The influence of sampling method on detecting benthic biodiversity patterns at the ecoregion scale on the South African west coast

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Declaration

I, Silke Brandt, hereby declare this thesis, submitted in partial fulfilment for the degree of Master of Science, is my own work, all sources used have been referenced, and that it has not been previously submitted for assessment to another University or for another qualification.

Signed by candidate

Silke Brandt

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Abstract

Long-term monitoring of marine benthic communities provides data which are essential for effective ocean management. However, long-term monitoring is limited by the difficulty and expense of sampling deep seafloor areas comprehensively enough to represent the whole benthic community. This has led to the development of a wide array of seafloor sampling methods. Consequently, the integration and prioritisation of data collected using different methods remains an area of concern. Demersal research trawling and grab sampling are two methods employed to sample the marine benthos in South Africa, targeting different habitats and fauna, at different scales and with different sampling efficiencies. Both datasets inform the national marine ecosystem classification, yet the consistency between biodiversity patterns detected by each sampling method has not yet been explored.

The aim of this thesis is to determine the influence of sampling method on the detection of benthic biodiversity patterns. This was explored using demersal trawl and grab datasets collected from twenty-four pairs of stations within the Southern Benguela Shelf ecoregion on the west coast of South Africa (70 – 600 m) between the years 2009 and 2020. Differences in benthic structure, univariate diversity indices, and multivariate assemblage structure were compared between demersal trawl and grab datasets using both taxonomic and trait-based approaches. This study utilised the rarely applied co-correspondence analysis (CoCA) to test for congruency in multivariate assemblage patterns sampled by trawls and grabs. Furthermore, the use of Biological Traits Analysis (BTA) allowed for the assessment of functional diversity patterns which is often a missing link when measuring biodiversity relative to ecosystem functioning.

The epifaunal community was dominated by Asteroidea, Decapoda and Gastropoda, whereas Polychaeta, Amphipoda and Bivalvia dominated infaunal communities. BTA found trawl samples to be dominated by epifauna exhibiting large sizes, dorso-ventrally flattened body forms, free-living and surface-crawling life habits, moderate mobility, predatory feeding, planktotrophic larval development and medium-long lifespans. Grab samples were dominated by infauna with small sizes, vermiform or laterally flattened body forms, low mobility, surface deposit feeding strategies, planktotrophic larval development and short lifespans. Demersal trawl and grab sampling detected significantly similar patterns in species abundance, species richness, species diversity, and functional richness values across the west coast. Species evenness, functional evenness, functional diversity, and functional redundancy gave no evidence of a significant relationship between the two sampling methods. CoCA found infaunal assemblage patterns to be highly correlated with epifaunal assemblage patterns across the study area using both taxonomic and trait-based approaches. Environmental and spatial gradients, including depth, longitude, and sediment characteristics, played key roles in structuring broad scale biodiversity patterns.

The results of this thesis have implications for how biological datasets from trawl and grab surveys should be prioritised or weighted at different ecological scales when incorporated in the South African marine ecosystem classification and mapping process. This is the first step in transitioning the current ecosystem classification from a data informed, expert driven approach to an expert informed, data driven approach through the use of quantitative multivariate statistical techniques. Furthermore, multi-method biodiversity studies are crucial to represent the entire benthic community and understanding the extent to which the choice of sampling method affects the biodiversity patterns detected is an integral component of accurate ecosystem delineation. The findings from this thesis can be applied to future assessments of South Africa’s marine ecosystem classification, increasing its accuracy, and therefore contributing to improved ecosystem-based sea-use management.

Chapter 1

Introduction

1.1. Background

Biodiversity studies inform marine resource management and can include ecosystem classifications, environmental impact assessments, predictive modelling, or taxonomic inventories. For whichever objective, data need to be collected from marine surveys to establish regional biodiversity patterns, their environmental drivers, and baseline conditions. Studying the marine benthos offers insight into ecosystem responses to anthropogenic impact. The physical, chemical and biological components of the seafloor are all monitoring variables. Benthic communities are particularly useful for study as they are long-lived, have relatively narrow ranges and changes in ecological processes happen over longer time frames (Jørgensen *et al*., 2011). Monitoring benthic community composition, structure and distribution over space and time provides useful information for conservation planning and management efforts but is often limited by the expense and difficulty of sampling deeper seafloor areas (Costello *et al*., 2010). This has led to the advancement of a wide range of seafloor sampling methods with different specialisations (Blomqvist, 1991).

1.1.1. Marine ecosystem classification

One of the uses of biological datasets collected using different benthic sampling methods is towards marine ecosystem classification schemes and mapping. Ecosystem classification schemes can be considered as a set of instructions to delimit habitats of distinct biological assemblages (Robinson & Levings, 1996). These instructions act as a classification process by which ecologically meaningful decisions can be made about the integration of different kinds of biological and environmental knowledge or data to delimit ecosystem boundaries. This process aids the conception of habitat maps by facilitating the delineation of discrete and continuous data into spatial units relevant to management objectives (Strong *et al*., 2019; Harris & Baker, 2020).

Although true natural continuities (e.g., biocoenoses and ecotones) cannot be strictly delineated by sharp boundaries, in most systems areas can be distinguished and categorised. Consequently, many different classification schemes have been developed (Harris & Baker, 2020). The hierarchical classification of ecosystems is the most commonly used approach as it effectively handles the multiple scales at which biodiversity patterns occur. Most hierarchical classification schemes are "rule-based" (Harris & Baker, 2020) and subdivisions within the hierarchy are based on biogeographical theories that explain the differences between the levels (Poiani *et al*., 2000). This qualitative approach lends itself to more subjectivity as opposed to more analytical approaches which make use of multivariate assemblage data to quantitatively define ecosystems or biotopes (Harris & Baker, 2020).

In South Africa, one of the uses of biological datasets collected using different benthic sampling methods is towards the marine ecosystem classification and map which underpins the National Biodiversity Assessment (NBA) produced by the South African National Biodiversity Institute (SANBI) every five to seven years (Sink *et al*., 2019). This scheme is an example of a "rule-based" hierarchical habitat classification (Sink *et al*., 2019). The first marine habitat map was initially produced for the 2004 NBA (Lombard *et al*., 2004). Since then, the map has been updated to include limited biological data (Sink *et al*., 2012) and most recently the addition of biological information collected using multiple sampling methods (Sink *et al*., 2019). However, the current ecosystem map is still data informed, expert driven. The advancement towards a more data driven approach has highlighted areas of concern, such as how to integrate or prioritise data collected by different sampling methods as such data cannot be directly compared in the same analysis using classical statistics (Sink *et al*., 2019).

1.1.2. Biodiversity surrogates and metrics

Regardless of the obtainability of data, intrinsic biodiversity is never fully known, so conservation planning is always based on surrogates from established data to represent broader biodiversity patterns and change (Magierowski & Johnson, 2006). Biodiversity surrogates are especially useful when data are scarce due to sampling limitations (McArthur *et al*., 2010). Surrogates are typically categorised as either biological (certain taxon groups) or physical (habitat features). Due to technological advances, physical data over broad ranges are easily obtained and mapped (Rodrigues & Brooks, 2007), however, the accuracy of delineating ecosystems increases with the inclusion of biological data. Biological surrogates can be based on univariate data (e.g., diversity indices, count, and biomass values across sites) or multivariate data (e.g., species presence/absence or abundance matrices; Mellin *et al*., 2011). Analysing univariate data as a measure of biodiversity may less accurately characterise or represent an ecosystem's biodiversity status compared to analysing multivariate data of the entire benthic community (e.g., sites which have low species richness but have rare or endemic species). Throughout this thesis, the use of the term ‘abundance’ will refer to all measures used to quantify species amount, including both numerical counts and biomass.

There are three different kinds of biological surrogates: higher-taxa, subset-taxa and cross-taxa surrogates (Mellin *et al*., 2011). Cross-taxa surrogacy is also referred to as community concordance or cross-taxon congruence (Corte *et al*., 2017). This approach compares the similarities between whole assemblages to determine to which degree they can represent one another’s biodiversity patterns (Corte *et al*., 2017). The approach is based on the extent that different assemblages show corresponding ordination patterns across comparable sites, and therefore, how well they represent each other’s biodiversity patterns. Strong congruence occurs when different taxa respond similarly to ecological processes and this indicates effective surrogacy taxa for monitoring objectives and conservation planning (Jackson & Harvey, 1993). Demersal trawling and grab sampling are two biological datasets which feed into ecosystem classification yet the degree of their community concordance has not yet been explored in South Africa and few studies have addressed this globally (Jørgensen *et al*., 2011; Flannery and Przeslawski, 2015).

The biological dataset used as a surrogate to represent biodiversity can also be measured using different metrics. There are three main units of measurement: taxonomic diversity (Magurran, 1988), functional diversity (Díaz and Cabido, 2001) and phylogenetic diversity (Cavender-Bares *et al*., 2009). The measurements are based on species abundance and composition, biological traits, and evolutionary history, respectively. Taxonomic diversity is the most commonly used measure of biodiversity, however, it is recognised that taxonomic diversity does not directly measure biodiversity change relevant to ecosystem functioning and services (Tribot *et al*., 2016). Taxonomic diversity is not always a substitute for functional diversity, and ecosystem functioning is more dependent on functional traits rather than species diversity (Wong & Dowd, 2015). For example, some species play a key functional role in an ecosystem which means loss of that species may result in greater functional diversity loss than loss of another species. The recognition of species functional traits is often a missing link and crucial for understanding species’ relationships to one another, their environment, responses to human impact, and measuring biodiversity change more accurately and relevantly to ecosystem functioning and management.

1.1.3. Sampling biodiversity

There are many gear types available to sample the biodiversity of marine benthic ecosystems and a range of equipment within gear type groups. Sled, dredges, trawls, grabs, corers, and underwater imaging systems can all be deployed from research vessels to sample seafloor fauna. The large range of gear types is a result of the diversity of benthic habitats which each require sampling by specific gear (Costello *et al*., 2017). Different gear types target different habitats, fauna, and sediment types with varying amounts of spatial coverage. Most biodiversity studies only use one sampling method since comparisons across methods pose a challenge - in addition to the constraints of sampling offshore or remote areas. The choice of sampling gear can have a major impact on the biodiversity patterns detected (Hessler & Sanders, 1967). Any type of sampling method has its advantages as well as biases (Costello *et al*., 2017) and few studies have explored the consistency of biodiversity patterns detected across different gear types.

1.2. Sampling Bias

The detection of benthic biodiversity patterns is determined by the characteristics of the sampling gear used and the species themselves. The ability of a sampling device to collect a species is affected by the species' size, abundance, mobility, behaviour, and position relative to the seafloor (Schiaparelli *et al*., 2016). To accurately represent the benthos, multiple sampling methods should be employed to target the diverse array of benthic habitats and fauna. Different sampling gear performs better in specific habitats and certain gear targets fauna which share similar morphology and life habits. No single sampling gear can sample the full benthic habitat and community structure.

The more topographically diverse a habitat is, a greater assortment of sampling gear is generally needed to capture the different elements of the ecosystem (Schiaparelli *et al*., 2016). For example, to study benthic infauna, the appropriate sampling devices are corers or grabs which sample meio- (63-500 µm) and macrofaunal (0.5 mm-5 cm) species. Large, mobile members of the epifauna are missed by these methods, whereas the use of towed gear such as dredges, sleds or trawls can collect megafaunal (>5 cm) species of the community. However, even if multiple gear types are used, the sampling biases of each method will still over- or under-sample some members of the targeted fauna.

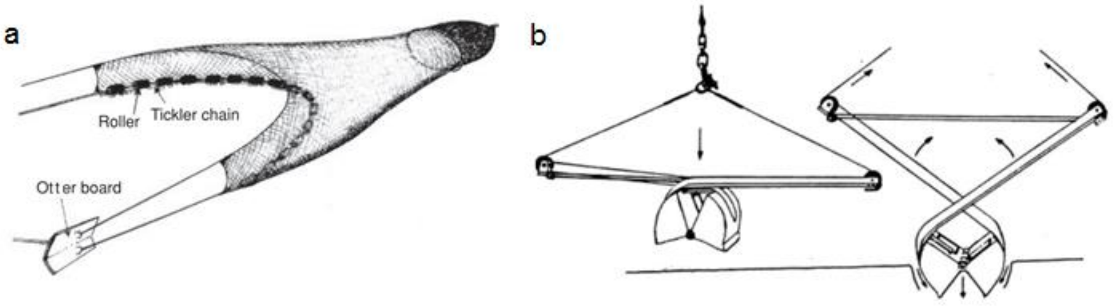

Figure 1.1. Otter trawl (a) and van Veen grab (b) (adapted from Eleftheriou & Moore, 2013).

