0	0	0	3	0	0	3	0	0	0

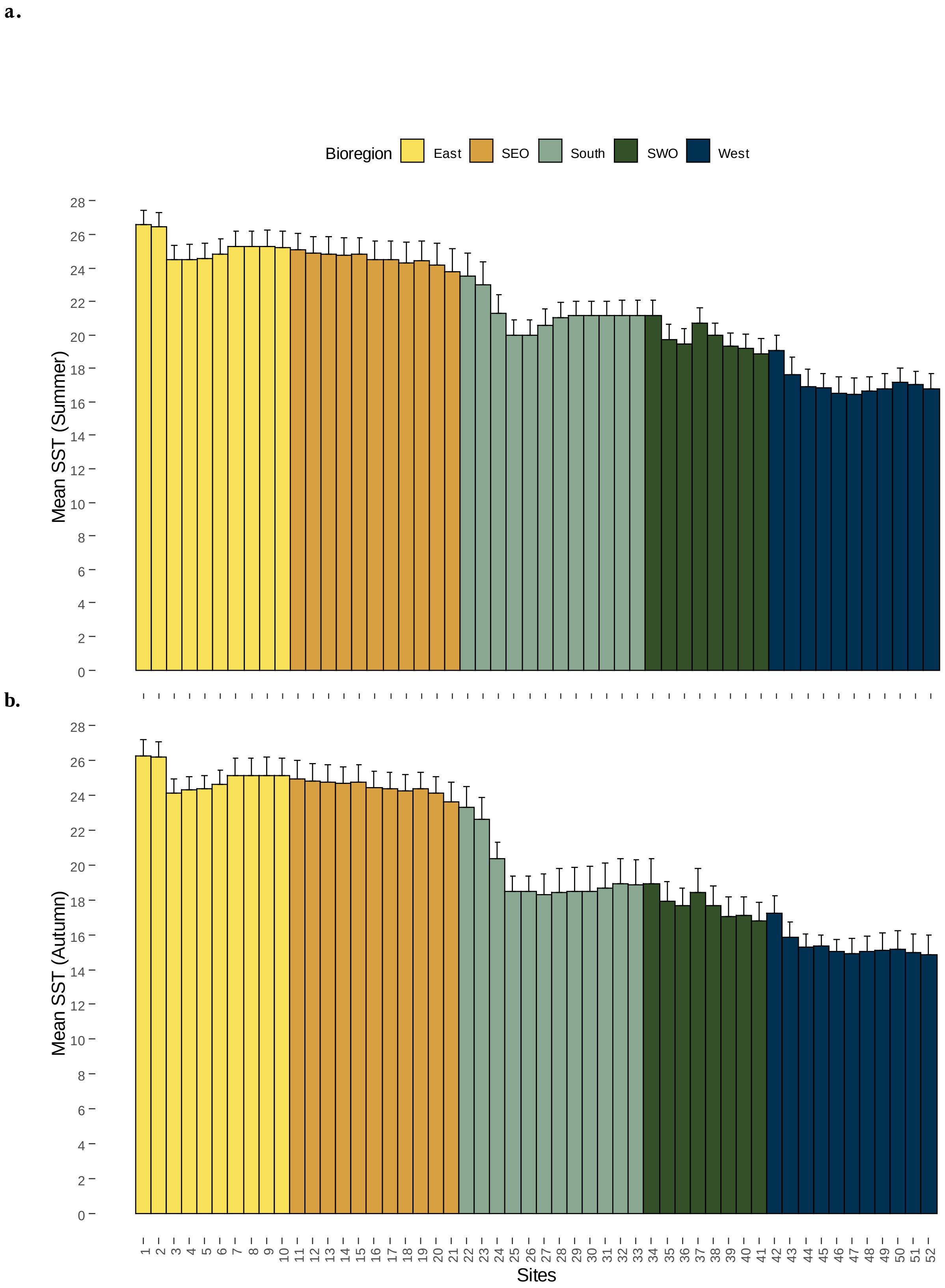
Species Code	**Species name**	**t6.1**	**t6.2**	**t6.3**	**t6.4**	**t7.1**	**t7.2**	**t7.3**	**t7.4**	**t8.1**	**t8.2**	**t8.3**	**t9.1**	**t9.2**	**t9.3**	**t9.4**	**t9.5**
sp31	*Parechinus angulosus*	1	3	0	0	0	3	0	0	0	0	3	0	3	0	0	0
sp32	*Crepidula sp 1*	0	3	0	0	0	0	3	0	0	3	0	0	3	0	0	0
sp33	*Eoacmaea albonotata*	2	3	0	0	0	0	3	0	0	3	0	3	2	0	0	0
sp34	*Siphonaria serrata*	1	3	1	0	0	3	0	3	3	0	0	0	3	0	0	0
sp35	*Scutellastra longicosta*	3	0	0	0	0	0	3	0	0	0	3	0	1	3	0	0
sp36	*Scutellastra cochlear*	3	0	0	0	0	0	3	0	0	0	3	0	0	3	1	1
sp37	*Austramegabalanus cylindricus*	1	3	0	0	0	0	0	3	0	3	0	0	3	0	0	0
sp38	*Burnupena lagenaria*	1	3	0	0	0	3	0	0	0	0	3	0	3	0	0	0
sp39	*Scutellastra sp*	3	0	0	0	0	0	3	0	0	3	0	0	3	0	0	0
sp40	*Pseudonereis podocirra*	0	0	3	0	0	3	0	0	0	3	0	0	0	3	0	0
sp41	*Platynereis dumerilii*	0	0	0	3	0	3	0	0	0	3	0	0	3	1	0	0
sp42	*Perinereis vallata*	0	3	0	0	0	3	0	0	0	3	0	0	1	3	0	0
sp43	*Actinia ebhayiensis*	0	3	0	0	0	3	0	0	1	3	0	0	3	0	0	0
sp44	*Cymbula compressa*	0	3	0	0	0	0	3	0	0	3	0	0	0	3	0	0
sp45	*Urothoe grimaldii*	0	0	3	0	0	0	0	3	3	0	0	3	0	0	0	0
sp46	*Ischnochiton oniscus*	1	3	0	0	0	3	0	0	0	3	0	0	3	0	0	0
sp47	*Onithochiton literatus*	1	3	0	0	0	3	0	0	0	3	0	0	3	0	0	0
sp48	*Ischnochiton bergoti*	1	3	0	0	0	3	0	0	0	3	0	0	3	0	0	0
sp49	*Acanthochitona garnoti*	1	3	0	0	0	3	0	0	0	3	0	0	1	3	0	0
sp50	*Cymbula miniata*	0	3	0	0	0	3	1	0	0	3	0	0	3	0	0	0
sp51	*Siphonaria sp 1*	1	3	0	0	0	0	3	0	3	0	0	0	3	0	0	0
sp52	*Scutellastra natalensis*	1	3	0	0	0	3	0	0	3	0	0	0	3	0	0	0
sp53	*Sipunculida sp*	3	0	0	0	1	3	0	1	2	3	0	0	3	0	0	0
sp54	*Scutellastra argenvillei*	1	3	0	0	0	1	3	0	0	3	0	0	1	3	0	0
sp55	*Siphonaria capensis*	1	3	1	0	0	1	3	0	0	3	0	0	3	0	0	0
sp56	*Gunnarea gaimardi*	1	3	0	0	0	3	1	0	0	3	0	0	0	3	0	0
sp57	*Sedentaria spp*	1	3	0	0	0	3	1	0	0	3	0	0	0	3	0	0
sp58	*Siphonaria anneae*	0	3	1	0	0	0	3	0	0	3	0	0	3	3	0	0
sp59	*Cymbula oculus*	0	3	0	0	0	0	3	0	0	3	0	0	0	3	0	0
sp60	*Tetralia cymodose*	3	0	1	0	0	3	0	0	0	3	0	0	3	0	0	0

Species Code	**Species name**	**t6.1**	**t6.2**	**t6.3**	**t6.4**	**t7.1**	**t7.2**	**t7.3**	**t7.4**	**t8.1**	**t8.2**	**t8.3**	**t9.1**	**t9.2**	**t9.3**	**t9.4**	**t9.5**
sp61	*Siphonaria concinna*	1	3	0	0	0	0	3	0	0	3	0	0	3	3	0	0
sp62	*Scutellastra exusta*	1	3	0	0	0	1	3	0	0	3	0	0	3	0	0	0
sp63	*Afrolittorina knysnaensis*	1	0	3	0	0	3	0	0	0	3	0	3	0	0	0	0
sp64	*Oxystele tigrina*	3	1	0	0	0	3	0	0	1	3	0	0	3	0	0	0
sp65	*Fissurella natalensis*	0	3	0	0	0	3	0	0	0	3	0	0	3	1	0	0
sp66	*Parvulastra exigua*	3	1	0	0	0	3	1	0	3	0	0	0	3	0	0	0
sp67	*Siphonaria oculus*	1	3	0	0	0	0	3	0	3	3	0	0	3	0	0	0
sp68	*Scutellastra barbara*	3	0	0	0	0	1	3	0	0	3	0	0	0	3	0	0
sp69	*Cymbula granatina*	1	3	0	0	0	1	3	0	0	3	0	0	0	3	0	0
sp70	*Burnupena pubescens*	1	3	0	0	0	3	0	0	0	0	3	0	3	1	0	0
sp71	*Scutellastra aphanes*	3	0	0	0	0	0	3	0	0	3	0	0	3	3	0	0
sp72	*Gibbula multicolor*	0	0	3	0	0	3	0	0	0	3	0	3	0	0	0	3
sp73	*Nucella squamosa*	0	3	1	0	0	3	0	0	3	0	0	0	3	0	0	0
sp74	*Vaughtia fenestrata*	0	0	0	0	0	0	0	3	3	0	0	0	1	3	0	0
sp75	*Siphonaria carbo*	0	3	0	0	0	0	3	0	3	0	0	0	3	0	0	0
sp76	*Oxystele sinensis*	3	1	0	0	0	3	0	0	0	3	0	0	3	1	0	0
sp77	*Botryllus sp*	1	3	0	0	3	0	0	0	0	3	0	3	0	0	0	0
sp78	*Isaurus tuberculatus*	0	0	3	0	3	0	0	0	3	0	0	3	0	0	0	0
sp79	*Fissurella mutabilis*	0	3	0	0	0	3	0	0	0	3	0	0	3	0	0	0
sp80	*Helcion pruinosus*	1	3	0	0	0	3	0	0	0	3	0	0	3	0	0	0
sp81	*Arenicola loveni*	0	3	0	0	0	3	0	0	0	0	3	0	0	0	0	0
sp82	*Ischyromene huttoni*	0	0	3	0	0	3	0	0	3	0	0	3	0	0	0	0
sp83	*Ischyromene ovalis*	0	0	3	0	0	3	0	0	3	0	0	3	0	0	0	0
sp84	*Listriolobus capensis*	3	0	0	0	0	3	0	0	0	3	0	0	3	0	0	0
sp85	*Dardanus arrosor*	3	0	0	0	0	0	3	0	3	0	0	3	0	0	0	0
sp86	*Nucella dubia*	0	3	1	0	0	3	0	0	3	0	0	0	3	0	0	0
sp87	*Parisocladus perforatus*	0	0	3	0	0	3	0	0	3	0	0	3	0	0	0	0
sp88	*Marphysa haemasona*	0	3	0	0	0	0	0	3	0	3	0	0	0	0	0	0
sp89	*Afrocominella capensis simoniana*	0	0	0	0	0	3	0	0	3	0	0	0	0	3	0	0
sp90	*Diodora crucifera*	0	0	3	0	0	3	0	0	0	3	0	0	3	0	0	0

Species Code	Species name	t6.1	t6.2	t6.3	t6.4	t7.1	t7.2	t7.3	t7.4	t8.1	t8.2	t8.3	t9.1	t9.2	t9.3	t9.4	t9.5
sp91	*Burnupena cincta*	1	3	0	0	0	0	0	3	3	0	0	0	3	0	0	0
sp92	*Dendrofissurella scutellum*	0	0	3	0	0	3	0	0	3	0	0	0	1	3	0	0
sp93	*Scutellastra tabularis*	1	3	0	0	0	0	3	0	3	0	0	0	0	3	0	0
sp94	*Oxystele impervia*	2	0	3	0	0	3	0	0	0	0	3	0	3	0	0	0
sp95	*Nephyts sp*	3	0	0	0	0	3	0	0	0	2	3	0	3	0	0	0
sp96	*Spirobranchus kraussii*	0	3	0	0	0	3	0	0	0	3	0	0	2	2	0	0
sp97	*Afropinnotheres dofleini*	0	0	3	1	0	0	0	3	0	3	0	3	0	0	0	0
sp98	*Rathbunixa occidentalis*	0	3	0	0	0	3	0	0	0	3	0	3	0	0	0	0
sp99	*Burnupena catarrhacta*	1	3	0	0	0	3	0	0	0	3	0	0	2	2	0	0
sp100	*Trochia cingulata*	0	3	0	0	0	3	0	0	3	1	0	0	3	0	0	0
sp101	*Crepidula porcellana*	3	1	0	0	0	0	3	0	0	3	0	0	3	0	0	0
sp102	*Striostrea margaritacea*	0	3	0	0	0	0	3	0	0	0	3	0	3	0	0	0
sp103	*Ostrea atherstonei*	0	3	0	0	0	0	3	0	0	0	3	0	0	3	0	0
sp104	*Burnupena papyracea*	1	3	0	0	0	3	0	0	0	3	0	0	3	0	0	0
sp105	*Ligia dilatata*	0	3	0	2	0	3	0	0	3	0	0	3	0	0	0	0
sp106	*Burnupena rotunda*	1	3	0	0	0	3	0	0	0	3	0	0	0	3	0	0
sp107	*Tetraclita rufotincta*	1	3	0	0	0	0	0	3	0	0	3	0	3	0	0	0
sp108	*Oxystele tabularis*	2	0	3	0	0	3	0	0	0	0	3	0	3	0	0	0
sp109	*Amphibalanus sp1*	2	3	1	0	0	0	0	3	0	0	3	0	3	0	0	0
sp110	*Mancinella capensis*	0	0	0	0	0	3	0	0	3	1	0	0	2	2	0	0
sp111	*Pyrene flava filmerae*	0	0	0	0	0	3	0	0	0	3	0	0	3	0	0	0
sp112	*Lysidice natalensis*	0	0	0	0	0	3	0	0	0	3	0	0	0	0	0	0
sp113	*Golfingia sp*	0	0	0	0	1	3	0	0	0	2	2	0	0	0	0	0
sp114	*Eunice aphroditois*	0	3	0	0	0	3	0	0	0	3	0	0	0	0	0	0
sp115	*Onchidium sp*	3	0	0	0	0	0	3	0	0	3	0	0	2	2	0	0
sp116	*Planocera gilchristi*	3	0	0	0	2	0	0	2	0	1	3	0	3	0	0	0
sp117	*Ochetostoma formosulum*	0	0	0	0	0	3	0	0	0	3	0	0	1	1	1	1
sp118	*Tenguella granulata*	2	3	0	0	0	3	0	0	0	3	0	0	3	0	0	0
sp119	*Eurythoe complanata*	3	0	0	0	3	3	0	0	0	3	0	0	3	0	0	0
sp120	*Glycera tridactyla*	0	0	3	0	0	3	0	0	0	3	0	3	0	0	0	0

Species Code	**Species name**	**t6.1**	**t6.2**	**t6.3**	**t6.4**	**t7.1**	**t7.2**	**t7.3**	**t7.4**	**t8.1**	**t8.2**	**t8.3**	**t9.1**	**t9.2**	**t9.3**	**t9.4**	**t9.5**
sp121	*Charybdis sp*	2	0	3	0	0	3	0	0	0	3	0	0	0	3	1	0
sp122	*Parisocladus stimpsoni*	0	0	3	0	0	3	0	0	0	3	0	3	0	0	0	0
sp123	*Scutellastra miliaris*	1	3	0	0	0	0	3	0	3	0	0	0	0	0	3	1
sp124	*Littorina saxatilis*	0	3	0	0	0	3	0	0	3	0	0	3	0	0	0	0
sp125	*Cirolana venusticauda*	0	0	3	0	0	3	0	0	3	0	0	3	0	0	0	0
sp126	*Heliacus variegatus*	0	0	0	0	0	0	3	0	0	3	0	0	3	0	0	0
sp127	*Afrolittorina africana*	1	0	3	0	0	3	0	0	0	3	0	3	0	0	0	0
sp128	*Diodora parviforata*	0	3	0	0	0	3	0	0	0	3	0	0	3	0	0	0
sp129	*Gibbula cicer*	0	3	0	0	0	3	0	0	0	3	0	0	3	0	0	0
sp130	*Grapsus tenuicrustatus*	0	0	3	0	0	3	0	0	0	3	0	3	0	0	0	0
sp131	*Arabella iricolor*	3	0	0	0	0	3	0	0	0	3	0	0	0	0	3	0
sp132	*Tylothais savignyi*	0	0	0	0	0	3	0	0	3	0	0	0	3	0	0	0
sp133	*Neorhynchoplax bovis*	0	0	3	0	0	3	0	0	0	3	0	3	0	0	0	0
sp134	*Acanthonyx scutellatus*	0	0	3	0	0	3	0	0	0	3	0	0	3	0	0	0
sp135	*Thalamita admete*	0	0	0	0	0	3	0	0	0	3	0	0	3	0	0	0
sp136	*Syllidae sp*	3	0	0	0	0	3	0	0	3	0	0	3	0	0	0	0
sp137	*Clibanarius virescens*	0	0	3	0	0	3	0	0	0	3	0	0	3	0	0	0
sp138	*Balanus glandula*	3	0	2	0	1	0	0	3	0	3	0	0	3	0	0	0
sp139	*Radsia nigrovirescens*	3	2	0	0	0	3	0	0	3	0	0	0	3	0	0	0
sp140	*Rhyssoplax polita*	0	3	0	0	0	3	0	0	0	3	0	0	3	1	0	0
sp141	*Pupillaea aperta*	0	3	0	0	0	3	0	0	0	3	0	0	1	3	0	0
sp142	*Argobuccinum pustulosum*	0	3	0	0	0	3	0	1	1	3	0	0	0	0	0	0
sp143	*Cabestana africana*	0	3	0	0	0	3	0	0	0	3	0	0	0	3	0	0
sp144	*Nucella wahlbergi*	0	3	1	0	0	3	0	0	3	0	0	0	3	1	0	0
sp145	*Lugubrilaria lugubris*	3	0	0	0	0	3	0	0	3	0	0	0	3	0	0	0
sp146	*Thyone aurea*	0	3	0	0	2	3	0	0	0	3	0	0	3	0	0	0
sp147	*Cymbula sanguinans*	0	3	0	0	0	0	3	0	0	3	0	0	0	3	0	0
sp148	*Notocomplana erythrotaenia*	0	0	0	0	0	0	0	3	0	3	0	0	3	0	0	0
sp149	*Ischnochiton textilis*	3	1	0	0	0	3	0	0	1	3	3	0	3	0	0	0
sp150	*Amphibalanus venustus*	2	3	1	0	0	0	0	3	0	3	0	3	0	0	0	0

2.11.2. Seasonal nearshore SST variability across sites and bioregions



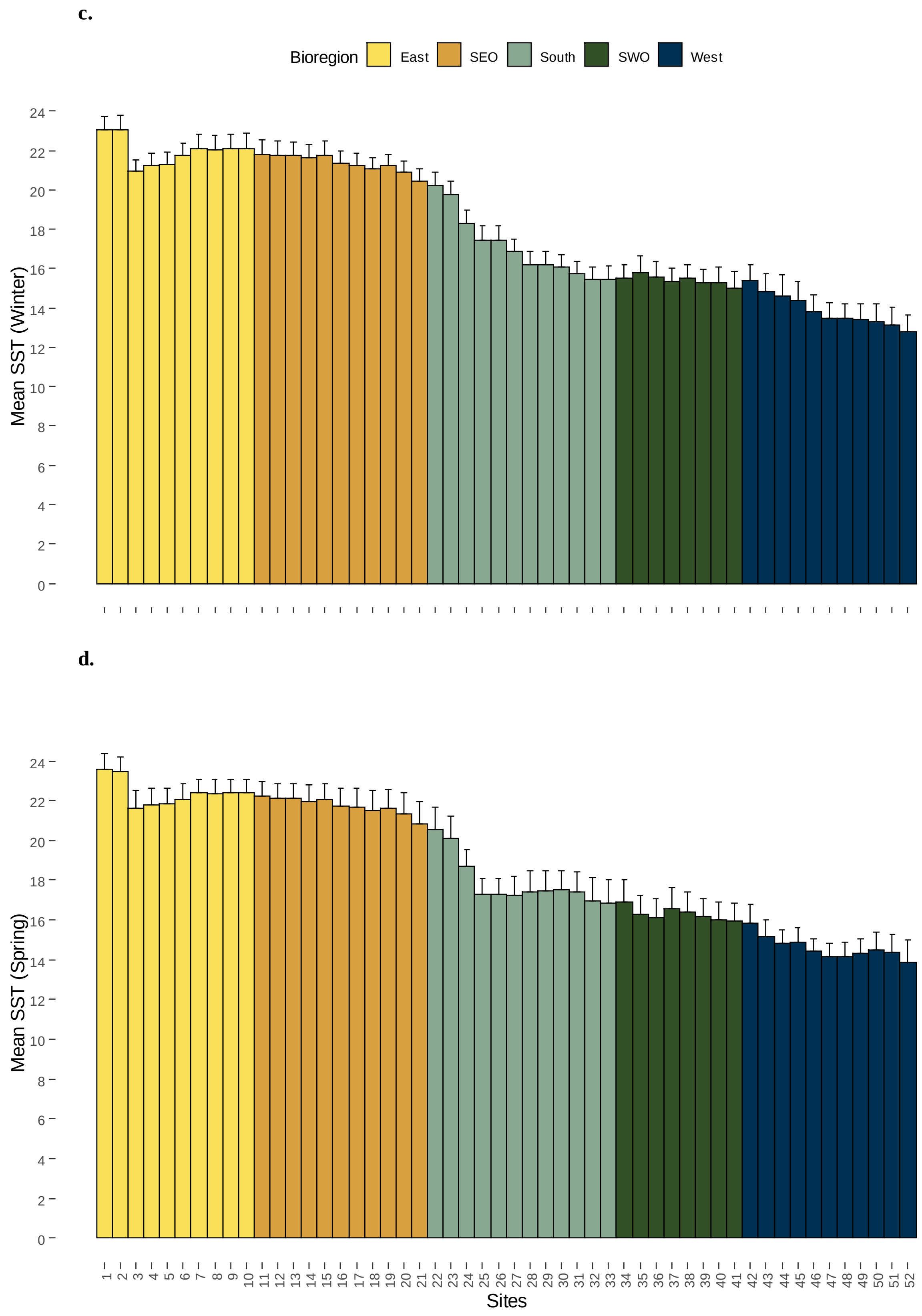
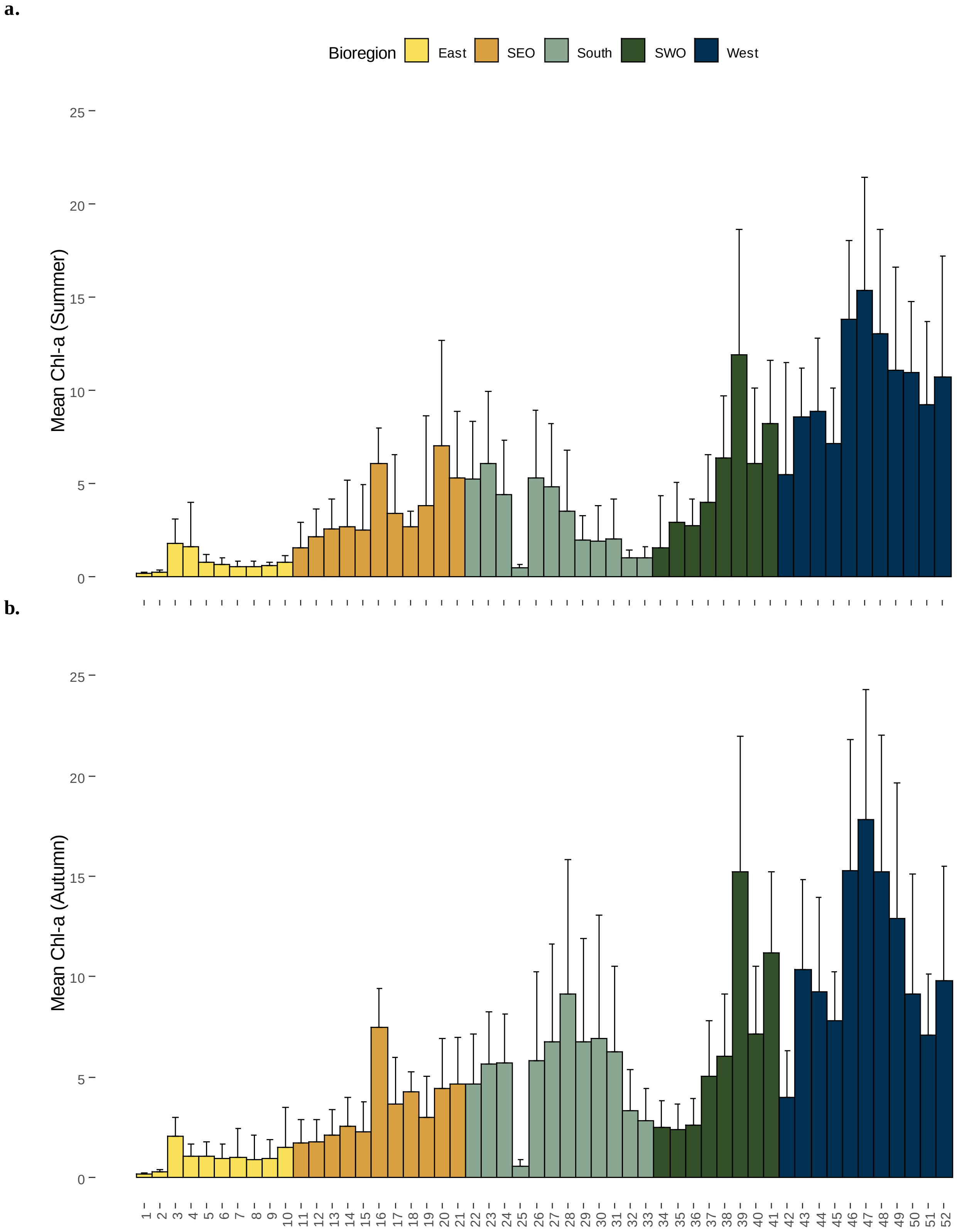


Fig.S2.1a-d.Mean SST values (+SD) across sites and seasons (summer, autumn, winter, and spring) from 2014-2020. Site numbers correspond with site codes in Table 2.2.

2.11.3. Seasonal nearshore chlorophyll-*a* variability across sites and bioregions



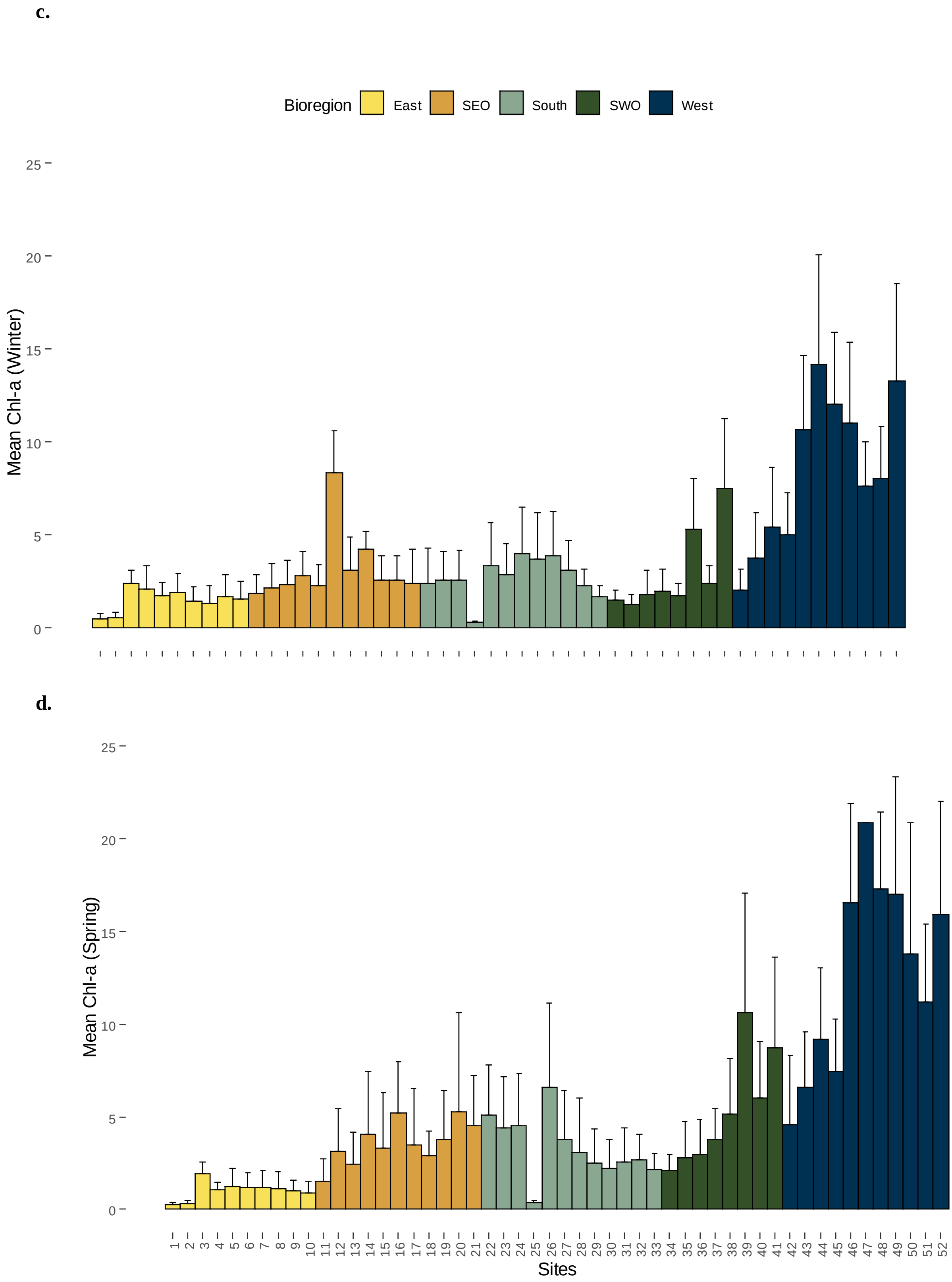


Fig.S2.2a-d. Mean chl-*a* values (+SD) across sites and seasons (summer, autumn, winter and spring) from 2014-2020. Site numbers correspond with site codes in Table 2.2.

CHAPTER 3

DO TAXONOMIC AND FUNCTIONAL DIVERSITY INDICES REVEAL CONCORDANT BIODIVERSITY RESPONSES TO HABITAT FILTERS ACROSS BIOGEOGRAPHIC TRANSITION ZONES?

One could safely predict that all physiological processes are influenced by the tide, could we but read delicately enough the indices. -E. F. Ricketts (Steinbeck, 1951)

Do taxonomic and functional diversity indices reveal concordant biodiversity responses to habitat filters across biogeographic transition zones?

3.1. Introduction

The concept of biogeography is suggested to proceed from two main themes, geographical biology, and biological geography. The former studies the space-related properties of species and focuses on distribution regularities (Baroni-Urbani et al., 1978; Hausdorf, 2002; Olivero et al., 2011), while biological geography attempts to divide the Earth's surface into geographic units based on similarities in the occurrence of species and ecosystems. A hierarchical system of these geographic units is termed a "biogeographical regionalisation," a concept of the geographical organisation of biota on Earth in response to past and current physical and biological forces (Kreft & Jetz, 2010). This geographical organisation provides frameworks for documenting species and ecosystems, analysing basic questions in historical and ecological biogeography, evolutionary biology, and/or assessing priorities for conservation (Carey et al., 1995; Morrone, 2008). Environmental characterisations of biotic regionalisations have been used to test and propose hypotheses about ecological factors conditioning the species composition of biological communities (e.g., Olivero & Hix, 1998; Moya et al., 2011; Martins et al., 2017).

In management and conservation policy, classifying geographical areas into regions with different species compositions is necessary to define contexts for representativeness, to ensure that the whole range of biotic variation (all areas with characteristic combinations of species) is represented in the selection of natural reserves (Carey et al., 1995). However, defining boundaries between different biogeographical regions is not straightforward. This is because limits between regions or along shorelines may form sharply defined boundaries along some parts of their borders, whereas elsewhere, they may consist of broad transition zones or gradients (Williams, 1996). Usually, different taxa show different boundaries, so a unique 'line' cannot be drawn, but instead, a 'transition zone' is represented (Morrone, 2008). This can also be seen through the vertical gradient of intertidal zones where although these zones are often distinguished by the most dominant species, e.g., cochlear zone, balanoid zone, littorina zone, they are regions where these zones become obscure as species transition into the next zone.

Transition zones are geographical areas of overlap, with a gradient of replacement and partial segregation between different biotas (Ferro & Morrone, 2014). They are usually described as complex and varied areas where diverse fauna and flora overlap and may be represented by strong gradients in species richness, high spatial species turnover, or a combination of both (Speziale et al., 2010). Even though species turnover or replacement does not necessarily imply an interaction between individual organisms or historical relationships, transition zones are often considered evolutionarily active zones where several speciation events have taken place in the past (Williams et al., 1999) and where biological and or functional interactions could potentially influence population dynamics. Kark et al. (2007) suggested that both evolutionary and ecological processes interact and are responsible for high richness and high rarity coincidence in transition zones. In this light, different tools have emerged to measure and understand the distribution and drivers of species composition within ecosystems.

3.1.1. Merging the old and new concepts

The majority of studies in the past on species assemblages across space and time have primarily used taxonomic-based indices to evaluate species abundance, diversity, and richness (Tilman et al., 2001). Although these methods may accurately describe spatial and temporal differences in community composition and summarise information about the relative abundances of species within a community or sample, they often ignore the degree of difference between species and fail to capture the causal mechanisms underlying these patterns (Botta-Dukát, 2005). This means they cannot account for the many different ecological functions of species comprising communities and ultimately do not account for the implications of changes in biodiversity for the functioning of ecosystems and their services for humans (Hillebrand, 2008).

As such, there is an increase in contemporary community ecology studies that have shifted from simply how many, and which species occur within a certain environment to how and by how much species differ in their functionality. This requires more understanding of the potential underlying mechanisms driving ecosystem functionality based on the relationship and interaction between species' functional traits and their environment. One approach to the analysis of community assembly and ecology is to assess functional trait values within a local community relative to a broader pool of species. This approach considers the environmental sorting of communities under certain environmental conditions (Weiher & Keddy, 1999), in which traits quantify the responses of species to and their effects on local conditions. Determining the relationship between taxonomic and functional diversity is critical for predicting the vulnerability of a community, shifts in community structure, and the effects of species loss due to anthropogenic drivers on ecosystem functioning (Micheli & Halpern, 2005). For example, from in-field personal observations, the excess subsistence harvesting, and removal of large-sized limpet and mussel species has consequently created niches that have become primarily occupied by seaweeds in the Transkei region on the east coast of South Africa. However, for the scope of this study, I will focus more on the environmental implications on community structure within and across main bioregions and transition zones using taxonomic- and functional diversity metrics.

3.1.2. Habitat filtering and ecosystem functioning in biogeographical regions

According to Mouchet et al. (2010), biogeographical changes in functional diversity and community assemblages across ecosystems and time can be attributed to two main factors or filters, i.e., environmental/habitat and limiting similarity. Habitat filtering and limiting similarity hypotheses are assumed to have antagonistic influences on species trait distribution. The former acts as a bottleneck as it "filters" out or selects against species based on their functional traits. This is founded on the habitat templet theory, where the habitat is thought of as a hierarchical filter, only allowing species with ecologically viable traits (also known as response traits) to proliferate and form local communities (Boersma et al. 2016). This defines the trait adaptive value of a species. Another assumption underlying the habitat templet theory is the occurrence of general trait-environment relationships, where the most dominant traits i.e., community-weighted mean (CWM), constitute a functional adaptation to a certain environmental gradient. More explicitly, it implies that the community-weighted mean (CWM) value of a trait can be used to predict the rate of ecosystem processes (Díaz et al., 2007). The CWM defines the most frequent trait value within a community. It is computed as an average of the trait values of species within a community weighted by either biomass or abundance (Garnier et al., 2004). CWM is based on the mass-ratio hypothesis, which states that a species' effect traits on a given ecosystem process or ecosystem function is proportional to its relative abundance within that community (Grime, 1998). This is because the participation of species in the processes of matter transformation and energy flux is proportional to their contribution to the community biomass (Bílá et al., 2014). I also included biomass as it is directly linked to the amount of energy and resources assimilated by a species.

Another way to predict ecosystem functioning is through the limiting similarity theory. This theory is an outgrowth of the competitive exclusion principle, which predicts that species can coexist if their niches complement one another but may be absent in a suitable environment because of interspecific competition (Botta-Dukát & Czucz, 2016). Limiting similarity aims to account for functional diversity, i.e., the community's variation in species trait values. Therefore, the functional diversity (FD) of a community is the extent of differences in the biological traits displayed within that community (Garaffo, 2018). FD also represents the diversity of species niches and how functional trait distribution differs between species assemblages across space and time. FD promotes nonadditive effects (i.e., effects not predictable from the sum of single-species) on the processes of matter transformation and energy flux (Heemsbergen et al., 2004). Nonadditive effects can emerge either due to antagonistic (competition or inhibition) or synergistic interactions (complementarity or facilitation), leading to more efficient utilisation of resources among coexisting species (Tilman et al., 1996; Petchey et al., 2004; Hooper et al., 2005; Mouillot et al., 2011). The three main independent components of functional diversity include functional richness, functional divergence, and functional evenness. These components aim to quantify the trait diversity in biological assemblages and act as a proxy to estimate the ecological functions performed by the community.

Lastly, it is important to mention that some of the approaches used to explain these two filters include searches into historical patterns of speciation, species dispersal, and migration patterns (Götzenberger et al., 2012). However, for this study, I focus on the contribution of species functional traits to the observed composition of community assemblages and patterns across large spatial scales using trait-based indices derived from the habitat filtering and limiting similarity theories. Thus, for the objective and design of this study, I evaluated the distributional patterns of rocky shore species along the South African coast across bioregions and transition zones based on functional, environmental, and biogeographical components. I hypothesised that the diversity in functional traits were the underlying biotic mechanism driving species distribution with the habitat limitations and environmental parameters acting as a filter or bottleneck. To test this hypothesis, I used multidimensional trait-based indices to evaluate the functional richness, evenness, divergence, and composition of rocky shore species across sites and bioregions. At the bioregion level, I expected the sites within the same bioregion to contain less variability in functional diversity than sites within transition zones where different large marine systems converge, where shifts in environmental parameters such as temperature are expected to be marked. This means I expected the most abundant species both in numbers and/or biomass (i.e., the mass ratio hypothesis to have a greater influence within the main bioregions (where environmental conditions are more stable to influence higher species persistence) than in transition zones. From the transition zones, I expected the effects of "hybrid zones" and range-edge effects associated with transition zones to drive biodiversity in these overlapping regions. Thus, I expected these transition regions to contain unique, functionally, and possibly taxonomically diverse species (from the limiting similarity hypothesis) from both distinct bioregions as they converge. For example, I expected species with traits associated with a short life span, small sizes, and limited dispersal to be more prevalent in biogeographic transition areas. I also expected to observe the influence of temperature on the composition of functional traits within communities as it is regarded as the main environmental filter driving species patterns in various systems, including coastal marine systems. I speculate that using functional traits would also further explain the taxonomic distribution of rocky shore species and their community dynamics.

3.2. Materials and Methods

3.2.1. Study Area and Data Analysis

I used the same study sites as Chapter 2 (Fig.2.1). However, the total sites varied between 48 and 52 to accommodate biomass- and abundance-related analyses depending on the analysis—the former excluded 4 sites within marine protected areas (MPA's). In addition, in this chapter, I used the same biological and environmental data collected for Chapter 2. See the previous chapter for sampling methods conducted and data processing methods.

3.2.2. Analysis of species abundances and diversity

Various multivariate analyses were used to compare taxonomic and functional composition among communities and for the spatial analysis of taxonomic and functional diversity. Before statistical analysis, macroinvertebrate community abundance and biomass data were transformed (log x+1) to ensure consistent comparability with the already standardised functional trait responses (see Chapter 2).

Rank abundance curves were used to assess the dominant species weighted by both abundance and biomass. Changes in the patterns of the macroinvertebrate species based on the abundance and biomass were assessed using the Abundance Biomass Comparison (ABC) method (Warwick, 1986). The ABC methods is a means of detecting the effects of anthropogenic perturbations on assemblages of organisms that have a theoretical background in the classical evolutionary theory of *r*- and *k*-selection. I used it however as a base exploratory technique to evaluate the relationship between abundance and biomass within and across bioregions. The ABC approach is a graphical approach that compares the abundance and biomass of organisms to predict the environmental stress level of an ecosystem (Dauer et al., 1993). It involves the plotting of separate *k*-dominance curves for species abundances and species biomasses on the same graph and comparing the forms of the two curves relative to each other. After computing the graphs, the shapes of the graphs were compared with the typical comparisons described by Warwick (1986). The graph is useful to explore the level of disturbance affecting assemblages. The W-statistic from the graph gives the difference between the two curves, which represents the area between them (Das et al., 2021). The method relies upon *k*-dominance curves as visual representations of the evenness of numbers of organisms and biomass distribution among species (Lambshead et al., 1983). It is expected that in undisturbed environments, if the community is dominated by *k*-selected species which are slow-growing, large and late-maturing, the biomass curve will lie above the abundance curve. On the other hand, with increasing disturbance, slow-growing species cannot survive, and the system is increasingly dominated by *r*-selected species (fast-growing, small, opportunistic), and the biomass curve will lie below the abundance curve. The contention is that these three conditions (unperturbed, moderately perturbed, or grossly perturbed) should be recognisable without reference control samples in time or space, the two curves acting as an internal control against each other and providing a snapshot of the condition of the assemblage at any one time or place (Warwick, 2008).

I also used the indices used in classical ecology approaches (i.e., Shannon diversity (H), Simpson's dominance (D), species richness (S), and Pielou's evenness (E)) to summarise community composition at site level. Species richness is the number of species represented within an ecological community or area. The Shannon diversity index characterises the diversity of species within a community. The index increases as both the community's richness and evenness increase. In addition, Simpson's dominance (D) measures the probability that any two individuals drawn at random from an infinitely large community will belong to the same species. 0 represents infinite diversity with this index, while 1 represents no diversity or complete evenness. The bigger the value of D, the lower the diversity. The main disadvantage of Simpson's index is that it is heavily weighted toward the most abundant species meaning the addition of rare species with one individual will fail to change the index. Pielou's evenness (J) index is a way to measure how evenly the species are distributed in a community. Pielou's index value is defined between 0 and 1. All taxon-based indices were computed in the ecodist package in R (Goslee & Urban, 2007). These indices were then statistically compared across bioregions. After calculating the taxonomic indices for each survey site with the ecodist package, I conducted Spearman rank correlation (rho) analyses (considering 9999 permutations) among species diversity metrics to examine if there was an association with the environmental parameters, including latitudinal effects. This correlation was done to test for changes in biological gradients along the biogeographic gradient. Differences in indices across biogeographic provinces were tested using the mantel correlogram analysis.

Lastly, to get a visual presentation on the patterns of richness and evenness across sites, I plotted Rényi diversity profiles also known as diversity ordering curves (Tóthmérész, 1993, 2005). The shape of the profile is an indication of evenness. The less horizontal a profile is, the less evenly species are distributed. Each value of the Rényi diversity profile is based on a parameter '*alpha*'. The profile values for *alpha*=0 provide information on species richness. The profile value is the logarithm of the species richness. The profile value for *alpha*=infinity provides information on the proportion of all individuals formed by the most abundant species. A larger evenness thus corresponds with lower proportions of the dominant species. The profiles were computed using the BiodiversityR package (Kindt & Coe, 2005). All R analyses were performed in R version 4.1.0 (R Core Team, 2021).

3.2.3. Analysis of biological traits

There is a significant scarcity of information pertaining to consolidated trait inventories of marine communities, including intertidal systems (Tyler et al., 2012; Beauchard et al., 2017; Degen et al., 2018). Thus, trait information (see Supplementary Information 1) was consolidated from various online sources of including WoRMS (World Register of Marine Species), BIOTIC (Biological Traits Information Catalogue), SeaLifeBase, journal articles, and books (e.g., Day, 1974; Branch & Branch, 2018). I selected nine trait categories based on their perceived importance to ecosystem functioning (effect traits) and/or how the environment influences their persistence (response traits) (see Table 2.3 for trait categories and rationale for trait selection). Trait categories are often subdivided into different trait modalities - i.e., within trait differences). Further, these trait categories and their respective modalities were grouped into two trait domains or suites of traits (which account for life-history strategies that determine the ability of an organism to deal with spatio-temporal variability of habitats) (Verberk et al., 2008). The trait domains considered in this study primarily characterised intertidal species' reproduction and development strategies. Because some species show plasticity or multi-faceted behaviour in trait responses, for example, a swimming species may also crawl. I used the fuzzy coding system to categorise species into trait modalities (Chevene et al., 1994; see Chapter 2 for detailed explanation).

3.2.4. Community trait assembly and response to environmental parameters

To analyse changes in the dominant traits or functional composition and expression across sites, I calculated community weighted means (CWM) value. CWM is an index that reveals the weights of each trait modality weighted by their relative abundance or biomass of species within a community. This index is sometimes referred to as the community functional composition or functional identity of a site or habitat. Using the betadisper function (which is a multivariate analogue of Levene’s test for homogeneity of variances), I computed multivariate homogeneity of group variances for (i) raw abundance, (ii) biomass data, and among CWM values for (iii) development traits and (iv) reproduction traits from each bioregion (weighted by abundance and biomass) in the vegan package (Oksanen et al., 2020). The betadisper function is primarily used as a means of assessing beta diversity.

Further, although the information yielded by fourth-corner interaction coefficients (Chapter 2) and CWM traits are expected to be similar, CWM values are useful for visualising the temporal trends in trait values (Lavorel et al., 2008). CWM computes trait modalities, for example, within the feeding trait category, there are trait modalities or within-trait differences such as filter feeders, grazers, or deposit feeders. Species possessing each modality will be weighted by their abundance or biomass. Just as the name suggests, CWM is also employed when the objective of the study is limited to the community level and is a useful indicator of dominant traits among habitats (Díaz et al., 2007). This is because CWM allows the observance of shifts in trait values within the community resulting from environmental selection of adaptive traits. It is directly related to the biomass ratio hypothesis, which assumes that the most abundant species traits determine ecosystem functioning (Garnier et al., 2004; Ricotta & Moretti, 2011). For example, CWM pools together the biomass of all filter-feeding species and weights them against all other traits modalities instead of using the taxon identification of the species within each site. To calculate the CWM average trait values for each site, I used Gower distances to calculate the species dissimilarity matrix using the dbFD function in the FD package (Laliberté & Legendre, 2010; Laliberté et al., 2014).

I used Mantel tests to examine the correlation between the ecological (species) and the environmental distance matrices (temperature and chl-*a*), including latitudinal gradients. The Mantel correlation test ensures that random patterns do not mislead interpretation of results. I then used separate one-way analysis of variance (ANOVA) to test the effect of bioregion on the CWM values and functional diversity indices. Correlations between the CWM traits and environmental properties were tested using Spearman's correlation coefficient. A principal components analysis (PCA) on standardised data was used to analyse the overall pattern of correlations between sites and specific trait modalities.

3.2.5. Functional trait complementarity across habitats

Various indices have been proposed to measure the different components of functional diversity of a community. In this study, I used all the main functional diversity indices available in the literature to examine how different components of functional diversity responded to different environmental gradients and across a large spatial scale. These include functional richness, functional evenness, functional divergence, functional redundancy, functional dispersion, and Rao's quadratic entropy.

Functional richness (FRic)- Functional richness reflects the volume of trait space for individual species or the niche space filled by a community (Villeger et. al., 2008). The calculation of FRic shows the total amount of functional space occupied by species within a community and is independent of species abundance. One limitation of FRic is that it has the same weighting for rare and common species even though the most common species may be expected to have more weight as they play a more critical role in ecosystem functioning.

Functional evenness (FEve)- Functional evenness can be used to address the limitation of FRic. FEve measures the evenness in the distribution of species abundances across traits. In other words, this index assesses if all available trait space is equally represented by the rare and/or common species within a community. FEve decreases when abundance is less evenly spread among traits or when there are empty niches. FEve is expected to be low in biogeographic transition zones because these regions are predicted to be highly productive and can be colonised by a wide variety of species from opposing bioregions.

Functional divergence (FDiv)- This index measures how dominant trait categories are distributed within the community, i.e., the proportion of total abundance supported by species with the most extreme trait values within a community. FDiv is related to how abundance is distributed within the volume of functional traits space (Casanoves et al., 2008). FDiv is high when the most abundant species exhibit extreme trait categories and low when the most abundant species occupy similar trait categories.

Functional redundancy (FRed)- Functional redundancy measures the degree of similarity in species traits within a community and is the relationship between taxonomic and functional diversity (Sasaki et al., 2009). It can be considered as an insurance policy against the loss of ecosystem processes when a species is lost. The larger the FRed index, the greater the possibility that ecosystem functioning will be maintained if a redundant species is lost (Diaz & Cabido, 2001; Loreau et al., 2001).

Functional dissimilarity- Two conceptually similar indices are often used to measure functional dissimilarity, i.e., functional dispersion (FDis) and Rao's quadratic entropy Q (Rao’s Q). Interestingly, they do this differently and are unaffected by species richness. FDis is the weighted mean distance of individual species to the weighted centroid of all species in multidimensional trait space, and weights here correspond to the relative abundances of the species (Laliberté & Legendre, 2010, Zhu et al., 2017). A larger FDis means a more functionally spread community in multidimensional trait space. On the other hand, Rao’s Q measures the mean functional distance between two randomly selected individuals. Rao’s Q is calculated as the sum of trait dissimilarities among all pairs of species weighted by the product of their relative abundances. When abundances are frequencies (i.e., counts of individuals), Rao's Q expresses the mean distance between two randomly selected individuals (Botta-Dukát, 2005).

All analyses were performed after the traits were standardised to ensure equal contributions from each trait. From the dbFD function, I was able to calculate various functional diversity indices which revealed the distribution of species in functional trait space across sites and bioregions. A complementary Monte-Carlo test (9999 permutations) was performed to test for differences among bioregions. As a *post hoc* test, I used the univariate pairwise PERMANOVA (Anderson, 2001) to test differences between groups in terms of FRic, FDiv, FDis, FEve, Rao's Q and FRed. All FD analyses and visualisations were performed using the packages; FD (Laliberté & Legendre (2010), adegraphics (Siberchicot et al., 2017), pairwiseAdonis (Arbizu, 2017), and ggplot2 (Wickham, 2016) in R v 4.1.0 (2021).

Lastly, to identify sites with similar suites of traits, I used a tree-clustering algorithm to assemble taxa into similarity clusters. The hierarchical cluster analyses were computed on abundance and biomass weighted CWM traits. The aim was to classify the sites into groups based on the degree of similarity in their patterns of biomass and abundance. To get the best cluster method, I calculated the agglomerative coefficient for each clustering linkage method. This function calculates the agglomerative coefficient of each method, which is a metric that measures the strength of the clusters. The closer this value is to 1, the stronger the clusters. In the end, I made this classification using Ward's linkage method (Ward, 1963) and Euclidean distances. Ward's linkage method uses an analysis of variance approach to evaluate the distance between clusters and minimises the sums of squares of hypothetical clusters that can be formed at each step.

3.3. Results

3.3.1. Spatial patterns of macroinvertebrate abundances and diversity

Computing the rank abundance curves highlighted the abundances of species from the highest to the least. Tables 3.1 and 3.2 each show the top 10 and 5 species of the highest and lowest abundances and biomass, respectively (i) across all sites and (ii) within each bioregion. The most abundant, species which also occurred in at least 3 bioregions, included the barnacles *Octomeris angulosa*, and *Tetraclita serrata*, the invasive blue mussel (*Mytilus galloprovincialis*), the native limpets (*Scutellastra granularis,* and *S. cochlear*) and the reef worm (*Gunnarea gaimardi*). On the other hand, there were no common species across bioregions for the least abundant species.

Table 3. 1. Most and least abundant species recorded across bioregions

Most abundant	All sites	East	South-East	South	South-West	West
	Zoanthus natalensis	*Zoanthus natalensis*	*Octomeris angulosa*	*Chthamalus dentatus*	*Balanus glandula*	*Mytilus galloprovincialis*
	Chthamalus dentatus	*Zoanthus durbanensis*	*Tetraclita serrata*	*Perna perna*	*Mytilus galloprovincialis*	*Balanus glandula.*
	Mytilus galloprovincialis	*Perna perna*	*Zoanthus natalensis*	*Mytilus galloprovincialis*	*Choromytilus meridionalis*	*Choromytilus meridionalis*
	Tetraclita serrata	*Octomeris angulosa*	*Chthamalus dentatus*	*Tetraclita serrata*	*Tetraclita serrata*	*Scutellastra granularis*
	Octomeris angulosa	*Palythoa natalensis*	*Perna perna*	*Octomeris angulosa*	*Scutellastra cochlear*	*Scutellastra cochlear*
	Perna perna	*Chthamalus dentatus*	*Gunnarea gaimardi*	*Gunnarea gaimardi*	*Bunodactis reynaudi*	*Gunnarea gaimardi*
	Zoanthus durbanensis	*Saccostrea cuccullata*	*Sedentaria sp*	*Scutellastra granularis*	*Scutellastra granularis*	*Aulacomya atra*
	Choromytilus meridionalis	*Scutellastra natalensis*	*Siphonaria serrata*	*Sedentaria sp*	*Octomeris angulosa*	*Cymbula granatina*
	Balanus glandula	*Isaurus tuberculatus*	*Cellana capensis*	*Siphonaria serrata*	*Gunnarea gaimardi*	*Pseudonereis podocirra*
	Palythoa natalensis	*Amphibalanus venustus*	*Scutellastra cochlear*	*Siphonaria capensis*	*Siphonaria capensis*	*Bunodactis reynaudi*
Least abundant						
	Neorhynchoplax bovis	*Neorhynchoplax bovis*	*Scutellastra obtecta*	*Rathbunixa occidentalis*	*Tetralia cymodose*	*Burnupena pubescens*
	Acanthonyx scutellatus	*Acanthonyx scutellatus*	*Nucella dubia*	*Cymbula granatina*	*Spirobranchus kraussii*	*Cymbula oculus*
	Botryllus sp	*Botryllus sp*	*Ischnochiton textilis*	*Austramegabalanus cylindricus*	*Siphonaria oculus*	*Acanthochitona garnoti*
	Cymbula sanguinans	*Cymbula oculus*	*Scutellastra barbara*	*Parisocladus perforatus*	*Fissurella mutabilis*	*Tetraclita serrata*
	Clibanarius virescens	*Cymbula sanguinans*	*Glycera tridactyla*	*Siphonaria sp*	*Rathbunixa occidentalis*	*Siphonaria serrata*

Table 3. 2. Highest and least species recorded across bioregions according to biomass.

Highest biomass	All sites	East	South-East	South	South-West	West
	Perna perna	*Perna perna*	*Zoanthus natalensis*	*Chthamalus dentatus*	*Bunodactis reynaudi*	*Mytilus galloprovincialis*
	Mytilus galloprovincialis	*Zoanthus natalensis*	*Perna perna*	*Perna perna*	*Mytilus galloprovincialis*	*Choromytilus meridionalis*
	Zoanthus natalensis	*Palythoa natalensis*	*Octomeris angulosa*	*Mytilus galloprovincialis*	*Scutellastra cochlear*	*Cymbula granatina*
	Choromytilus meridionalis	*Octomeris angulosa*	*Saccostrea cuccullata*	*Tetraclita serrata*	*Choromytilus meridionalis*	*Bunodactis reynaudi*
	Octomeris angulosa	*Saccostrea cuccullata*	*Scutellastra cochlear*	*Octomeris angulosa*	*Octomeris angulosa*	*Scutellastra cochlear*
	Tetraclita serrata	*Zoanthus durbanensis*	*Siphonaria serrata*	*Gunnarea gaimardi*	*Scutellastra granularis*	*Scutellastra argenvillei*
	Scutellastra granularis	*Roweia frauenfeldii*	*Argobuccinum pustulosum*	*Scutellastra granularis*	*Cymbula oculus*	*Aulacomya atra*
	Palythoa natalensis	*Scutellastra natalensis*	*Roweia frauenfeldii*	*Sedentaria sp*	*Aulacomya atra*	*Octomeris angulosa*
	Scutellastra cochlear	*Cellana capensis*	*Cellana capensis*	*Siphonaria serrata*	*Gunnarea gaimardi*	*Burnupena lagenaria*
	Cymbula granatina	*Gunnarea gaimardi*	*Gunnarea gaimardi*	*Siphonaria capensis*	*Siphonaria capensis*	*Gunnarea gaimardi*
Least biomass						
	Tylothais savignyi	*Eurythoe complanata*	*Scutellastra obtecta*	*Grapsus tenuicrustatus*	*Rathbunixa occidentalis*	*Nucella squamosa*
	Diodora crucifera	*Ischnochiton oniscus*	*Nucella dubia*	*Rhyssoplax polita*	*Afrocominella capensis simoniana*	*Vaughtia fenestrata*
	Neorhynchoplax bovis	*Afropinnotheres dofleini*	*Ischnochiton textilis*	*Parisocladus perforatus*	*Spirobranchus kraussi*	*Afropinnotheres dofleini*
	Grapsus tenuicrustatus	*Neorhynchoplax bovis*	*Scutellastra barbara*	*Urothoe grimaldii*	*Urothoe grimaldii*	*Tetraclita serrata*
	Afrolittorina africana	*Sipunculida sp*	*Glycera tridactyla*	*Charybdis sp*	*Ischyromene huttoni*	*Diodora crucifera*

3.3.2. Abundance-biomass comparison curves

As a follow-up on the rank abundance curves (Table 3.1), I attempted using the cumulative percentage abundance and biomass of the top ten dominant species to create the abundance biomass curves (ABC curves) for each bioregion and across all sites i.e., Fig.3.1. Overall, when all sites were pooled, the cumulative dominance of the biomass curve appeared higher than that of the abundance curve. For the separate bioregions and transition zone, the east and south-east regions suggested low disturbance levels, as indicated by the proximity of the abundance and biomass. The south and west coast indicated relative stability or less disturbance as indicated by the biomass curves lying on top of the abundance curves. On the other hand, the south-west ABC curves suggested a disturbed system as indicated by the abundance curve being notably higher than the biomass curve.

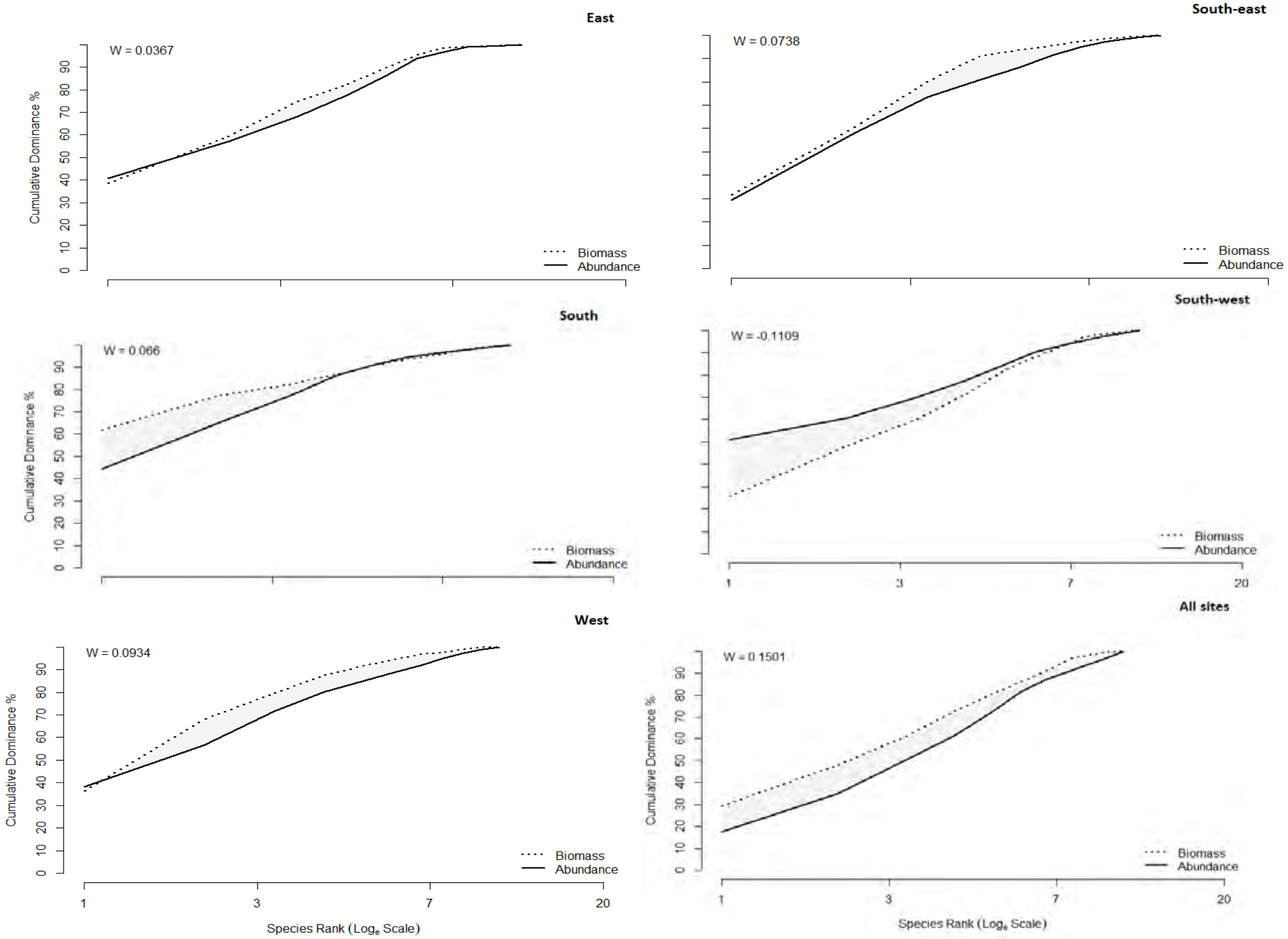


Fig.3.1. Combined k-dominance curves of biomass and abundance and the ABC index values for each bioregion and across all sites. Species are ranked in order of importance on the x-axis (logarithmic scale) with percentage dominance on the y-axis (cumulative scale).

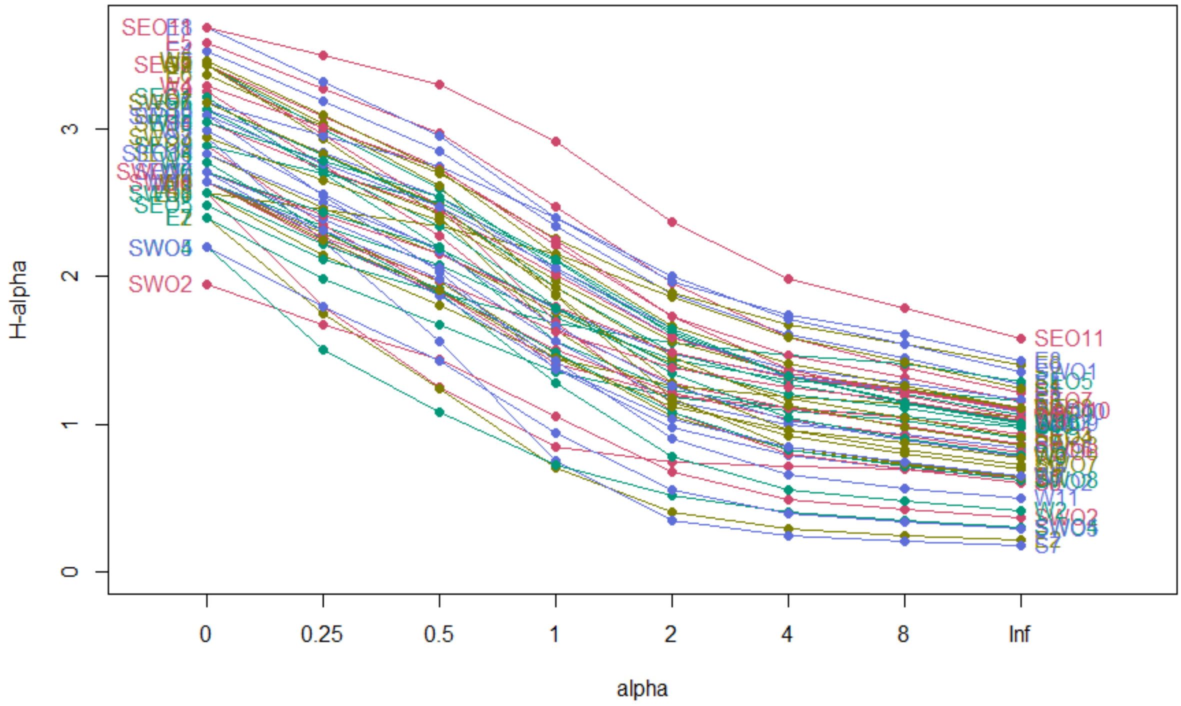


Fig.3.2. Combined Rényi diversity plot showing diversity slope for each sampled site.

A combined Rényi diversity plot for all sites indicated the south-east and east coasts to have the highest diversity (Fig.3.3). These sites include Kidd's Beach (SEO11), Umhlanga (E5), and Margate (E8).

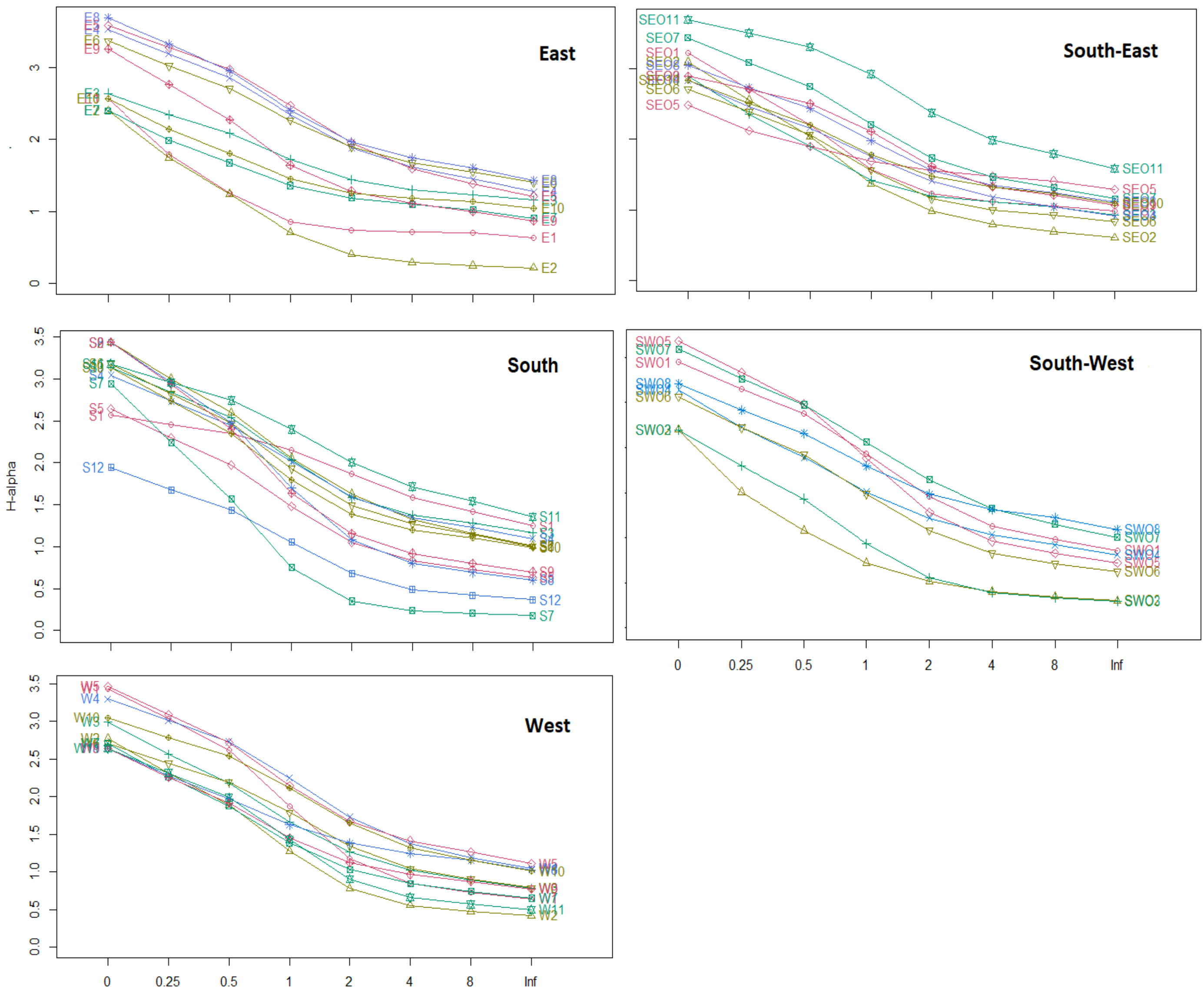


Fig.3.3. A Rényi diversity plot highlighting the variation in species diversity and evenness for each site within each bioregion. Each panel is labelled according to the bioregion.

The Rényi diversity plots show species diversity and evenness for each sampled site (Fig.3.4**)**. Within the transitional zone site, SEO11 and SWO8 (Kidd's Beach, -33.152581°, 27.700416° and Fish Hoek, -34.143593°, 18.436926°, respectively) contained the highest diversity. On the other hand, within the main bioregions, sites E2 and S7 (Cape Vidal, -28.143895, 32.556132 and Harold's Bay -34.056321°, 22.400024°, respectively) exhibited the least diversity (Fig.3.4**)**. Based on the higher alpha values (i.e., a range of 2.5–3.5), all profiles show that many sites have a significant count of dominant species.

The taxonomic diversity indices, i.e., Shannon diversity (*H*) and Pielou's evenness (*J*), revealed similar patterns when weighted with either biomass or abundance. Both metrics showed the east coast's diversity and evenness was significantly higher than the rest of the bioregions and trans-regions. Further, there was a notable decrease in (*H*) and (*J*) index values from the east to the west. Both indices were significantly correlated with latitude, min, mean and max temperature, and chl-*a* ($p<0.05$). Further, a line graph also showed notable site-to-site variability in all 4 taxonomic indices (Fig.S3.1). A general trend observed was that for richness (*S*) and diversity (*H*), the main bioregions exhibited the highest peaks. On the other hand, Simpson's dominance (*D*) showed no significant differences across the biogeographic gradient. Overall, the south-west overlap indicated the lowest values across all taxon-based indices.

3.3.3. Biogeographic patterns of community trait composition

Multivariate dispersion of community trait composition also referred to as community-weighted means CWM of development traits weighted by both abundances and biomass showed no significant differences across bioregions and transition zones. However, the east coast did not overlap with the south-west and west regions (i.e., for development traits weighted by biomass, Fig.3.5E). Further, there was a significant overlap in the ellipses of CWM for reproduction traits weighted by abundance data across all regions. Likewise, for CWM of development traits weighted by abundance, the *p*-adjusted Tukey's HSD *post hoc* test showed no differences across all bioregions.

On the other hand, there were significant differences among regions for the suite of reproduction traits weighted by biomass($p=0.004$). A Tukey's *post hoc* with p-adjusted showed some regions marginally different i.e., south and south-east regions ($p=0.04$), west and south-east ($p=0.04$). Likewise, the CWM of reproduction traits (weighted by abundances) differed significantly between the east and west coasts ($p= 0.04$). Non-overlapping ellipses suggest differences in community trait composition, for example, between the east and south-west regions (Fig.3.5C).

In addition, significant correlations were observed between traits and environmental variables. The Mantel tests showed a significant correlation between latitude and CWM for each suite of traits, reproduction traits (Mantel r=0.166, $p=0.002$), development traits (Mantel r=0.1158, $p=0.007$). Moreover, there was a significant correlation between temperature and CWM for each suite of traits, reproduction traits (Mantel r=0.2133, $p=0.001$), and development traits (Mantel r=0.1243, $p=0.001$). However, there was no correlation between chl-*a* and CWM for development traits (Mantel r=0.0595, $p=0.08$), while a significant correlation was observed between chl-*a* and reproduction traits (Mantel r= 0.09876, $p=0.023$).