Epifauna and infauna have different spatial distribution patterns across environmental gradients which operate at varying scales and degrees of influence. Furthermore, the different methods used to sample epifauna and infauna also operate at different scales and have their own sampling biases specific to the gear type (Table 1.1). Due to these factors, datasets acquired using different methods cannot be amalgamated when conducting biodiversity studies (Flannery & Przeslawski, 2015). The most commonly used epifaunal and infaunal samplers in South African biodiversity studies are trawls (Fig. 1.1.a) and grabs (Fig. 1.1.b).

1.2.1. Demersal trawls

Demersal trawls consist of ropes or wires attached to a metal frame or doors, which tow a net along the seabed over the sediment surface. Trawls are used as commercial fishing gear and are a common method to sample benthic macro- and megafaunal communities (Eleftheriou & Moore, 2013). There are four main types of bottom trawl: otter and shrimp trawls (trawl doors spread the net and hold it open), and beam and Agassiz trawls (mouth of the net is held open by a rigid frame). Otter trawls (Fig. 1.1.a) make use of trawl doors (‘otter boards’) to spread the net mouth and hold it open. Wires connect the trawl net to the doors. The angle of the doors is determined by the towing brackets which are connected to the warps of the vessel (Clark *et al.*, 2016). Otter trawls are commercially used in South African fisheries and abundance estimate surveys but the trawl netting can have varying mesh sizes (Axelsen & Johnsen, 2015). During annual demersal trawl abundance estimate surveys, invertebrates are collected, identified, counted and weighed, providing a source of biological data for offshore invertebrate biodiversity studies on the South African continental shelf.

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Table 1.1. Summary of factors causing disparities in datasets collected by demersal trawl and grab.

		Demersal trawl	**Grab**
Substrate type		Large sedimentary areas across all habitats	Soft sediment across all habitats
Target fauna		Epibenthic macro- and megafauna	Meio- and macro-infauna
Biological data		Qualitative/Semiquantitative	Semiquantitative/Quantitative
Environmental data		Generally measured separately and varies across sampling unit	Direct measurement of sediment characteristics from same locality as infaunal samples
Capture efficiency		Poor Varies across substrate types	Good (less so than corers) Generally decreases with depth
Scale	**Spatial**	Large area ~ 1000s m^2 Integrated sample	Small area 0.1 – 0.25 m^2 Replicates needed to characterise an area
	Temporal	Annual surveys	Sporadic/opportunistic
	Thematic (taxonomic resolution)	Poor for Polychaeta, Amphipoda, and Isopoda	Poor for Ophiuroidea, Anthozoa, and Holothuroidea
	Thematic (biological trait resolution)	Low accuracy for the above groups. Species-level biological traits are more scarcely available for epifaunal species	Low accuracy for the above groups. Species-level infaunal biological traits have been more extensively collated into accessible databases
	Intrinsic	Varies with scale Large, mobile epifauna decoupled from environment at fine scales	Varies with scale Small, sessile macrofauna closely coupled with habitat at fine scales
	Observational	~1000s m^2	0.1 – 0.25 m^2

Trawl sampling is limited to large homogenous areas of soft sediment. This provides the first filtering of what species trawls can sample. Within the trawlable grounds, trawls target epifauna which includes fish and mega and macro-invertebrates. Trawl sampling is biased towards certain animal morphologies and life habits. Typically, larger, firmer bodied epifauna are more efficiently sampled. Trawl nets can damage soft-bodied or fragile, stalked epifauna. Smaller organisms can pass through the net and burrowing animals are missed (Eleftheriou & Moore, 2013). Otter trawls are most effective at sampling larger animals such as demersal fish and macro- and mega-invertebrates (Clark *et al*., 2016). Echinoderms and crustaceans dominate invertebrate megafauna (Schiaparelli *et al*., 2016). The bias in the selectivity of the gear for the morphology and life habits of certain species will influence the interpretation of data obtained by the trawl. For example, megafauna are known to have wider depth ranges than macrofauna, which will influence the biodiversity patterns trawls detect in comparison to sampling methods which mainly target macrofauna.

Because of the variability in gear performance with each trawl, data collected by trawls are qualitative to semi-quantitative, therefore, generally limited to relative abundance or biomass and community composition (Clark *et al*., 2016). Multiple factors influence gear performance. These factors include trawl deployment (shooting and warp depth), trawling speed, substrate type, bottom contact, tow distance, trawl duration and direction, location, weather conditions, spreading of the trawl doors and the number of tickler chains (Eleftheriou & Moore, 2013). Further biases affecting samples collected by trawls occur during sample collection from the net, sorting and processing.

Attempts to standardise tows are made to estimate population densities and therefore quantify the data. Devices which can aid standardisation include time-depth recorders, digital timing devices, mechanical openers, measuring wheels and underwater cameras. Due to the qualitative nature of the data, the capture efficiency of trawls (ability to sample all animals in the sweep; Eleftheriou & Moore, 2013) is difficult to quantify and only meaningful for semi-quantitative and quantitative gear. However, studies have determined that the numbers of animals relative to the area swept by the trawl net is low and biased towards particular species (Eleftheriou & Moore, 2013; Clark *et al*., 2016).

1.2.2. Grabs

The development of grabs (and corers) allowed for the quantification of faunal richness and abundance because the size of area or volume sampled can be accurately estimated and species are effectively retrieved from that volume (Blomqvist, 1991). Grabs are normally composed of two buckets that pivot around a hinge and, when closed, encase a semi-circular volume of sediment. The van Veen grab (Fig. 1.1.b) has long arms attached to each bucket which improves leverage for closing compared to other grabs such as the Peterson grab (van Veen, 1933; Eleftheriou & Moore, 2013). The long arms also prevent the grab being jerked off the seafloor if the ship rolls while the buckets are closing. The Day grab features a frame to keep the grab level on the seafloor and two trigger plates for prompting the release. However, there are no springs to push the buckets into the sediment (Day, 1978; Eleftheriou & Moore, 2013); rather, the greater weight of the grab allows it to penetrate the seafloor sediment. Although corers improve on the grab due to increased accuracy and ability to maintain an undisrupted portion of sediment (Blomqvist, 1991; Narayanaswamy *et al.*, 2016) and sampling fixed volumes (Clark *et al.*, 2016), grabs are the standard infaunal sampling tool currently used in South Africa. Grabs are comparatively cheaper than corers and simpler to use, however, deep-sea ecologists mainly use corers for quantitative sampling work due to the decreased performance and capture efficiency of grabs as depth increases (Clark *et al.*, 2016).

Like epibenthic trawls, grabs are limited to sampling soft sediment substrate since the grab needs to penetrate the seafloor and sample a measurable volume. Therefore, the targeted fauna are meio- and macro-infauna but can include small, sessile epifauna (Eleftheriou & Moore, 2013; Narayanaswamy *et al.*, 2016). Grab sampling is less destructive than demersal trawling so soft-bodied organisms are successfully sampled, however, large, mobile epifaunal species can avoid the grab (complementary to trawl sampling). The depth of penetration is limited to the size and weight of the grab (McIntyre, 1956) and large deep-burrowing infauna may be missed. Polychaetes generally dominate benthic macro-infaunal samples, followed by small crustaceans, bivalves and gastropods (Schiaparelli *et al.*, 2016). The bias in the selectivity of the gear for certain animal morphology and life habits will influence the data obtained by grabs and the biodiversity patterns detected.

The data obtained by grabs is semi-quantitative to quantitative since the area of seafloor sampled is relatively constant across grab samples (Blomqvist, 1991; Eleftheriou & Moore, 2013; Narayanaswamy *et al.*, 2016). This allows for more meaningful capture efficiency estimates (Long & Wang, 1994) which is defined for a grab as the proportion of the number of animals in the volume of sediment collected to the number present in the same volume *in situ* (Eleftheriou & Moore, 2013). Grabs sample infauna relatively well and the capture efficiency is therefore greater than the low capture efficiency estimated for trawls. The type of grab and performance of the grab will affect the capture efficiency. Factors which affect the performance of the grab across sampling stations can include operator bias, depth, substrate type, weather conditions, depth of penetration, bite profile, amount of 'washout', sorting and processing the samples, and taxonomic identification of the macro-infauna.

1.2.3. Scale in ecology

An important biasing factor which differs across sampling gear is the scale at which the method samples. Biodiversity, habitat and communities are ecological concepts which vary across scales (Poiani *et al.*, 2000; Underwood & Chapman, 2013). Biodiversity patterns of benthic fauna vary depending on the spatial scale being assessed. For this thesis, diversity patterns are being assessed at the ecoregion scale (10s-100s km), but the gear types (trawls and grabs) are different sized sampling units. This creates disparities in the datasets collected by each method, hindering comparisons (Table 1.1). Changes in patterns with scale are understood in ecology, however, the significance of scale was not recognised until more recently (Lecours *et al.*, 2015). Research on the influence of scale and relating patterns across different scales is an important component of many sciences.

In ecological literature, three types of scale are recognised: spatial, temporal and thematic (Brown *et al.*, 2011; Lecours *et al.*, 2015). The grab and trawl datasets used in this thesis differ in all three (Table 1.1). Spatial scale refers to the geographic extent and the spatial resolution or level of detail (Schneider, 1994). Grabs sample a small area (0.1 - 0.25 m^2) well, whereas trawls can cover an area across tens of kilometres, however, doing so less efficiently. Temporal scale is also characterised by extent and resolution (Schneider, 1994). However, data from different sampling surveys will generally be mismatched temporally when incorporated into classification or mapping studies which make use of data collected over time. Therefore, this mismatch in temporal scale is less of a concern when comparing datasets but rather an inherent bias.

Thematic scale is the organisational scale, or ecological organisation level at which objects of a study are described (Lecours *et al.*, 2015). Taxonomic resolution is an example of thematic scale and needs to be considered when exploring taxonomic diversity patterns. Epifauna and infauna contain members across many taxonomic groups and the data are identified to species level when possible. However, taxonomic resolution mismatches do occur during the identification process (Table 1.1). For example, polychaetes obtained in the trawls are often identified to Class level whereas in the grab data, they are the dominant fauna and identified to species level. Thus, the same species may be identified to a lower taxonomic level and higher resolution in grab samples than in trawl samples. This in turn affects the accuracy of biological trait information in functional diversity studies, creating further disparities across thematic scales. Though, the proportion of species for which this specific mismatch occurs is likely quite low.

There are also a distinctions between the scale at which a process or pattern occurs (intrinsic scale) and the scale of observation (Lechner *et al.*, 2012). The intrinsic scale (scale at which ecological processes relate to the environment) is ultimately measured by the observational and analytical scale. The observational scale (sampling unit applied to measure the environment) refers to the data used to describe the natural process or pattern. The patterns being compared are the taxonomic and functional diversity patterns (intrinsic scale) between epifauna and infauna, which are different (Table 1.1). For example, the associations of infauna and epifauna species with their environment vary with spatial scale. Generally, mobile (epifaunal) species show decoupling from environmental correlates at fine scales and have closer associations to their habitat at broader scales, compared to the close association of sessile or less mobile species to their habitat at fine scales (Lecours *et al.*, 2015).

1.3. Biodiversity Congruence

Based on known biogeographical theory and the biases associated with different benthic sampling methods (discussed in the previous section), it is predicted that different sampling methods will detect different biodiversity patterns. Existing research also provides evidence in support of different biodiversity patterns being detected across different gear types. Although few studies have directly compared whether different sampling methods detect different benthic community patterns (Jørgensen *et al.*, 2011; Flannery & Przeslawski, 2015), this result can also be extrapolated from some biodiversity studies (Flannery & Przeslawski, 2015). Biodiversity studies which make use of multiple gear types to explore community patterns and their potential environmental drivers provide information on whether ecological patterns are consistent across different gear types. Studies which have sampled both epifauna and infauna (and therefore used both epifaunal and infaunal sampling methods across the same scales) and identified their main environmental drivers provide some insight into the influence of sampling method on biodiversity results.