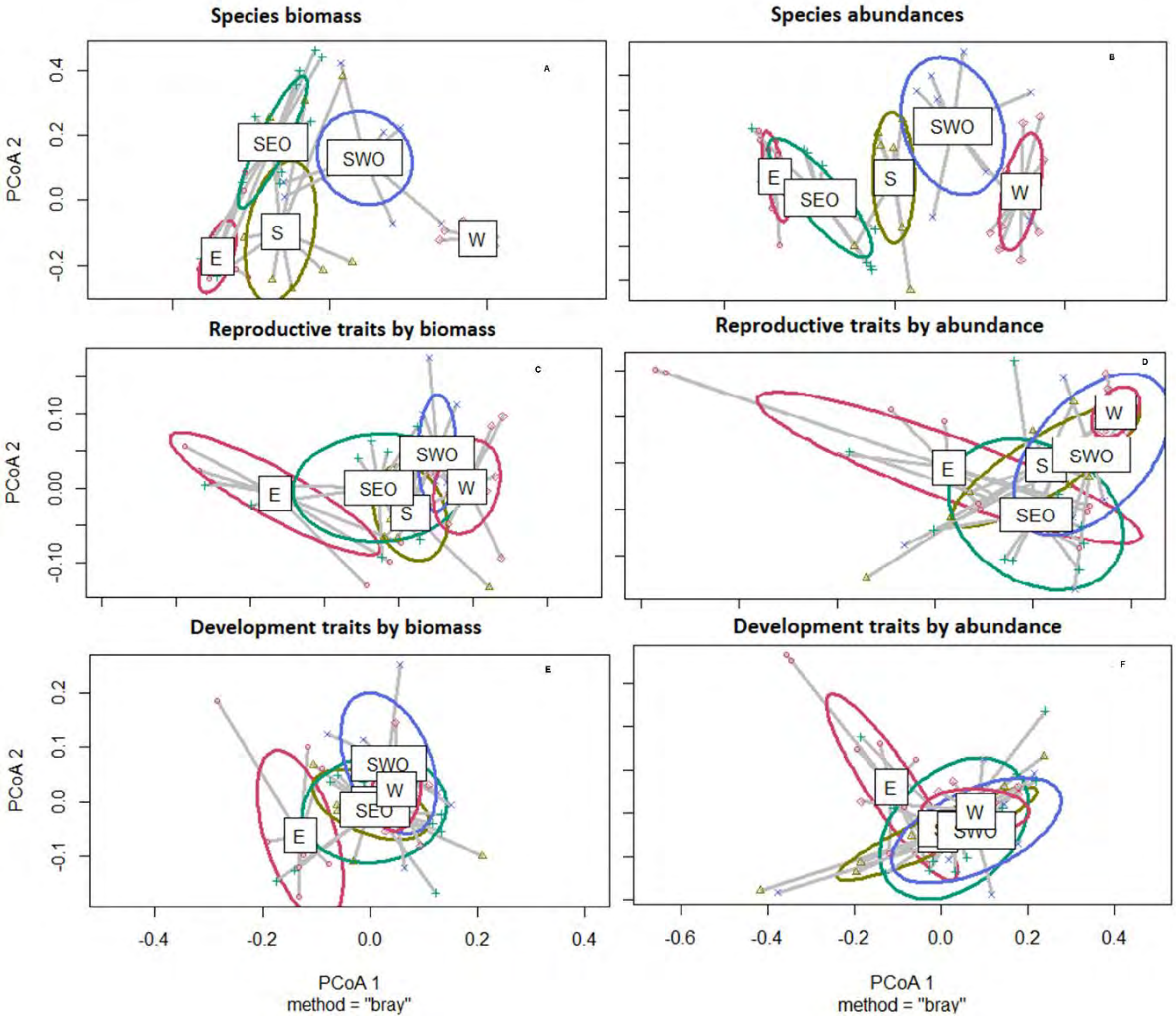


Fig.3.5A-F. A visual presentation of the multivariate analyses used to compare taxonomic and functional composition between communities across bioregions. All plots to the left were weighted by biomass and plots to the right by abundance. The top two plots compare ecological distances using biomass *vs* abundance; the middle plots compare ecological distances for the reproduction trait domain based on biomass *vs* abundance. Lastly, the bottom 2 plots compare development traits weighted by biomass *vs* abundance.

A hierarchical cluster analysis comparing the actual species abundance *vs* biomass showed notable differences in patterns across sites (Fig.3.6a & b). Most sites clustered together by bioregion for biomass data, e.g., the west coast. Further, the sister clades of both transition zones were in the closest proximity. In contrast, species abundances did not show similar patterns.

Another hierarchical cluster analysis comparing the abundance *vs* biomass weighted traits showed notable differences in patterns across sites. For example, when CWM was weighted by biomass, the main bioregions, particularly sites within the west coast, clustered together (Fig.3.7a). When these findings were compared with abundance-weighted data, no distinct patterns or clusters in sites were observable (Fig.3.7b). Likewise, sites from the main bioregions (especially the west and east coast sites) for CWM weighted by biomass formed distinct clusters. In addition, the sites from both transition zones (i.e., the SEO and SWO) also clustered together.

Lastly, when the CWM for reproduction traits was weighted by abundances, the hierarchical cluster analysis showed no similar patterns in dominant trait composition for sites in closest proximity within bioregions suggesting similar abundance patterns compared to sites farther from each other within the same bioregions (Fig.3.8a & b).

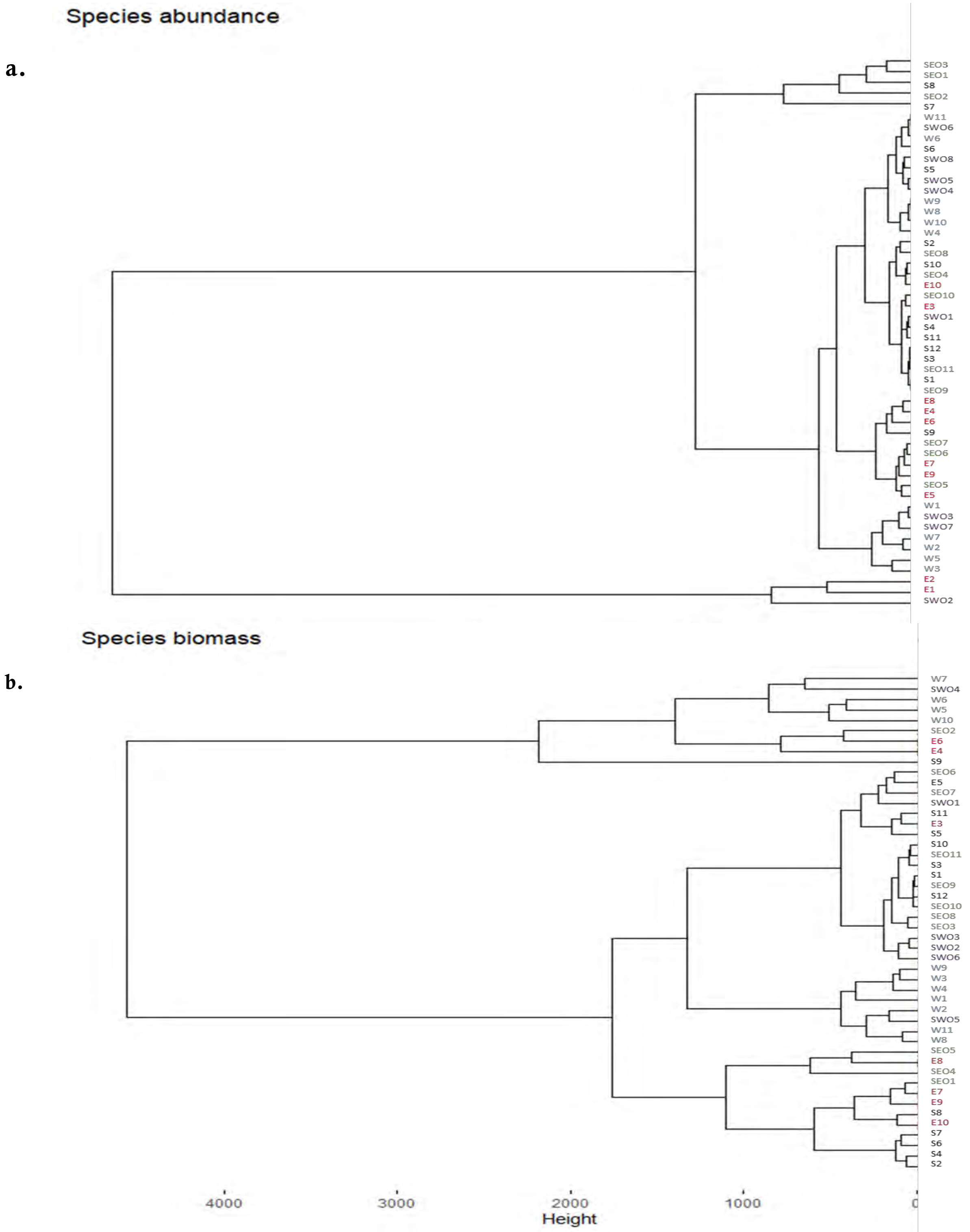


Fig.3.6. Hierarchical cluster plots showing species abundance *vs* biomass similarities among sites. Height represents the ecological distance metric at which the clusters are formed.

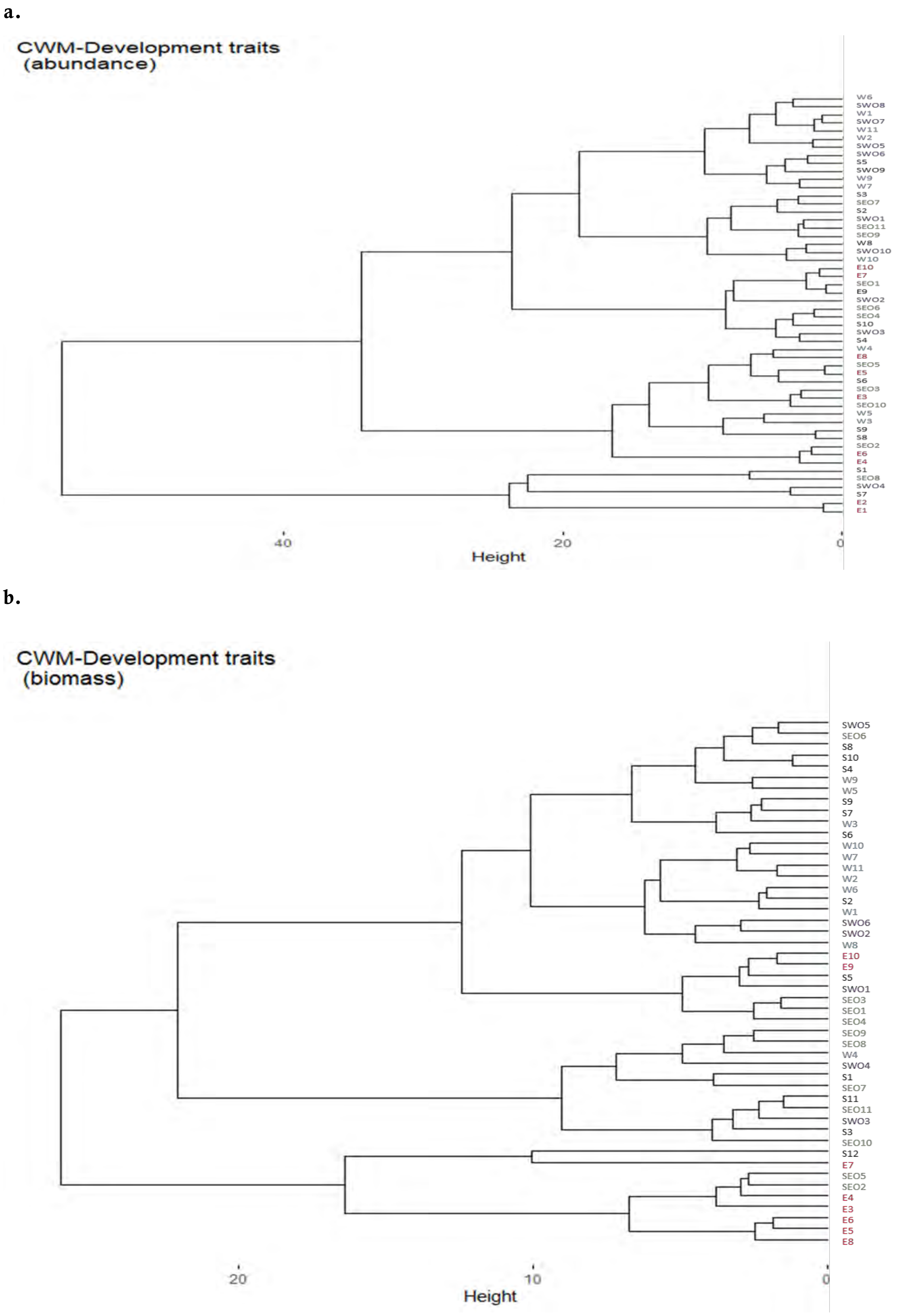


Fig.3.7. Hierarchical cluster plots comparing abundance *vs* biomass weighted CWM of development traits similarities among sites. Height =represents the ecological distance metric at which the clusters are formed.

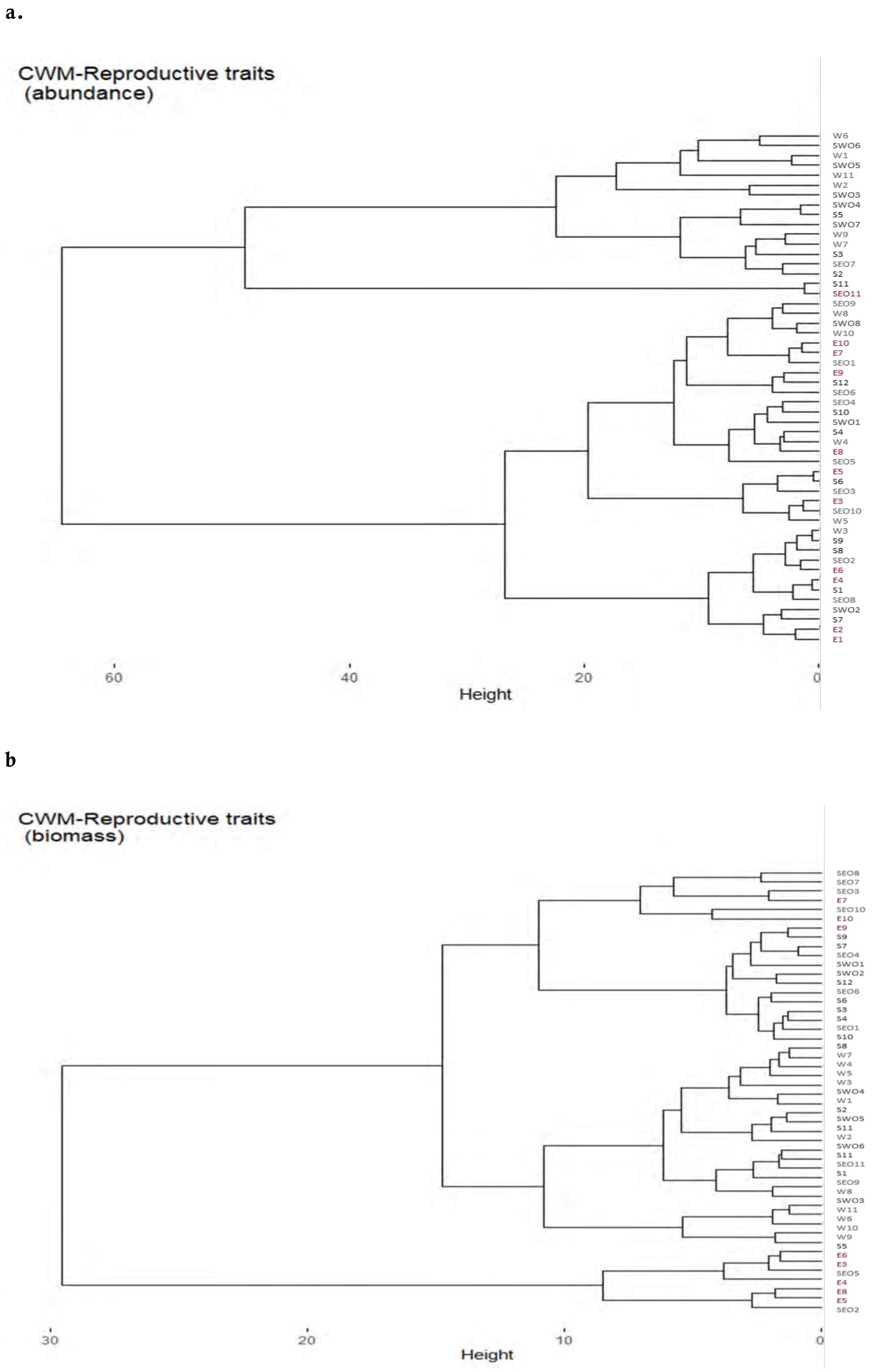


Fig.3.8. Hierarchical cluster plots comparing abundance *vs* biomass weighted CWM of reproduction traits among sites. Height =represents the ecological distance metric at which the clusters are formed.

No distinct patterns were observed between the development traits (weighted by biomass) and sites/ bioregions (Fig.3.9.1). For example, sites on the west coasts and SEO shared similar dominant trait compositions e.g., grazer and herbivore feeders (t1.2), deposit feeders (t1.3), and species with intermediate body form (t5.2). Lastly, due to the assumed importance of biomass over abundance in predicting ecosystem functioning, the biomass results are reported here while the CWM weighted by abundance is reported in Supplementary Information (Fig.S3.7).

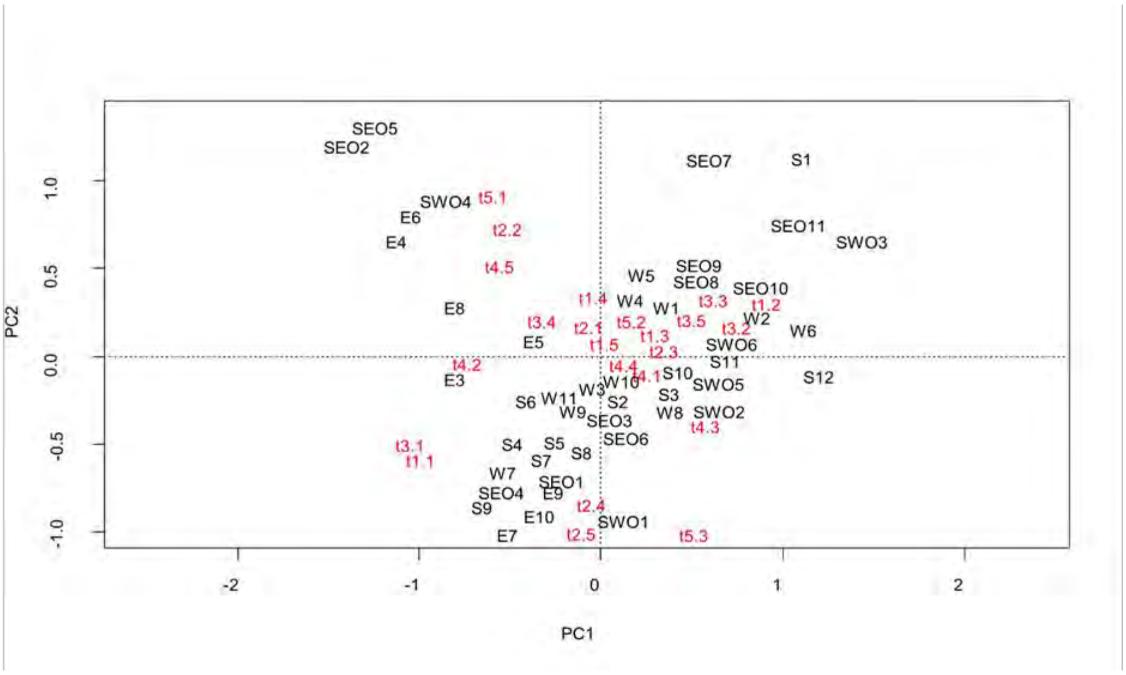


Fig.3.9.1. A PCA ordination showing the association between sites and specific trait modalities within the development trait domain (weighted by biomass). The sites are coded in black where the first letter represents the bioregion e.g., E8 denotes site 8 on the east coast. The trait modalities are indicated in red. Refer to trait codes in Table 2.7.

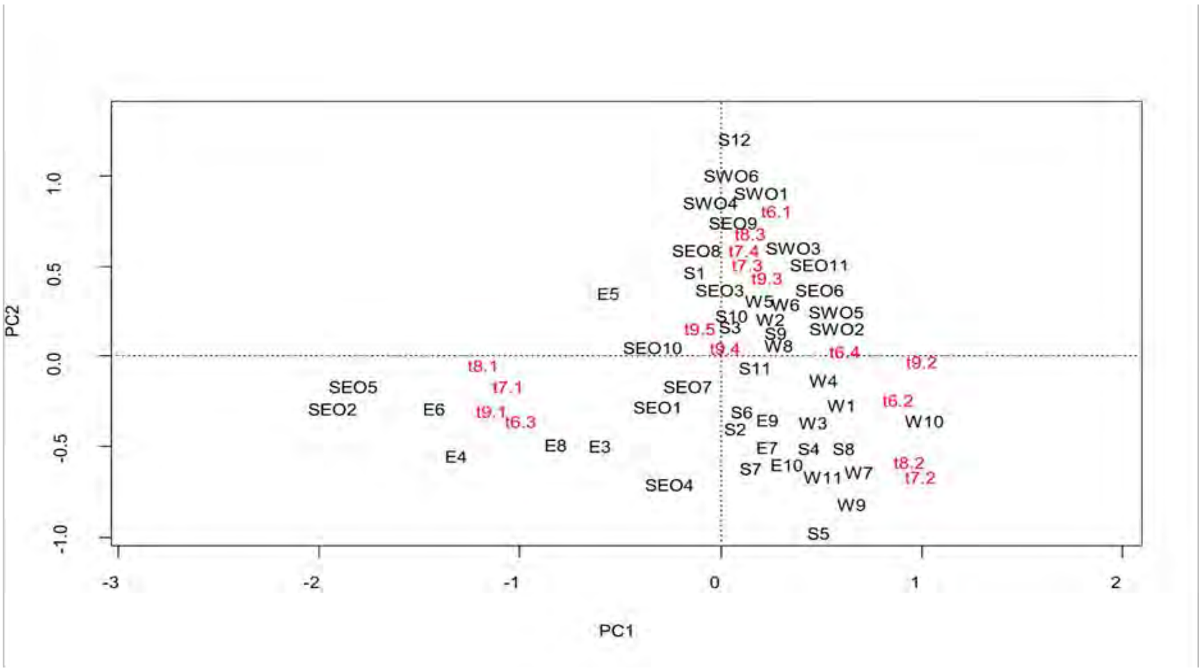


Fig.3.9.2. PCA ordination showing the association between sites and specific trait modalities within the reproduction trait domain (weighted by biomass). The sites are coded in black where the first letter represents the bioregion e.g., W10 represents site 10 on the west coast. The trait modalities are indicated in red. See trait codes in Table 2.7.

The PCA plot for the reproduction trait domain weighted by species biomass (Fig.3.9.2) showed some distinct patterns in trait modality distribution. For example, sites within the south and west bioregions were associated with species with gonochoristic reproductive type (t7.2), species with episodic reproductive frequency (t6.2), species attaining reproductive at larger sizes (t9.4 and t9.5) and species with planktotrophic direct development mechanism (t8.2). Further, the sites within the 2 transition zones predominantly comprised species with traits such as annual, protracted reproductive frequency (t6.1), lecithotrophic development (t8.3), sequential (t7.3) and simultaneous hermaphroditism (t7.4).

3.3.4. Evaluating community trait diversity among bioregions using functional diversity indices based on reproduction traits weighted by species biomass

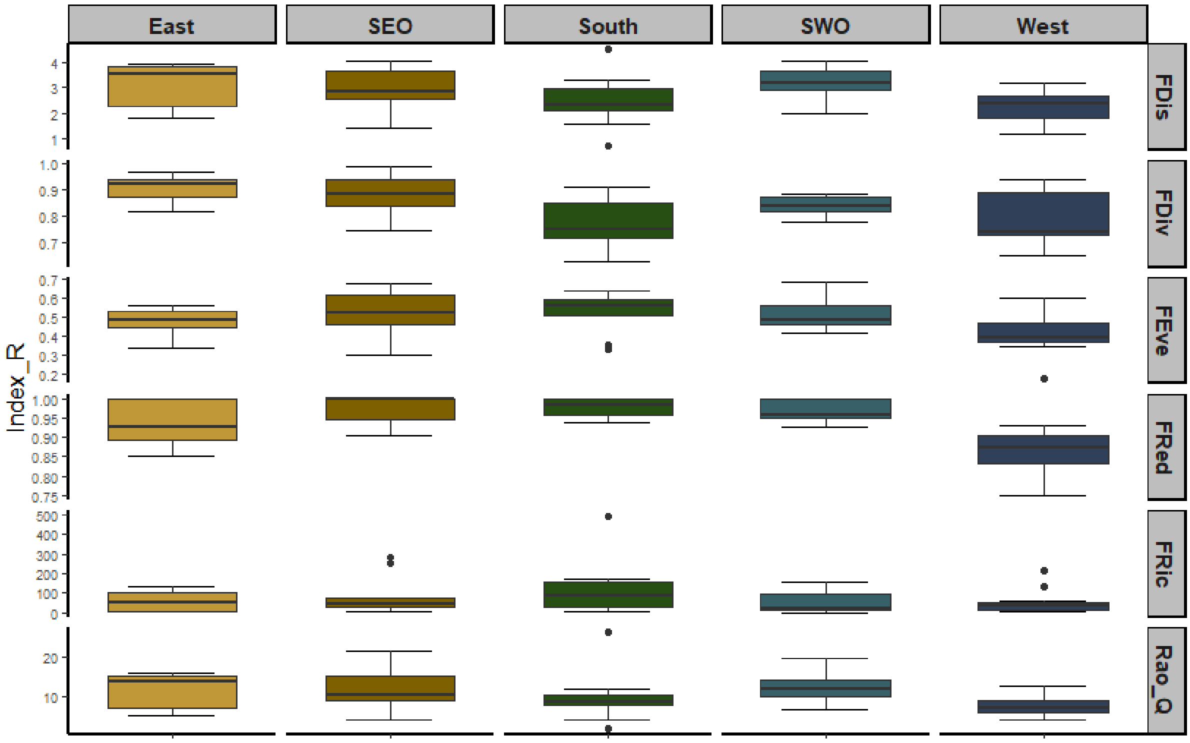


Fig.3.10.1. Boxplots for the various FD indices computed using reproduction traits (weighted by biomass) showing variability across the bioregions and transition zones. The points show outliers.

The one-way ANOVA showed that different functional indices differed across bioregions (Fig.3.10.1). For example, functional evenness (FEve), functional redundancy (FRed) and functional divergence (FDiv) were significantly different across bioregions (p<0.0001). For reproduction traits weighted by abundances FDiv for the east and SEO was significantly higher than the other 3 bioregions. FDiv also showed higher variability on the SWO and west regions than the eastern sites (Figs.S3.2 & S3.3). On the other hand, for biomass weighted traits, the east coast was significantly different from the south and west coasts. (Fig.3.10.1 and Fig.S3.6). In addition, the (FRed) index weighted by biomass was significantly lower (p<0.0001) for the west coast in comparison to the other two bioregions and the transition zones (Fig.3.10.1). The Tukey's *post hoc* showed that the FEve was significantly different between SWO *vs* the south and SEO (p<0.006) but not different from the east and west coasts. Functional dispersion (FDis) was marginally different across bioregions (p<0.05). Although indices such as functional richness

(FRic) and functional evenness (FEve) did not differ significantly among bioregions a site-to-site comparison showed that some of the highest peaks in FRic, and FEve among reproduction traits occurred on the SEO region (Fig.S3.2). Rao's Q was also highly variable across sites; however, some of the highest readings were recorded within transition zones, e.g., sites 9 and 11 along with the SEO and site 7 along the SWO.

3.3.5. Evaluating community trait diversity among bioregions using functional diversity indices based on development traits weighted by species biomass

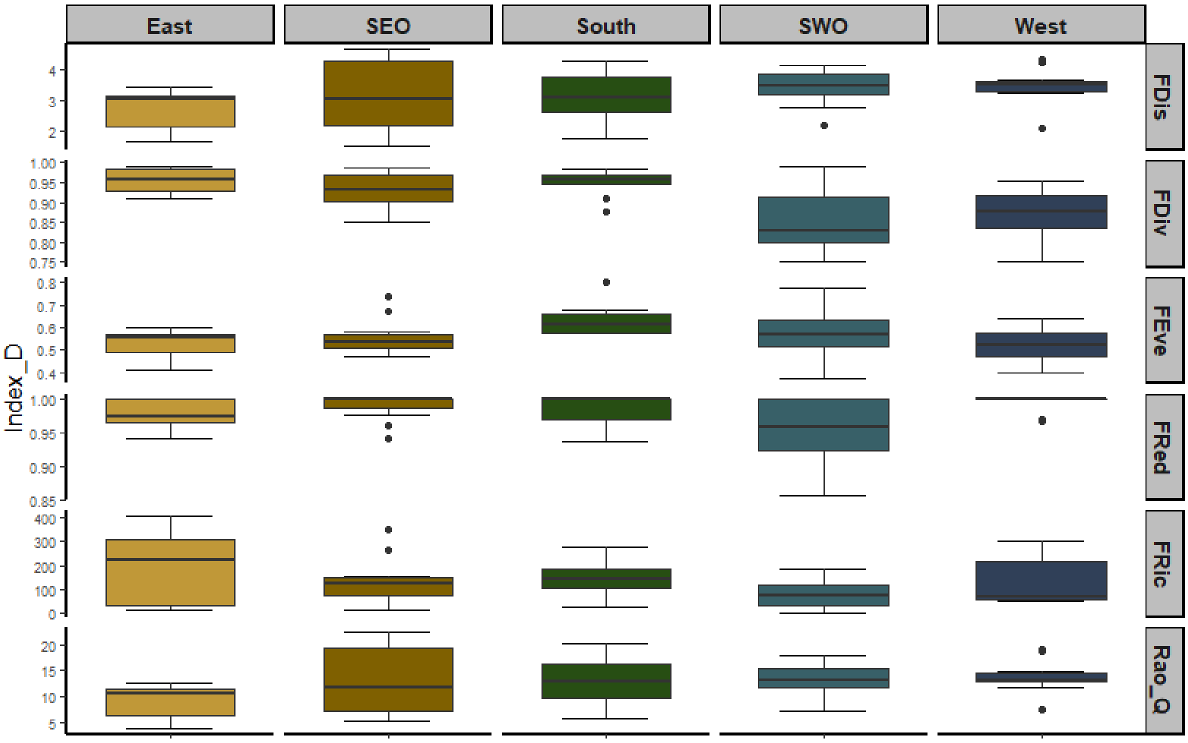


Fig.3.10.2. Boxplots for the various FD indices computed using development traits (weighted by biomass) showing variability across the bioregions and transition zones. The points show outliers.

The functional dissimilarity index (Rao's Q) was notably lower for the east coast and the SEO for the development trait domain however, there were no differences among bioregions (Fig.3.10.2). Further, the SEO, south, SWO, and west did not significantly differ in the size of the dissimilarity metric. Additionally, the *post hoc* tests also revealed some biogeographically linked differences in Rao's Q, FRed, and FDis metrics. Based on all FD indices except FDiv, the sites farthest east (i.e., E1 and E2) had the lowest FD indices. ANOVA showed FDiv and FRed were significantly different across bioregions, $p<0.0001$ and $p< 0.01$, respectively. In addition, SWO exhibited the lowest FRic. FRed in development traits was highest on the SEO and west coasts, while FEve was highest on the east and south coasts (Figs.S3.4 and S3.5). Tukey's *post hoc* tests revealed that the two transition zones differed significantly in FRed. Lastly, the FDiv for the east and south-east coasts was notably higher and less variable across sites in comparison to that of the west and SWO regions. Lastly, for both suites of traits, the east and SWO bioregions had higher FRed than the other regions (SEO, south, and west). Rao's Q and FDis exhibited similar patterns, i.e., both metrics differed significantly between the east coast and the SEO, with higher dissimilarity on the SEO than the east. In contrast, both metrics were similar among the east, south, SWO, and west.

3.4. Discussion

The two different understandings of how ecological processes (stochastic and deterministic) govern community assemblages come from one of two broad models, which differ fundamentally in their perspectives of the role of species' demographic characteristics (Sommer et al., 2014). The former proposes that species are ecologically equal, and coexistence patterns result from random demographic processes, dispersal limitation, and ecological drift (Hubbell, 2001). On the other hand, deterministic niche-based theories explain the variation of community structure based on interspecific trade-offs and stabilising mechanisms that facilitate coexistence (Chase & Myers, 2011). While it is widely acknowledged that deterministic and stochastic processes occur concurrently, their balance in their relative influence continues to fuel contemporary debate (Chase & Myers, 2011; Dini-Andreote et al., 2015).

The deterministic theory hypothesises that ecosystem functioning, or ecosystem processes may be driven by the traits of the most dominant species or by niche complementarity (as determined by either abundance or biomass weights), with the environment acting as a bottleneck to the persistence of these traits. Whether or not a species can pass through this environmental filter depends on its functional traits. On this premise, I conducted a large-scale study to assess how species distribution (taxon identity) and functional distribution (biological trait identity) respond to the environment, subsequently influencing secondary production and overall ecosystem functioning. Because most coastal species significantly respond to environmental parameters such as temperature, I evaluated species distribution patterns and community structure in response to nearshore SST and chl-*a* based on species functional traits. Questions concerning trait distribution are also particularly pertinent to ecosystems at the transition of biogeographical zones, which are often understood by the assumptions of these two hypotheses of the deterministic theory. In most instances, they show different demographic characteristics from those in main bioregions (Sommer et al., 2014).

The first step was to evaluate the species diversity patterns based on taxonomic diversity indices across sites and bioregions. This was done because it is widely suggested that one fundamental aspect to consider when comparing the structure of complex ecological networks across environmental gradients is species richness (Lurgi et al., 2020). Several aspects of network structure are influenced by changes in species richness and how connected these species are (Bengtsson, 1994; Riede et al., 2010; Dunne et al., 2013). Also, based on basic food web ecology, the average number of links per species increases as communities become larger (Riede et al., 2010). However, although species richness is critical, there is a growing consensus that the presence and survival of species in an ecosystem depend on the ability of the species themselves to maximise fitness, growth, and reproduction within that given environment (Pecuchet et al., 2016). This fitness has been linked to the functional characteristics of the species, also termed biological traits, and may be driven by the environment. The premise of trait-based ecology seeks to condense species into a few functional traits (Verberk et al., 2008). However, because knowledge of the species' identity is the first critical to place them into trait categories, all species in this study were identified to the lowest taxonomic level possible.

3.4.1. Species diversity and functional trait distribution patterns

The patterns in species diversity indices among the bioregions did not mirror the patterns observed in functional diversity indices. This is similar to results obtained by other authors, who found that the response of functional diversity to environmental changes is not closely related to species diversity (Bílá et al., 2014; Šímová et al., 2015; Niu et al., 2016). For example, the highest species diversity and richness peaks were recorded at sites within the main bioregions (Fig. S3.1). This is contrary to FRic and FEve, which peaked in the transition zones (Figs.S3.2 and S3.3). FDis was also relatively higher on sites on the SEO region. At the same time, FRed was notably high in both transition zones and the west coast, with the latter recording the lowest species diversity.

Moreover, the Renyi diversity plots revealed many intersecting sites/profiles, meaning many sites could not be ranked from highest to lowest diversity (Figs.3.3 and 3.4). However, all profiles showed a steep downward slope from left to right, indicating that many sites are clearly dominated by a few species. This was corroborated by the significant differences in FDiv across bioregions. FDiv reveals how abundances are distributed on the outer margins of the functional space, weighted by functional richness (Mason et al., 2005). In this sense, high levels of functional divergence recorded on the east and SEO bioregions suggest a high degree of niche differentiation among dominant species within communities (Dolbeth et al., 2016). On the other hand, sites within the west and SWO showed large variability in FDiv across sites for both trait domains (Figs.S3.2, S3.3, S3.4, and S3.5). In addition, environmental filtering, such as brought about by large shifts in temperature, can decrease functional divergence due to the increased abundance of optimally adapted species, and I expected this trend in biogeographic transition zones. Needless to say, the similarity in patterns between FDis and Rao's Q was expected, given that both indices aim at estimating the dispersion of species in trait space, weighted by their relative abundances or biomass.

Another possible explanation for the low FDiv is the Environmental favourability hypothesis which predicts redundancy in species and their functional traits. The hypothesis suggests that sites or landscapes with favourable environmental conditions for native species potentially also have favourable conditions for non-native species (Davies et al., 2007), which may, in turn, have similar functional traits. In natural localised communities, species are rarely assumed to be functionally different (de Bello et al., 2006; Petchey & Gaston, 2006), and as a result, it is reasonable to expect that a certain degree of functional redundancy is always present (Naeem, 1998), this subsequently reduces functional divergence. In this study, a moderate level of functional redundancy (an approximate index of ~0.5) was maintained at the regional scale when the range-center and range-edge sites were compared. This finding illustrates that functional redundancy in these rocky shores may be an insurance against the diverse environmental conditions known to prevail in these ecosystems, thereby maintaining ecosystem processes and services (Diaz et al., 2007) at regional scales. This concept of stability is to some extent corroborated by the ABC curves (for the species with the highest abundances), where the biomass curves were relatively higher than the abundance curves across all bioregions with the exception of the SWO (Fig.3.1).

In addition, the results from this study also indicated the west coast as one of the regions with more consistently higher FRed for most sites for both trait domains than other bioregions (Figs.S3.3 and S.3.4). One explanation for this may be that the Southern Benguela along the west coast has exhibited the highest number (a record of 67 species) of biological invasions to date (Robinson et al., 2020). Further, the west coast is minimally disturbed by anthropogenic factors such as harvesting for subsistence. At the same time, there is higher resource availability due to frequent upwelling episodes in contrast to the east coast. Based on this, one would expect higher species diversity, but it is likely that other factors, such as lack of disturbance, may also be critical in explaining the high functional redundancy through domination of space by relatively few species. This may in turn affect or limit the possibility of other species colonising the west coast, ultimately keeping the species diversity low.

In addition, the within-trait variability among species may also explain how distinct species/ taxon-based diversity was notably variable among bioregions. For example, 10 species of mussels were recorded in this study (Table S2.1.1), and, although their suite of development traits may not vary significantly, there is likely environmentally driven within-trait variability in reproduction traits such as age or size at reproductive maturity or duration of reproductive frequency potentially driving the observed patterns in diversity/composition/presence/abundance across bioregions. As a recommendation, it would be informative to investigate intra-trait variability for different species within communities because, at this stage, the few studies that have investigated this have been limited to laboratory-based work or single-species studies.

In conclusion, the relationship between species diversity and functional diversity is a perpetual debate (Banaszak-Cibicka & Dylewski, 2021). This relationship is largely regulated by the versatility of some species and by functional redundancy. Due to the latter, random species loss, which primarily influences species diversity, is unlikely to affect functional diversity. As a result, although there is a potential relationship between species diversity and functional diversity, this relationship is influenced by a variety of factors. It is known that different components of biodiversity may vary independently of each other along environmental gradients giving insights into the mechanisms that regulate species coexistence.

3.4.2. Community composition: Abundance *vs* biomass-weighted patterns at regional scale

The Shannon diversity and Pielou's evenness indices weighted by both biomass and abundance showed different patterns. For example, there was an overlap in composition based on actual species abundances (i.e., Fig.3.5B) for the east and SEO coasts. However, when traits were weighted by biomass, the bioregions were separate, suggesting a shift in the size of species between regions. The east coast had a higher richness index, suggesting more diverse ecological networks than other regions. This was expected as the east coast is known to be more diverse than the other bioregions (Griffiths et al., 2010). One of their main findings in the study by Griffiths et al. (2010) was that some groups, including fishes, bivalves, gastropods, brachyurans, and echinoderms, become progressively more species rich to the (more tropical) east, whereas other taxa, such as amphipods, isopods, and polychaetes, attain maximum species richness in the temperate southwest. The traits of the sampled species from the east coast fit into the predictions of both the mass ratio and niche complementarity hypotheses, as analysed by CWM and FD indices, respectively. This is based on the results that: (i) FRed was relatively high on the east coast and SEO, (ii) likewise FDiv was also very high i.e., close to 1 (and with fewer fluctuations) for the same bioregions, and (iii) the CWM trait values of both trait domains for the east coast were significantly different from other bioregions. It seems the most dominant traits were also functionally redundant. Based on the hierarchical cluster analyses (Figs.3.7 & 3.8), the sites on the east coast clustered together, suggesting they shared similar redundant and dominant traits.

This study further showed how the SWO species abundances and biomass ellipses (i.e., Fig.3.5A&B) were separated from other the bioregions suggesting some distinct changes or differences from the south and west coast populations. In addition, apart from the analysis of development traits weighted by abundance (i.e., Fig.3.5 C, D, F), the east coast was notably different in both development and reproduction trait domains. This brings me to the conclusion that differences in species diversity, particularly beta diversity, in itself, may mask any underlying or causal mechanisms driving community assemblages. Further, considering the random permutation tests (with 49999 reps), on the combined fourth corner Model 6 highlighting the significant effects of reproduction traits on species persistence (See Chapter 2, Fig.2.6), the results of this study argue against the suggestion that stochastic mechanisms drive species persistence across these different regions.

Contrary to my expectations, there were no differences in community composition (CWM) between any of the transition zones and the main bioregions as the former are considered as "hybrid zones" areas that allow the mixture of taxa belonging to different biogeographic components. Although this is a common assumption, Ferro & Morrone, (2014) point out that such generalisations are not always true for all transition zones. They highlight the fact that the nature of the barrier and taxa under study may not always result in a clear-cut change in species richness and/or composition. Ferro & Morrone (2014) also distinguish two main types of transition zones: (i) subtraction transition zones and (ii) addition transition zones. Firstly, there is a low overlap in species within subtraction zones and progressive loss of taxa from one region to another, and the zones are expected to be depauperate. On the other hand, addition transition zones occur when there is a high overlap of species leading to a species-rich transition zone due to the progressive gain of taxa from each bioregion. Building on this idea, it was worth evaluating these concepts to assess the relative species gains or losses for the transition zones in my study. Looking at the coast of South Africa, I speculate that for the SWO region, the observed species dynamics are driven primarily by species with cold temperate affinities. Examples include the increased presence of mussel species such as *Choromytilus meridionalis* and *Mytilus galloprovincialis,* which also contributed towards the high levels of biomass on the west coast (Table 3.2). The most abundant species, however, was the alien barnacle *Balanus glandula. B. glandula* is an invasive species in the cold and temperate waters of Argentina and Japan (Kado, 2003). Its presence on the South African Atlantic shores, which are influenced by the cold Benguela Current, and its subsequent absence from the warmer Indian Ocean coast, are indicative of its adaptation to a cold-water habitat (Laird & Griffiths, 2008). Its present expansion and dominance in its new South African territory indicates its competitive superiority over *Chthamalus dentatus* in the intertidal region. While *Balanus glandula* likely penetrated into an under-utilised niche on this coast, it appears to also have the ability to out-compete *C. dentatus* (Simon-Blecher et al., 2008).

Considering the other transition zone on the coastline of South Africa, although there are debates over the geographic limits of the SEO, my results (Fig.3.5A-F) suggest that both the trait modalities under both reproduction and development [weighted by biomass] trait domains and to a lesser extent actual taxonomic identity of species within the SEO reflect or show greater affinity to the subtropical environment. For example, for the reproduction traits, the east coast only overlaps with the south-east coast (Fig.3.5C). Further, this was true to a lesser extent for the development traits, although there is a slight overlap of 3 regions, including the south coast (Fig.3.5E). In essence, using the terminology of Ferro & Morrone (2014), there is a higher chance of addition from the subtropical and low subtraction from the south coast. I suggest the latter because the south coast is known for its high level of endemism. Thus, one would, to some extent, expect fewer species with higher tolerances to warm temperate systems to disperse to the subtropical environment. Reverting to the SWO, I speculate that the SWO seems to be a classic example of a subtraction transition zone as it recorded the least species counts in comparison to other bioregions. The SWO community structure comprised mostly of *Balanus glandula* which is a small-sized but high reproductive turnover species. This species showed the highest abundance but very low biomass. In addition, based on the importance of the mass-ratio hypothesis to understanding ecosystem functioning and persistence, the abundance biomass comparison (ABC) curves were computed using species abundances and biomass to predict the potential environmental stress level across the bioregions. The responses to changing environmental conditions can be expressed by changes in their population structure and composition through changes in abundance and biomass (Wijeyaratne & Bellanthudawa, 2018). In the broadest sense, I speculate that the SWO showed signs of instability according to the assumptions of ABC curves (Warwick, 1986). The reasons for this speculation are attributed to the challenges associated with the ABC methodology. These include the inappropriate classification of stress due to the susceptibility of the procedure to the absence, or presence, of several or even single dominant species. For example, considering the placement of the abundance curve, the unexpected presence of abundance-dominating species, such as after dense recruitment of small-sized individuals, may result in a community considered unstressed being classified as stressed (see Beukema, 1988). In this particular study, the barnacle *Balanus glandula* had the highest abundance at the time of sampling. In essence, the absence of expected abundance-dominating species, or the presence of unexpected biomass-dominating species, may occur due to small shifts in relative dominance of individuals or biomass in communities with low absolute numbers of individuals, or biomass, resulting in a community considered stressed being classified as unstressed. I therefore conclude that applying abundance/biomass comparison curves to communities across large spatial scales may be a weak tool for the detection of environmental-related gradients in rocky shore assemblages, however it may be useful in exploratory phases.

Overall, the most common feeding type along the entire coast of South Africa consisted of filter-feeders and grazer/herbivorous invertebrates and these two modalities also constituted the most/highest biomass (Tables 3.1 and 3.2). Across different bioregions however, the ratios of these two modalities changed slightly and included other trait modalities such as deposit feeders, and carnivorous/predatory/omnivorous species. These species also fall into other trait modalities such as sessile, and intermediate to robust body forms. Also, the east coast had a substantially higher number of filter-feeders while the SEO had a balanced ratio of filter-feeders to grazer/herbivores. The south, SWO and west coasts included deposit feeders and carnivorous/predatory/omnivorous species. On the contrary, the least represented/common feeding modality across the coastline was for scavenging species. Lastly, the two most notable differences between the most abundant and least species abundance and biomass were mostly adult body size and size at reproductivity maturity. The majority of the least abundant species were relatively small in body size and exhibited low biomass.

Looking at the reproduction traits across all bioregions, some of the most common trait modalities for the species with high abundances and biomass included small size at reproductive maturity (<30mm i.e., t9.1 and t9.2), planktotrophic development mechanism, and annual episodic reproductive frequency (t6.2). On the east coast, zoanthid species were amongst those with the highest biomass and abundance; they also possessed traits such as continuous and simultaneous hermaphroditic reproductive frequency and asexual reproductive type. Some studies have linked reproductive frequency or spawning times with geographic location. For example, some limpets on the cool-temperate west coast tend to have a single spawning period, usually in winter (Branch, 1974). On the contrary, limpets from the eastern, warm water locations (i.e., south, and east coasts) either have biannual spawning periodicity with the main reproductive period occurring in summer and autumn, or protracted spawning in which it is difficult to detect seasonality (Henninger & Hodgson, 2001; Nakin & McQuaid, 2016). Although these trait differences could not be fully explored in this study, I speculate that these differences may account for the differences in species reproductive vigour, which may ultimately cause trait trade-offs and spin-offs first at individual level and secondly in overall variation in species presence or absence across communities and across different bioregions or geographical locations.

On the SWO and west coasts, the mussel *Mytilus galloprovincialis* exhibited notably higher abundances and biomass compared to the indigenous *Aulacomya atra* and *Choromytilus meridionalis* most likely because of its higher growth rate, superior reproductive output, and also higher tolerance of desiccation. It has also been observed that *M. galloprovincialis* displaces the limpet *Scutellastra argenvillei* from its primary habitat space (Steffani & Branch, 2005). These competitive interactions between sessile species and limpets are not unusual. Branch (1976) also noted that the barnacles; *Chthamalus dentatus, Octomeris angulosa* and *Tetraclita serrata* compete with *Scutellastra granularis* for space and deny it access to food, resulting in reduced limpet size, growth, and reproductive output. Lastly, in this study, the high *Balanus glandula* abundances maybe an indication of its higher reproductive frequency and leading to its success over the native granular limpet (*S. granularis*). In a nutshell, the use of the ranked abundance analysis showed a variety of species with considerable trait overlap and at the same time some differences in trait combinations among species that allow them to coexist in healthy numbers. Nonetheless, it is important to realise that site-to-site variability brought about by spatial variation may have contributed to the observed results because the analyses were conducted at the bioregion level where a number of sites were pooled together and not at single site level.

3.5. Conclusion

The results obtained for this study showed how species abundances and biomass responded to biogeographic gradients and how their reproduction traits (instead of development traits) may drive some of the observed patterns, particularly across large spatial gradients (100s to 1000s of km) along the coast of South Africa. Comparing abundance *vs* biomass weighted traits, the results showed that the CWM differed slightly across bioregions for each metric. Overall, the filter-feeder species and grazer/herbivore species showed the highest biomasses and abundances. On the other hand, FD indices yielded similar results when either biomass or abundance weighted data were used. Overall, based on the high functional redundancy index across many sites, the rocky shore systems of South Africa by bioregion can be considered as relatively functionally stable and the loss of some species may not negatively affect overall ecosystem functioning. This interpretation is made in the context of biogeographical/environmental influences and may change if other ecosystem processes or services are considered. Lastly, due to the scale of the project design, it is acknowledged that some information was lost by disregarding intra-trait variability, and this information may be needed to fully understand the contribution of species traits to intertidal ecosystem functioning. However, this study is one of the few for the coast of South Africa that goes beyond functional and/or trophic group analysis. In conclusion, both the mass ratio and limiting similarity hypotheses showed complementary effects. Interestingly, different bioregions seemed to conform to the predictions of these two hypotheses independently; however, the mass ratio hypothesis (weighted by species biomass) received stronger support and may be more useful to the interpretation of ecosystem functioning and persistence within rocky shore systems.

3.6. Supplementary Information

3.6.1. Taxonomic- and functional trait-based indices across sites and bioregions

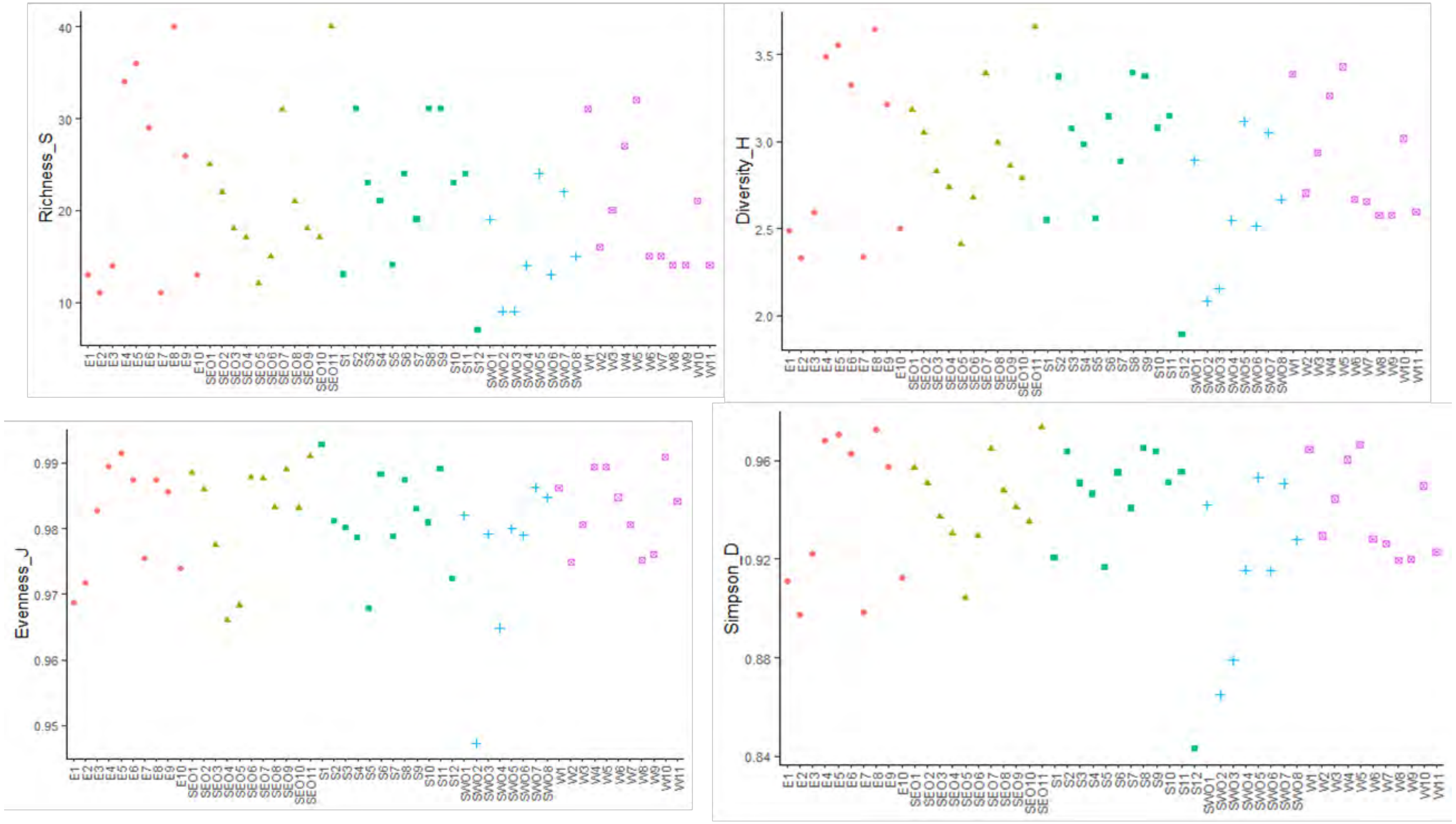


Fig.S3.1. Species diversity indices across sites and bioregions.

3.6.2. Functional diversity indices for the reproduction trait domain across sites and bioregions

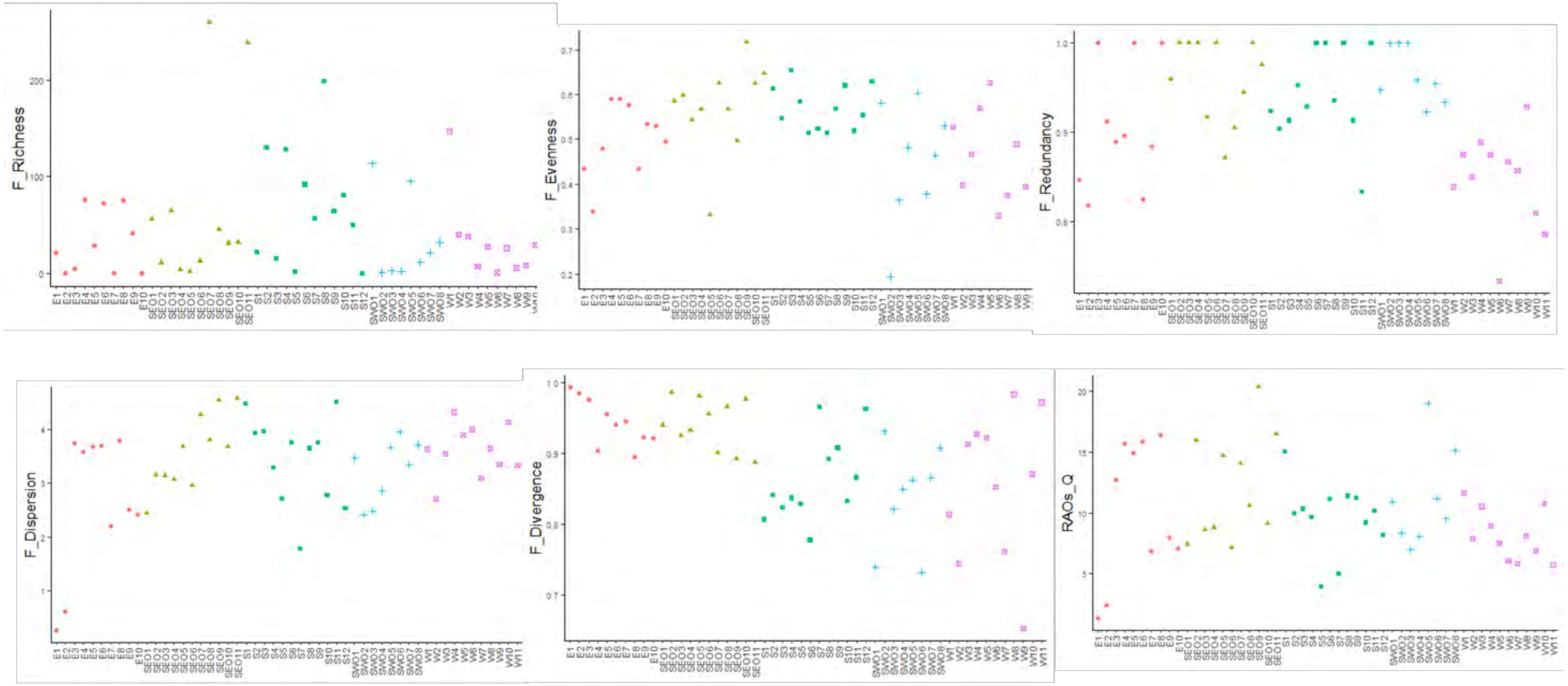


Fig.S3.2. FD indices for reproduction traits weighted by abundance showing patterns across sites and bioregions

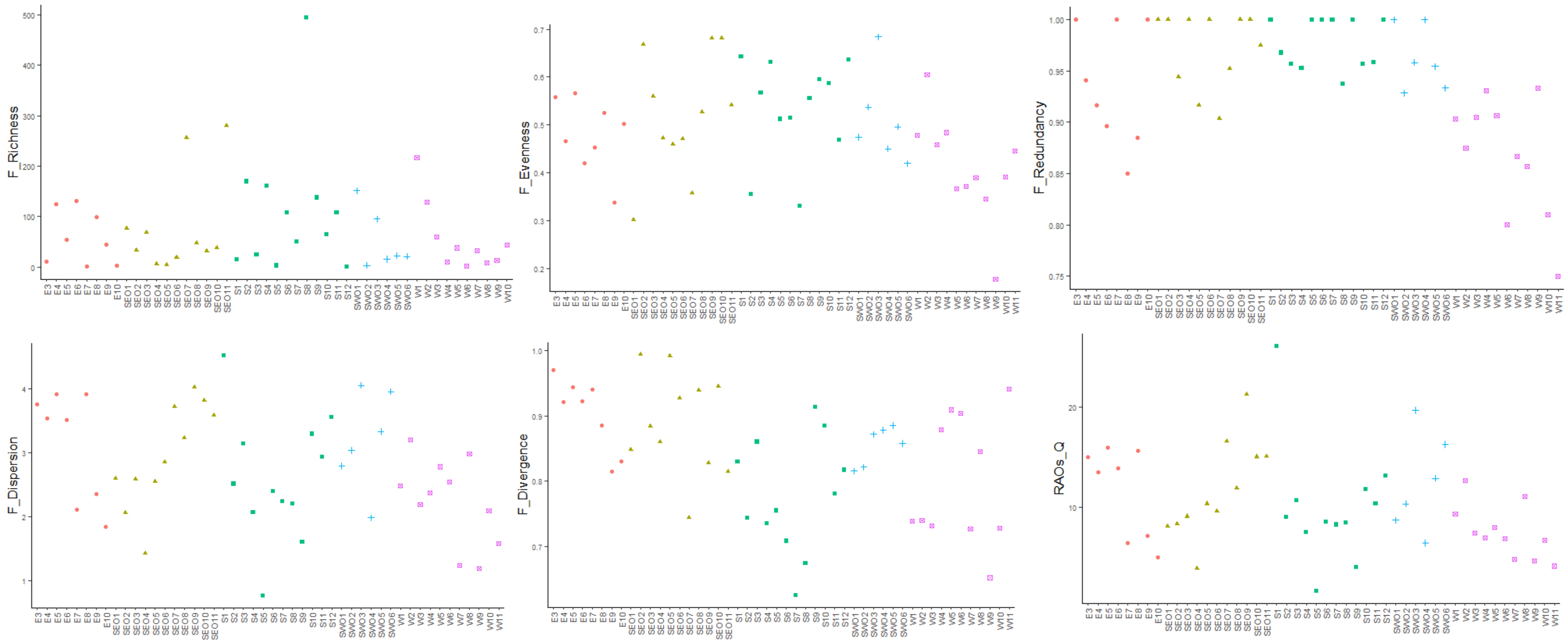


Fig.S3.3. FD indices for reproduction traits weighted by biomass showing patterns across sites and bioregions.

3.6.3. Functional diversity indices for the development trait domain across sites and bioregions

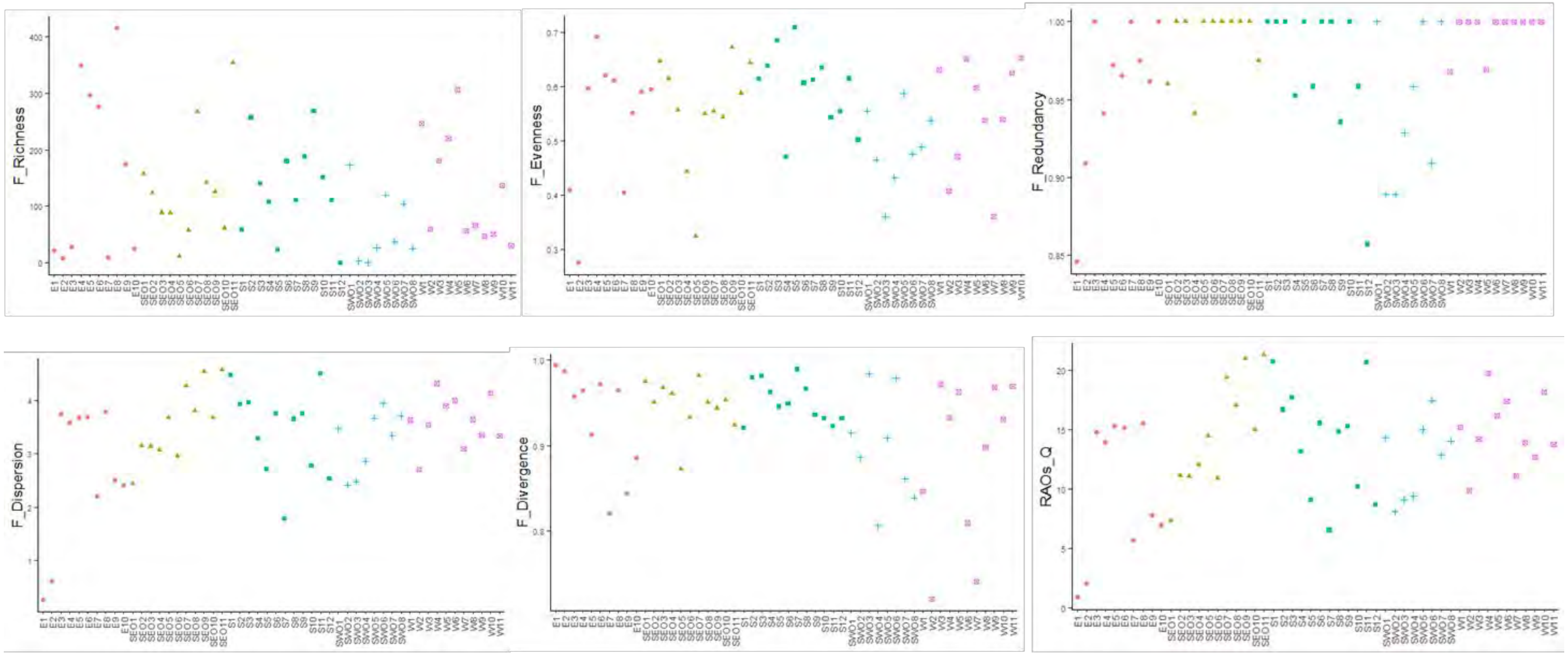


Fig.S3.4. FD indices for development traits weighted by abundance showing patterns across sites and bioregions.

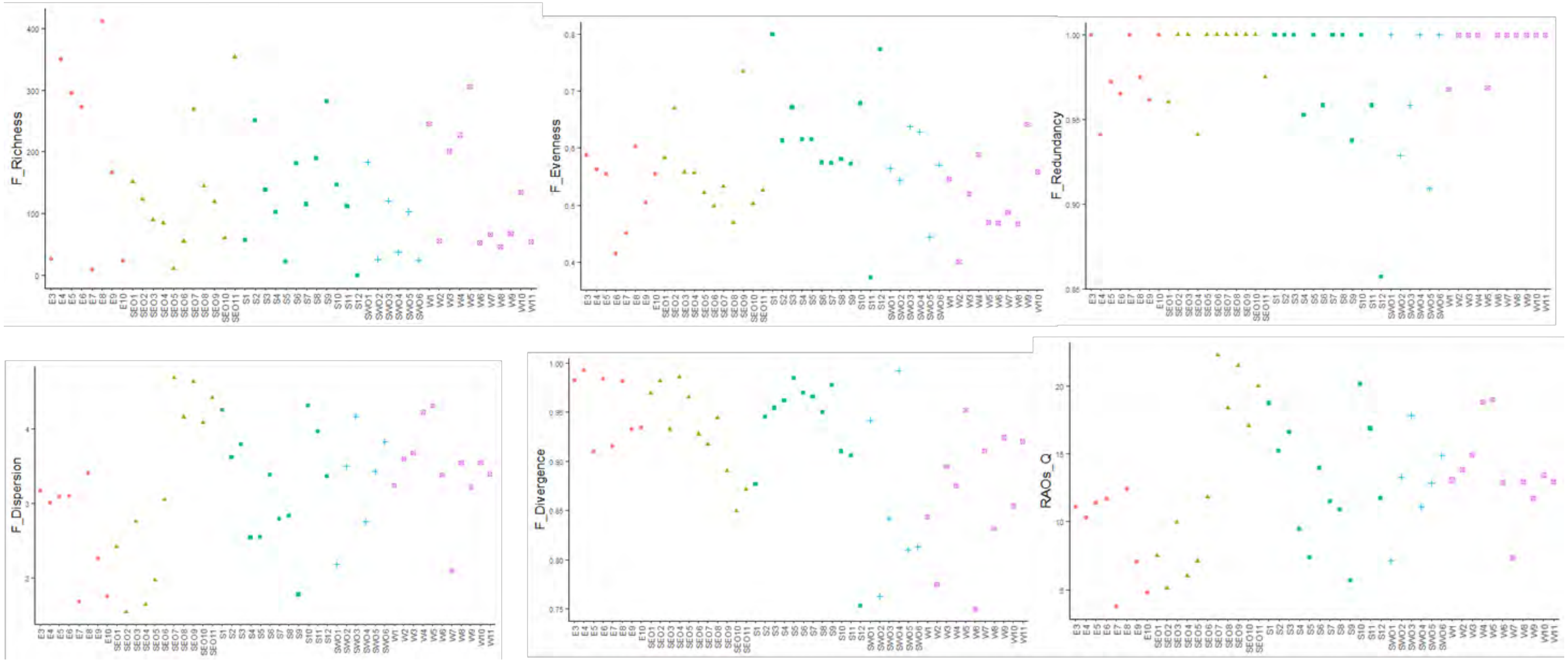


Fig.S3.5. FD indices for development traits weighted by biomass showing patterns across sites and bioregions.

3.6.4. Evaluating community trait diversity among bioregions using functional diversity indices based on development traits weighted by species abundance

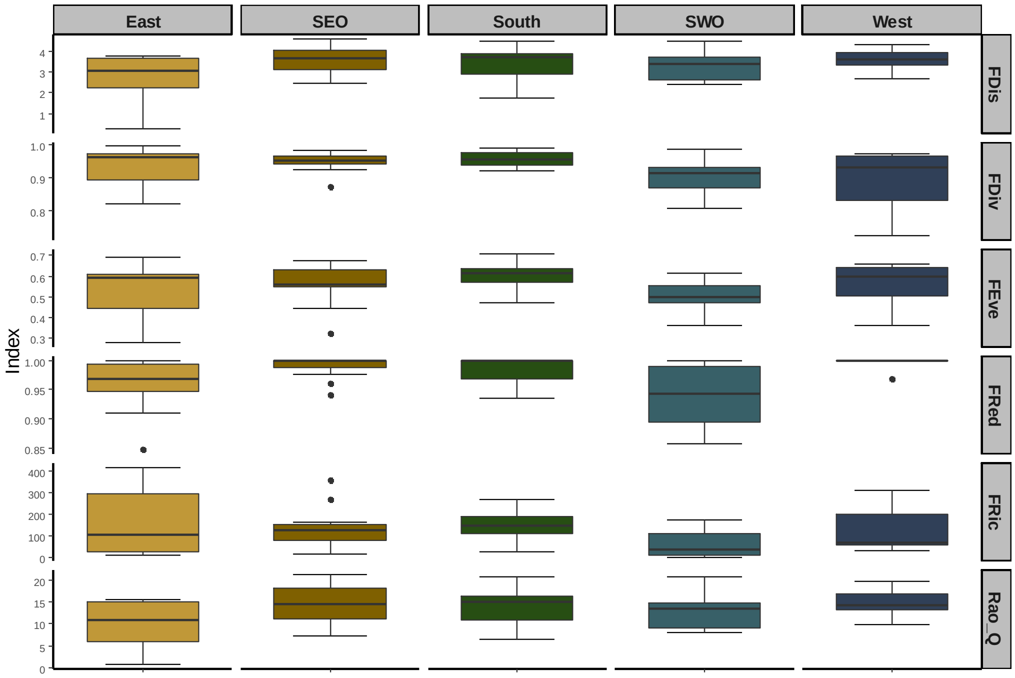


Fig.S3.6.1. Boxplots for the various FD indices computed using development traits (weighted by abundance) showing variability across the bioregions and transition zones. The points show outliers.

The box plots showed similar patterns with (Fig.3.10.1) and no significant changes in functional diversity indices when species abundance data were used. The results showed similar patterns as to when species biomass data were used in computing the FD indices.

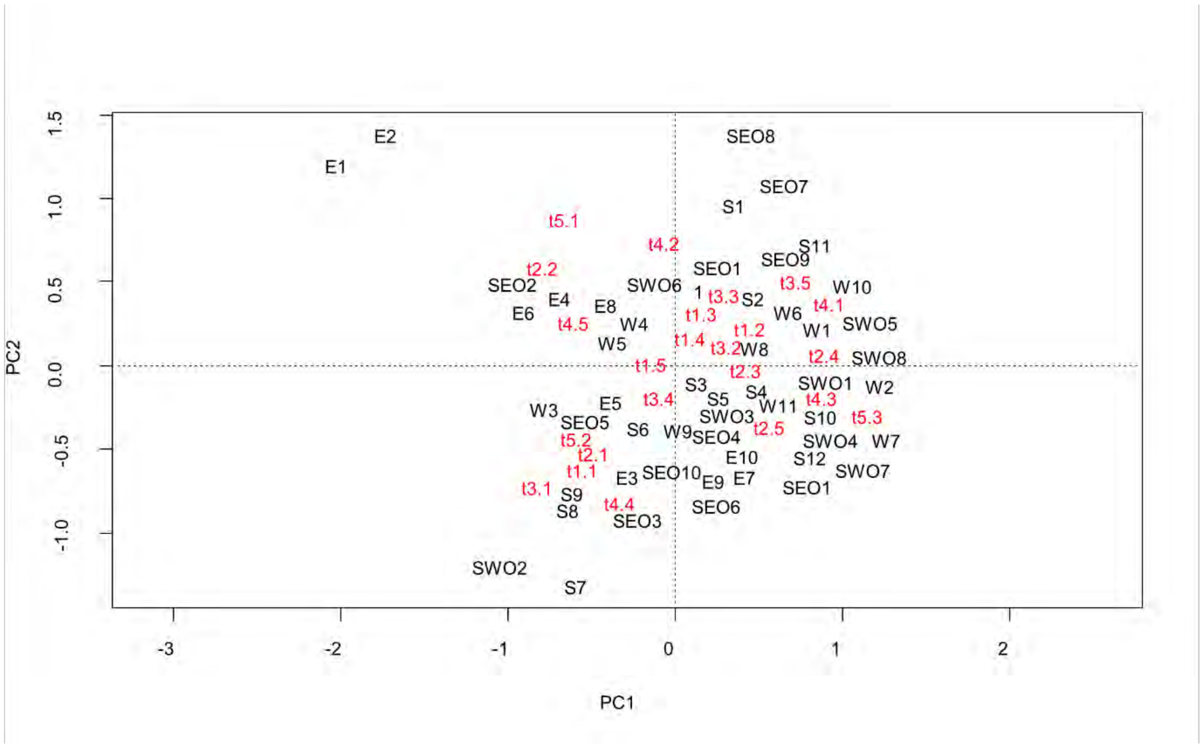


Fig. S3.7. A PCA ordination showing the association between sites and specific trait modalities within the development trait domain (weighted by abundance). The sites are coded in black where the first letter represents the bioregion e.g., E8 denotes site 8 on the east coast. The trait modalities are indicated in red. Refer to trait codes in Table 2.7.