1.3.1. Epifauna and infauna congruence

Out of twelve studies reviewed, nine gave evidence of inconsistent patterns between epifauna and infauna biodiversity patterns. Univariate measures of diversity show varying responses to environmental gradients and disturbance between epifauna and infauna. Some studies have found consistent patterns in species number, species richness (Buhl-Mortensen *et al.*, 2012), species diversity (Reiss *et al.*, 2010), trait abundance (Muntadas *et al.*, 2016) and functional diversity (Trannum *et al.*, 2019) between epifauna and infauna. However, studies have also found inconsistent patterns in species diversity, species evenness, abundance, biomass (Buhl-Mortensen *et al.*, 2012), trait richness, and functional redundancy (Muntadas *et al.*, 2016) between epifauna and infauna. Multivariate community patterns almost always showed inconsistent patterns between epifauna and infauna to environmental drivers (Basford *et al*., 1990; Rees *et al*., 1999; Ganesh & Raman, 2007; Currie *et al*., 2009;;Silberberger *et al*., 2019). Similarly, trait assemblage patterns also show inconsistent responses (Fleddum *et al*., 2013; Muntadas *et al*., 2014; Tiano *et al*., 2020). Few studies found consistent responses of epifaunal and infaunal communities to environmental variables and these were only found at broad spatial scales (Reiss *et al*., 2010; Silberberger *et al*., 2019).

1.3.2. Sampling method congruence

Two studies directly compared the influence of sampling gear (including samples collected by trawls and grabs) on the detection of benthic biodiversity patterns. Flannery and Przeslawski (2015) investigated whether broadscale biodiversity patterns are consistent among community data acquired from different sampling gear types and which methods together provide the most accurate results for biodiversity assessments. Overall, they found little consistency in biodiversity patterns between different gear types. The exception was the consistent response of univariate biological data from sled and video sampling methods to geomorphic groups. Similarly, the multivariate faunal assemblage data for all the gear types were significantly related to geomorphology, showing some consistency in ecological relationships across all gear types. Jørgensen *et al*. (2011) investigated how biodiversity assessments characterise the whole benthic community by comparing taxonomic and functional components sampled by trawls and grabs. Mean species richness, density, abundance of individuals, and overall biomass were compared between grab and trawl samples and had varying results. Faunal communities and functional components collected by grabs were found to differ widely from those collected by trawls.

1.4. Gaps and Limitations

1.4.1. Statistical limitations

The main challenge when incorporating different biological datasets into ecosystem classification is that disparate datasets collected by different sampling methods cannot be directly compared using classical statistical methods. Jørgensen *et al*. (2011) standardised the grab and trawl data both to unit/100 m^2 to directly compare measures of biodiversity for each gear type, amalgamating the datasets and analysing them together in the same correspondence analysis. However, this approach may obscure any similarities in assemblage structure because it compares species or trait datasets which are inherently different across grab and trawl samples and not necessarily indicative of differences in relative assemblage structure. Although, it does allow for some comparison of assemblage structure (but this is not a direct comparison nor statistical test).

Flannery and Przeslawski (2015) used a different approach to compare the influence of sampling methods on ecological patterns using a taxonomic-based approach. They compared the responses of fauna sampled by different methods to environmental drivers. The biological data could not be compared directly by classical statistics because of the different sampling methods used and the inability to standardise for them. By relating biodiversity measures to environmental drivers, the authors determined ecological patterns to be inconsistent across gear types. This indirect comparison of the biological data is not ideal because environmental variables are measured to different degrees of accuracy for each gear type. For example, grabs allow for *in situ* sediment sampling, whereas other integrated sampling methods do not allow for this fine scale biological and environmental coupling. This creates discrepancies in the data when determining consistent ecological patterns across gear types.

1.4.2. Co-correspondence analysis (CoCA)

Recently, the rarely utilised co-correspondence analysis (CoCA; ter Braak & Schaffers, 2004) has been applied in terrestrial and freshwater studies to directly relate two sets of communities. The only limitation on the data is that communities need to be collected from the same sampling location or unit, otherwise all other differences in scale or parameters between the samples can differ. CoCA maximises the weighted covariance between the weighted averaged species scores of two communities. By doing this, CoCA can identify the patterns similar to both communities. CoCA can be symmetric (descriptive) or asymmetric (predictive).

CoCA is not a widely used statistical method in the literature with few studies using it to investigate community associations. Studies which do apply it are almost all terrestrial or freshwater ecosystem studies (Gioria *et al*., 2010; Mitchell *et al*., 2010; Hanson *et al*., 2015; Zhang *et al*., 2018), although it has recently been used to compare marine microbial communities (Alric *et al*., 2020). One reason for the lack of studies directly relating different sets of community data to each other was the previous absence of appropriate statistical methods to do so (ter Braak & Schaffers, 2004; Schaffers *et al*., 2008). The lack of the method being used in the marine realm may be a result of the general lag of marine science behind terrestrial or freshwater counterparts due to sampling difficulties. Also unique to this study is the application of CoCA to compare functional trait datasets for the first time.

1.4.3. Functional diversity: the missing link

Taxonomic diversity is the most commonly used measure of biodiversity; however, it is recognised that it does not always directly measure biodiversity change relevant to ecosystem functioning and services (Tribot *et al.,* 2016). The recognition of species functional traits is often a missing link relevant to ecosystem functioning. Of the multi-method biodiversity studies reviewed, less than half of the studies incorporated a functional trait-based approach (Fleddum *et al.,* 2013; Muntadas *et al.,* 2014; Muntadas *et al.,* 2016; Trannum *et al.,* 2019; Tiano *et al.,* 2020). Functional analysis of benthic assemblages can delineate communities differently and generally reveal more detail than using only traditional taxonomic analysis (Fleddum *et al.,* 2013; Wong & Dowd, 2015). If the taxonomic diversity patterns detected by trawls and grabs are found to be similar, this is only relevant to management if the functional aspects are also similar as this would suggest similar community sensitivity to impact or disturbance. The functional role of benthic animals provides the crucial link between individual species and benthic ecosystem functioning. There is a need to understand how sampling gear biases affect our ability to sample certain functional components and structure of the benthic community and predict biodiversity responses to environmental change.

1.4.4. Biological Traits Analysis (BTA)

Biological traits analysis (BTA) is an approach used to characterise species diversity and function within their ecosystem. It is an effective tool which can be applied to benthic macrofauna to assess their trait responses to their environment (Bremner *et al.*, 2006). Traits are defined as measurable or categorisable properties of an organism and are generally described at species level when information is available (McGill *et al*., 2006; Tyler *et al*., 2012). The selection of traits which are included in the BTA is an important step and should be based on the research objectives, scale of assessment, and the availability of reliable biological information. Traits most appropriate to broad scale community ecology include life history, reproduction, feeding ecology and behaviour (Webb *et al*., 2009; Tyler *et al*., 2012). BTAs are becoming more frequently applied to study benthic macrofauna (Degen *et al.,* 2018) but have rarely been used in studies focusing on South African offshore macrofaunal invertebrate communities (Fleddum *et al*., 2013).

1.4.5. Geographical gaps

Sampling effort is geographically biased towards coastal areas and developed nations (Costello *et al*., 2010), resulting in a lack of knowledge of deep-water species biogeography which varies regionally. This lack of information reflects the challenges of sampling deep-sea biota due to gaps in capacity, expertise, and adequate technology. Results of regional revisions from the Census of Marine Life indicated that deep-sea areas in South African waters are poorly known in comparison to coastal shelf waters. In South Africa it was estimated that only 17% of benthic invertebrate marine samples were collected from water deeper than 100 m despite the large extent of offshore habitats (Griffiths *et al*., 2010). Furthermore, benthic invertebrates are understudied in comparison to marine vertebrates and plants (Costello *et al*., 2010). The taxonomic knowledge of South African offshore marine invertebrates is particularly lacking in comparison to other taxa (Gibbons, 1999).

Multi-method biodiversity studies are concentrated in the coastal regions of UK, Norway, and Australia (Flannery & Przeslawski, 2015). There are a limited number of studies from South America and Africa and from offshore areas. Very few biodiversity studies which make use of multiple sampling methods within the same study have been conducted in South Africa (e.g., Fleddum *et al*., 2013). Biological data gaps exist in South African marine ecosystem classification since this process is mainly facilitated by physical data. Physical data across broad areas are more attainable and act as proxies for biodiversity patterns, however, biological data inform more accurate ecosystem type delimitation (Karenyi, 2014; Harris & Baker, 2020). Further data-driven approaches that can combine large datasets covering multiple ecosystem types collected by different methods have been encouraged to inform the next South African marine ecosystem classification and map (Sink *et al*., 2019).

1.4.6. The Southern Benguela Shelf ecoregion

In this thesis, samples are compared from unconsolidated sediment habitats of the west coast of South Africa across the Southern Benguela Shelf ecoregion. This addresses the geographical bias identified by Flannery and Przeslawski (2015) regarding the lack of multi-method studies from Africa. The data are biological samples of offshore benthic invertebrates, an understudied group, providing information regarding the influence of sampling methods on the detection of biodiversity patterns. This will inform the integration of data collected by multiple sampling methods and deepen our understanding of factors influencing the accurate detection biodiversity patterns. The west coast of South Africa has higher sampling effort compared to the south and east coasts (Griffiths *et al*., 2010), enabling the availability of biological data for analysis. The regional scale is the broadest operating scale for national management and testing at the ecoregion scale is relevant to management practices and allows for global comparisons of findings.

1.5. Thesis Aim and Objectives

1.5.1. Thesis aim

The aim of this thesis is to determine the influence of sampling method on the detection of benthic biodiversity patterns. This study will identify the main disparities between ecological results derived from data collected by two different benthic sampling methods currently employed in South Africa. These data include demersal research trawl and grab data sampled at the ecoregion scale on the South African west coast. To compare the similarities in biodiversity patterns detected by the two sampling methods, two predictive hypotheses will be tested: 1) demersal trawling and grab sampling detect different taxonomic diversity patterns and 2) demersal trawling and grab sampling detect different functional diversity patterns (addressed in Chapter 2 and 3, respectively). CoCA will be utilised to address both hypotheses and directly compare assemblage patterns. Chapter 4 synthesises the results of these chapters and places the finding into the greater marine context.

1.5.2. Chapter aims and objectives

The aim of Chapter 2 is to determine whether demersal trawling and grab sampling detect different taxonomic diversity patterns at the ecoregion scale on the South African west coast. The objectives of the chapter are:

i) to compare community composition and structure
ii) to compare trends in taxonomic diversity indices
iii) to compare community assemblage patterns between demersal trawl and grab sampling methods

The aim of Chapter 3 is to determine whether demersal research trawling and grab sampling detect different functional diversity patterns at the ecoregion scale on the South African west coast. The objectives of the chapter are

i) to compare functional trait assemblage composition and structure
ii) to compare trends in functional diversity indices
iii) to compare functional trait assemblage patterns between demersal trawl and grab sampling methods

Chapter 2

The influence of sampling method on detecting benthic biodiversity patterns using a taxonomic-based approach

2.1. Introduction

Monitoring benthic communities to determine species or habitat occurrence and change is an important component of marine management. Benthic community composition, structure and geographical distribution can be monitored over time to provide useful information on ecological responses to environmental change or human impact. Offshore benthic invertebrates often have narrow ranges and are relatively long-lived compared to their shallower counterparts and are therefore useful indicators of slow changes in ecological processes and ecosystem status (Gray, 1974; Warwick, 1993; Salas *et al*., 2006). Being sensitive to human activities and having important functional roles makes benthic communities a key ecological metric (Koslow *et al*., 2001). However, monitoring offshore benthic communities is hindered by the elevated expense and the difficulty of accessing deep seafloor areas (Costello *et al*., 2010) which has led to the development of a wide array of seafloor sampling methods with different specialisations (Blomqvist, 1991).