The CWM for each suite of traits (weighted by abundance) were plotted to assess the association between trait modalities and sites using the PCA ordination technique. No clear associative patterns were observed between the development traits and sites (Fig. S3.7). Nonetheless, some patterns were observed. Most transition zones (i.e., SEO and SWO) and sites at the range edge of bioregions (E9, E10, S11, S12) showed similar dominant trait compositions. These traits include species with hard or robust body forms (t5.3), small adult sizes (t2.1), scavengers (t1.5). Further, the majority of the main bioregions particularly the south and west coasts comprised traits modalities such as deposit feeders (t1.3), grazers and herbivores (t1.2), semi-sessile and sessile (t3.2) and crawlers (t3.2).

3.6.5. Evaluating community trait diversity among bioregions using functional diversity indices based on reproduction traits weighted by species abundance

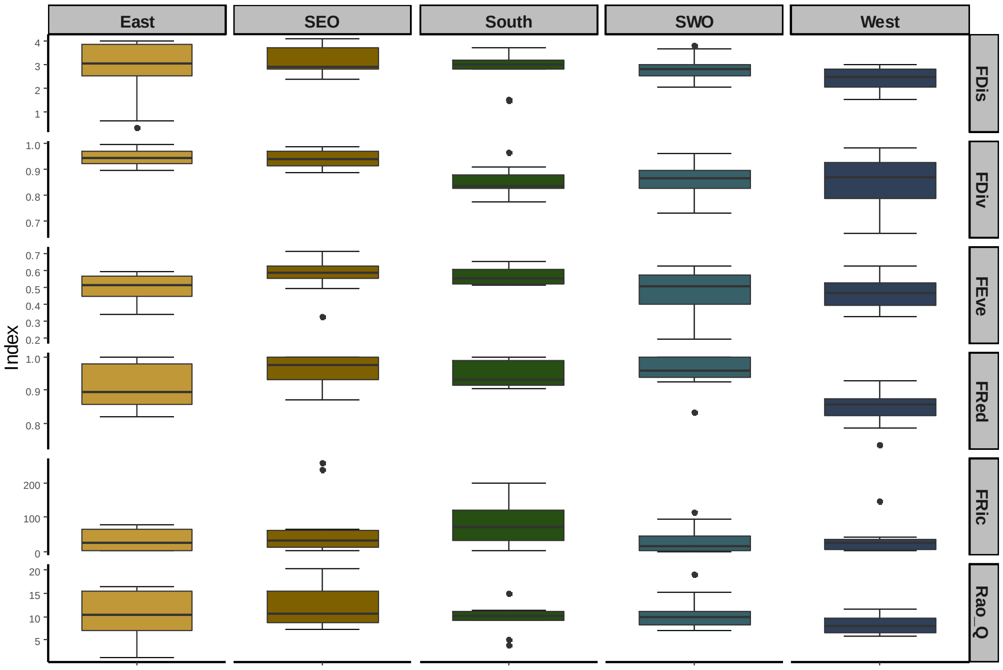


Fig.S3.6.2. Boxplots for the various FD indices computed using reproduction traits (weighted by abundance) showing variability across the bioregions and transition zones. The points show outliers.

The box plots showed no significant differences in patterns of functional diversity indices across bioregions when the analyses were performed using data weighted by species abundances *vs* when weighted by biomass (Fig.3.10.2).

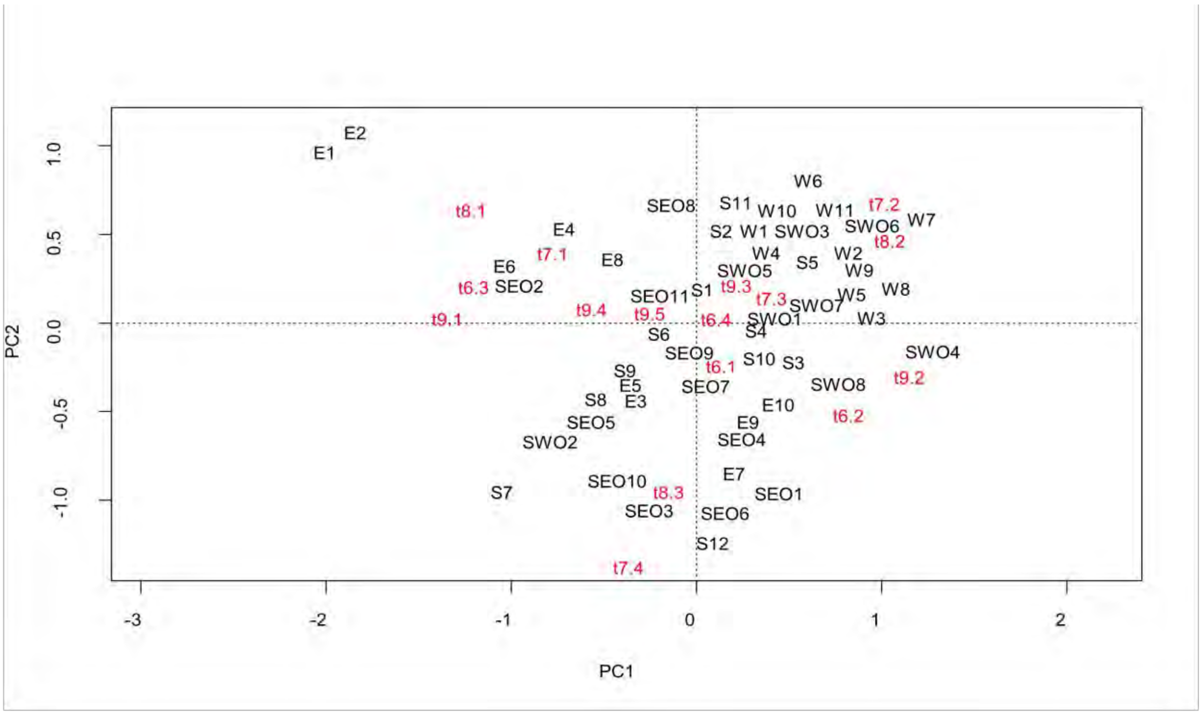


Fig.S3.8. A PCA ordination showing the association between sites and specific trait modalities within the reproduction trait domain (weighted by abundance). The sites are coded in black where the first letter represents the bioregion e.g., E8 denotes site 8 on the east coast. The trait modalities are indicated in red. Refer to trait codes in Table 2.7.

Sites within the east coast (Fig.S3.8) were associated with species that attained reproductive maturity at very small sizes (>10mm– t9.1), with more continuous reproductive maturity (t6.3), direct developers (t8.1), and with asexual reproductive type (t7.1). In addition, both transition zones contained species with simultaneous hermaphroditism (t7.4), both annual protracted (t6.1) and annual episodic (t6.2), lecithotrophic species (t8.3), and a few semelparous species (t6.4). Lastly, the west coast predominantly had species that attained reproductive maturity when much larger in size, i.e., (>30mm–t2.2), planktotrophic developers (t8.2), and gonochoristic reproductive type (t7.2).

CHAPTER 4

EVALUATING THE INFLUENCE OF GENICULATE CORALLINE ALGAE ON EPIFAUNAL DIVERSITY AND COMPOSITION: A POTENTIAL FUNCTIONAL CASCADE OR SIMPLY THE EFFECTS OF BIOGEOGRAPHY?

Eventually, it was realised that the whole method of approach–Fragestellung–of this essentially static zoogeography was wrong. Instead of thinking of fixed regions, it is necessary to think of fluid faunas (Mayr, 1946).

Evaluating the influence of geniculate coralline algae on epifaunal diversity and composition: A potential functional cascade or simply the effects of biogeography?

4.1. Introduction

Research into the identification of recurring species assemblages is perhaps the oldest form of marine community research. It forms the basis of subsequent work into examining diversity and distribution patterns (Zacharias & Roff, 2001; Pereira et al., 2006). Habitat structure, both physical and biogenic, in ecosystems influences the diversity and distribution of species assemblages. Based on the habitat templet theory, one of the main underlying assumptions of the influence of habitat structure is that species pass through a hierarchical set of these physical and biogenic 'filters' and only the best adapted species persist within the particular environment in question. This 'filtering' process provides a spectrum of benefits and challenges to species across different spatio-temporal scales. For example, the intertidal zone is a dynamic and stressful habitat for organisms because of the rapid changes in physical conditions (such as desiccation resulting from temperature fluctuations) associated with the fluctuation between terrestrial and marine conditions (Flores-Molina et al., 2014). The Crain & Bertness (2006) environmental stress model predicts that one of the main community-structuring mechanisms in extreme environments, such as on wave-exposed rocky intertidal shores, is abiotic stress. Changes in intertidal height of even a few centimetres can result in significant differences in emersion time and exposure to aerial stress (Umanzor et al., 2019). Consequently, intertidal organisms often must continuously deal with environmental conditions that can severely limit their abundance and distribution (Denny, 1987).

4.1.1. Habitat modifiers and their influence

Despite all the aforementioned stresses, some species benefit from the presence of other species which modify the habitat particularly those species provide what is referred to as the biogenic habitat. The organisms with this facilitative ability to ameliorate stressful conditions and provide shelter for other species have the highest relative importance (Gutiérrez & Iribarne, 2004; Sueiro et al., 2011; Watt & Scrosati, 2013). These organisms are termed habitat-formers, foundation species, ecosystem engineers, or bioengineers (Watt & Socrati, 2013). There is, however, considerable ambiguity about the usage of these terms (Jones et al., 1997). Because the physical habitat is assumed to be more influential in ecosystem functioning, for this study, I focus on and define the species that influence or moderate effects of environmental elements as habitat modifiers instead. Key examples of these habitat modifiers include seaweeds and mussels, with the latter having a wider research pool to date (see e.g., Karatayev et al., 2002; Gutiérrez et al., 2003; Borthagaray & Carranza, 2007; Arribas et al., 2014; Capelle et al., 2019). The former was therefore the focus of this chapter. In addition, the selection of seaweeds over mussels was arguably based on their importance as autotrophs at the base of the food chain.

4.1.2. Seaweeds as habitat modifiers

Seaweeds are high-yielding producers occupying a basal position in aquatic food webs and form part of the foundation species of coastal and estuarine ecosystems (Vettori et al., 2020). There are other attributes that warrant the inclusion of a species as a foundation species or habitat modifier. These include functional trait attributes which relate to morphological characteristics (Chemello & Milazzo, 2002), tissue composition (Belovsky, 1981), and chemical defences (Duffy & Paul, 1992). The morphology, structure, and persistence of seaweeds have been recognised as vital in maintaining overall biodiversity of marine ecosystems (Seed & O'Connor, 1981; Manríquez & Castilla, 2007; O'Brien et al., 2018). Primary production in certain aquatic biomes can be determined based on marine seaweeds' morphological, life history, and tolerance traits (Jänes et al., 2017). In addition, small canopy-forming macroalgae can ameliorate extreme physical conditions within their environment by modifying local hydrodynamic regimes, stabilising sediments, and providing protection from competition and predation.

The role of seaweed morphology as a determinant of intertidal epifauna abundance and diversity is, however, often species-specific (Seed et al., 1981; Kelaher et al., 2001; Parker et al., 2001; Chemello & Milazzo, 2002; Christie et al., 2003). Many intertidal seaweeds show a tremendous gradient of morphological form, ranging from spatially separated thalli to thalli that are aggregated into dense turfs. All these morphological forms have varying effects on benthic species that are trapped within them or use them as a habitat. For example, *Ascophyllum* sp, a branched brown seaweed, significantly reduces heat and desiccation pressure in the intertidal zone and positively affects the recruitment, survival, and growth of macroinvertebrates (Bertness et al., 1999). Further, the red seaweed *Gracilaria vermiculophylla* provides milder biophysical conditions, increasing the survival of the amphipod *Gammarus mucronatus* (Wright et al., 2014). Locally, on the west coast of South Africa, the lanceolate or rosette thalli of *Porphyra* sp provides shelter to gastropods, *Afrolittorina* spp and *Oxystele antoni*, during low tide (Stegenga, 1997). Given these different species-centric results, my work was focused on evaluating the epifaunal species associated with macroalgal species from the sub-family Corallinoideae. The majority of species within this sub-family occur as single species and also as turfs. The choice of a single sub-family turf was an effort to reduce confounding factors (e.g., see Jompa & McCook, 2003; Schiel, 2006) seeing monospecific algal communities are in themselves already not homogeneous, and that morphological differences and interactions with other biological substrates can influence the mobile and sometimes host-specific epifaunal assemblages.

Turf-forming seaweeds are relatively common around the South African coast (particularly the east and south coasts). Like other seaweed species, turfs provide a complex structural habitat and food source directly to grazers and indirectly by trapping suspended material for deposit feeders and detritivores. Their morphological characteristics likely induce a functional cascade on intertidal epifauna through habitat provision. For example, aggregation of seaweeds into turfs decreases productivity per gram of organic weight as a result of crowding of thalli but increases resistance to desiccation (Taylor & Hay, 1984). At the community level, the intertidal distribution of the turf growth form is correlated with the intensity of desiccation stress. Although I could not examine this, it is reasonable to expect that while desiccation stress is ameliorated inside the coralline matrix, it may not be the same around its exterior surroundings; thus, the effect of coralline algae on epiphytes may not always be positive.

Considering the taxon of choice in this study, coralline algae are considered as relatively structurally complex, where the crustose holdfast or base is perennial and grows apically, like encrusting corallines such as *Lithothamnia* and *Phymatolithon* spp. The basal crust may grow continuously until stimulated to produce fronds (Colthart & Johansen, 1973). More specifically, geniculate coralline species of the Division Rhodophyta, Order Corallinales, are a versatile and cosmopolitan group with tropics-polar distributions (Adey & Macintyre, 1973; Bosence, 1983; Wray, 1998). These species are categorised as amongst the most crucial foundation taxa in the photic zone (Walker & Kendrick, 1998; Watt & Scrosati, 2013; Cornwall et al., 2019). Consequently, this makes their performance tightly linked to a suite of biotic and abiotic factors mainly associated with the intertidal zone. Although not all are turf-forming, I examined whether all collected geniculate coralline species are potential habitat modifiers with a functional cascading influence on epifaunal assemblages. This is because fronds of most corallines have a high surface area to volume ratio compared to other seaweeds (Coull & Wells, 1983). In addition, these species consist of an upright portion with a segmented structure due to the alternation of calcified fragments (intergenicula) with noncalcified portions (genicula). Their cell walls are also encrusted with calcium carbonate, which occurs as a crystal or calcite. The geniculum also gives the otherwise rigid and brittle thallus the ability to bend at these points, resulting in flexibility that allows coralline algae to grow up to 30 cm tall (Bold & Wyne, 1985).

It is important to acknowledge that understanding the mechanisms behind the effects of ecological engineers requires manipulative experiments, which were logistically impossible on the scales addressed. The objective of this chapter was therefore to evaluate some of the basic assumptions of the habitat templet theory i.e., to explore the interaction and effects of the biotic and abiotic filters of the habitat on epifaunal assemblages. I evaluated whether the turf morphological structure, total biomass, and thallus dry matter content (TDMC) of coralline seaweeds induce a functional cascade on intertidal epifauna by influencing the composition and abundances of their communities across different bioregions. TDMC is the ratio between dry and wet mass which represents the proportion of structural compounds and water-filled and therefore mainly photosynthetically active tissues (Mauffrey et al., 2020). TDMC has also been regarded as an effective indicator of seaweed palatability to generalist grazers (Elger & Wilby, 2003). The knowledge of the influence of species (and trait) relatedness on associated fauna and ecosystem functioning has proven useful to estimating global species diversity and performance (Ødegaard et al., 2005) and understanding community assembly. Calculating and evaluating TDMC and total dry weight (DW) biomass across space can reveal the potential effects of grazing (especially in instances where the same grazer species are observed within the same seaweed species). In most cases, grazers have negative effects on seaweed. For example, lesions of the apical meristem limit the growth of the thallus in height and promote the formation of new lateral branches because of the elimination of apical dominance. This results in the formation of low compact densely branched thalli, dense tufts, or crustose forms. An example is the case of the coralline *Lithophyllum congestum*, which forms semispherical crusts on reef slopes at a high concentration of herbivorous fish (Shibneva & Skriptsova, 2015).

The three most abundant species within the coralline community which provide the highest microhabitat space and structure sampled in this study include: *Jania verrucosa, Jania adhaerens,* and *Corallina sp 1* (previously assumed to be *Corallina officinalis*). Based on the biomass ratio hypothesis (which proposes that the effect of a species on a given ecosystem process is proportional to its relative abundance in the community), I expected these 3 species to have more influence on epifauna diversity and abundances than the rarer coralline species such as *Jania sagittata* and *Jania subulata*. The objectives of this chapter were to: (1) provide a description of the patterns of distribution of coralline dwelling crustaceans including Amphipoda and Isopoda identified along the rocky shores of South Africa and (2) make a preliminary attempt to test the relationship between patterns of distribution of crustacean epifauna and conspicuous geniculate coralline species. I also assessed the effects of biogeographical changes in patterns of epifaunal assemblages within and among the geniculate coralline community. I expected that the epifauna observed within the coralline use the seaweed for reasons including feeding and temporary and/or permanent habitat or refuge.

On a last note, while herbivory is a significant form of parasitism that negatively influences seaweeds in general, coralline species are assumed to be protected from herbivory because of the calcium carbonate deposition (Cronin & Hay, 1996; Kurimoto & Tokeshi, 2010). Key-hole limpets are, however, are not deterred by the calcium carbonate deposits and feed on coralline seaweeds. I, therefore, expected to find herbivorous limpets such as the key-hole limpets (e.g., *Fissurella* spp) within the coralline seaweed species. Lastly, to evaluate the possible influence or contribution of overall seaweed community structure on the observed patterns of epifauna, I also analysed the diversity of other seaweeds from the same heights on the shore as those where the coralline species were sampled.

4.2. Materials and Methods

4.2.1. Study Area

The biogeographic boundaries of seaweeds for the South African coastline do not fully conform to the three traditional bioregions (i.e., the west, east, and south coasts). Two main criteria have generally been used for delineating marine provinces. One method proposes using endemism as a primary criterion (Eckman, 1953; Briggs, 1974). These authors suggested that > 10% endemicity of species within a locality warrants that area as a separate marine province. In contrast, using the second method, seaweed biologists have resorted to Hoek & Donze (1967), who regarded an algal phytogeographic province as ‘‘a part of the coast characterised by homogeneous flora and separated from other such parts by comparatively small stretches of coast with a rapidly changing flora, i.e., by floristic discontinuities’’. This simple discontinuity to delimit marine provinces has also been followed by botanists and zoologists on the South African coast (e.g., Emanuel et al., 1992; Farrell et al., 1994; Procheş & Marshall, 2002).

There are, however, several different ideas in the literature on the overlap between tropical and temperate regions along the South African coastline. Zoogeographers have documented the existence of an overlap region between the south and east coasts, as well as a sub-tropical east coast region or marine province, although the proposed boundaries given vary considerably (Day, 1967; Brown & Jarman, 1978; Thandar, 1989; Emanuel et al., 1992; Farrell et al., 1994; Turpie et al., 2000). The east coast of South Africa (refer to Fig.2.1), comprising the coast of Kwazulu-Natal Province (KZN), formerly known as Natal, was described as "sub-tropical" by Stephenson (1939). While working with seaweed data, Bolton & Anderson (1997) differed from Stephenson (1939) in not recognising a sub-tropical east coast region or marine province. Instead, they postulated an extended overlap region (SEO; Fig.4.1). Their opinion was that ‘‘although this matter is not resolved, at this stage we consider an Eastern Overlap' between Agulhas and Indo–West Pacific marine provinces comprising the coastline from around East London to the Mozambique border" (Bolton et al., 2004, page 53). For simplicity, this eastern overlap will be referred to as the south-east overlap (SEO) in this study. Therefore, what is regarded as the east coast falls within the south-east overlap region, resulting into two transition zones (south-west and south-east) and two bioregions (west and south), (Fig.4.1).

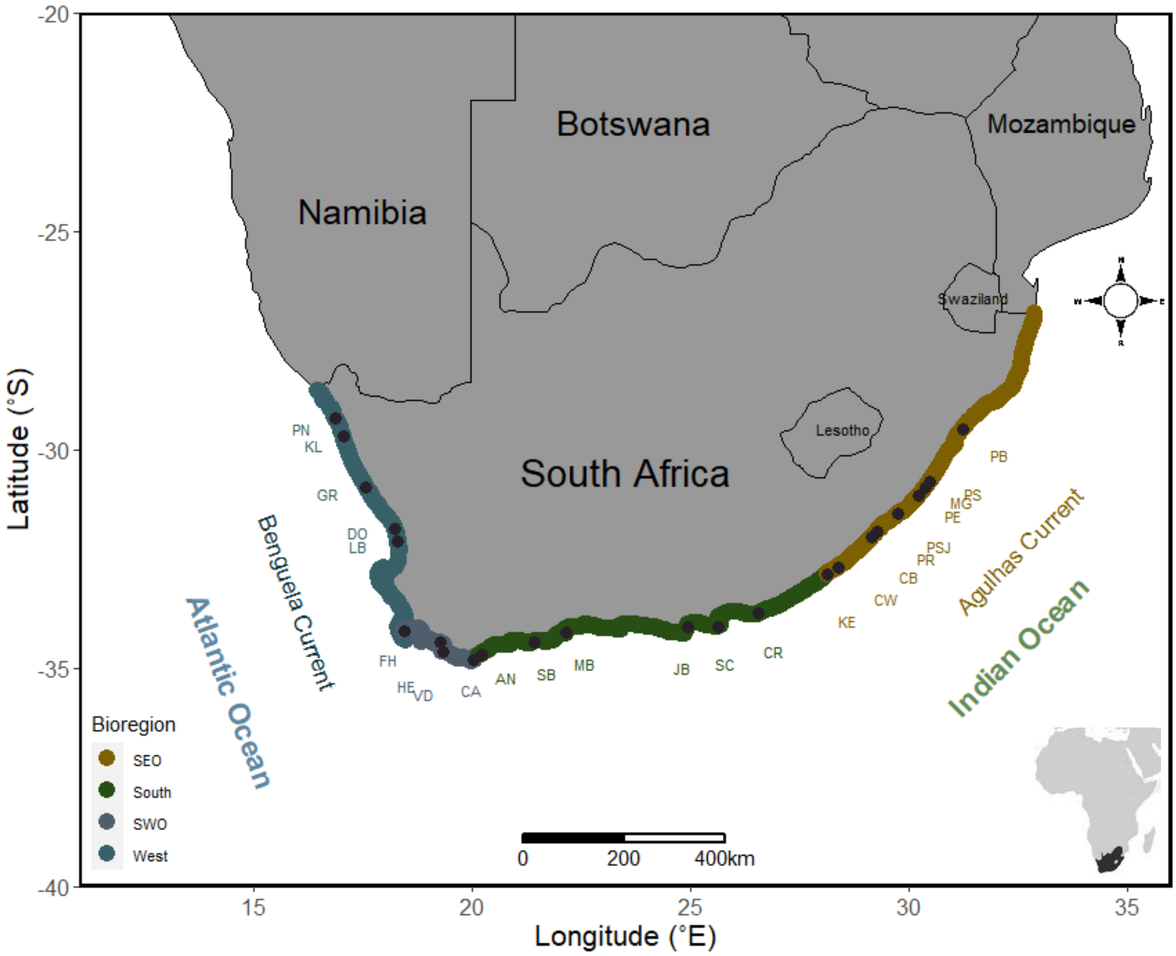


Fig.4.1. A map showing the location of all sites (indicated as black dots) where geniculate coralline seaweed specimens were recorded and sampled for epifaunal assemblages. Sites names are PB= Pebble Beach, PS= Port Shepstone, MG=Margate, PE= Port Edward, PSJ= Port St Johns, PR=Presley Bay, CB= Coffee Bay, CW= Cintsa West, KE= Kei Mouth, CR= Cannon Rocks, SC= Schoenmakerskop, JB= Jeffrey's Bay, MOS= Mosselbaai, SB= Stillbaai, AN= Arniston, CA= Cape Agulhas, VD= Van Dyks, HE=Hermanus, FH=Fish Hoek, LB=Lambert's Bay, DO=Doringbaai, GR= Groenriviermond, KL= Kleinsee, PN=Port Nolloth.

4.2.2. Data Collection

Out of the fifty-two sites sampled for macroinvertebrates (Fig.2.1), twenty-four sites had coralline species. Sampling was therefore conducted at these twenty-four sites which were spread across all four bioregions (Fig.4.1). The field survey was conducted between October and December 2019. Before specimen collection, a pre-survey was undertaken to identify approximately 25x25cm monospecific patches of coralline seaweeds. All selected quadrats had a minimum of 50% percentage cover of the geniculate coralline. Other seaweeds present (i.e., not geniculate corallines) were collected for community composition assessment. Seaweed specimens were collected by removing the specimen within the quadrat from the substratum at the holdfast using a paint scraper. Across 90% of the sites, coralline seaweed occurred mainly in two zones i.e., lower balanoid zone (i.e., excluding the sublittoral fringe zone) and mid (mid balanoid) zones (herein referred to as zone 1 and zone 2, respectively). These zones are consistent with those of Branch & Branch (1981, 2018). From each zone specimens were collected from replicate quadrats (n=3) along 50m wide transects placed parallel to the coast.

A plastic bag was placed over the quadrat during seaweed collection to minimise the escape of highly mobile epifauna such as amphipods. The samples (from each quadrat and site) were immediately placed in Ziploc bags after collection and preserved in a 5% formalin solution (prepared with seawater). In the laboratory, all seaweed specimens were rinsed out to collect all epifauna. The procedure was done by rinsing the seaweed under flowing water through a 500 μm mesh sieve into a collecting jar. The epifaunal specimens retained in the sieve were sorted under a dissecting microscope using appropriate taxonomic keys (Branch et al., 1991), books (Day, 1974, Kilburn & Ripley, 1982), and monographs (Day, 1966; 1967). Seaweed species identity was conducted to the lowest taxonomic level. Each seaweed specimen was inspected under the microscope to remove any remaining organisms or dead matter before taking weight measurements. All epifauna were identified and counted to the lowest possible taxon. Organisms included in the study were within a size (length or diameter) range from roughly 0.1 to 10 cm (including small crustaceans and annelids). Only the heads were counted for highly fragile organisms such as annelid worms. Epifaunal specimens that could not be identified to genus level were excluded from the study. Dry weight biomass (grams) estimates were obtained for the seaweed after drying at 60 °C for ~48h. Seaweed dry weight biomass and thallus dry matter content estimates of the corallines were calculated and recorded. Overall seaweed species diversity for each site was also recorded. These data were used (1) as a proxy to estimate the biomass output of each site at the time of sampling and (2) to suggest the possible shifts in the diversity of the epifaunal community observed at each site as a result of changes in biomass and coralline species identity. The identification of all seaweeds sampled at each site was based on the books including Stegenga, (1997); Seagrief (1967); De Clerck et al. (2005) and online seaweed databases such as Seaweeds of the South African south coast (Anderson et al., 2016) and AlgaeBase (Guiry & Guiry, 2020). Seaweed names and authorities were checked on AlgaeBase.org between the 22-25th February 2020. Epifaunal names and authorities were checked on the World Register of Marine Species (WoRMS) between the 16-20th of October 2021.

4.2.3. Data Analysis

Before all statistical analyses, data were tested for normality using the Shapiro-Wilk test. Epifaunal abundance data were log (x+1) transformed. This transformation was done to reduce differences in scale among variables while preserving information about the relative abundances of species among samples. On the other hand, because the seaweed richness and coralline biomass data were not normally distributed, these data were analysed using non-parametric Kruskal-Wallis and Wilcox tests, respectively. These hypothesis testing statistics were performed in R v 4.1.0 (R Core Team, 2021). Tukey's HSD (honestly significant difference) *post hoc* tests were used for pairwise comparisons where significant differences in abundance amongst different bioregions had been observed.

To identify sites with similar species composition, I used a hierarchical tree-clustering algorithm to assemble epifaunal taxa into similarity clusters. The hierarchical cluster analyses were computed on epifaunal abundance, coralline DW biomass, and community data for all other seaweeds present at each sampled site. The aim was to classify the sites into groups based on the degree of similarity in their patterns of biomass, and abundance. To get the best cluster method, I calculated the agglomerative coefficient for each clustering linkage method. This function calculates the agglomerative coefficient of each method, which is a metric that measures the strength of the clusters. The closer this value is to 1, the stronger the clusters. In the end, I made this classification using Ward's linkage method (Ward, 1963) with Euclidean distance measures as it closely matches the purpose of clustering (Tufféry, 2011; Govender & Sivakumar, 2020). Ward's linkage method uses an analysis of variance approach to evaluate the distance between clusters and minimises the sums of squares of hypothetical clusters that can be formed at each step. Lastly, a Correspondence Analysis (CA) was used to display differences in epifaunal community composition (based on abundance data) within bioregions. Epifaunal data were ordinated for each bioregion for better visualisation.

To test the effects of Bioregion, Site and Zone on the abundance of epifauna and coralline dry weight biomass data, I used the permutational multivariate analysis of variance (PERMANOVA; Anderson, 2014) analysis. A nested PERMANOVA with interactions was performed for each dataset. Bioregion (4 levels: south-east, south, south-west, and west) and 'Zone' (2 levels: low and mid) were fixed factors while Site (24 levels) was treated as a random factor nested within Bioregion. Type III sums of squares and 999 permutations were selected for the analysis. The Bray-Curtis dissimilarity measure was used to compute all the resemblance matrices with transformed data to characterise variation in the epifaunal community and coralline DW biomass within and across sites. These multivariate analyses were done in PRIMER software version 6 with the PERMANOVA+ add on (Anderson, 2001).

4.3. Results

4.3.1. Composition patterns of geniculate coralline species across sites and bioregions

Table 4.1. PERMANOVA results showing the effects of bioregions, zones, sites, and transects and pairwise comparison across bioregions for coralline species DW biomass.

Source	df	SS	MS	F	*p*
Bioregion	**3**	**94154**	**31385**	**4.3609**	**0.001**
Zone	1	286.81	286.81	0.39013	0.86
Site [Bioregion]	**20**	**1.43E+05**	**7196.8**	**4.4954**	**0.001**
Bioregion*Zone	3	1337.9	445.98	0.60663	0.853
Site [Bioregion]*Zone	20	14703	735.17	0.45921	1
Residuals	96	1.53E+05	1600.9		
Total	143	4.08E+05			

PAIR-WISE TESTS

Term 'Bioregion'

Groups	T	*p*
SEO, South	**1.5283**	**0.05**
SEO, SWO	**2.1106**	**0.001**
SEO, West	**2.5433**	**0.002**
South, SWO	0.88025	0.641
South, West	**2.8786**	**0.005**
SWO, West	**2.2523**	**0.031**

The nested PERMANOVA analysis on the influence of Bioregion, Zone, and Site on coralline dry weight biomass showed a strong significant effect of Site nested in Bioregion. Similarly, there was also a strong significant main factor effect of Bioregion on coralline DW biomass. The SEO and south coasts also had higher variability in biomass estimates for the coralline species than the SWO and west coasts (Fig.4.2). Moreover, of these two bioregions, the SEO contained the highest coralline species richness. Subsequently, the highest variability in both DW biomass and TDMC were observed in the SEO bioregion (Fig.4.2 and Fig.4.3) and the least on the SWO and west bioregions. The pairwise comparisons among bioregions for DW biomass showed that all other bioregions were significantly different from each other (Table 4.1) with the exception of the south and SWO coasts

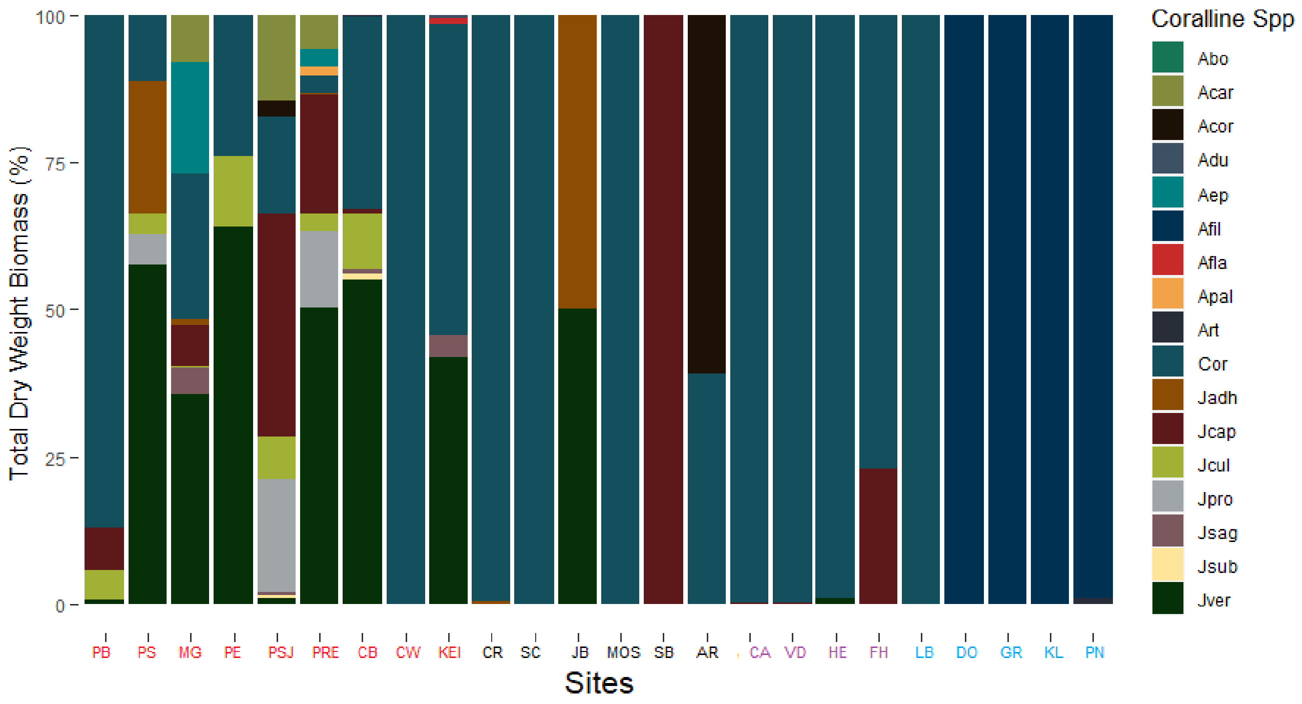


Fig.4.2. Frequency distribution for coralline seaweeds DW biomass across sampled sites. Abo=*Amphiroa bowerbankii,* Acar= *Arthrocardia carinata*, Acor= *Arthrocardia corymbosa*, Adu=*Arthrocardia dutheae*, Aep= *Amphiroa ephedraea*, Afil= *Arthrocardia filicula*, *Arthrocardia flabellata*, Apal=*Arthrocardia palmata*, Art=*Arthrocardia* sp, Cor= *Corallina sp 1*, Jadh= *Jania adhaerens*, Jcap= *Jania capillacea*, Jcul= *Jania cultrata*, Jpro= *Jania prolifera,* Jsag= *Jania sagittata*, Jsub= *Jania subulata*, Jver= *Jania verrucosa.* Sites names are PB= Pebble Beach, PS= Port Shepstone, MG= Margate, PE= Port Edward, PSJ= Port St Johns, PRE=Presley Bay, CB= Coffee Bay, CW= Cintsa West, KEI= Kei Mouth, CR= Cannon Rocks, SC= Schoenmakerskop, JB= Jeffrey's Bay, MOS= Mosselbaai, SB= Stillbaai, AR= Arniston, CA= Cape Agulhas, VD= Van Dyk's Bay, HE=Hermanus, FH=Fish Hoek, LB=Lambert's Bay, DO=Doringbaai GR= Groenriviermond, KL= Kleinsee, PN=Port Nolloth. Sites are coded by bioregion where red= SEO, black= south coast, purple= SWO and blue=west coast.

The highest biomass and TDMC were recorded for *Corallina sp 1* across most sites on the SEO, south and SWO regions (Fig.4.2 and Fig.4.3). The SEO region, however, had the highest variability in species composition. Species within the genus *Jania* were the most common on the SEO while on the south and SWO bioregions it was *Corallina sp 1* and *Arthrocardia filicula* being the most common for the west coast. A multivariate Wilcox test further confirmed that of all 17 geniculate corallines species collected, only *Corallina sp 1*, *Jania verrucosa, Jania capillacea,* and *Jania cultrata* significantly varied ($p<0.01$) in total biomass across all sites (Fig.4.3).

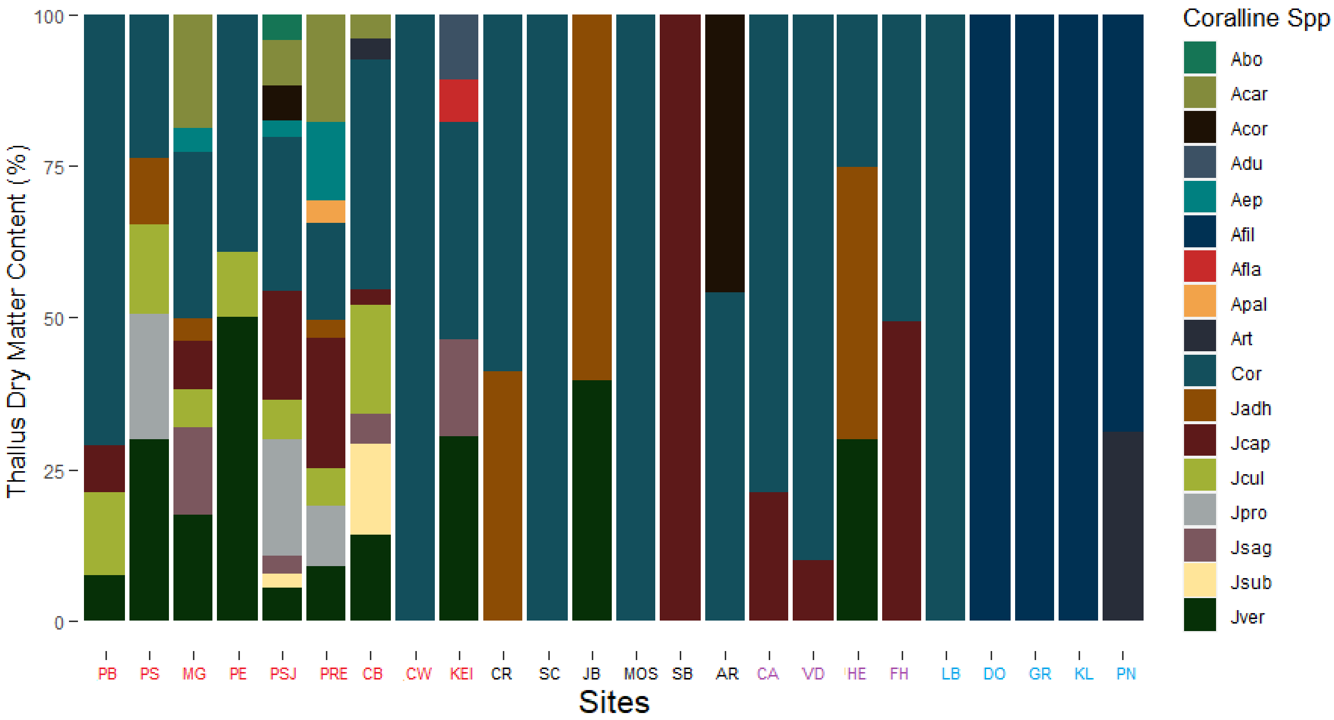


Fig.4.3. A frequency distribution plot shows the thallus dry matter content of geniculate coralline seaweeds identified at the sampled sites. Abo=*Amphiroa bowerbankii,* Acar= *Arthrocardia carinata*, Acor= *Arthrocardia corymbosa*, Adu=*Arthrocardia dutheae*, Aep= *Amphiroa ephedraea*, Afil= *Arthrocardia filicula*, *Arthrocardia flabellata*, Apal=*Arthrocardia palmata*, Art=*Arthrocardia* sp, Cor= *Corallina sp 1*, Jadh= *Jania adhaerens*, Jcap= *Jania capillacea*, Jcul= *Jania cultrata*, Jpro= *Jania prolifera,* Jsag= *Jania sagittata*, Jsub= *Jania subulata*, Jver= *Jania verrucosa.* Sites names are PB= Pebble Beach, PS= Port Shepstone, MG= Margate, PE= Port Edward, PSJ= Port St Johns, PRE=Presley Bay, CB= Coffee Bay, CW= Cintsa West, KEI= Kei Mouth, CR= Cannon Rocks, SC= Schoenmakerskop, JB= Jeffrey's Bay, MOS= Mosselbaai, SB= Stillbaai, AR= Arniston, CA= Cape Agulhas, VD= Van Dyk's Bay, HE=Hermanus, FH=Fish Hoek, LB=Lambert's Bay, DO=Doringbaai GR= Groenriviermond, KL= Kleinsee, PN=Port Nolloth. Sites are coded by bioregion where red= SEO, black= south coast, purple= SWO and blue=west coast.

Similar patterns as observed for coralline DW biomass in Fig.4.2 were observed for the distribution of TDMC across sites (Fig.4.3). The SEO had the most variability in TDMC values among species across sites in comparison to other bioregions and sites. Similarly, a multivariate Wilcox test showed that only *Corallina sp 1*, *Jania verrucosa, Jania capillacea,* and *Jania cultrata* significantly varied ($p<0.01$) in TDMC across all sites (Fig.4.3).

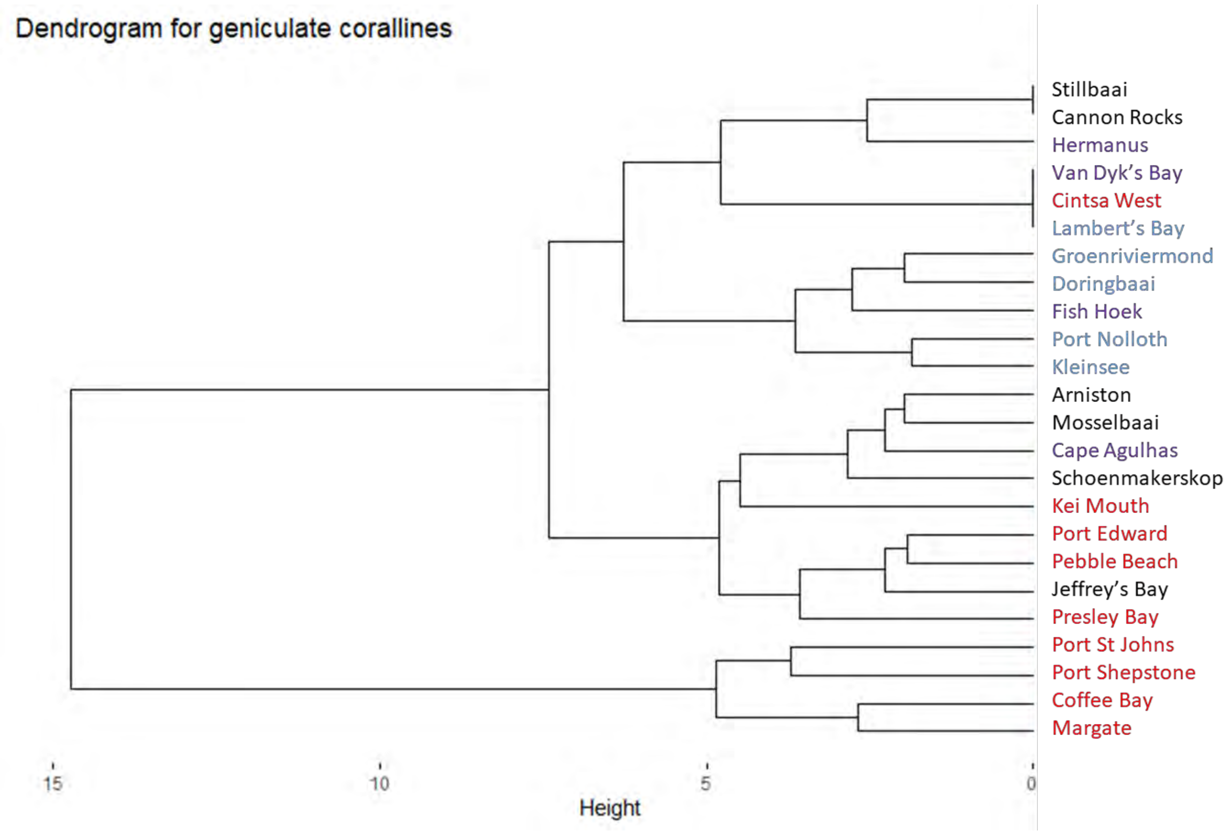


Fig.4.4. Hierarchical cluster plots comparing similarities in geniculate coralline species composition among sites. Height =represents the ecological distance metric at which the clusters are formed. Sites are coded by bioregion where red= SEO, black= south coast, purple= SWO and blue=west coast.

The cluster plot for geniculate corallines showed 2 main patterns (Fig.4.4). The majority of the SEO and south coast sites formed one cluster while the SWO and west sites formed another cluster. These results are corroborated by the pairwise comparisons (Table 4.1).

4.3.2. Epifauna abundance distribution and composition patterns in coralline seaweeds across sites and bioregions

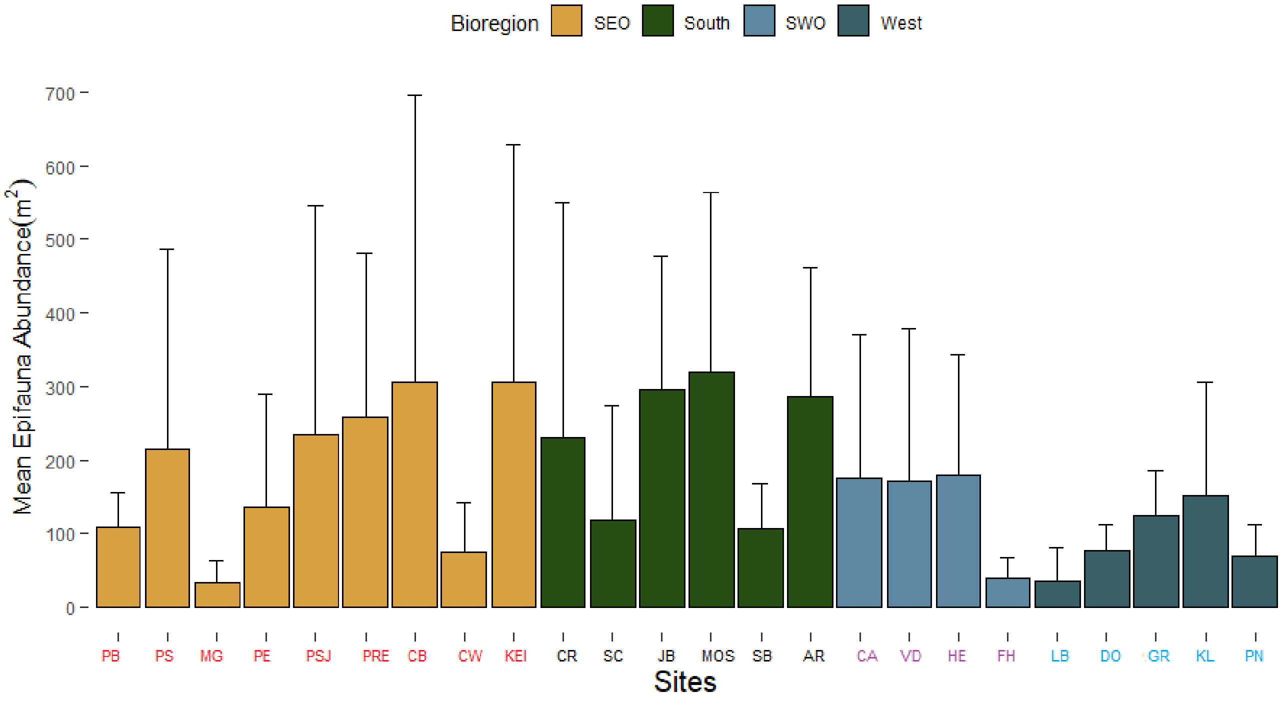


Fig.4.5. The bar graphs show the mean abundance of epifauna per m^2 across bioregions. Error bars indicate SD. Where PB= Pebble Beach, PS= Port Shepstone, MG= Margate, PE= Port Edward, PSJ= Port St Johns, PRE=Presley Bay, CB= Coffee Bay, CW= Cintsa West, KEI= Kei Mouth, CR= Cannon Rocks, SC= Schoenmakerskop, JB= Jeffreys' Bay, MOS= Mosselbaai, SB= Stillbaai, AR= Arniston, CA= Cape Agulhas, VD= Van Dyks Bay, HE=Hermanus, FH=Fish Hoek, LB=Lambert's Bay, DO=Doringbaai, GR= Groenriviermond, KL= Kleinsee and PN=Port Nolloth. Sites are coded by bioregion where red= south-east, black= south coast, purple= south-west and blue=west coast.

The SEO had the highest epifaunal species richness (121) among all the bioregions, followed by the south (98), then the SWO (41) and lastly the west coast (33). The SEO and south coasts also had higher variability in abundances within sites as indicated by large standard deviations (Fig.4.5). In these 2 bioregions, the sites at the centre and also at the range edge in terms of geographic location had the highest richness and abundances. For the SEO, these most central sites were Port St Johns, Presley Bay, and Coffee Bay while the furthest range edge site was Kei Mouth. On the other hand, along the south coast the most central sites were Jeffrey's Bay and Mosselbaai, while the range edge site was Arniston (Fig.4.5). The PERMANOVA results, however, showed a significant main factor effect of Bioregion on epifaunal abundance (Table 4.2). Site nested in Bioregion also had a significant effect on epifaunal assemblages. Pairwise comparison among Bioregions further indicated that all bioregions were significantly different from each other.

Table 4.2. Nested PERMANOVA results showing the effects of bioregion, sites, and shore height (zone) on the abundance of epifaunal assemblages.

Source	df	SS	MS	Pseudo-F	*P*
Bioregion	**3**	**68284**	**22761**	**2.7115**	**0.001**
Zone	1	4364.8	4364.8	0.95746	0.511
Site [Bioregion]	**20**	**1.68E+05**	**8405**	**2.9424**	**0.001**
Bioregion*Zone	3	10759	3586.3	0.78653	0.847
Site [Bioregion]* Zone	**20**	**91258**	**4562.9**	**1.5974**	**0.001**
Residuals	96	2.7422E+05	2856.5		
Total	143	6.17E+05			

PAIR-WISE TESTS

Term Bioregion

Groups	t	*P*
SEO, South	**1.4714**	**0.004**
SEO, SWO	**1.8311**	**0.001**
SEO, West	**1.7977**	**0.002**
South, SWO	**1.6327**	**0.001**
South, West	**1.4643**	**0.011**
SWO, West	**1.6178**	**0.001**

The highest and least abundant epifaunal species recorded across all sites and bioregions are presented (Table 4.3). The four-eyed ampipod (*Ampelisca palmata*), the segmented worms (*Platynereis dumerilii* and *Pseudonereis podocirra*) and native brown mussel recruits (labelled as *Perna perna_* R) were amongst the common epifaunal species within the coralline seaweed species. On the other hand, all the limpet species such as *Scutellastra granularis, Cymbula granatina, and Siphonaria carbo* recorded the least abundances.

Table 4.3. Most and least abundant epifaunal species recorded across all sites and within each bioregion

	ALL SITES	SEO	SOUTH	SWO	WEST
Most abundant	*Ampelisca palmata*	*Apohyale grandicornis*	*Ampelisca palmata*	*Platynereis dumerilii*	*Ampelisca palmata*
	Platynereis dumerilii	*Platynereis dumerilii*	*Ischyromene huttoni*	*Afrolittorina sp*	*Urothoe grimaldii*
	Apohyale grandicornis	*Diopatra sp*	*Eatoniella sp*	*Lysianassa ceratina*	*Pseudonereis podocirra*
	Pseudonereis podocirra	*Melita zeylanica*	*Sipuncula sp*	*Perinereis vallata*	*Cymodocella magna*
	*Perna perna*_(R)	*Ampelisca palmata*	*Apohyale grandicornis*	*Pseudonereis podocirra*	*Griffithsus sp*
	Ischyromene huttoni	*Perna perna*_(R)	*Griffithsus sp*	*Perna perna*_(R)	*Eatoniella sp*
	Afrolittorina sp	*Ischyromene sp 1*	*Perna perna*_(R)	*Griffithsius sp*	*Aulacomya atra*
	Griffithsus sp	*Cymodoce valida*	*Nephyts sp*	*Exosphaeroma varicolor*	*Nephyts sp*
	Eatoniella sp	*Pseudonereis podocirra*	*Ischyromene ovalis*	*Ischyromene huttoni*	*Perinereis vallata*
	Lysianassa ceratina	*Phascolosoma sp*	*Thelepus sp*	*Mytilus galloprovincialis*	*Parisocladus perforatus*
Least abundant	*Oxystele sinensis*	*Lepidonotus durbanensis*	*Choromytilus meridionalis*	*Eurythoe complanata*	*Onithochiton literatus*_(R)
	Trochus nigropunctatus	*Griffithsus sp*	*Griffithsius latipes*	*Betaeus jucundus*	*Eurythoe complanata*
	Moerella tulipa	*Euphrosine capensis*	*Ischyromene sp 1*	*Pentacta doliolum*	*Betaeus jucundus*
	Barbatia obliquata	*Ampelisca sp*	*Tricholia sp*	*Temnophlias capensis*	*Pentacta doliolum*
	Tenguella granulata	*Ophionereis dubia*	*Scutellastra granularis*	*Ampelisca palmata*	*Temnophlias capensis*
	Lepidonotus durbanensis	*Conus mozambicus*	*Eurythoe complanata*	*Listriolobus capensis*	*Listriolobus capensis*
	Tripneustes gratilla	*Griffithsius latipes*	*Betaeus jucundus*	*Nephyts sp*	*Arabella iricolor*
	Thalamita admete	*Scutellastra granularis*	*Pentacta doliolum*	*Siphonaria carbo*	*Siphonaria carbo*
	Cymbula granatina	*Temnophlias capensis*	*Siphonaria carbo*	*Natatolana hirtipes*	*Natatolana hirtipes*
	Charybdis sp	*Natatolana hirtipes*	*Aora sp*	*Aora sp*	*Aora sp*

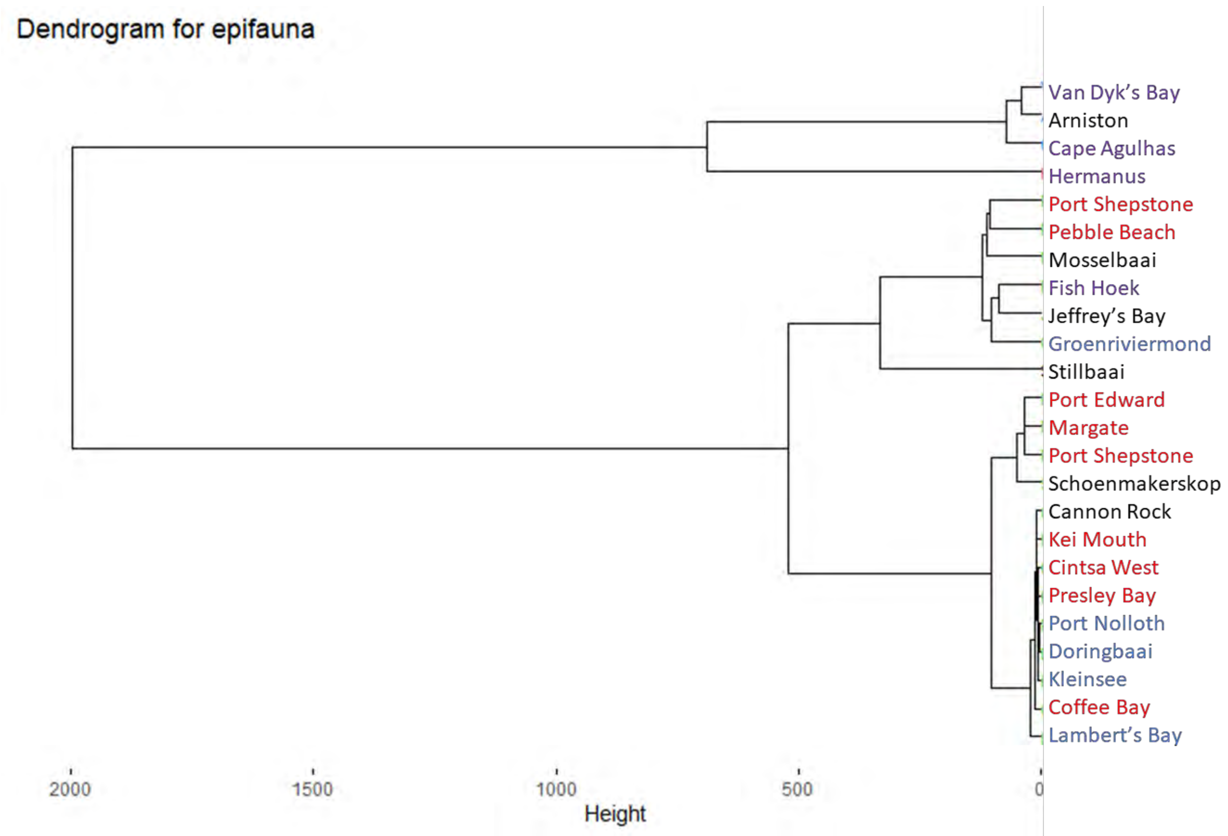


Fig.4.6. Hierarchical cluster plots comparing similarities in epifaunal species composition among sites. Height =represents the ecological distance metric at which the clusters are formed. Sites are coded by bioregion where red= SEO, black= south coast, purple= SWO and blue=west coast.

The hierarchical cluster analysis comparing the epifauna distribution across bioregions showed the sister clades of the west and SEO sites clustering independently of the SWO sites (Fig.4.6).

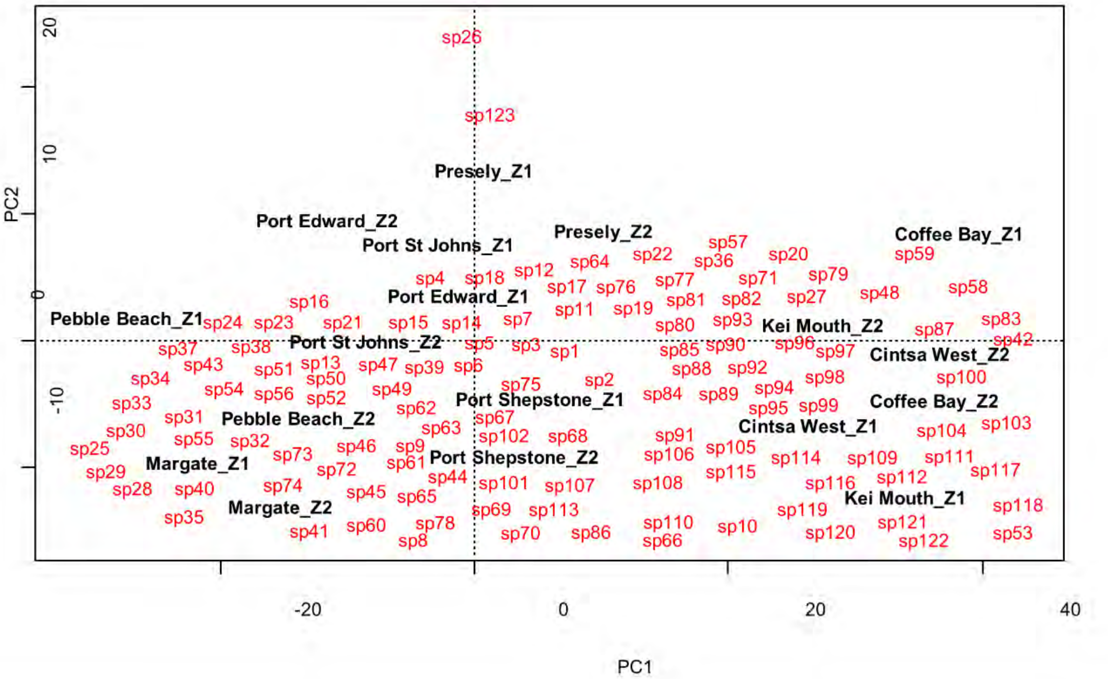


Fig.4.7.1. Correspondence Analysis for the SEO region showing the distribution of epifaunal assemblages across sites. Full species names are provided in Table 4.4.

The correspondence analysis (CA) plot (Fig.4.7.1) was performed as a follow-up to the dendrogram on epifauna. Across all main bioregions, the CA showed that sites close to each clustered together implying similar epifaunal assemblages on the basis of species presence/absence. For example, sites further to the east in the subtropical Natal region including Port Edward, Port Shepstone, and Port St Johns, had different diversity patterns from sites towards the west of the Natal region, including Coffee Bay and Cintsa West (Fig.4.7.1). Segmented worms, limpets and (amphipods and sea cucumbers), were the top three taxa contributing to the highest diversity in epifaunal communities on the SEO region (Table 4.4).

Table 4.4. List of epifaunal species collected on the SEO

Taxon	Spp Code	Species name	Taxon	Spp Code	Species name
Segmented worms	sp4	*Lepidonotus semitectus*	**Unsegmented worms**	sp31	*Sipuncula sp*
	sp5	*Euphrosine capensis*		sp39	*Anisakis pegreffii*
	sp6	*Syllidae sp*		sp45	*Listriolobus capensis*
	sp9	*Pseudonereis podocirra*		sp46	*Phascolosoma sp*
	sp23	*Eurythoe complanata*		sp87	*Golfingia capensis*
	sp24	*Nephyts' sp*		sp117	*Anisakis sp*
	sp26	*Gunnarea gaimardi*			
	sp32	*Perinereis nuntia vallata*	**Mussels**	sp10	*Perna perna_Recruits*
	sp33	*Flabelligera affinis*		sp11	*Septifer bilocularis*
	sp34	*Orbinia angrapequensis*		sp50	*Brachidontes sp*
	sp36	*Platynereis dumerilii*		sp80	*Brachidontes variabilis*
	sp37	*Arabella iricolor*		sp101	*Striarca symmetrica*
	sp47	*Marphysa sp*		sp91	*Gregariella petagnae*
	sp48	*Lysidice sp*			
	sp51	*Euphrosine capensis*	**Isopods**	sp2	*Cymodoce valida*
	sp52	*Glycera tridactyla*		sp3	*Ischyromene sp*
	sp53	*Thelepus sp*		sp60	*Ischyromene ovalis*
	sp57	*Spirobranchus krausii*		sp81	*Ischyromene huttoni*
	sp58	*Marphysa corallina*		sp111	*Exophaeroma truncatitelson*
	sp59	*Polyphysia sp*			
	sp64	*Eunice aphroditois*	**Amphipods**	sp121	*Melita zeylanica*
	sp65	*Arenicola loveni*		sp7	*Paramoera capensis*
	sp70	*Orbinia sp*		sp12	*Ampelisca palmate*
	sp67	*Scolelepis squamata*		sp25	*Apohyale grandicornis*
	sp72	*Notomastus sp*		sp35	*Jassa sp*
	sp76	*Diopatra cuprea*		sp62	*Leucothoe spinicarpa*
	sp78	*Polynoe erythrotaenia*		sp77	*Urothoe grimaldii*
	sp85	*Diopatra neapolitana capensis*		sp114	*Aora sp*
	sp88	*Eunice siciliensis*		sp73	*Leucothoe spinicarpa*
	sp94	*Harmothoe aequiseta*			
	sp95	*Lysidice natalensis*	**Sea cucumbers**	sp8	*Roweia frauenfeldi frauenfeldi_Recruits*
	sp98	*Lumbrineris sp*		sp17	*Neostichopus grammatus*
	sp99	*Prionospio sp*		sp18	*Pseudocnella sykion*
	sp100	*Polydora sp*		sp71	*Holothuria parva*
	sp107	*Syllidae variegata*		sp74	*Pentacta doliolum*
	sp110	*Perinereis sp*		sp79	*Roweia stephensoni*
	sp116	*Scoloplos johnstonei*		sp118	*Aslia spyridophora*
	sp120	*Dendronereis arborifera*		sp119	*Stichopus chronotus*
	sp96	*Leodice antennata*		sp113	*Pseudocnella sykion*
	sp82	*Diopatra sp*			
	sp61	*Lumbrineris cavifrons*			

Table 4.4 continued. List of epifaunal species collected on the SEO

Taxon	Spp Code	Species name	Taxon	Spp Code	Species name
Limpets	sp13	*Eoacmaea albonotata*	**Whelks**	sp27	*Vaughtia fenestrata*
	sp14	*Fissurella natalensis*			*Nucella dubia*
	sp15	*Dendofissurella scutellum*		sp66	*Tenguella granulata*
	sp19	*Scutellastra natalensis*			
	sp41	*Cymbula oculus*	**Topshells**	sp22	*Gibbula cicer*
	sp42	*Fissurella mutabilis*		sp28	*Heliacus variegatus*
	sp43	*Scutellastra longicosta*		sp97	*Oxystele tabularis*
	sp44	*Scutellastra cochlear*		sp56	*Oxystele antoni*
	sp63	*Helcion pruinosus*		sp86	*Oxystele impervia*
	sp68	*Crepidula porcellana*		sp90	*Trochus nigropunctatus*
	sp93	*Siphonaria carbo*			
	sp102	*Helcion concolor*	**Sea urchins**	sp40	*Parechinus angulosus*
	sp109	*Siphonaria concinna*		sp112	*Tripneustes gratilla*
	sp106	*Scutellastra obtecta*			
Crabs	sp103	*Acanthonyx scutellatus*	**Shrimps**	sp115	*Betaeus jucundus*
	sp104	*Neorhynchoplax bovis*			
	sp105	*Thalamita admete*	**Periwinkles**	sp1	*Littoraria coccinea*
	sp108	*Charybdis sp*		sp29	*Tricolia sp*
	sp83	*Rathbunixa occidentalis*			
			Sea anemones	sp30	*Actinia ebhayiensis*
Chitons	sp38	*Acanthochitona garnoti*			
	sp55	*Onithochiton literatus*	**Sea slugs**	sp69	*Aplysia sp*
	sp89	*Ischnochiton oniscus*		sp92	*Onchidium sp*
	sp16	*Onithochiton literatus_Recruits*			
			Worm shells	sp49	*Clionella rosaria*
Barnacles	sp84	*Amphibalanus amphitrite*			
	sp75	*Amphibalanus sp*			
	sp20	*Octomeris angulosa*			
	sp21	*Tetraclita serrata*			

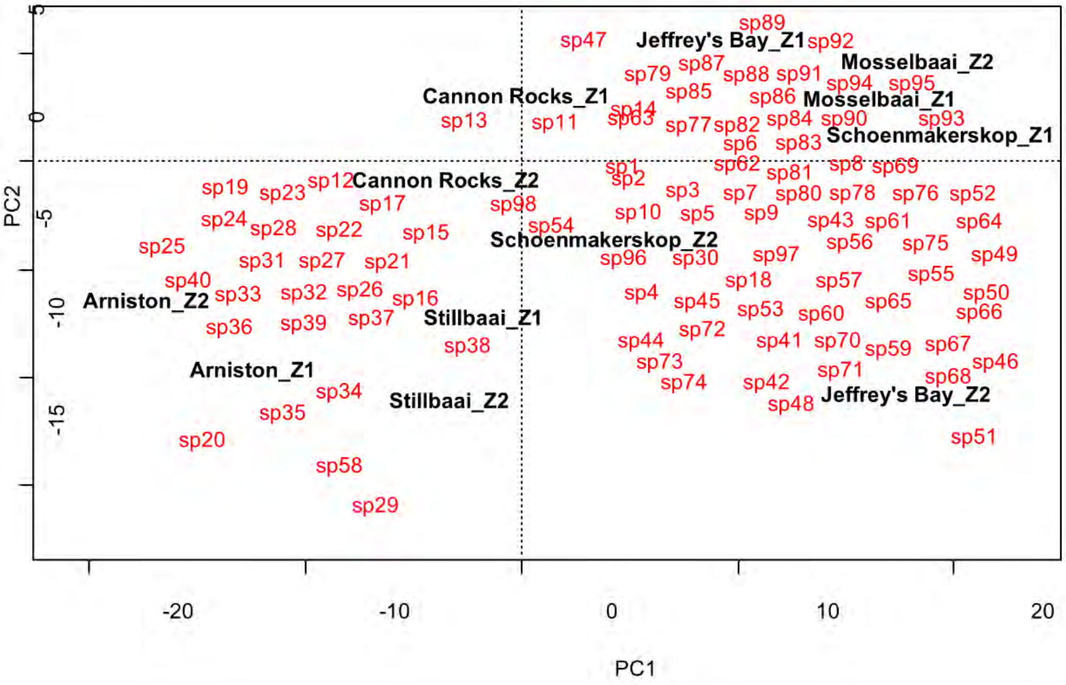


Fig.4.7.2. Correspondence Analysis for the south coast region showing the distribution of epifaunal assemblages across sites and bioregions. Full species names are provided in Table 4.5.

The CA for the south coast (Fig.4.7.2) indicated higher composition along the most centre sites i.e., Jeffrey's Bay, Schoenmakerskop and Mosselbaai. The community of Stillbaai and Arniston was notably dissimilar from more central south coasts sites including Cannon Rocks, Jeffrey's Bay and Schoenmakerskop. Segmented worms, amphipods and isopods were the top three taxa contributing to the highest diversity in epifaunal communities on the south coast (Table 4.5).

Table 4.5. List of epifaunal species collected on the south coast

Taxon	Species Code	Species name	Taxon	Species Code	Species name
Segmented worms	sp1	*Lepidonotus semitectus*	**Unsegmented worms**	sp72	*Listriolobus capensis*
	sp2	*Syllidae sp*		sp17	*Sipuncula sp*
	sp3	*Pseudonereis podocirra*		sp22	*Anisakis pegreffii*
	sp11	*Nephyts' sp*		sp25	*Phascolosoma sp*
	sp13	*Gunnarea gaimardi*		sp86	*Golfingia capensis*
	sp18	*Perinereis vallata*		sp93	*Anisakis sp*
	sp19	*Platynereis dumerilii*			
	sp20	*Arabella iricolor*	**Mussels**	sp56	*Barbatia obliquata*
	sp26	*Spirobranchus krausii*		sp84	*Mytilus galloprovincialis*
	sp29	*Marphysa sp*		sp33	*Brachiodontes sp*
	sp30	*Lysidice sp*		sp4	*Perna perna_Recruits*
	sp39	*Euphrosine capensis*		sp5	*Septifer bilocularis*
	sp47	*Pontobdella sp*			
	sp48	*Glycera tridactyla*	**Limpets**	sp7	*Dendrofissurella scutellum*
	sp51	*Lepidonotus durbanensis*		sp8	*Scutellastra natalensis*
	sp52	*Thelepus sp*		sp24	*Scutellastra longicosta*
	sp58	*Glycera tridactyla*		sp41	*Diodora parviforata*
	sp61	*Antinoe lactea*		sp92	*Siphonaria concinna*
	sp67	*Arabella sp*		sp57	*Cymbula granatina*
	sp75	*Eunice aphroditois*			
	sp80	*Arenicola loveni*	**Chitons**	sp54	*Onithochiton literatus*
	sp81	*Glycera sp*		sp21	*Acanthochitona garnoti*
	sp87	*Lysidice natalensis*			
	sp88	*Polydora sp*			
Mitres	sp50	*Mitra sp*	**Sea snails**	sp28	*Naria ocellata*
				sp31	*Moerella tulipa*
Starfish	sp42	*Henricia ornata*			
	sp77	*Parvulastra exigua*	**Periwinkles**	sp95	*Afrolittorina knysnaensis*
				sp63	*Afrolittorina knysnaensis*
Barnacles	sp9	*Octomeris angulosa*		sp64	*Afrolittorina sp*
	sp10	*Tetraclita serrata*		sp49	*Eatoniella sp*
				sp15	*Tricolia sp*
Crabs	sp90	*Acanthonyx scutellatus*			
	sp27	*Trapezia cymodose*	**Cirolanids**	sp76	*Natatolana hirtipes*
				sp78	*Cirolana sp*

Table 4.5 *continued*. List of epifaunal species collected on the south coast

Taxon	Species Code	Species name	Taxon	Species Code	Species name
Isopods	sp43	*Exosphaeroma porrectum*	**Amphipods**	sp96	*Temnophlias capensis*
	sp44	*Exosphaeroma planum*		sp97	*Ampelisca sp*
	sp45	*Ischyromene huttoni*		sp98	*Melita zeylanica*
	sp79	*Ischyromene magna*		sp12	*Apohyale grandicornis*
	sp68	*Parisocladus perforatus*		sp46	*Apohyale grandicornis*
	sp89	*Exosphaeroma truncatitelson*		sp83	*Cyproidea ornata*
	sp59	*Parisocladus stimpsoni*		sp37	*Monocorophium acherusicum*
	sp60	*Ischyromene ovalis*		sp38	*Griffithsus sp*
				sp70	*Leucothoe spinicarpa*
Topshells	sp73	*Gibbula sp*		sp74	*Amaryllis macrophthalma*
	sp85	*Oxystele impervia*		sp6	*Ampelisca palmata*
	sp55	*Oxystele antoni*			
	sp91	*Oxystele tigrina*	**Shrimps**	sp62	*Ostracoda sp*
	sp94	*Oxystele sinensis*			
	sp40	*Granata sulcifera*	**Worm shells**	sp32	*Clionella rosaria*
Whelks	sp66	*Afrocominella sp*	**Sea anemones**	sp16	*Actinia ebhayiensis*
	sp69	*Burnupena pubescens*			
	sp53	*Nucella dubia*	**Brittle stars**	sp34	*Ophiothrix fragilis*
	sp71	*Nucella sp*		sp35	*Ophionereis dubia dubia*
	sp14	*Vaughtia fenestrata*		sp36	*Amphiura capensis*
Bubble-shells	sp65	*Haminoea alfredensis*	**Sea urchins**	sp23	*Parechinus angulosus*

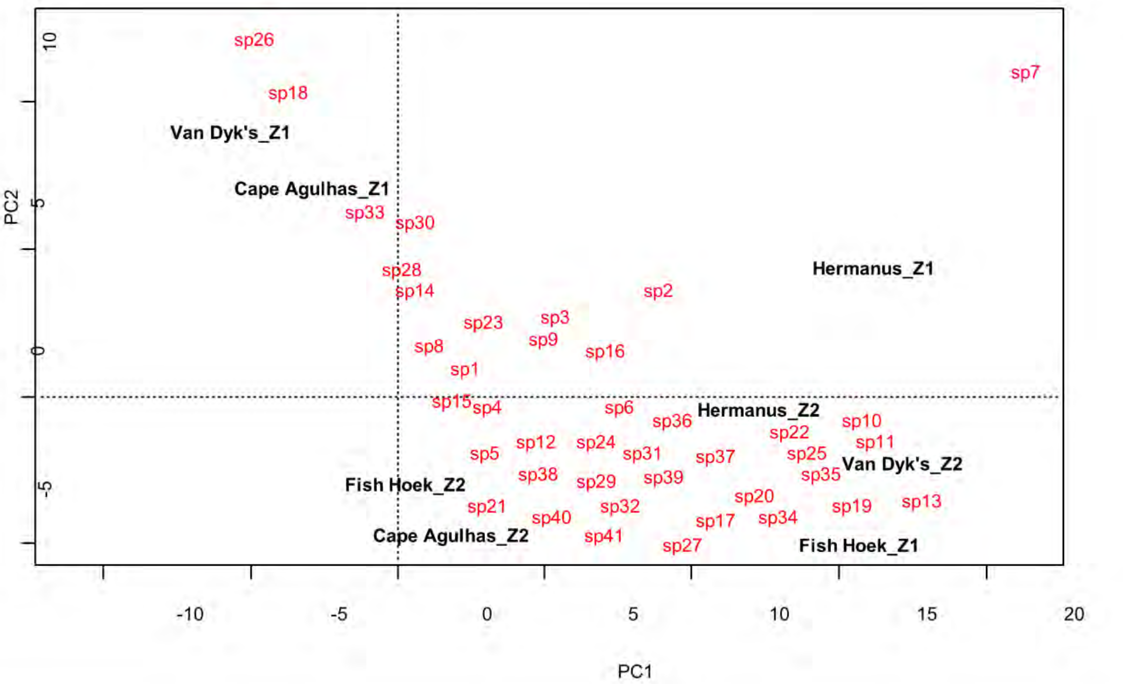


Fig.4.7.3. Correspondence Analysis for the SWO region showing the distribution of epifaunal assemblages across sites and bioregions. Full species names are provided in Table 4.5.