Data collected using different sampling methods are not readily incorporated into the same analyses using classical statistical methods. Consequently, biodiversity studies tend to use only one benthic sampling method (which may target a certain habitat or faunal group) to represent the benthic community as a whole (Flannery & Przeslawski, 2015). This type of biological surrogacy can be referred to as cross-taxon congruence (Mellin *et al*., 2011; Corte *et al*., 2017) by which whole assemblages are used as biodiversity surrogates. This approach is based on the extent to which distinct assemblages show corresponding ordination patterns across the same sites (Jackson & Harvey, 1993; Paavola *et al*., 2006; Thomaz *et al*., 2007) and the surrogate effectiveness varies depending on the sampling method employed. As every sampling method has advantages and biases, the reliability of biodiversity patterns detected using only one sampling method needs more research attention (Flannery & Przeslawski, 2015).

One of the uses of biological data collected by different sampling methods is towards the marine ecosystem classification and mapping process in South Africa. The most recent ecosystem classification was informed by several biological datasets collected using different sampling gear types, including epifauna, infauna, and underwater imagery (Sink *et al*., 2019). These biological datasets essentially act as biodiversity surrogates based on benthic taxonomic diversity patterns. Demersal trawling and grab sampling are two common sampling methods employed to monitor the benthos. Trawl and grab surveys should be combined to improve benthic monitoring (Jørgensen *et al*., 2011), however, their datasets are generally analysed separately due to data disparities. Datasets collected by demersal trawls and grabs differ mainly in the faunal group and habitat they target, the sampling efficiency, and the scale at which they sample.

Demersal research trawling targets epifaunal species and the number of animals in relation to the area swept by the net is generally low and selective for particular species (Eleftheriou & Moore, 2013; Clark *et al*., 2016). Grabs target meio- and macro-infaunal species (and some small, sessile epifaunal species) residing within the soft sediment (Narayanaswamy *et al*., 2016). Grab sampling is quantitative since the volume of sediment sampled is relatively constant across grabs, and the sampling efficiency is more reliable and greater than that achieved by trawling (Blomqvist, 1991; Long & Wang, 1994). The scale of demersal trawling and grab sampling differs spatially, temporally and thematically (Brown *et al*., 2011; Lecours *et al*., 2015).

Spatially, the geographical extent covered by demersal trawls is broad (~80 000 m^2) and may cover multiple habitat and ecosystem types in a sweep – missing distinctions between these habitats as species from different habitats are collected in a single sampling event. In contrast, grabs efficiently sample fine scale detail at the resolution of meters (0.1–0.25 m^2), but may fail to represent communities at a broad scale due to the patchy nature of benthic habitats (Eleftheriou & Moore, 2013). Although, on the South African west coast, grab samples have been used to some extent to classify ecosystems at the broad scale (Karenyi, 2014).

Temporally, trawl and grab datasets which contribute towards the ecosystem classification and mapping process are often mismatched as they are collected by different biodiversity studies conducted at different times. The thematic scale (the organisational scale which is linked to the level at which objects of a study are described) sampled by trawls and grabs differ when comparing the taxonomic resolution of certain taxa (e.g., Polychaeta and Ophiuroidea are often identified to different taxonomic levels when collected by the different sampling methods). A change in scale affects faunal groups differently (Brown *et al*., 2011; Lecours *et al*., 2015);

even if sampling occurred at the same scales, patterns in epifaunal and infaunal habitat coupling may still diverge due to the characteristics of the taxa.

Biodiversity studies which sampled both epifauna and infauna at the same scale and assessed their ecological responses to the environment using a taxonomic-based approach have almost all found inconsistent community patterns and drivers between epifauna and infauna (Basford *et al*., 1990; Rees *et al*., 1999; Ward *et al*., 2006; Ganesh and Raman, 2007; Currie *et al*., 2009; Buhl-Mortensen *et al*., 2012; Silberberger *et al*., 2019). Studies directly comparing community patterns detected by different sampling methods have found little consistency in biodiversity trends between different gear types (Flannery & Przeslawski, 2015). More specifically, demersal trawls and grabs have been found to sample widely different communities (Jørgensen *et al*., 2011, Flannery and Przeslawski, 2015). The influence of sampling method on study results is highly dependent on sampling location and design, the types of data and the statistical methods used to draw comparisons.

This study was conducted using data from the South African west coast collected by demersal research trawl and grab sampling. The aim of this chapter is to determine whether demersal trawling and grab sampling detect different taxonomic diversity patterns at the ecoregion scale on the South African west coast. The objectives of the chapter include determining whether demersal trawls and grabs i) sample different taxonomic compositions and structure, ii) detect different trends in taxonomic diversity indices, and iii) detect different community assemblage patterns. Both qualitative and quantitative methods are used to address the objectives.

2.2. Methods

2.2.1. Study area and sampling design

The west coast of South Africa is a sediment habitat in an eastern boundary upwelling region: the Southern Benguela Shelf ecoregion (Sink *et al*, 2019). This is the most productive of South Africa's six ecoregions and it is distinguished by the cold equatorward flowing Benguela current and nutrient-rich water from large-scale upwelling events (Field & Shillington, 2006). Unconsolidated sediment communities are environmentally structured and driven by many local processes. Specifically, depth and sediment type have been found to be important drivers of benthic faunal patterns in the region (Lange & Griffiths, 2014; Steffani *et al*., 2015; Karenyi *et al*., 2016).

The study includes a total of 24 sites off the west coast of South Africa (Fig. 2.1). The sites are located across ten ecosystem types within the ecoregion, spanning the mid shelf, outer shelf, shelf edge, and upper slope depth zones (70 m–600 m) and diverse substratum types including muddy, muddy sand, sandy, and rocky sand mosaics (Table 2.1). Each site was selected based on whether both a grab and trawl station were available at approximately the same location. A 25’x25’ grid block with both a trawl and grab station present was used to select sites (the size of the demersal trawl research survey grid blocks; Fig. 2.1). The trawl and grab stations are subsets taken from previous research and monitoring initiatives.

A further criterion for the selection of sites is that the trawl and grab station pairs fall within the same ecosystem type (Sink *et al.*, 2019), therefore, likely sharing similar depth and sediment characteristics. Site pairs differed by no more than 50 m, except for site 11 which had a 123 m difference in depth between trawl and grab stations, however, this was the only site from the upper slope of the continental shelf, and it was included in the study to represent the ecosystem type.

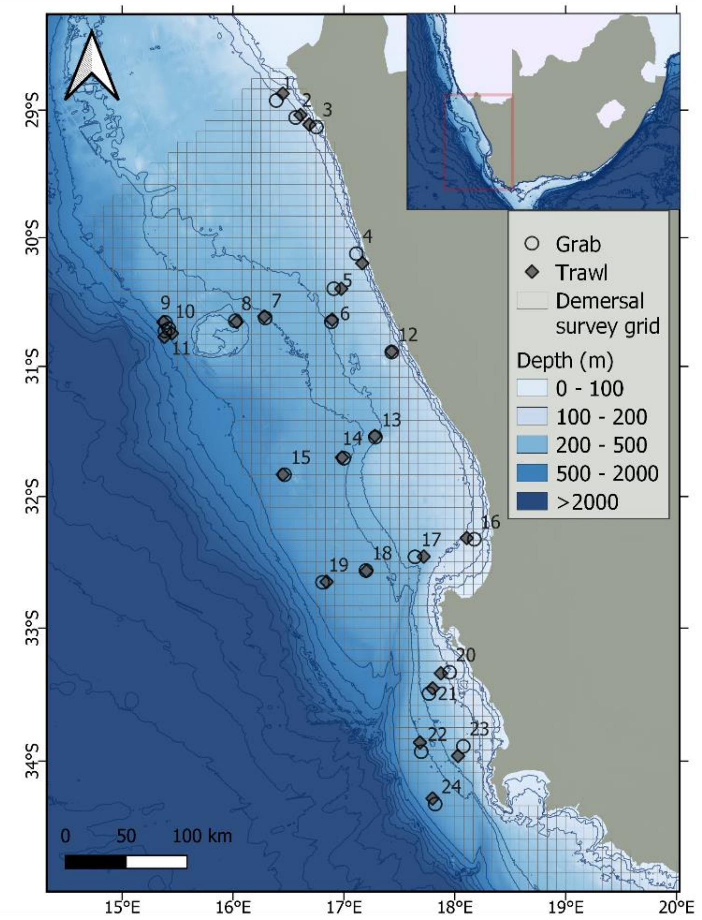


Figure 2.1. Demersal trawl and grab stations sampled from 24 sites on the west coast of South Africa. The demersal survey grid is shown with trawl and grab station pairs falling within the area of a grid block.

Table 2.1. Sites consisting of demersal trawl and grab station pairs across the Southern Benguela Shelf ecoregion on the west coast of South Africa sampled during various research and monitoring initiatives.

Site	Station ID		Grab type	Grab size (m^2)	Year		Latitude (°S)		Longitude (°E)		Depth (m)		Ecosystem type
	Trawl	Grab			Trawl	Grab	Trawl	Grab	Trawl	Grab	Trawl	Grab	
1	A32180	De Beers N1-C2	Van Veen	0.2	2012	2014	-28.86	-28.92	16.44	16.38	79	122	Orange Cone Muddy Mid Shelf
2	A33891	De Beers Bio2A	Van Veen	0.2	2019	2014	-29.03	-29.05	16.60	16.56	95	121	Orange Cone Muddy Mid Shelf
3	A34488	PN St 3A	Van Veen	0.2	2020	2014	-29.11	-29.13	16.68	16.75	82	70	Orange Cone Muddy Mid Shelf
4	A33895	Platbaai St 4	Van Veen	0.2	2019	2014	-30.20	-30.12	17.16	17.11	112	118	Namaqua Muddy Mid Shelf Mosaic
5	A33896	PSBS 01/05 A	Van Veen	0.2	2019	2014	-30.39	-30.39	16.97	16.90	162	165	Southern Benguela Muddy Sands
6	A31437	Platbaai St 5A	Van Veen	0.2	2011	2014	-30.63	-30.65	16.89	16.88	186	187	Southern Benguela Muddy Sands
7	A33175	ALG13451-28	Day	0.25	2017	2020	-30.61	-30.62	16.28	16.29	248	250	Southern Benguela Outer Shelf Rocky Sand Mosaic
8	A31432	ALG13450-27	Day	0.25	2011	2020	-30.65	-30.64	16.03	16.02	204	202	Child's Bank Plateau and Sandy Slope
9	A32161	BTE-14-5-1c I	Van Veen	0.1	2012	2014	-30.65	-30.66	15.37	15.39	383	362	Southern Benguela Sandy Shelf Edge
10	A33166	BTE-18-4-5c I	Van Veen	0.1	2017	2018	-30.74	-30.70	15.45	15.42	387	380	Southern Benguela Sandy Shelf Edge
11	A32160	BTE-14-1-4d I	Van Veen	0.1	2012	2014	-30.77	-30.72	15.38	15.38	608	485	Southern Atlantic Upper Slope
12	A33899	ALG13461-40	Day	0.25	2019	2020	-30.88	-30.89	17.43	17.43	132	132	Namaqua Muddy Mid Shelf Mosaic
13	A32207	ALG13435-41	Van Veen	0.2	2012	2020	-31.53	-31.54	17.27	17.28	212	209	Southern Benguela Sandy Outer Shelf
14	A33795	ALG13434-42	Van Veen	0.2	2019	2020	-31.70	-31.70	16.98	16.99	272	268	Southern Benguela Outer Shelf Rocky Sand Mosaic
15	A33083	ALG13433-1	Van Veen	0.2	2017	2020	-31.83	-31.83	16.44	16.46	368	366	Southern Benguela Hard Shelf Edge Mosaic
16	A31408	SHB St 3A	Van Veen	0.2	2011	2014	-32.31	-32.32	18.10	18.17	90	75	Namaqua Muddy Mid Shelf Mosaic
17	A33182	SHB St 6A	Van Veen	0.2	2017	2014	-32.45	-32.46	17.72	17.64	162	187	Southern Benguela Sandy Outer Shelf
18	A32220	SHB St 8A	Van Veen	0.2	2012	2014	-32.56	-32.56	17.20	17.19	275	286	Southern Benguela Outer Shelf Rocky Sand Mosaic
19	A34512	SHB St 10	Van Veen	0.2	2020	2014	-32.65	-32.65	16.84	16.80	352	391	Southern Benguela Sandy Shelf Edge
20	A33905	PSBS 11/03 A	Van Veen	0.2	2019	2014	-33.34	-33.33	17.87	17.95	145	94	Cape Rocky Mid Shelf Mosaic
21	A33906	Yz St 5A	Van Veen	0.2	2019	2014	-33.45	-33.49	17.80	17.76	170	191	Southern Benguela Sandy Outer Shelf
22	A33093	Melkbos St 6A	Van Veen	0.2	2017	2014	-33.96	-33.93	18.02	17.69	256	274	Southern Benguela Sandy Outer Shelf
23	A34442	PSBS 14/05	Van Veen	0.2	2020	2014	-33.86	-33.89	17.68	18.07	170	150	Southern Benguela Outer Shelf Rocky Sand Mosaic
24	A33117	Lara Point L1	Van Veen	0.2	2017	2014	-34.27	-34.32	17.80	17.82	350	348	Southern Benguela Sandy Shelf Edge