The species for the SWO were relatively very few in comparison to the SEO and south coasts (Figs.4.7.1 & 4.7.2). All species were almost equally distributed across all sites and zones with the exception of Van Dyk's Bay Z1 and Cape Agulhas Z1. Amphipods, limpets, and mussels were the top three taxa contributing to the highest diversity in epifaunal communities on the SWO region (Table 4.6).

Table 4.6. List of epifaunal species collected on the SWO

Taxon	Species Code	Species name	Taxon	Species Code	Species name
Segmented worms	sp1	*Pseudonereis podocirra*	**Unsegmented worms**	sp9	*Sipuncula sp*
	sp7	*Nephyts' sp*		sp11	*Anisakis pegreffii*
	sp8	*Gunnarea gaimardi*			
	sp15	*Thelepus sp*	**Amphipods**	sp18	*Paramoera capensis*
				sp19	*Amaryllis macrophthalma*
Isopods	sp13	*Ischyromene huttoni*		sp22	*Ceradocus rubromaculatus*
	sp20	*Paridotea reticulata*		sp21	*Lysianassa ceratina*
	sp35	*Exosphaeroma truncatitelson*		sp33	*Griffithsius latipes*
	sp36	*Exosphaeroma varicolor*		sp34	*Urothoe grimaldii*
				sp27	*Monocorophium acherusicum*
Limpets	sp38	*Scutellastra granularis*		sp4	*Ampelisca palmata*
	sp39	*Siphonaria concinna*			
	sp12	*Scutellastra longicosta*	**Mussels**	sp26	*Mytilus galloprovincialis*
	sp17	*Helcion pruinosus*		sp28	*Semimytilus patagonicus*
	sp24	*Helcion dunkeri*		sp40	*Aulacomya atra*
	sp25	*Scutellastra barbara*		sp41	*Choromytilus meridionalis*
	sp5	*Scutellastra natalensis*		sp2	*Perna perna_Recruits*
				sp3	*Septifer bilocularis*
Topshells	sp16	*Gibbula sp*			
	sp37	*Oxystele tigrina*	**Chitons**	sp32	*Ischnochiton textilis*
				sp10	*Acanthochitona garnoti*
Periwinkles	sp31	*Afrolittorina sp*			
	sp14	*Eatoniella sp*	**Barnacles**	sp6	*Octomeris angulosa*
Whelks	sp23	*Burnupena lagenaria*	**Cone shells**	sp29	*Conus mozambicus*
Dogwhelks	sp30	*Nassarius sp*			

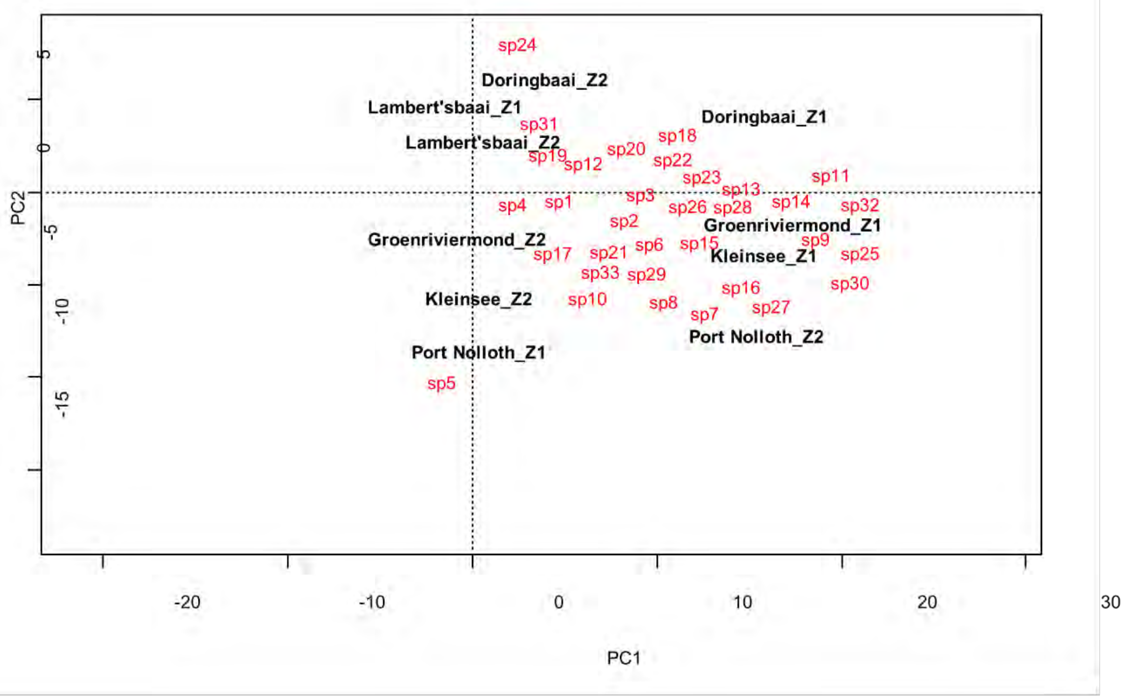


Fig.4.7.4. Correspondence Analysis for the west region showing the distribution of epifaunal assemblages across sites and bioregions. Full species names are provided in Table 4.6.

Similar patterns as observed for the SWO were also observed for the distribution of epifauna on the west coast (4.7.4). All species were almost equally distributed across all sites and zones within the bioregion. The west coast had the lowest species counts (Table 4.7) relative to all other bioregions (Tables 4.4, 4.5 & 4.6). Just like the south coast, segmented worms, amphipods, and isopods were the top three taxa contributing to the highest diversity in epifaunal communities on the west coast (Table 4.7).

Table 4.7. List of epifaunal species collected on the west coast

Taxon	Species Code	Species name	Taxon	Species Code	Species name
Segmented worms	sp1	*Lepidonotus semitectus*	**Unsegmented worms**	sp12	*Anisakis pegreffi*
	sp3	*Pseudonereis podocirra*		sp7	*Sipuncula sp*
	sp6	*Nephyts' sp*			
	sp8	*Perinereis vallata*	**Mussels**	sp31	*Aulacomya atra*
	sp10	*Perinereis dumerilii*		sp4	*Perna perna_Recruits*
	sp13	*Spirobranchus krausii*			
	sp18	*Terebella pterochaeta*	**Topshells**	sp20	*Gibbula sp*
	sp17	*Thelepus sp*			
Amphipods	sp2	*Paramoera capensis*	**Isopods**	sp24	*Cymodocella magna*
	sp5	*Ampelisca palmata*		sp25	*Paridotea reticulata*
	sp9	*Jassa sp*		sp19	*Parisocladus perforatus*
	sp14	*Griffithsus sp*		sp32	*Paridotea sp*
	sp21	*Caprella equilibra*		sp33	*Sphaerame polytylotos*
	sp22	*Amaryllis macrophthalma*			
	sp26	*Lysianassa ceratina*	**Starfish**	sp23	*Parvulastra exigua*
	sp27	*Ceradocus rubromaculatus*		sp15	*Callopatiria granifera*
	sp29	*Griffithsius latipes*			
	sp30	*Urothoe grimaldii*	**Chitons**	sp11	*Acanthochitona garnoti*
Whelks	sp28	*Burnupena lagenaria*	**Periwinkles**	sp16	*Eatoniella sp*

4.3.3. General seaweed community diversity patterns

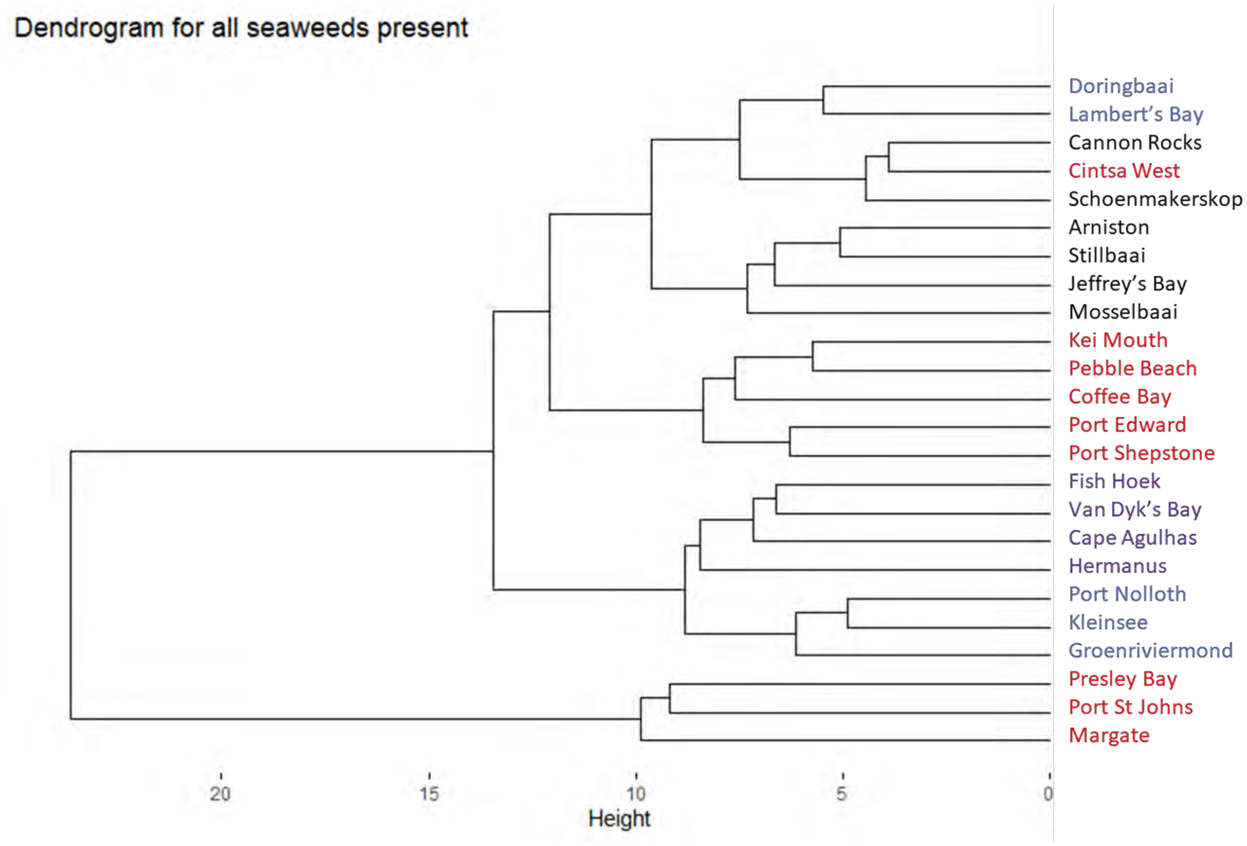


Fig.4.8. Hierarchical cluster plots comparing similarities in seaweed species composition among sites. Height =represents the ecological distance metric at which the clusters are formed. Sites are coded by bioregion where red= SEO, black= south coast, purple= SWO and blue=west coast.

The dendrogram for all other seaweeds collected showed significant overlap in clusters across all bioregions (Fig.4.8). For example, sites on the SWO and south coast clustered independent of each other.

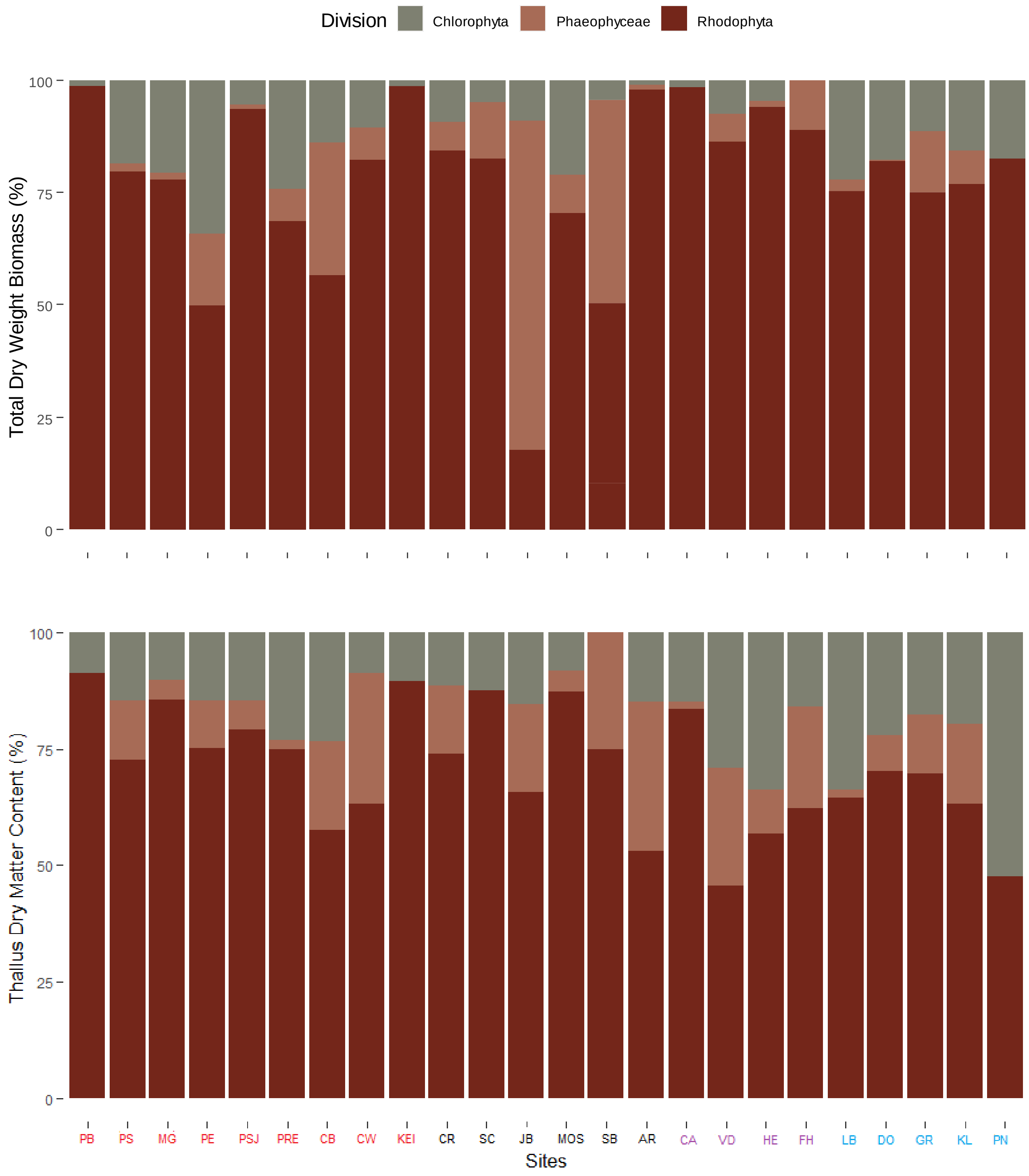


Fig.4.9. A frequency distribution showing the total DW biomass and TDMC for each seaweed Division across the 24 sampled sites. Sites are coded by bioregion where red= south-east, black= south coast, purple= south-west and blue=west coast. Refer to Fig.4.3 for site names.

The TDMC and biomass for all the other seaweed species detected and collected at each site and bioregion (Fig.4.9) were further evaluated at the Division level (i.e., Chlorophyta, Ochrophyta and Rhodophyta). However, the Kruskal Wallis test showed no significant differences in total biomass or TDMC among either bioregions or sites. In terms of richness, DW biomass, and TDMC, the most abundant group comprised the red seaweeds (rhodophytes). For the other 2 groups, the green seaweeds (chlorophytes) and brown seaweeds (ochrophytes), total DW biomass and TDMC was variable across sites. For example, chlorophytes and ochrophytes had more similar values in TDMC than DW biomass e.g., compare sites PS, CB, and GR (Fig.4.9). In terms of DW biomass, overall chlorophytes exhibited the lowest biomass across all sites. A Kruskal Wallis test, however, showed no significant differences in dry weight (DW) biomass and thallus dry matter content (TDMC) across these bioregions.

4.4. Discussion

The biodiversity found at any given location is determined by the ability of species to colonise and tolerate site conditions including food and habitat supply, as well as their interaction with other organisms (Connell 1972; Engels et al., 2011). These assumptions on biodiversity and the environment are rooted within the habitat templet theory of Southwood (1977). The heterogeneity of the environment is essential for species co-existence. Structurally complex habitats offer a variety of different microhabitats and niches, therefore allowing species to exist in greater abundances (Levin, 1992; Tuya et al., 2011). It is commonly acknowledged that one of the most limiting resources for benthic species within rocky intertidal habitats is space (Dayton, 1971; Cacabelos et al., 2010). Some species have thus survived by living on other surface or within other organisms. These organisms which essentially provide habitat are termed foundation species or habitat modifiers and have a major influence on the organisation of nearshore communities by diversifying the spatial resources and providing refuges against unfavourable environmental conditions (Monteiro et al., 2002).

Most coralline seaweeds are warm-water species, and they have shown a long-term increase in species richness through most of their history (Steneck, 1983; Aguirre et al., 2000). Therefore, because they are highly distributed and less disturbed, providing relatively stable microhabitats, I expected their diversity, and biomass to contribute to the abundance of and possibly distinct patterns in the diversity of the epifauna on the coast of South Africa. In addition, the survival of these epifauna (due to the small body sizes of most epifauna <10mm), may largely depend on seeking refuge within or on other organisms that alleviate the harsh conditions of the intertidal environment during emersion. The inclusion of the effect of biogeography was to assess the overall influence of large spatial variability simultaneously with microhabitat effects. For this study, I evaluated the small- and large-scale effects of biogenic habitat on epifaunal assemblages. One of the main assumptions was that the microhabitat offered by corallines as biogenic habitat modifiers (based on total DW biomass and turf morphological structure) might have a more significant influence on the abundance, diversity, and composition of marine epifauna, therefore distinct patterns of change could be observed at these small-scale spatial scales than at the level of bioregion.

Moreover, due to the intricate connections between biogenic habitat structure and benthic organisms, I speculated that the abundance and diversity of epifauna might be influenced in ecosystems in which the turf foundation species have been lost or replaced by morphologically different species. Therefore, I analysed the species diversity, biomass and TDMC composition of the entire seaweed community (i.e., at Division [i.e., greens, reds, and browns] and species level). This was done to evaluate other potential influences of community diversity and structure on the observed epifaunal dynamics. I hypothesised that the more diverse the seaweed community is at each site, the higher the likelihood that more microhabitats are available for epifauna to colonise macroalgae other than the corallines.

4.4.1. The biogenic habitat: Effects of geniculate coralline diversity on epifaunal assemblages

While the physical structure of seaweed is often a strong determinant of the abundance and diversity of epifaunal assemblages, isolating the effects of the physical structure within multiparameter driven systems such as in coastal systems remains challenging (Cacebelos et al., 2010; Gestoso et al., 2010; Kovalenko et al., 2012). Host specimen architecture can strongly influence epifaunal abundances and species composition; seaweeds with higher morphological complexity are usually preferred by organisms (Gee & Warwick, 1993; Jacobi & Langevin, 1996). For instance, in a study by Parker et al. (2001), amphipods responded particularly strongly to the coarsely branched red seaweed (*Gracilaria verrucosa*). Their experimental results supported a strong effect of species composition, and little effect of species diversity *per se*, on the motile macrofauna they studied.

For example, in this study, because there was a biogeographic influence on epifaunal assemblages, it was imperative to evaluate epifaunal community structure at site and within bioregion levels, to isolate the influence of biogeography. The results showed high variability in the most abundant species among bioregions. For example, on the south coast, the most abundant species included the isopod (*Ischyromene huttoni*), amphipod (*Ampelisca palmata*), and peanut worms (*Sipuncula spp*). In contrast, the epifauna of the south-east region predominantly comprised the amphipod

(*Apohyale grandicornis*), peanut worms (*Phascolosoma spp*) and annelids (*Lysidice spp*). Further, the mussel worm (*Pseudonereis podocirra*) and catworm (*Nephyts sp*) were most common in both the south and south-east bioregions. In contrast, mussel, and barnacle recruits (i.e., *Perna perna,* and *Octomeris angulosa,* respectively) were common across all bioregions. Moreover, the amphipods *Griffithsius latipes* and *Urothoe grimaldii,* and the isopod (*Exosphaeroma truncatitelson*) were most common on the south-west transition zone. The highest abundances of the amphipods *Lysianassa ceratina* and *Ceradocus rubromaculatus* and the molluscs *Gibbula* spp and *Eatoniella nigra* were recorded on the west coast. These differences may be related to variation in the physical environment, or the physiological tolerances of the organisms (Lancelloti & Trucco, 1993; Viejo, 1999).

Of the four bioregions, the SEO had the highest epifaunal species richness (121 species) compared to the south coast with 98 species, the SWO with 41 species and the west with 33 species. I speculate that the higher species composition and variability in biomass of geniculate coralline seaweeds may have contributed to the richness of epifaunal species on the SEO (Fig.4.3, Table 4.4) in comparison to other bioregions. Mean epifaunal abundances (see Fig.4.5) were notably more variable across sites on the SEO and south coasts than within other bioregions. Overall epifaunal species abundances were highest on the SEO coast compared to other bioregions where the most common coralline species were from the genus *Jania.*

These findings can have conflicting interpretations. Firstly, the increase in epifaunal richness on the SEO could corroborate the assumption that epifaunal assemblages are not host–specific. Secondly, considering that the majority of corallines on the south coast comprised *Corallina sp 1*, the results could also be interpreted as indicating that specific epifaunal species may increase in numbers as a preference for this particular coralline. Although both interpretations are plausible, the influence of biogeography seems to be an underlying driving force behind these findings more than the species composition of corallines themselves. This is because, when the relationship between epifaunal diversity, abundance, and seaweed diversity and biomass was analysed at the bioregion level, it was evident that, within the south-east region, both epifaunal abundance and richness increased with coralline diversity at site level. This may go back to illustrate that epifauna may not be species–centric as commonly assumed, and the higher diversity of epifaunal diversity may well be simply because those corallines are the available habitat within that part of the coastline, in this instance the SEO.

Comparing the results of this study to other related questions of turf-forming seaweed species influences on epifaunal communities showed varying conclusions. For example, previous studies on the coast of South Africa (see Beckley, 1982; Ndlovu et al., 2021) which have already looked at other key habit-forming turf species such (*Gelidium pristoides*). From the results of Ndhlovu et al., (2021), epifaunal community composition showed significant variability across sites, with the epifauna of sites close together being more similar in composition as observed and expected on the basis of Tobler's First Law of Geography. Their study also concluded that the effects of indirect biotic interactions might strongly influence epifaunal communities. Moreover, comparing the composition of epifauna from both these studies against my own data set, striking similarities in the most abundant epifauna species were observed. In another study, geniculate coralline algae were found to have similar invertebrate composition to leathery, corticated terete, corticated foliose, and foliose functional groups (Bates & DeWreede, 2007). Crustose and corticated foliose functional groups harboured similarly sparse assemblages. This evidence supports the suggestion that there are often few to no significant differences based on seaweed functional groups.

4.4.2. Effects of biogeography on seaweeds and epifaunal assemblages

Temperature tolerance has generally been regarded as a conservative trait in seaweeds (see Lüning, 1990). Tolerance to high temperatures (summer maximum) defines the biogeographical boundaries of seaweeds (Van den Hoek, 1982; Lüning, 1984). The temperature gradients that cause geographic changes in abundance and composition of seaweed communities are often associated with continental-scale features of oceanography (Leliaert et al., 2000; Wernberg et al., 2003). Cheney (1977) showed a clear pattern in the ratio of red and green to brown seaweed species in the North Atlantic, with higher ratios in warmer waters. Bolton (1986), however, pointed out that this pattern does not apply in southern Africa, as the cool-water brown seaweed flora in this region is relatively species-poor. In a later study by Bolton (1995), a change in the ratios of major groups was observed, with a clear increase in the green algal component (from 15% to 25% of total species diversity) moving from the temperate/tropical overlap region to the tropical flora at sites between Sodwana Bay and Bhanga Nek. Sodwana Bay is close to Mabibi while Bhanga Nek is located north of Mabibi on the east coast (refer to Fig.2.1).

In this present study, from the 24 sites I analysed, the rhodophytes clearly exhibited the highest diversity (Table S4.1) and proportion of total biomass across most sites (Fig.4.9), while the percentage biomass composition of the greens and browns were almost similar across sites. Interestingly, the thallus dry matter content (TDMC) for green seaweed was notably highest for Jeffrey's Bay and Schoenmakerskorp in the South bioregion. Jeffrey's Bay was one of the 2 sites with the highest total epifaunal abundance and richness. It is, however, important to note that these findings may be scale dependent and may change when more sites are considered e.g., all 52 sites sampled for this thesis [Chapters 2 & 3], and as other physical factors come into play. For example, it has been shown that TDMC decreases in low salinity environments for species such as the rockweed–*Fucus vesiculosus* (Klindukh et al., 2021). This is possible because the thallus' ability to change water content within certain limits prevents the cellular metabolic processes from being permanently compromised. This mechanism determines the tolerance limits of littoral seaweed and is responsible for their growth boundaries. It can be speculated that TDMC is an effect trait, with cascading influences on the ecosystem functioning. Thus, it would be worth analysing the salinity gradient of the coastline to investigate its correlation with TDMC as some bioregions have little or no freshwater input, while others include the mouths of large rivers.

Further, although epifaunal abundances were not strongly affected by the composition of geniculate coralline, there were observable changes in epifaunal diversity and composition among sites and bioregions (Table 4.2). Results from the pairwise comparisons results highlighted the epifaunal assemblages of the south and south-east bioregions as being significantly different from each other. It appears that either the shift in the physical habitat or microalgal food supply either provided by the nearshore environment or other seaweed within the community and possibly other aspects of their complex structure are the mechanisms supporting different biogeographic epifaunal diversity and composition. I also think that the low diversity in epifauna diversity within the corallines at some sites may be due to the diversity in non-coralline seaweeds (Table S4.1) which potentially increased microhabitats that the non-host-specific epifauna can occupy.

The cluster plots for both corallines and epifauna also indicated 2 interesting patterns which may conform to the observed patterns of SST and chl-*a,* respectively (see Chapter 2). For epifaunal communities, there were 2 major breaks i.e., the SEO, south and west *vs* SWO while for corallines 2 breaks were also observed with sites on the SEO and south clustering independently of the west and SWO sites. In essence, epifaunal assemblages seem to directly respond to the chl-a gradient while coralline species are more directly driven by changes in SST. This conclusion may however require more investigation i.e., identifying the functional composition of the epifauna. It is also very likely that other components of the biological communities vary along this biogeographical gradient, which could affect the seaweed distributions and epifaunal abundances. For example, a great increase in fish species diversity moving northwards in Kwazulu-Natal has been recorded in the past, with many of these fish species being grazers or omnivores (Turpie et al., 2000). Another study also suggested a region of change in the echinoderm fauna in St. Lucia (Bolton et al., 2001). These community changes will undoubtedly affect the nature of the seaweed communities along this stretch of coastline. It would, however, be very difficult to assess the effects of other seaweeds within the community without analysing the epifaunal assemblages from those seaweeds.

Further, some epifauna species may exploit distinct habitats during different phases of their life cycle. For example, Arrontes & Anadon (1990) found that many isopod species displayed marked seasonal variation in seaweed occurrence, with seaweeds providing habitats for juvenile stages, while adults occurred elsewhere. Lastly, other traits, such as feeding behaviour, vagility or response to predators, may also contribute to the high variation in epifaunal abundance and composition observed among different algal species (Pavia et al., 1999) or even different thalli of similar species (Gunnill, 1982; Kelaher et al., 2001).

4.4.3. Other possible indirect biotic influences on epifaunal assemblages

Although examples of seaweed host specialisation do exist (Sotka, 2005), the lack of a strict host specialisation by epifauna was observed in this study and has been corroborated by other authors (Russo, 1997; Attrill et al., 2000; Parker et al., 2001). Attrill et al. (2000) specifically highlighted the lack of evidence for the effects of structural complexity of seaweeds on faunal composition. However, Crisp & Mwaiseje (1989) found that structural complexity within corallines can be enhanced by the presence of attached epiphytes. These epiphytes increase the number and variety of microhabitats within the seaweed, which can in turn lead to changes and differences in faunal composition and diversity. Also, the presence of coralline turf increased recruitment of the colonial ascidian *Pseudodistoma novaezelandiae* in New Zealand (Stocker & Bergquist, 1987). In addition, by providing a refuge from herbivory, turfs of *Corallina* spp facilitated the recruitment of the kelp *Lessonia nigrescens*, which is regarded as a key structuring component of the intertidal zone in northern Chile (Bussel, 2003). In my study, the most common epiphytes I observed while sorting the coralline turfs included *Champia compressa, Tayloriella tenebrosa, Acrosorium acrospermum, Ceramium* and *Polysiphonia* spp. From personal observations, these epiphytes made the turf more compact, especially when *C. compressa* was the epiphyte. However, this aspect could not be directly verified and linked to the observed patterns in epifaunal assemblages.

Steneck et al. (1991) also suggested that coralline diversification was directly promoted by a coeval increase in herbivores, notably limpets, echinoids, and teleost fish, that removed soft algal overgrowth. The densely packed thalli and low-lying form of algal turfs cause accumulations of sediments (Whorff et al., 1995) which fill the spaces between the axes and prevent the settlement of other algal spores on the rock (Sousa, 1979). The ability of turf-forming species to pre-empt space in the intertidal despite their low-lying form ensures their success (Lobban & Harrison, 1994) and is possibly why they attract and provide refuge for various epifaunal species. This could explain the high epifaunal densities in the south-east and south coasts. I speculate it is on this basis that Crisp & Mwaiseje (1989), Chemello & Milazzo (2002) and Kelaher (2003) considered algal structural architecture or traits as influential on epifaunal diversity and abundance. Lastly, although some limpets were observed within the seaweed specimens, it was not possible to conclude whether they were using the seaweed as a refuge or as food or whether they were feeding on trapped materials within the seaweed because the study did not include gut content analysis.

On the other hand, although the presence of epiphytes provides structural integrity, their presence is associated with reduced growth rates, biomass production, and disrupted photosynthesis and damage to the thalli (Hurtado et al., 2006; Mulyaningrum et al., 2019), which subsequently compromises available habitat within the turf matrix and overall ecosystem functioning. I calculated the thallus dry matter content (TDMC) of the geniculate coralline seaweed and other seaweed species recorded from each site as a proxy for evaluating the contribution of seaweed to overall ecosystem functioning across sites. TDMC showed no variability across bioregions for the corallines, possibly because of the low diversity in epiphytes observed on the corallines. However, high TDMC of the chlorophytes may have indirectly contributed to the stability of the ecosystem in the most central sites, such as Jeffrey's Bay (see site location on Fig 4.1).

4.5. Conclusion

The biogenic habitat showed conflicting influences on epifaunal diversity and distribution. I conclude this may be because, the presence and composition of seaweeds may have both positive and negative effects on different epifaunal species based on their body sizes. For example, sediment trapping turf-forming species could suffocate some species of small-bodied epifauna, while simultaneously providing refuge for other larger limpets. Some authors have concluded that this is because marine intertidal epifauna are likely more amenable than other organisms (in more stable environments) to find a new host due to the harshness of the rocky shore habitat.

This study showed more substantial site-to-site variability in epifaunal assemblages than within coralline species composition along the vertical gradient at site level (i.e., height on shore). This result suggests that the horizontal scale gradient (10 – 100s of km) overall had stronger effects on epifaunal communities than coralline morphological structure. However, these site-to-site attributes could not be fully assessed in-depth at this stage. Therefore, it is advised that replication at small-scale and seasonal experiments be performed to distinguish transient organisms from true host-residents, which are more likely to be affected by changes in the environmental gradient. Despite this being a once-off sampling effort, the seaweed and epifaunal communities showed distinct biogeographical dissimilarities. These results indicate that the biogeographic structure was the stronger environmental filter on epifauna assemblages than potential microhabitat modification induced by different coralline species. Seaweed host–specificity does not appear a strong determinant for epifaunal diversity and distribution in the rocky shore system of the South African coastline. Both epifauna and all seaweeds including the geniculate corallines, however, do show distributional patterns that are aligned with the oceanographic patterns influencing the South African coastline. More interestingly was how epifauna communities' distribution patterns conforming to the chl-*a* patterns while coralline assemblages showed patterns consistent with the SST gradient. For more predictive results, I do recommend conducting small scale *in situ* feeding or grazing experiments across different habitats and turf seaweeds to determine the interaction among the environment, seaweeds and epifaunal composition.

4.6. Supplementary Information

Table S4.1. List of other seaweeds collected

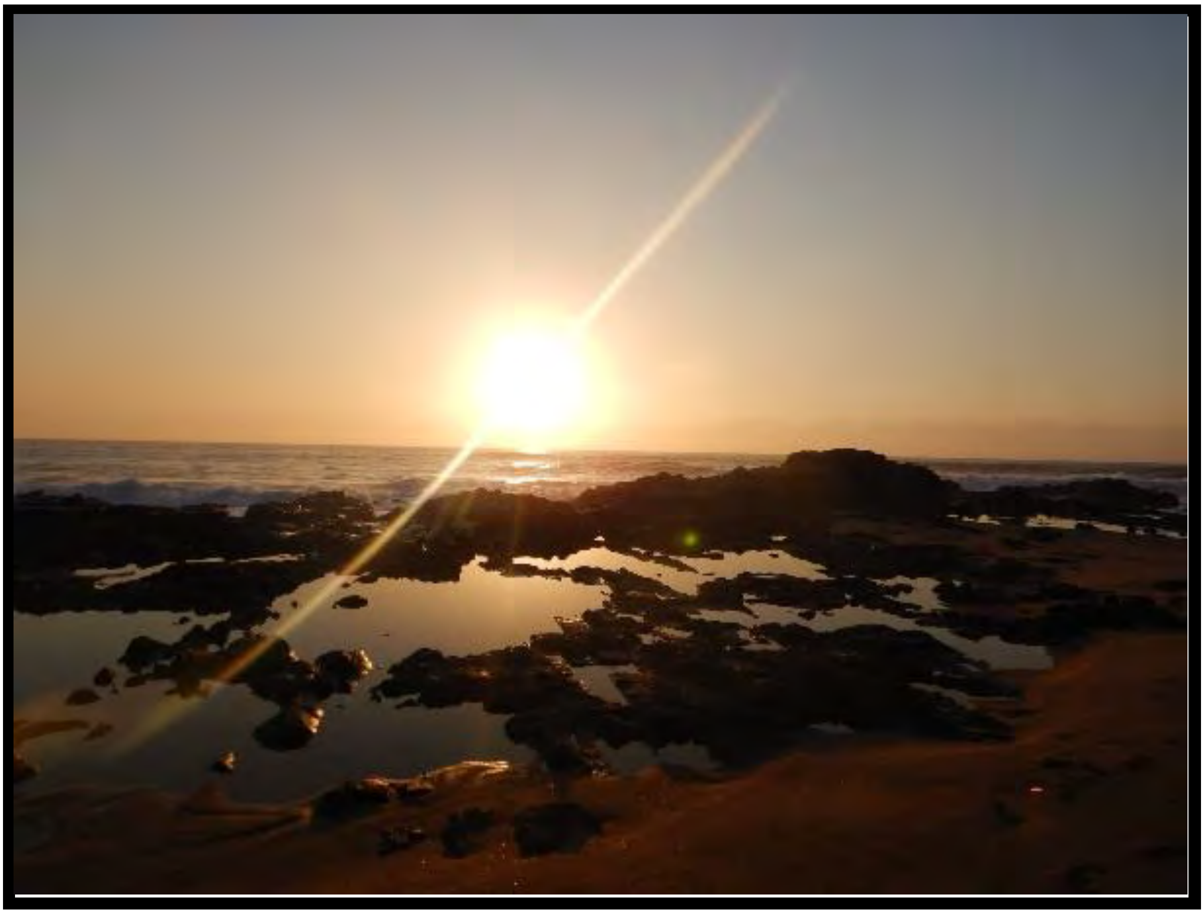
Group	Species Code	Species name	Group	Species Code	Species name
Rhodophyta	sp2	*Acrosorium acrospermum*	**Rhodophyta**	sp65	*Laurencia digitata*
	sp3	*Acrosorium maculatum*		sp66	*Laurencia flexuosa*
	sp4	*Amphiroa ephedraea*		sp67	*Laurencia glomerata*
	sp5	*Aplogosum ruscifolium*		sp68	*Laurencia riseaviolacea*
	sp10	*Bostrychia intricata*		sp69	*Laurencia multiclavata*
	sp7	*Arthrocardia corymbosa*		sp70	*Laurencia pumila*
	sp8	*Arthrocardia palmata*		sp71	*Nothogenia ovalis*
	sp19	*Centroceras clavulatum*		sp72	*Pachymenia orbitosa*
	sp20	*Ceramium arenarium*		sp73	*Phymatolithon acervartum*
	sp21	*Ceramium camoui*		sp74	*Platysiphonia delicata*
	sp22	*Ceramium centroceratiforme*		sp75	*Plocamium beckeri*
	sp23	*Ceramium papenfussianum*		sp76	*Plocamium corallorhiza*
	sp14	*Callithamnion collabens*		sp77	*Plocamium cornutum*
	sp15	*Callithamnion stuposum*		sp78	*Polysiphonia foetidissima*
	sp16	*Caulacanthus ustulatus*		sp79	*Polysiphonia incompta*
	sp26	*Champia compressa*		sp80	*Polysiphonia scopulorum*
	sp27	*Champia lumbricalis*		sp81	*Polysiphonia sp 1*
	sp28	*Champia parvula*		sp82	*Porphyra agulhensis ined*
	sp29	*Chondria armata*		sp83	*Porphyra capensis*
	sp30	*Chondria sp indet*		sp84	*Portieria hornemannii*
	sp42	*Dasyclonium incisum*		sp85	*Portieria tripinnata*
	sp45	*Gelidium abbottiorum*		sp86	*Pterosiphonia cloiophylla*
	sp46	*Gelidium pristoides*		sp87	*Pterosiphonia sp indet*
	sp47	*Gelidium reptans*		sp88	*Pterosiphonia spinifera*
	sp48	*Gigartina minima*		sp89	*Pterosiphonia stangerii*
	sp49	*Gigartina paxillata*		sp90	*Pterosiphonia stengengae*
	sp50	*Gigartina polycarpa*		sp91	*Pyropia saldanhae*
	sp51	*Herposiphonia heringii*		sp92	*Rhodymenia natalensis*
	sp52	*Hildenbrandia lecannellierii*		sp93	*Sarcothalia stiriata*
	sp53	*Hypnea rosea*		sp96	*Shepleya elixithamnia*
	sp54	*Hypnea spicifera*			
	sp55	*Hypnea tenuis*			
	sp57	*Tayloriella tenebrosa*			
	sp64	*Laurencia cf. corymbosa*			

Table S4.1 (continued). List of other seaweeds collected

Group	Species Code	Species name	Group	Species Code	Species name
Chlorophyta	sp12	*Bryopsis africana*	**Ochrophyta**	sp1	*Acitenospora crinita*
	sp13	*Bryopsis hypnoides*		sp6	*Acitenospora crinita*
	sp17	*Caulerpa chemnitzia*		sp9	*Bifurcariopsis capensis*
	sp18	*Caulerpa filiformis*		sp11	*Brassicophycus brassicaeformis*
	sp24	*Chaetomorpha aerea*		sp31	*Chordariopsis capensis*
	sp25	*Chaetomorpha robusta*		sp56	*Iyengaria stellata*
	sp32	*Cladophora flagelliformis*		sp44	*Dictyota dichotoma*
	sp33	*Codium isaacii*		sp40	*Colpomenia sinuosa*
	sp34	*Cladophora radiosa*		sp41	*Splachinidium rugosum*
	sp35	*Cladophora rugulosa*		sp94	*Sargassum elegans*
	sp36	*Codium lucasii*		sp95	*Sargassum incisifolium*
	sp37	*Codium prostratum*			
	sp38	*Codium stephensiae*	**Plankton**	sp43	Diatom sp
	sp39	*Codium capitatum*			
	sp58	*Ulva capensis*			
	sp59	*Ulva compressa*			
	sp60	*Ulva flexuosa*			
	sp61	*Ulva rhacodes*			
	sp62	*Ulva rigida*			
	sp63	*Ulva tanneri*			

CHAPTER 5

SYNTHESIS



"If we do not develop a strong theoretical core that will bring all parts of ecology back together, we shall all be washed out to sea in an immense tide of unrelated information"

Watt, 1971

Synthesis

Understanding biogeography has been rooted in the species concept (Violle et al., 2014). Species distribution models have provided projections of the effects of global change on species diversity patterns (Thomas et al., 2004; Phillips et al., 2006; Thuiller et al., 2009). Nonetheless, due to the limitations of species-based approaches in explaining causal mechanisms to species distribution, predictions of how ecological communities respond to the past, and the projected future have increasingly been a challenge (Lavergne et al., 2010; Wisz et al., 2013). This is because, if we treat species as qualitative entities, then we need to study each one of them, which is often logistically impossible. In contrast, the advent of trait-based biogeography or functional biogeography has helped us to model species interactions, dispersal ability, and physiological tolerance more simply and generically across large spatial scales (Green et al., 2008). Patterns of trait variation particularly shed light on fundamental questions in biology, including what drives organisms to live where they do and how they are predicted to respond to environmental change. It was on this premise that this research was conducted.

5.1. An evaluation of methods: How well do trait-based approaches explain community assembly patterns?

Since its inception in the 1990s, functional trait-based ecology has connected evolutionary ecology, classical population, and community ecology. More specifically, this approach offers an alternative to classical species-centric approaches with the potential to describe complex ecosystems in simple ways and to assess the effects of environmental change on ecosystem structure and function. This has revolutionised the understanding of biodiversity-ecosystem functioning (BEF) concepts (Cadotte et al., 2011). There is also a growing consensus that the effects of community composition on ecosystem processes and services are mediated by the identity, variation, and relative abundance of functional traits in a community (Díaz & Cabido, 2001; Villéger et al., 2010; Friesen et al., 2011; Funk et al., 2017). To tie these facets together, several multivariate analyses have been developed to explain these various processes. In this study, I considered biological trait analysis (BTA), functional identity measured as community weighted mean trait values (CWM), and functional diversity (measured as functional richness, functional evenness, functional divergence, functional dispersion, and functional redundancy indices). The performance of these functional indices was also compared to the classical taxonomy-based indices (i.e., Shannon diversity, Pielou's evenness, Simpson's dominance and Margalef's richness).

The aims of the BTA were first to identify and present a graphical presentation of trait distribution (via RLQ analyses – Figs. 2.6.1, 2.6.2, 2.6.3 & 2.6.4), second to evaluate how functional traits responded to spatial variability in temperature and chl-*a* gradients (via the combined fourth corner approach – Figs. 2.7.1 & 2.7.2) and lastly to evaluate how these traits subsequently contribute and relate to the species abundance and biomass patterns on the coast of South Africa. From the RLQ analyses, temperature and chl-*a* explained >95% of trait distribution (Tables 2.6 & 2.8) of temperature and chl-*a* on trait distribution. The combined fourth corner test revealed how some of the reproduction trait modalities showed significant positive and negative associations with variability in the temperature and chl-*a* gradient over time. These results of the combined fourth-corner method for BTA (in Chapter 2) corroborated the findings of the CWM trait analyses (in Chapter 3). Further, results from the combined fourth corner method revealed that both environmental parameters had significant effects on reproduction traits ($p<0.05$) but not on development traits. The influence of environmental temperature on a variety of organismal processes in ectotherms, including growth, reproduction, and survival is well recognised (Hochachka & Somero, 2002) and is rooted in early studies linking thermal tolerances to species distributions (Hutchins, 1947).

Further, I compared CWM (which is based on the mass ratio hypothesis) and FD indices (which are based on niche complementarity). Although CWM and FD express different aspects of community trait composition, they are not mutually exclusive. They both explain a significant part of the variation among various ecosystem processes (Mouillot et al., 2011; Roscher et al., 2012; Conti & Díaz, 2013). The results of this study showed that CWM weighted by biomass was notably more responsive to temperature and chlorophyll-*a* than FD weighted by biomass. In addition, across both suites of traits, CWM weighted by biomass *vs* CWM weighted by abundance values showed different results, while FD indices gave almost similar results whether based on abundance or biomass. The CWM results suggest that variability in biodiversity is likely to predict total biomass more strongly if the identity and traits of the dominant species are more critical for biomass production. In this case, it seems both diversity and dominance effects are important determinants of biomass production.

Moreover, the results for the east coast also show how the traits of the species analysed meet the main assumptions of both the biomass ratio and niche complementarity hypotheses. This is indicated by the fact that FRed was almost one (suggesting complete redundancy) for most sites on the east coast and SEO. Secondly, likewise, FDiv was also close to one (and exhibited less fluctuation) for the same bioregions. Lastly, the CWM trait values of both trait domains for the east coast were significantly different from the other bioregions. According to Hillebrand et al. (2008), the most dominant species have a significant role in the spatio-temporal variability and compositional stability of communities. Species dominance affects regional species' coexistence by altering metacommunity dynamics. Local species dominance is assumed to lead to high beta diversity with the persistence of rare species due to source-sink dynamics. Hillebrand et al. (2008), further state that, in instances where species are dominant locally, this reflects abiotic heterogeneity among locales. Species attain dominance in habitats where they are the best competitors for local niche conditions. Based on the results obtained in this study, I speculate that the populations of dominant species are primarily driven by species adapting to specific trait strategies or having higher stress tolerance. This occurs through compensatory dynamics where an increase in dominance or abundance of one species is associated with a decrease in other species as corroborated by Grman et al. (2010). This may, in turn, promote ecosystem stability because competing species may overlap in the ecosystem services they provide.

The use of the trait-based approach in this study provides insights that help in evaluating how deterministic theories based on the assumptions of the biomass ratio and niche complementarity hypotheses explain patterns and distribution of species assemblages. At the same time, this study corroborates other studies which showed that it is difficult to disentangle the relative importance and unique contributions of CWM and FD (Thompson et al., 2005; Mokany et al., 2008; Schumacher & Roscher, 2009) using only observational data. Therefore, simultaneously testing the unique and shared contributions of these two functional metrics will improve our understanding of how community trait composition affects ecosystem processes. This is especially important in a context of environmental change, where shifts in species composition can promote distinct changes in the CWM and FD of communities. Dias et al. (2013) suggested that specifically designed manipulative experiments are necessary to tease apart the effects of CWM and FD on ecosystem processes. In summary, beyond CWM, functional diversity has been shown to be an accurate predictor of ecosystem functioning reinforcing the importance of niche complementarity for enhancing ecosystem processes (Fargione et al., 2007). Recent studies have since shown that both community-weighted means of trait values and functional trait diversity can both explain variation in productivity of other ecosystems such as in semi-natural grasslands (Roscher et al., 2012). For example, higher community biomass correlates positively with functional trait diversity (Ricotta, 2005) or a combination of functional trait diversity and CWM of trait values (Mouillot et al., 2011). In the coastal system selected in this study, however, higher community biomass showed a positive correlation with community-weighted means.

There is no doubt that one of the current limitations to the use of trait-based approaches is the time and effort it takes to compile a database of trait information, especially in instances where whole communities are considered, as in this study. To date, the main databases containing some trait information include the World Register of Marine Species (WoRMS), AlgaeBase and SeaLifeBase. Although these databases are useful, sometimes they do not have comprehensive trait information and researchers often must rely on the literature to adequately capture information for species with high trait plasticity. Therefore, one of the objectives of this study was to compare the performance of trait-based approaches *vs* species-centric classical methods. In Chapter 3, the results showed the patterns in classical taxonomy-based indices among the bioregions did not completely mirror the patterns observed in functional diversity analysis. The multivariate dispersion analyses using actual abundances indicated each bioregion to be a stand-alone region (Fig.3.5B). This does not give a true representation of the coast of South Africa as species composition along the coastline is known to form a gradient (Emanuel et al., 1992). Interestingly the hierarchical cluster analyses on the actual species biomass showed the transition zones as clustering close to each other. These patterns also closely resemble the CWM patterns for the reproduction trait domain but not the development trait domain (see Figs.3.6, 3.7 & 3.8). Therefore, it can be said that functional diversity outperforms taxonomic diversity in elucidating the importance of reproduction traits on community assemblage patterns for the coast of South Africa. In a nutshell, functional diversity analyses elucidate the relationship between the environment and functional trait-based strategies which different species possess which in turn makes them better candidates for similar and/or different habitats. Thus, I conclude that, although analyses of ecosystem functioning and patterns of species assemblages based on species traits may be tedious to consolidate, the information is invaluable for predictive ecology in comparison to taxonomic based approaches.

On another note, considering individual traits and their responses to the environment in this study, most modalities within the feeding type trait were correlated with chl-*a*. This is different from the findings by Wieters et al. (2006) who found filter-feeder growth to be related to temperature instead. Earlier on, Bustamante & Branch (1996) had found that, for filter-feeders, wave action plays an overwhelming role, leading to biomass values that are more different over short distances than over a gradient of productivity spanning hundreds to thousands of kilometres. These findings suggest that a variety of factors inevitably contribute to the persistence of filter-feeders. There is a possibility that each of these factors could have contributed to other traits of filter-feeders such as their reproductive efficiency or dispersal ability which may not have been the focus of their studies. This interpretation is based on one of the key findings of this study which is that species are multi-trait organisms driven by the relationship between intra- and interspecific trade-offs, spin-offs among-trait modalities, and consequently the environment. These predictions about the role of biotic interactions are often not easy to make due to complex interactions between physical and biological processes. Lastly, superimposed on these natural factors influencing trait dynamics are a set of anthropogenic impacts and disturbances, including socio-political issues that impinge on all ecosystems.

Despite some of the aforementioned challenges arising when using trait-based approaches, these results stress the importance of a multi-pronged analytical approach when evaluating the complex relationships that underlie multivariate patterns. Firstly, the combined fourth-corner analysis primarily used for trait-based questions has brought us one step closer to an understanding of which suite of functional traits/ trait modalities respond to conditions of temperature and chl-*a*. Secondly, considering the habitat filtering concept which is primarily explained by the mass ratio and limiting similarity, the results from the community weighted mean trait (CWM) and functional diversity (FD) analyses in this study suggest that differences in patterns of functional trait distribution observed within and across bioregions conform to these two hypotheses. Between the two trait domains, the CWM (weighted by species biomass) was more responsive to the environmental parameters considered. On this premise, I make the conclusion that the mass ratio hypothesis is likely more meaningful in the interpretation of ecosystem functioning and persistence within coastal rocky shore systems. Future research should be directed at assessing whether the generality of the finding that CWM instead of FD holds for other ecosystem processes such as biogeochemical/nutrient cycling and energy flow. Detecting general rules for various ecosystem processes and community functioning might elucidate future scenarios of biodiversity threats due to global changes, such as increasing climatic extremes or biological invasions, and thus help in preventing further ecosystems' impoverishment (Bílá et al., 2014).

5.2. Does environmental filtering precede biotic filtering on the functional diversity patterns of transition zones?

As alluded in the General Introduction (Chapter 1), the environmental filtering concept excludes the biotic influence. In itself, environmental filtering is regarded as one of the major driving forces of gradients in ecosystem structure and functioning (Sommer et al., 2014). Among other contributing factors (e.g., see Kraft et al., 2014), the concept of environmental filtering proposes that species sorting along an environmental gradient is based on their functional traits and their adaptations to prevailing environmental conditions (Chase & Leibold, 2003). The ability of these species to pass through these filters is therefore dependent on their functional traits. This suggests that species experiencing the same environmental conditions are functionally similar, however biotic interactions are thought to limit the extent of similarity (Cavender-Bares et al., 2004). This biotic influence is further explained by the favourability hypothesis, which proposes that in climatically stressful habitats, environmental filtering in itself may produce a regional assemblage that is less functionally diverse than that expected given the species richness and the global pool of traits (Swenson et al., 2012). In turn, this is expected to promote increased similarity of ecological traits that affect how species respond to marginal environmental conditions at their range edges or in transition zones (Sommer et al., 2014).

Transition zones are often considered to be evolutionarily active zones where several speciation events have taken place (Williams, 1999). Understanding how and why communities are similar at biogeographic transition zones or differ along environmental gradients is therefore crucial to predicting how they may respond to environmental change (Beger et al., 2011). Shifts in species abundances, diversity and interaction patterns can be indicative of environmental filtering in areas with high abiotic stress such as these transition zones. In turn, this should subsequently promote increased similarity of ecological characteristics among co-occurring species.

Rao's Q, a functional dissimilarity measure, was notably different across sites. Some of the highest dissimilarity indices were recorded within transition zones. For example, both Rao's Q and FDis were significantly different between the east coast and the south-east transition zone, with higher dissimilarity in the south-east overlap region. This indicates more variability in the composition of traits exhibited. Further, species abundances and biomass within the SWO (i.e., Fig.3.5 A&B) also dispersed independently of the bioregions, suggesting distinct differences from the south and west coast populations. Interestingly, the hierarchical cluster analyses showed an overlap in CWM reproduction trait values of the south-west transition zone (SWO) and south-east transition zone (SEO). This seems to suggest that the dominant reproduction traits were similar in transition zones irrespective of the geographical distance between them.

Based on the interpretation of ABC curves (Warwick, 1986), however, the SWO showed indications of instability or stress. A plausible explanation is highlighted by Ferro & Morrone (2014) and involves the concept of subtraction and addition zones. Addition transition zones occur when there is a high overlap of species leading to a species-rich transition zone due to the progressive gain of taxa from each bioregion. On the other hand, in most instances, subtraction zones may not have the ideal conditions for species persistence and thus are expected to be depauperate, leading to generally low species diversity. The SWO offers a classic example of a subtraction transition zone. The results show that, although the species composition for the SWO may be similar to or resemble that of the west and south coasts, species diversity was the lowest recorded among all bioregions. This finding can be corroborated by Awad et al. (2002) who while working on the distribution of marine invertebrates along the South African coastline found that many south coast species reach their eastern limits at Cape Point (which is the western range edge of the SWO), while some extend some distance up the west coast away from Cape Town. Further, for the SWO region, the results from this study suggest that more species with cold temperate affinities may be driving the observed species dynamics. Examples include the increased presence of mussel species such as *Choromytilus meridionalis* and *Mytilus galloprovincialis,* which also contributed to the high biomass on the west coast (Table 3.2). The highest abundance, however, primarily comprised *Balanus glandula,* a small-sized barnacle, with high reproductive turnover. This species showed the highest abundance but relatively very low biomass.

A strong relationship also exists between monthly changes in the average surface water temperature and gonad development of South African marine invertebrates (Thum & Allen, 1976; Laudien et al., 2001; Schleyer et al., 2004). For most species on the coast of South Africa, gametogenesis occurs as sea-surface temperatures are rising and the breeding season occurs when water temperatures are at or about their warmest. This close relationship between changes in the average surface water temperature and gonad development of South African marine invertebrates, has led many authors to speculate on a link between temperature and the overall reproductive attributes of species (e.g., Schleyer et al., 2004). Through this study, I identified some specific reproductive attributes/trait modalities linked to temperature. These include species with direct development, simultaneous hermaphrodism, continuous reproductive frequency, gonochoristic reproductive type, and those species attaining reproductive maturity at small sizes (Figs.2.7.1 & 2.7.2). According to Fernández et al. (2009), species with direct development show a strong negative relationship with sea surface temperature (SST). For instance, low temperature at high latitudes might favour direct developers as the cost of brooding increases with temperature (e.g., oxygen provision; Brante et al., 2003). Moreover, the distributions of many marine animals follow the temperature–size rule phenomenon. This is when they mature at larger sizes in lower temperature environments and at smaller sizes in higher temperature environments (Hosono, 2011).

For the coastline of South Africa, this phenomenon has been widely observed between the east and west coasts, which are profoundly influenced by two large marine ecosystems i.e., the Agulhas Current on the east and the Benguela on the west. These systems bring dynamic changes to coastal climate and habitat properties, consequently influencing species diversity and ecosystem functioning. The two distinct environmental differences between these currents which were the focus of this study were temperature and nutrients (with chl-*a* used as a proxy for the latter). The former is regarded as one of the main abiotic factors influencing species distribution and community structure (Boland, 1997a; Munguia et al., 2006; Ma et al., 2015). At the scale of the biogeographic provinces on the coast of South Africa and depending on the group of organisms considered, the west coast is relatively depauperate for macroinvertebrate species compared to the east coast. However, there is a notable trend of macroinvertebrate diversity on the west coast, increasing from north to south (i.e., towards the south coast). On the other hand, for macroalgal assemblages, it has been suggested that the west coast is supports a higher average species richness and biomass than the east and south coasts (Bolton et al., 2004).

Considering the link between environmental cues, specifically temperature and reproduction, the effect of temperature on reproduction may be an indirect one with warm water promoting phytoplankton blooms, in turn triggering spawning. For example, research by Himmelman et al. (2008) showed that spawning of the sea star (*Asterias vulgaris*) coincided with sharp increases in sea temperature caused by downwelling. Starr et al. (1990) also observed that the spawning of green sea urchins and blue mussels may be triggered by a heat-stable metabolite released by various species of phytoplankton. Mussels require a higher phytoplankton density for a maximum response than urchins, most likely because mussels are exposed to higher concentrations of phytoplankton because of their filter-feeding mechanism. Further, phytoplankton as a spawning cue appears to integrate numerous physical and biotic factors to indicate favourable conditions for larval growth and survival. For example, the sequential spawning observed for three species (the sea urchin (*Strongylocentrotus droebachiensis*) followed by the brittle stars (*Ophiura robusta* and *Ophiopholis aculeata*) could mean either that each species was triggered to spawn by a different environmental signal such as weak to moderate currents, changes in the lunar cycle or by different thresholds to the same signal.

In summary, to date, there has been insufficient work on the community diversity within transition zones to draw concrete conclusions. Therefore, I conclude that, although the habitat filtering concept (in this case both temperature and chl-*a*) may have an effect on species diversity and subsequently traits, the abiotic filter i.e., SST in this study may be influencing trait diversity patterns. It is important to remember, however that the concept of environmental filtering is difficult to conclusively determine from observational data and there may also be other underlying factors at play and worth investigating further including those raised in the review by Kraft et al. (2014). Together with other authors (e.g., Cornwell & Ackerly 2009; Katabuchi et al., 2012; Shipley et al., 2012), I also speculate that some key elements influencing species assemblages along transition zones include the geographical size of the region and dispersal limitation and this may be true for the observations made on the SWO. Lastly, some important factors which could help the understanding the effects of the environmental filtering concept which were not fully investigated in this study, that may have influenced the results include air temperature and wave exposure. For example, studies on benthic species presence or absence have reported highly variable effects of wave exposure, in some instances weak relationships have been observed (Thomas, 1994; Chappuis et al., 2014) but see Heaven et al. (2008) and Christofoletti et al. (2011). Weak relationships are found for other environmental variables, including salinity. In addition, some specific small influences of substratum type on species presence are found but in general, the relationship is weak (McQuaid & Branch, 1984) and was not considered in this study.

5.3. Influence of large- *vs* small-scale biogenic habitat effects on epifaunal species diversity and distribution

The assembly of species within a community is thought to result from a hierarchical process in which species must pass a set of abiotic and biotic filters acting at various spatio-temporal scales

(Zobel, 1997), selecting the species best adapted to local conditions. For terrestrial environments, biogenic filters at microscales often have more easily observable effects on insects and are thus more host-specific (Janz et al., 2001), whereas marine invertebrates tend to be much more generalised in their host usage (Arrontes, 1999). Given the strong relationships that have been observed between the diversity of plants and invertebrates in terrestrial systems, it was interesting to ask why marine algal diversity and associated epifauna are not more tightly linked. It has been suggested that in most scenarios, epifaunal assemblages are robust to changes in seaweed biodiversity (Bates & DeWreede, 2007) and this seems to have been the case in Chapter 4.

Of all the four bioregions sampled for seaweed in Chapter 4, the highest epifaunal species richness (121 species) was recorded from the SEO while the south coast had 98 species. Forty-one species were recorded from the SWO and 33 species from the west. I speculate that the higher species composition and variability in biomass composition of geniculate coralline seaweeds may have contributed to the richness of epifaunal species on the SEO in comparison to other bioregions. The mean epifaunal abundances were notably more variable across sites on the SEO and south coasts than in other bioregions (see Fig.4.5). Overall epifaunal species abundance was highest on the SEO coast compared to other bioregions where the most common host algal species were from the genus *Jania.* Conflicting interpretations can be drawn from these findings. Firstly, the increase in epifaunal richness on the SEO could corroborate the assumptions that epifaunal assemblages are not host-specific. On the other hand, considering that the majority of coralline species composition on the south coast comprised *Corallina sp 1*, the results may be interpreted as specific epifaunal species increasing in numbers as a result of a preference to this particular coralline. This is because, when the relationships among epifaunal diversity and abundance, and seaweed diversity and biomass are examined at the bioregion level, it was evident that epifaunal diversity increased with diversity of the corallines on the south-east region at the site level. This may go back to support the idea that epifauna may not be species–centric, as commonly assumed, and the higher diversity of epifaunal species may be simply because the corallines may be the only potential or safer habitat on the SEO bioregion.

From this study, it is evident that the relative importance that seaweeds as environmental modifiers may have within their habitats could largely depend on the harshness of physical conditions of their environments. In this study, biogeography was at the top of the hierarchy of factors influencing epifaunal diversity, having a stronger effect than small-scale biogenic habitat structure at the site or zone level. This study showed higher site-to-site variability in epifaunal assemblages than within-site variability among coralline species. This suggests that effects operating at a horizontal scale of 10 – 100s of km had stronger overall effects on epifaunal communities than coralline morphological structure. It also appears that there are other mechanisms supporting different biogeographic epifaunal diversity and composition such as (i) shifts in the physical habitat

(ii) microalgal food supply provided by the nearshore environment and (iii) the presence of other seaweeds within the community. These site-to-site attributes, however, could not be fully assessed in depth at this stage. Therefore, I suggest that replication at small-scales and seasonal experiments be performed to distinguish transient organisms from true host residents, which are more likely to be affected by changes in the environmental gradient. In addition, due to time constraints, the functional traits of the epifauna could not be compiled and analysed to evaluate their responses to the environmental gradient. Lastly, despite this being a once-off sampling effort, the seaweed and epifaunal communities showed distinct biogeographical dissimilarities. These results indicate that the biogeographic structure was a stronger environmental filter on epifaunal assemblages than potential microhabitat modification induced by different coralline species. Seaweed host–specificity does not appear a strong determinant for epifaunal diversity and distribution in the rocky shore system of the South African coastline. Both epifauna and all seaweeds, including the geniculate corallines, do however show distributional patterns that are aligned with the oceanographic patterns influencing the South African coastline. In conclusion, although I concur that the concept of fluid faunas is true, the influence of biogeographic regions based on oceanography still has superior effects and influences zoogeography, contrary to Mayr (1946). Thus, biogeographical regionalisations are realised as instruments for a comprehensive rethinking of biogeographical concepts and aid in developing integrative biogeography (Morrone, 2018), including other facets such as functional biogeography.

5.4. Functional diversity and its implications on coastal ecosystems

The most abundant species are expected to be functionally dissimilar and to compete weakly with one another (Mouchet et al., 2010). Data collected for this study showed that the most abundant species were generally filter-feeders followed by grazers (see rank abundance curves (Table 3.1). The dominant filter-feeders also possessed R1 and R4 reproduction strategies (refer to Chapter 2, Discussion). An R1 strategy entails sequential reproduction and active dispersal while an R4 strategy involves early age at first reproduction with no active flight/dispersal. The South African coastline is assumed to favour the existence of pelagic planktonic larvae for most species and these species have prolonged spawning linked to temperature and chl-*a* gradients. Therefore, by spreading the reproductive effort over a longer period and larger spatial scales, species with this reproduction strategy minimise the probability of total reproductive failure. In addition, in as much as the most dominant species were primarily filter-feeders on both the east and west coasts, the reproduction strategies for these filter-feeders were different. This could be one of the reasons why the CWM showed no overlaps in the ellipses of the east and west coasts (Fig.3.5 A-F). Further, based on the BTA (Chapter 2), the east coast had R4 strategists as the most common trait strategy while on the west coast the R1 strategy was more common. This in itself could essentially highlight the greater influence of reproduction strategies over development strategies. Further, throughout this study, the response of reproduction traits has been more prominent than development traits.

In addition, the second most abundant trophic group also possessed a strategy that could not be fully incorporated in the current strategies by Verberk et al. (2008) which involves simultaneous reproduction with many small eggs and high dispersal. Common organisms with this strategy include limpet species (e.g., *Siphonaria capensis* and *Siphonaria serrata*). These two species lay large benthic egg masses, however, slightly differ in their dispersal dynamics. For example, *S. capensis* has planktonic development (eggs hatch after 3-4 days as planktotrophic larvae), *S. serrata* has direct development (eggs hatch after c. 30 days as crawl-away larvae). *S. serrata* also possessed the S4 strategy (i.e., high *per capita* investment with no active flight). Another S4 strategist species is the limpet *Scutellastra granularis* which is gonochoristic and spawns once annually. Species with the S4 strategy have shorter dispersal ranges than planktotrophic developers which in turn could mean increased local persistence. In this study, however, *S. granularis* showed a relatively large spatial range (100s to 1000kms) and it was among the dominant species on the south, south-west, and west coasts. According to Vat (2000), synchronised development has been observed from the south coast populations of *S. granularis* where gametogenic activity has coincidentally increased at the same time that microalgal biomass on intertidal rocks increased. In addition, Hill & McQuaid (2008), through IsoSource models showed that *Ulva* sp made large contributions to the diets of the two grazers (*Siphonaria capensis* and *Scutellastra granularis*) and this dietary dependence increased when moving from west to east coast. Moreover, *S. granularis* densities have been reported to increase as a result of the invasion by *Mytilus galloprovincialis* which provides favourable settlement and recruitment substratum (Griffiths et al., 1992; Hockey & van Erkom Schurink, 1992; Branch et al., 2008). In addition to the reproduction and development suite of traits that *S. granularis* possesses, these findings highlight the possible interplay of various factors to the persistence of other organisms, not just limpets. On the other hand, it can be speculated that the fact that the native brown mussel *Perna perna* and the limpets *Scutellastra cochlear, Cellana capensis,* and *Siphonaria serrata* are amongst the most widespread/abundant species could be a classic fit for the stochastic theory of community assembly. As native species on the coast of South Africa, their persistence may naturally be because it is endemic to the habitat.

In summary, it can be concluded that the extent to which biogeographical differences in functional trait dissimilarity and redundancy translate into differences in ecosystem function depends on how regional pools of species assemble at local scales, accounting for the abundance and trait variability of individual species. For functional redundancy to enhance the resilience of high-richness regions compared to depauperate ones, redundant species must exhibit response diversity (i.e., have different tolerances to environmental change) or have different regeneration capacities after a perturbation (Green et al., 2008). Numerous traits influence species responses, including reproductive capacity, dispersal ability, and growth rate. However, low redundancy in key groups can reduce the diversity of these traits and limit the extent of response diversity among species (Lavorel et al., 2002; Phillips et al., 2006). Response diversity is common in highly redundant marine and terrestrial ecosystems (Thuiller et al., 2005; Wisz et al., 2013; Reichstein et al., 2014). Nevertheless, the stabilising influence of response diversity becomes weaker as the severity of multiple stressors increases. For example, response diversity within similar guilds of terrestrial plants diminishes under land-use intensification (Suding et al., 2008). In this study, it was evident that the functional redundancy of organisms was high not only at the single trait level but also even at the trait domain level. Overall, at the gamma diversity level, the loss of species with developmental and reproduction traits analysed in this study may not have observable negative effects on the overall ecosystem functioning of the rocky shore system of South Africa. Except for the south-west overlap region, the high level of functional redundancy observed suggests that the rocky shore system of the coastline of South Africa is stable at this stage.

5.5. Predictions into the future using trait-based approaches

Given the links between species' traits and invasion/extinction and the fact that the resistance of marine assemblages to such events may be linked to the characteristics of member species (Arenas et al., 2006; Stachowicz & Byrnes, 2006), it seems reasonable to assert that a trait-based approach may also play a part in predicting and possibly mitigating the consequences the effects of future environmental change. Horizontal shifts in species distributions from tens to hundreds of kilometres and small changes in vertical distribution are expected with the mean surface temperature predicted to rise by 1.4–5.8°C rise in by 2100. (Suárez, 2002). Different species are expected to respond in different ways depending on their life-history traits, dispersal characteristics, and habitat requirements (Hiscock et al., 2004; Helmuth et al., 2006), with recent range extensions of some barnacle species (e.g., *Balanus perforatus*) being recorded (Herbert et al., 2003). The influence of climate on the distribution and abundance of invertebrates is also mediated through reproductive output (Kendall et al., 1985; Lewis, 1996). In a separate study on herbivores in plant-arthropod systems, the significance of species functionality and habitat filtering (both biotic and abiotic parameters) is recognised as critical in shaping species coexistence (Wang et al., 2022).

This thesis illustrates that trait-based approaches are useful for improving our understanding of how species and communities respond to the marine environment and how these communities of species subsequently influence ecosystem processes. Although this study was observational, not experimental, in design, it was meant as a baseline for future studies testing specific mechanisms, and studies adding more complexity by including multiple ecosystem processes, and integrating trait-based, phylogenetic, and demographic approaches. Some recent findings suggest a tight linkage between functional traits and demography (Adler et al., 2014), which represents a promising step in the development of an integrative and dynamical theory of functional biogeography. The mechanisms driving species co-occurrence are varied and include biotic interactions, abiotic factors, and scale-dependent processes. It is without a doubt, however, that trait-based approaches are unifying across these different scales/processes and should help improve our understanding of the biogeographical patterns of species diversity and, ultimately, may allow us to predict more conclusively the consequences of global changes for ecosystem functions and services.

Learn from yesterday, live for today, hope for tomorrow. The important thing is not to stop questioning.
– Albert Einstein

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