2.2.2. Benthic data collection

Biological data

Macrobenthic samples were collected for previous research (Karenyi, 2014; Benthic Trawl Experiment, unpublished data) and monitoring initiatives (South African Environmental Observation Network (SAEON)/Department of Forestry, Fisheries and Environment (DFFE) annual demersal trawl research surveys; DFFE Marine Benthic Survey, 2021; Table 2.1). The trawl samples were collected during 2011, 2012, 2017, 2019 and 2020. These surveys target commercially important demersal fish species such as hake, monk and kingklip on the west coast continental shelf of South Africa. However, from 2011 onwards, benthic invertebrates have also been consistently recorded. Research trawls were conducted using a 180 ft otter trawl with a 9 m sweep (Atkinson *et al*., 2011; Kirkman *et al*., 2015). The stretched mesh size of the codend is 60 mm and the stretched mesh size of the codend liner is 40 mm (Axelsen & Johnsen, 2015). The trawl was fitted with sensors to measure headline, wing spread, and door spread and deployed for thirty minutes at each station. Once the net was brought aboard, the epifaunal invertebrates were retained and most specimens were identified to species level (Atkinson & Sink, 2018). The total weights (blotted wet weight) and count for each species were recorded.

The grab samples were collected during 2014, 2018 and 2021. Either a 0.1 m^2 van Veen grab, 0.2 m^2 van Veen grab or a 0.25 m^2 Day grab were used to sample the benthic macro-infauna (Table 2.1). Samples were washed over a 1 mm mesh sieve to retain macrofauna greater than 1 mm in size. Though there are discussions around the correct sieve mesh size to collect infauna, the absence of organisms <1 mm is not expected to have a large impact on the biodiversity patterns detected as 1 mm mesh size captures most of the macrofauna species (Smith, 1995; Hemery *et al*., 2017). Specimens were later identified to the lowest taxonomic level (mostly species level) in the laboratory using identification keys (Day, 1967; Griffiths, 1976; Kensley, 1978; Olbers *et al*., 2019) and a stereomicroscope. Species were counted and weighed (blotted wet weight).

Environmental data

Depth, latitude, and longitude were available for both trawl and grab datasets. Sediment particle size analysis was done for the sediment samples collected from the grab samples. Sediment variables included percentage mud, very fine sand, fine sand, medium sand, coarse sand, very coarse sand and gravel.

2.2.3. Statistical analysis

Various approaches were used to compare the biodiversity patterns detected between the grab and trawl samples, including univariate and multivariate analyses of the community datasets. The datasets compared were epifaunal biomass (from trawl sampling) and infaunal counts (from grab sampling) collected from the 24 sites. Although biomass was recorded for both datasets, using infauna count and epifauna biomass abundance measures best characterise the different faunal groups and have been used in previous ecosystem classification studies (Sink *et al.*, 2019). The statistical methods employed accounted for the difference in abundance measurements between the two datasets. Invertebrates were excluded from the datasets if they were not epifaunal or infaunal organisms, such as pelagic jellyfish or zooplankton species. Singleton records (species occurring only once in the dataset) were retained to include the entire range of species richness detected by each method. The World Registry of Marine Species (WoRMS, 2022, www.marinespecies.org) was used to validate all species names and update unaccepted ranks to ensure the most recent scientific names were applied in this study.

The faunal biomass and numbers were standardised within respective gear types because the sampling methods cover vastly different sampling unit sizes and could not be reliably standardised to the same unit. Grab samples were scaled up from individuals per $0.2m^2$ to individuals per m^2. Trawl samples were scaled down from biomass (kg) per average swept area ($84\ 800\ m^2$) to biomass (g) per $1000\ m^2$. Both datasets were fourth root transformed to downweigh the effect of the dominant species and account for the effect of rarer species. This transformation thus incorporates the whole benthic community as sampled by the different methods which is the focus of the comparisons. The datasets were used to calculate resemblance matrices based on Bray-Curtis similarity.

Comparison of taxonomic diversity indices

The transformed species abundance matrices were used to calculate taxonomic diversity across trawl stations and grab stations, including total abundance, Margalef's richness index (*d*), Pielou's evenness index (J') and the Shannon diversity index $H'_{(loge)}$ (Margalef, 1958; Pielou, 1966). Pearson's product-moment correlation was used to determine the strength of the relationship between the diversity indices detected by trawl and grab samples. The associations between indices detected by trawls and by grabs were compared using Pearson correlations. Linear regression was applied to significant correlations to visualise the associations between the diversity indices detected by each sampling method.

Comparison of community assemblage patterns

Using the ‘vegan’ package in R (Oksanen *et al.*, 2020), non-metric multidimensional scaling (nMDS) ordinations were applied to the trawl and grab Bray-Curtis resemblance matrices to visualise the similarities among trawl stations and among grab stations in two-dimensional space, where stress values <0.20 indicate adequate representation and accurate ordinations (Clarke & Warwick, 2001). The multivariate analyses on the unconstrained data for each sampling method provided the foundation for further *a posteriori* hypothesis driven analyses to test the similarities in the biodiversity patterns detected by the two sampling methods. SIMPER analyses determined the characteristic species detected by each sampling method and the contribution towards the similarity between sites for each sampling method. A SIMPROF analysis was conducted on the trawl and grab resemblance matrices to determine significant communities *a posteriori.* This was discussed further in Chapter 4 (Fig. 4.1).

Direct comparisons between the two datasets were achieved using symmetric co-correspondence analysis (sCoCA; ter Braak and Schaffers, 2004) in R using the ‘cocorresp’ package (Simpson, 2009). The symmetric form was applied because neither sampling type was assumed to predict the other. Rather, the model was used to identify the structural similarities between the two sampling methods’ data tables. The axes were produced by maximising the covariance between the community assemblages. The number of important axes explaining most of the co-structure between data tables were identified to preserve the main variability in community assemblages by removing noise. Pearson product-moment correlations between the important axes of trawl and grab species and sample scores were calculated. Correlations indicated co-correspondence between species assemblages detected by different sampling methods.

A Monte-Carlo permutation test with 9999 permutations was used to test the significance of the covariance between the two datasets for the first constrained axis and then again for all axes. A randomisation test such as this one was more appropriate to test the significance of constrained ordinations as opposed to using classical statistical testing which would always detect a significant result. This permutation test examined the null hypothesis that compositional variation is independent between the two communities sampled by the different methods. A null distribution was estimated from the covariance calculated for the permuted data. The inertia was recalculated for every permutation by reapplying the sCoCA. However, the row samples of the trawl dataset were randomised for each permutation, while preserving the biomass values of the species columns. The null distribution of the permutated covariance was compared to the observed covariance to obtain a significance measure. The number of important axes were identified to remove noise, preserve the main variability in community structure and determine the level of association between biodiversity patterns detected by the different sampling methods.

Correlations between latitude, longitude, depth, and sediment variables were determined by plotting draftsman plots. No environmental variables were highly correlated (i.e., $r>0.95$) so all were retained. Significant environmental variables were fitted to the sCoCA ordination represented by vectors using the function ‘envfit’ from the ‘vegan’ package in R (Oksanen *et al.,* 2020). The projection of points onto vectors had maximum correlations with corresponding environmental variables.

Ordination triplots were constructed from the sCoCA by plotting the species and sample scores of each dataset for the first two axes (ter Braak and Schaffers, 2004) using the ‘compositions’ package in R (van den Boogaart *et al.*, 2021). The axes were produced by maximising the covariance between the community structures. The covariance was captured by the plots as opposed to the total variation in each individual dataset. The plots were based on the principle of weighted averaging. Samples were therefore plotted at the centre of the species they contain, and species were plotted in the centre of the samples they were recorded in. To plot the environmental vectors, the projection of sample points had maximum correlation with corresponding environmental variables.

2.3. Results

The demersal trawl and grab community datasets consisted of 82 epifaunal and 240 infaunal species, respectively, from the 24 sites. The average number of species collected by grab was 21.88 (±2.27) species per m^2. In contrast, 12.13 (±1.20) species were sampled by trawl per 1000 m^2 area of seabed. Despite sampling a much smaller area than trawls, grabs collected more species per m^2 than trawls did per 1000 m^2. Trawls sampled an average biomass of 569.75 g (±231.75 g) over 1000 m^2. The mean biomass per 1000 m^2 detected by trawling is likely an inaccurate representation of the true epifaunal population mean biomass based on the large standard error. The mean number of individuals sampled by grab per m^2 was 560.92 (±99.87). This value was likely a more accurate representation of infaunal abundance than the biomass sampled by trawls for epifaunal species.

2.3.1. Taxonomic structure of the benthic community

Trawls and grabs sampled different suites of fauna and shared only three species across the two datasets: the heart urchin Brissopsis lyrifera capensis, the gastropod Nassarius vinctus and the mantis shrimp Pterygosquilla capensis. The invertebrate abundance collected by each sampling method was also composed of and dominated by different groups of taxa (Fig. 2.2 & 2.3). Trawl samples were composed of 16 known Classes. Malacostraca (35%), Asteroidea (16%), Anthozoa (14%) and Gastropoda (11%; Fig. 2.2.a & 2.3.a) dominated the epifaunal biomass. Grab samples were also composed of 16 known Classes with infaunal count being dominated by Polychaeta (33%), Malacostraca (23%) and Bivalvia (15%; Fig. 2.2.b & 2.3.b). Samples were composed of similar Classes for each sampling method, however, the dominant Class varied among the sites (Fig. 2.2).

Malacostraca were similarly represented by each sampling method, however, when this Class was explored at the Order level, these similarities were less comparable (Fig. 2.3.c & 2.3.d). The Malacostraca biomass sampled by trawls were composed of only three Orders: Decapoda (68%), Stomatopoda (31%) and Isopoda (1%; Fig. 2.3.c).

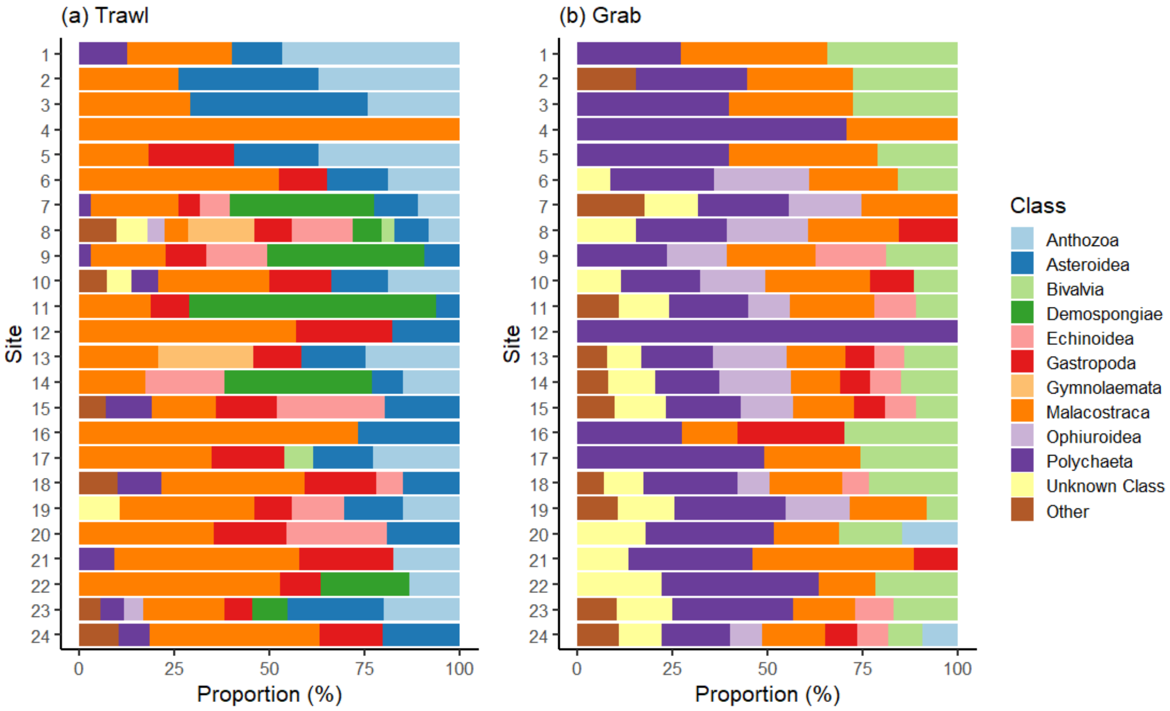


Figure 2.2. Abundance based proportions of invertebrate taxa Classes sampled by two gear types: trawl (a) and grab (b) from 24 offshore sites on the west coast of South Africa.

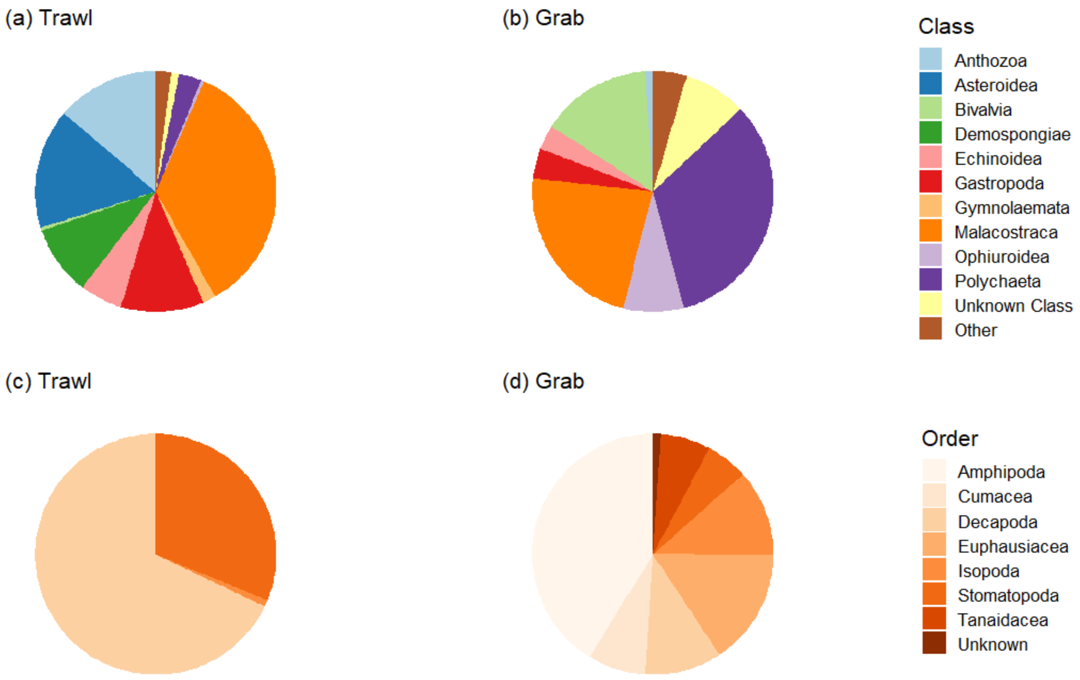


Figure 2.3. Abundance based proportions of invertebrate taxa Classes (a; b) and Malacostraca Orders (c; d) sampled by two gear types: trawl (a; c) and grab (b; d) pooled from 24 offshore sites on the west coast of South Africa.

The Malacostraca count sampled by grabs showed more variation at the Order level, consisting of seven known Orders dominated by Amphipoda (41%), Euphausiacea (16%), Isopoda (12%) and Decapoda (10%). The remaining 21% was composed of Stomatopoda, Cumacea and Tanaidacea (Fig. 2.3.d).

2.3.2. Comparison of taxonomic diversity indices

There were significant positive linear correlations between trawl and grab species abundance (r=0.44, t=2.312. df=22, $p<0.05$; Fig. 2.4.a), species richness (r=0.48, t=2.574, df=22, $p<0.05$; Fig. 2.4.b) and species diversity (r=0.55, t=3.118, df=22, $p<0.05$; Fig. 2.4.d), although these relationships were only moderately strong. Species evenness was the only taxonomic diversity metric that did not show evidence of a linear relationship (Fig. 2.4.c).

2.3.3. Comparison community assemblage patterns

The average Bray-Curtis similarity between all trawl samples based on species biomass per 1000 m^2 was 20.51% which was greater than grab samples which were 12.44% similar based on species count per m^2 (Table 2.2). Four epifaunal species (4.88% of total species) contributed to 50% of the average similarity between trawl samples (Table 2.2). The species which contributed the most (17.21%) to the average similarity within trawl samples was the Cape Mantis Shrimp, *Pterygosquilla capensis*. Eight infaunal species (3.32% of total species) contributed to 50 % of the similarity within grab samples. The species which contributed the most (10.86%) to the average similarity between samples was the spionid polychaete, *Paraprionospio pinnata*. No species had a consistently large presence across the west coast continental shelf based on the low ratios of their average contribution to its SD across the within-group similarities.

Table 2.2. Species contributing towards 50 % of the mean Bray-Curtis similarity between demersal trawl and grab samples collected from the same offshore sites on the west coast of South Africa. Sim/SD is the ratio of the average contribution divided by the standard deviation (SD) of those contributions across all pairs of samples making up this average.

Trawls **Mean similarity=20.51%**			**Grabs** **Mean similarity=12.44%**		
Species	Sim/SD	Contribution to similarity (%)	Species	Sim/SD	Contribution to similarity (%)
Pterygosquilla capensis	0.58	17.21	*Paraprionospio pinnata*	0.51	10.86
Sympagurus dimorphus	0.64	15.34	*Mediomastus capensis*	0.52	9.29
Exodromidia spinosa	0.70	9.39	*Nephtys hombergii*	0.42	8.58
Actinostola capensis	0.41	6.83	*Dosinia lupinus orbignyi*	0.38	5.10
			Nyctiphanes capensis	0.43	4.77
			Scoletoma tetraura	0.38	4.18
			Diopatra monroi	0.20	3.38
			Scalibregma inflatum	0.32	3.09

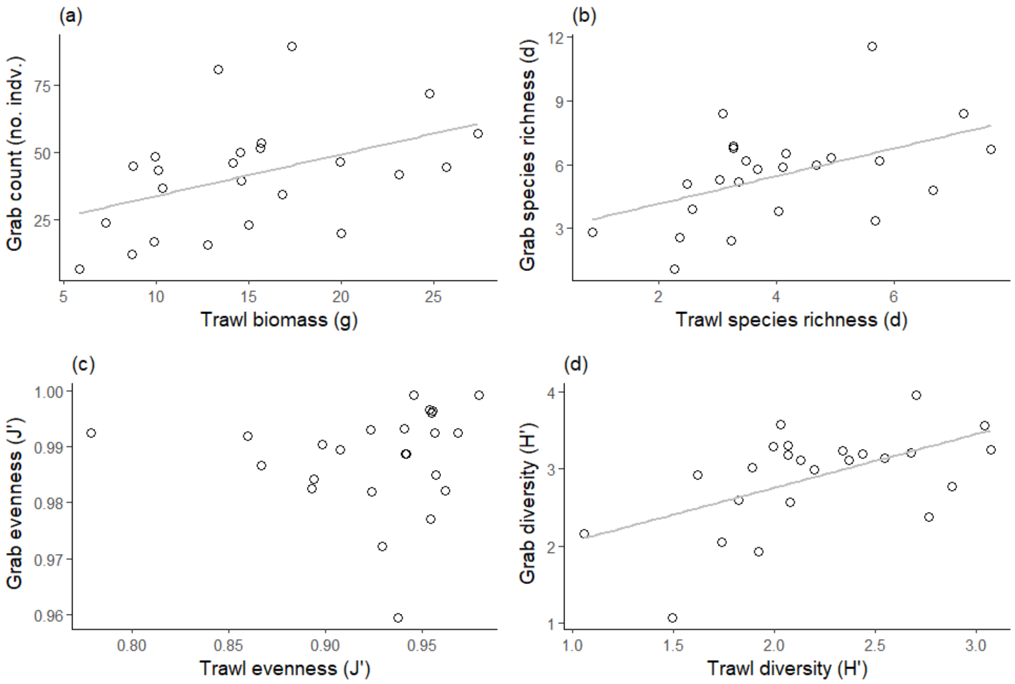


Figure 2.4. The relationships between taxonomic diversity metrics: species abundance (a), richness (b), evenness (c), and diversity (d) detected by demersal trawl and grab sampling from the same offshore locations on the west coast of South Africa.

When the trawl and grab species abundance datasets were analysed separately using distance-based multivariate techniques (i.e., nMDS ordination) similarities between the community patterns detected by each sampling method were evident (Fig. 2.5). There were no prominent structures or clustering of sites in either dataset and the sites were quite evenly spread. However, samples separated along the ordination axes similarly for trawl samples and grab samples.

(a) Trawl

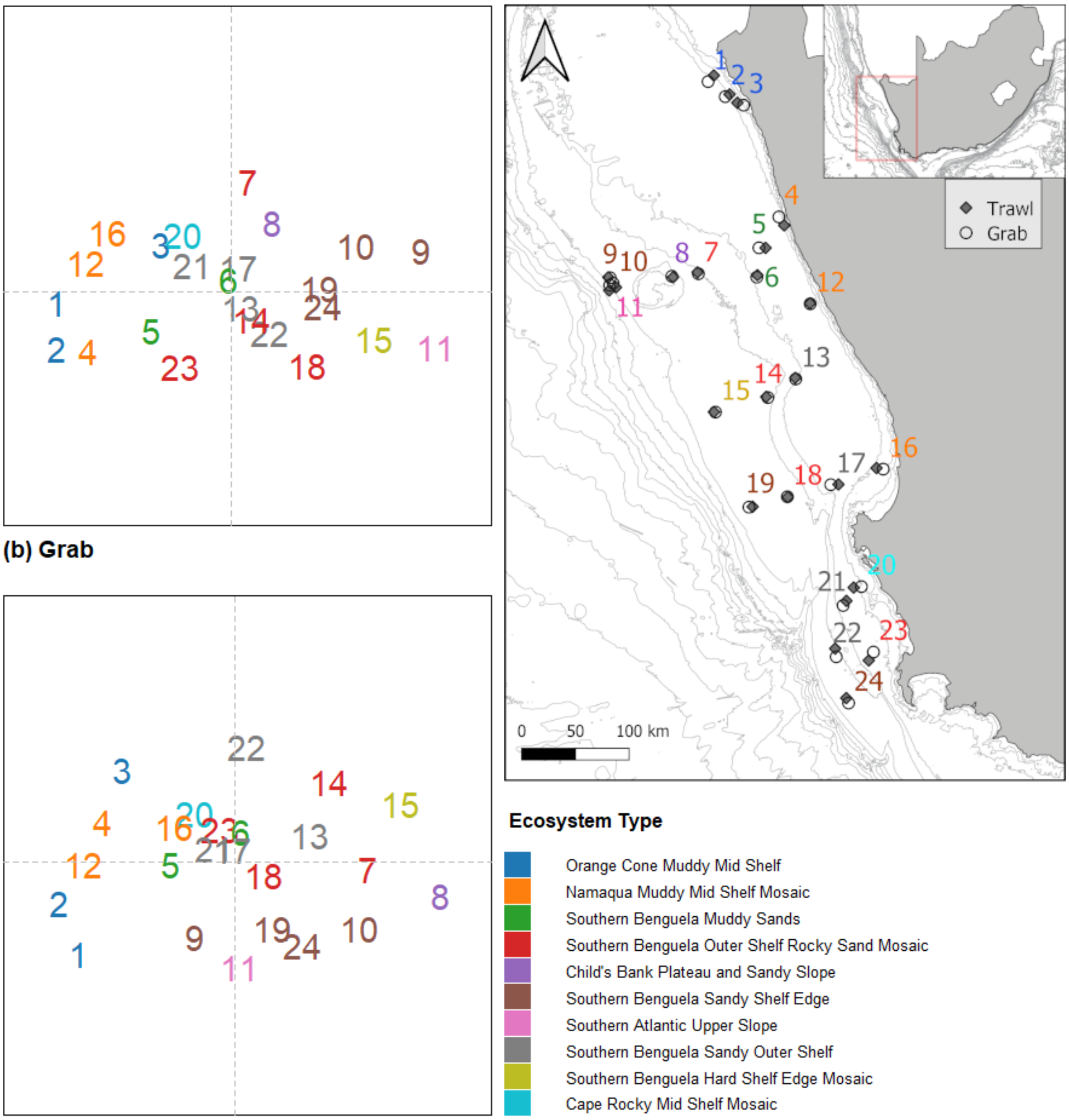


Figure 2.5. nMDS ordination plots showing benthic invertebrate community patterns from samples collected by demersal trawl (a) and grab sampling (b) from the same sites on the west coast of South Africa. Ecosystem types are denoted by colour, and stress values are <0.2. Colours represent the ecosystem type based on the national marine ecosystem classification (Sink *et al*., 2019).

Sites located in the same ecosystem type appeared to share similarities in communities detected by trawls and grabs, and these similarities were consistent between the sampling methods. For example, sites belonging to the Southern Benguela Sandy Shelf Edge ecosystem type (sites 9, 10, 19 and 24) were dispersed across the longitudinal band seen in the map of the study area (Fig. 2.5), yet clustered closely in the nMDS ordination based on species abundance data for both datasets.

The common variance between the two sampling type datasets explained 18.93% of the total variation of grab species data and 32.41% of the total variation of trawl species data. Of the common variance, 44.18% was accounted for by the first three axes of the sCoCA (axis 1: 21.37%, axis 2: 12.31%, axis 3: 10.50%). The first three ordination axes of the trawl species biomass were significantly ($p<0.05$) and highly correlated with the first three axes of the grab species numbers: r=0.96, 0.97 and 0.98. This demonstrated a high degree of similarity in how communities sampled by trawl and grab changed in assemblage structure along environmental gradients on the west coast.

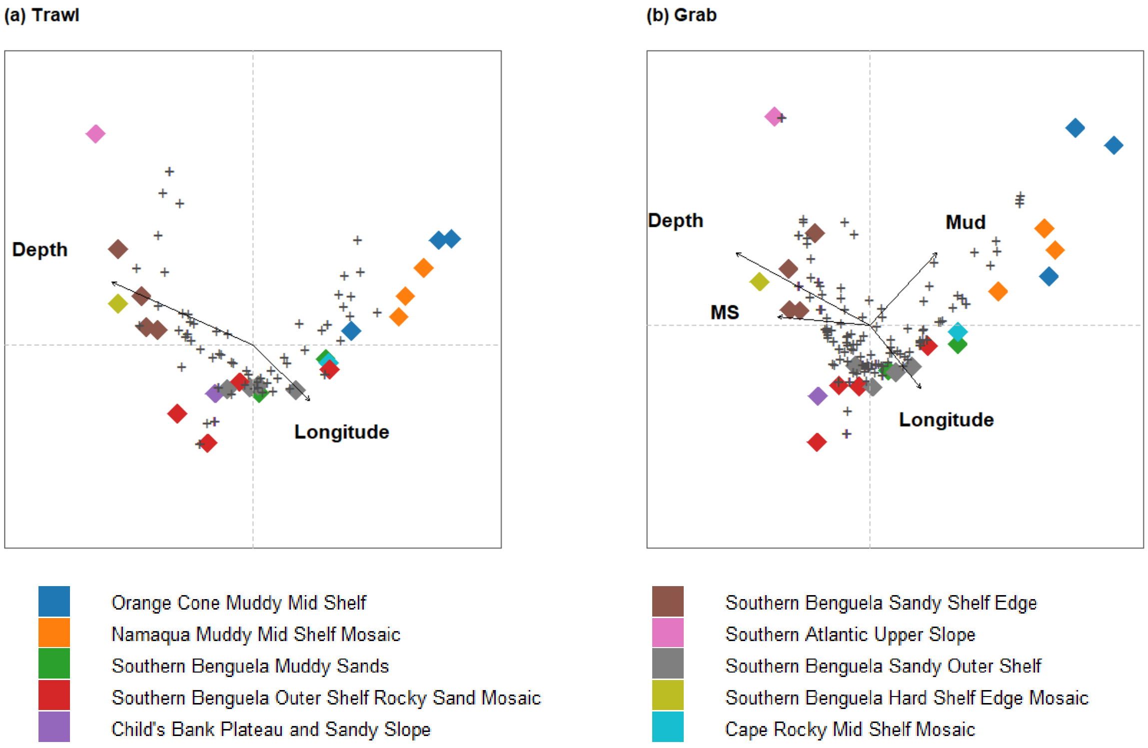


Figure 2.6. Ordination triplots representing the position of sites (diamonds) and species (grey crosses) on the first two axes of the symmetric co-correspondence analysis for data collected by demersal trawl (a) and data collected by grab (b) from the same offshore sites on the west coast of South Africa. Arrows represent the direction of significant environmental variables: depth, longitude, percentage mud and percentage medium sand (MS). Colours represent the ecosystem type based on the national marine ecosystem classification (Sink *et al*., 2019).

The test for community independence was significant for both the first constrained axis ($p=0.001$) and all constrained axes ($p=0.04$). Therefore, there was evidence to support dependence between the communities sampled by demersal trawl and grab based on the results of the Monte-Carlo permutation tests. Epifaunal communities detected by trawls and infaunal community patterns detected by grabs co-varied in assemblage structure along environmental gradients (Fig. 2.6). Depth ($R2=0.93$, $p<0.05$) and longitude ($R2=0.28$, $p<0.05$) were significantly correlated with the trawl site axes scores (Fig. 2.6.a). Depth ($R2=0.89$, $p<0.05$), longitude ($R2=0.26$, $p<0.05$), percentage mud ($R2=0.37$, $p<0.05$) and percentage medium sand ($R2=0.33$, $p<0.05$) were significantly correlated with grab site axes scores (Fig. 2.6.b). The similarities in biodiversity patterns detected by both sampling methods shown in the sCoCA were likely a result of the same environmental gradients experienced by both suites of benthic fauna (epifauna and infauna) operating at the scale sampled (i.e., ecoregion scale). Depth (in particular) explained similar and large proportions of the variation in site scores for both trawl and grab sCoCA axes.

2.4.1. Taxonomic structure

The taxonomic structure of trawl and grab samples was very dissimilar, which is as expected due to the differences in sampled size classes and positions in the sediment. Trawl samples were dominated by Decapoda, Asteroidea, Gastropoda and Anthozoa. These taxa are representative of epifaunal communities where crustaceans and echinoderms are known to dominate invertebrate megafauna (Schiaparelli *et al*., 2016; Clark *et al*., 2016; Atkinson & Sink, 2018). Grab samples were mainly composed of Polychaeta, Amphipoda and Bivalvia – also representative of infaunal communities where polychaetes are known to dominate, followed by small crustaceans, bivalves and gastropods (Schiaparelli *et al*., 2016; Narayanaswamy *et al*., 2016).

Communities occupying the benthos are composed of taxa which have traits adapted to their specific environment. The sampling gear’s ability to collect a species is affected by these various traits, such as size, mobility, behaviour, and position relative to the seafloor (Eleftheriou & Moore, 2013; Shiaparelli *et al*., 2016). Trawling targets epibenthic fish and macro- and mega-invertebrates (Clark *et al*., 2016) and is biased towards certain animal morphologies and life habits. Grabs target meio- and macro-infauna but can include small sessile epifauna (Elefteriou & Moore, 2013; Narayanaswamy *et al*., 2016). As a result of their different gear components and function, demersal trawls and grabs clearly targeted different (complementary) components of the benthic community.

2.4.2. Species diversity

Although trawls and grabs detected different species abundance, richness, and diversity values in this study, when compared relatively, there were moderate positive relationships between univariate measures detected by the two sampling methods (excluding species evenness). It is therefore feasible to consider that when grabs detect a change in species abundance, richness, or diversity, trawls may detect a reciprocal linear pattern. Flannery and Przslawski (2015) compared univariate diversity measures, including richness and diversity, by relating the metrics to environmental variables and comparing the responses. They found inconsistent responses of richness and diversity to environmental drivers measured by trawl and grab sampling. In contrast, this study found some measurable positive relationship.

The significant relationships of species abundance, richness, and diversity between trawls and grabs are likely attributed to epifauna and infauna both being components of the benthic habitat and therefore responding similarly to overlapping key environmental drivers, such as depth and sediment type. However, trawls and grabs also target distinct faunal (and functional) groups of the benthic community which have varying responses to these key drivers (Jørgensen *et al*., 2011). For example, infauna and epifauna both respond strongly to depth and sediment type; yet depth has been found to affect epifaunal patterns more strongly and sediment type is more closely associated to infaunal organisms (Basford *et al*., 1990). They are both key drivers for both faunal groups, but their importance varies between them.

There are other possible factors affecting the strengths of the relationships. Epifauna biomass and infauna count show evidence of being proportionate, likely due to the reasons mentioned above. However, using different abundance measures for each faunal group could result in more disparate abundance estimates and decreased relationship strength. Furthermore, univariate biodiversity measures can be inaccurate surrogates for biodiversity patterns and using multivariate-based methods is recommended (Mellin *et al*., 2011). There is evidence for this in the stronger associations found between multivariate community data sampled by the different methods in this study. Univariate measures could be biased towards detecting infaunal biodiversity patterns more so than epifaunal biodiversity patterns. Additionally, the sampling method used may obscure a stronger intrinsic relationship. Grabs perform more consistently across each sampling location whereas the sampling efficiency of trawling is lower and tends to vary more considerably between tows (Eleftheriou & Moore, 2013; Clarke *et al*., 2016). Lastly, the number of taxa observed depends strongly on sampling effort at that location. Trawls may miss or damage certain taxonomic components of the epibenthos, affecting the species abundance, richness or diversity measures and thus the biodiversity patterns detected. In addition, the opportunistic sampling design resulted in a small sample size which most likely decreased the strengths the relationships.

2.4.3. Community assemblage patterns and drivers

The greatest similarity between the two sampling methods was evident in the patterns of community assemblages detected by demersal trawls and grabs. There was a high degree of similarity in assemblage structure between communities sampled using trawl and grab, which acts as proxies for patterns in biodiversity across the region. Despite sampling different habitats, taxa, abundances, richness, and diversity; the multivariate community structure at the ecoregion scale presented very similar patterns. This was not predicted based on previous research exploring community patterns of epifauna and infauna (Basford *et al*., 1990; Rees *et al*., 1999; Ward *et al*., 2006; Ganesh and Rama, 2007; Currie *et al*., 2009; Buhl-Mortensen *et al*., 2012; Silberberger *et al*., 2019), studies directly comparing patterns detected by different gear types (Jørgensen *et al*., 2011; Flannery & Przeslawski, 2015), the difference in community composition between sampling methods, and the differences in spatial, temporal and thematic scale between the sampling methods (Brown *et al*., 2011; Lecours *et al*., 2015).

The co-variation between taxonomic diversity patterns detected by the two methods can be attributed to environmental gradients operating at the broadscale. Strong congruence occurs when different taxa respond to the same ecological processes (Jackson & Harvey, 1993; Corte *et al*., 2017). The main environmental drivers of epifauna and infauna are likely similar. These are most consistently found to be sediment characteristics and depth (Gray, 1981) and this was reflected in the assemblage responses to their assigned ecosystem types. Trawl and grab communities separated clearly along sediment and depth gradients, from muddy mid shelf sites to mosaic outer shelf sites to sandy shelf edge and sandy upper slope sites. In addition, there was a longitudinal gradient operating on the mid shelf.

Spatial variables such as depth, longitude and latitude are indirect drivers of epifaunal and infaunal community patterns acting as proxies for other environmental drivers (McArthur *et al*., 2010). Direct gradient drivers (environmental drivers which are directly link to animal responses) associated with sediment characteristics explained a large proportion in the infaunal community structure variability. Percentage mud and percentage medium sand were both significantly correlated with community structure. Sediment characteristics (such as substrate type) are likely also important for epifaunal community structure, but these data were not available for the trawl samples which is a notable disadvantage compared to grab sampling (Basford *et al*., 1990; Lange & Griffiths, 2014). Grab sampling allows for a volume of sediment to be retained *in situ* and later used in analyses with biological data.

Physical surrogate effectiveness has been found to increase in soft sediment habitats as opposed to highly complex benthic habitats (Mellin *et al*., 2011). Environmental variables play a key role at the broadscale (100s of kilometres), especially in unconsolidated sediment communities which are physically controlled (Gray, 2002). At meso- (20 km) and fine scales (1.5 km), epifauna and infauna have been found to have different spatial patterns and responses to different drivers despite having similar responses at the broadscale (Silberberger *et al*., 2019). Epifaunal and infaunal co-variation may decouple at finer scales when close physical associations to the environment and biological relationships become more important. However, at the broadscale, epifauna and infauna have shown similar structural responses to hydrography, strongly reflecting the boundary of water masses (Reiss *et al*., 2010; Silberberger *et al*., 2019). The effect of hydrography was not considered in this study due to insufficient data accuracy and availability. Depth and longitude could be surrogates for variables associated with west coast hydrographical patterns (e.g., salinity, oxygen, temperature, current speed, and water movement).

The west coast of South Africa has very distinct physical boundaries. Biogeography, temperature, nutrients, and productivity define the Southern Benguela Shelf ecoregion. The ecoregion itself is characterised by the cold Benguela current, large-scale upwelling (Field & Shillington, 2006) and low oxygen events (Jarre *et al*., 2015). The Namaqua and Cape sub-regions divide the area between Cape Columbine and Donkin Bay (Sink *et al*., 2019). The Namaqua bioregion also consists of two muddy middle shelf biotopes. Taxonomic diversity studies conducted in this region provide some insight to the known drivers of epifaunal and infaunal community patterns. Depth has been found to be a main driver of epifaunal community patterns (Lange & Griffiths, 2014). Infaunal community patterns have been explained by depth, latitude, distance from the Orange River mouth, sand and mud content, sediment grain size, slope and upwelling related variables including maximum chlorophyll concentration, bottom oxygen concentration and sediment organic carbon content (Karenyi *et al*., 2014 unpublished; Steffani *et al*., 2015; Karenyi *et al*., 2016).

2.4.4. Taxonomic detail

Results from this study showed that grabs sampled a greater level of taxonomic detail than demersal trawls. When comparing the community compositions, grabs sampled a greater number of Orders and species than trawls. At the Class level the communities were most similar but once finer taxonomic resolution was examined, the taxa were from different Orders. At high taxonomic levels, the communities collected by grabs and trawls have been found to be more similar but composed of different taxa (Jørgensen *et al.*, 2011). Grabs also tended to sample greater species density, richness, and diversity than demersal trawls (Jørgensen *et al.*, 2011), despite sampling an area 1000s of metres smaller than trawls. At the broadscale, samples collected by grabs were slightly less similar than trawls based on species abundance data, alluding to the greater detail in community structure detected by grabs.

There could be many reasons for grabs sampling greater taxonomic detail than trawls. This result could be representative of the intrinsic taxonomic diversity patterns found in benthic habitats. Infauna could be more diverse than epifauna in unconsolidated sediment communities (Kingston, 2001). Another likely reason is based on the differences between the sampling gear. Grabs sample more quantitatively than trawls and therefore more accurately represent the community at the site where the sample was collected (Blomqvist, 1991; Clark *et al.*, 2016; Narayanaswamy *et al.*, 2016). However, grab sample data are more effected by benthic habitat patchiness, potentially creating additional variation in the samples collected which may not be an accurate representation of patterns across the region. In contrast, trawls cover a greater area, including many different habitats in a sweep which could homogenise samples and decrease the detail of the true community variation across the region. Additionally, trawling is more selective for particular taxa, especially larger-bodied individuals (Eleftheriou & Moore, 2013; Clark *et al.*, 2016). Trawls potentially oversampled groups such as Malacostraca, contributing to the greater average similarity between samples and a loss of taxonomic detail.

2.4.5. Conclusion

Trawls and grabs targeted different habitats and faunal groups, therefore, neither method can replace the other entirely as a surrogate. Species datasets from both sampling methods are complementary and are most valuable when used in combination. Yet, the epifaunal and infaunal community assemblages detected at the broadscale were structurally similar. The environmental drivers of the west coast of South Africa are key to understanding the organisation of regional biodiversity patterns. Further research is needed to identify and quantify epifaunal and infaunal community drivers and how these change within the west coast ecoregion. Taxonomic diversity is the most commonly used measure of biodiversity, however, it does not always represent ecosystem functioning (Wong & Dowd, 2015; Tribot *et al*., 2016). The functional diversity patterns of the west coast should be explored further in conjunction with these findings.

Chapter 3

The influence of sampling method on detecting benthic biodiversity patterns using a functional trait-based approach

3.1. Introduction

Many sectors which make use of ocean space are expanding, such as fishing, mineral extraction, and offshore wind energy. In addition, new uses of ocean space are emerging, such as new types of recreation and deep-sea mining. With these new and expanding sectors come unprecedented impacts on marine ecosystems. Maintaining healthy ecosystems provides environmental, economic, and social benefits at national and international levels. Ecological monitoring is an important step in identifying and managing human impact on ecosystems (Douvere & Ehler, 2009). Within ecosystems, various marine habitats, faunal and functional groups are monitored, including microbial communities, and benthic and pelagic fish and invertebrate communities. These groups are likely to respond differently to environmental drivers and ecological impact.

Benthic invertebrates are important monitoring variables. They have significant functional roles as ecosystem engineers by creating and changing seafloor habitats for other species (Meadows, Meadows & Murray, 2012). They construct burrows, feed on other organisms, excrete extracellular polymeric substances, and produce faeces (Mermillod-Blondin *et al*., 2003; Mermillod-Blondin & Rosenberg, 2006). These activities affect the trophic structure and physical and chemical characteristics of the surrounding sediment by influencing sediment particle size distribution, erodibility, permeability, shear strength, redox and nutrients (Meadows *et al*., 2012). Benthic macrofauna are therefore vital components of healthy ecosystem functioning.

However, benthic macrofauna are vulnerable to human activities which affect seafloor habitats. Anthropogenic activities such as bottom fishing, dredging, sediment disposal, renewable energy strategies, and the oil and gas sectors are associated with sediment abrasion, sediment removal, smothering, and infrastructure, altering community structure as species respond differently to pressures and across different habitats (Kenny *et al*., 2018). For example, the impacts of bottom fishing, dredging and disposal activities are all considered to be most significant when conducted in deep, sedimentary habitats and these activities effect functional groups differently (Kenny *et al*., 2018). Trawling has been found to shift community structures, allowing burrowing short-lived infauna to persist while fragile long-lived epifaunal species decline (Fleddum *et al*., 2013, Muntandas *et al*., 2014; Tiano *et al*., 2020). Trannum *et al*., (2019) found that both infauna and epifauna experienced a decline in sessile, deposit-feeders and a dominance of mobile, burrowing omnivores or carnivores when impacted by heavy mine tailings deposition. In general, opportunistic species abundances have shown to increase in areas affected by human activities and specialists are negatively impacted (Johansen *et al*., 2018). These disturbances cause measurable changes in the abundance and diversity metrics of stress-tolerant or sensitive species and influence community trophic and functional structure.

The biological traits of benthic macrofauna make them particularly useful for long-term monitoring to inform marine management and assess human impact (e.g. having small ranges and long lifespans relative to other marine communities). Monitoring initiatives frequently use the benthic macrofauna community structure as a measurement for biodiversity or ecological condition since benthic macrofauna reflect the seafloor environment (Gray & Elliott, 2009; Josefson *et al*., 2009). Benthic macrofauna biological datasets informed the South African marine ecosystem classification component of the recent National Biodiversity Assessment (NBA) and act as surrogates for intrinsic seafloor biodiversity patterns (Sink *et al*., 2019). The datasets consist of species occurrence, abundance, and composition (i.e., taxonomic diversity) to measure biodiversity.

Taxonomic diversity (Magurran, 1988) is the most commonly used metric for measuring biodiversity, although, functional diversity (Diaz & Cabido, 2001) may more accurately represent ecosystem functioning (Tribot *et al.*, 2016). The taxonomic diversity of benthic communities is not always an adequate proxy for functional diversity (Wong & Dowd, 2015; Henseler *et al*., 2019) which provides the missing link between taxonomic nomenclature of an animal and how it interacts with its immediate environment (Bremner *et al*., 2003). Biological traits analysis (BTA) is an approach used to characterise species diversity and function within their ecosystem. BTA is being more frequently applied to study benthic macrofauna (Degen *et al*., 2018) but has rarely been used in studies focusing on South African offshore macrofaunal invertebrate communities.

Fleddum *et al*. (2013) sampled benthic fauna along the west coast of southern Africa to assess the impact of trawling using a trait-based approach. The authors found varying responses of infauna (sampled by grab) and epifauna (sampled by trawl) to trawl disturbance providing support for the two gear types sampling different functional diversity patterns on the west coast of South Africa. Other biodiversity studies which sampled both epifauna and infauna at the same scale and assessed their ecological responses to the environment using a trait-based approach have almost all found inconsistent assemblage patterns and drivers between epifauna and infauna biological traits (Muntadas *et al*., 2014; Muntadas *et al*., 2016; Pecuchet *et al*., 2018; Tiano *et al*., 2020). There is little consistency between benthic community functional diversity trends when directly compared between demersal trawl and grabs (Jørgensen *et al*., 2011).

This chapter compares the functional diversity patterns of benthic macrofauna collected by demersal research trawling and grab sampling – two sampling methods which have provided biological datasets incorporated into the latest marine ecosystem classification (Sink *et al*., 2019). The aim of this chapter is to determine whether demersal trawling and grab sampling detect different functional diversity patterns at the ecoregion scale on the South African west coast. The objectives of the chapter are to i) compare functional trait assemblage composition and structure, ii) compare trends in functional diversity indices, and iii) compare functional trait assemblage patterns between demersal trawl and grab sampling methods. Similarly to Chapter 2, both qualitative and quantitative methods are used to address the objectives.

3.2. Methods

The study area, sampling design and benthic data collection methods are outlined in Chapter 2, pages 20-23.

3.2.1. Biological Traits Analysis (BTA)

To assess the functional diversity of the mega- and macrofauna sampled by demersal trawl and grab on the west coast of South Africa, eight biological traits were selected representing morphological, behavioural and life history characteristics important to ecosystem functioning (Table 3.1). Two separate data tables were created for epifauna collected by trawl and infauna collected by grab. The eight traits include 35 trait modalities (trait sub-categories) for the trawl data table and 34 trait modalities for the grab data table. To ensure consistency and comparability with past and future studies in the region, similar traits and trait modalities to those defined by Fleddum *et al.*, (2013) were used. Information on faunal traits were collected from personal observation (e.g., trait “Body form”), web databases, scientific publications, field guides, theses and expert knowledge (Appendix C). Wherever species level information was lacking, trait information was recorded at a higher taxonomic level such as genus or family level. Singletons and species which were unidentifiable at the species or genus level were excluded from the study.

The biological trait information was summarised into fuzzy coded species by trait array matrix (Q-tables) with fuzzy codes ranging from 0 (no affinity) to 3 (high and exclusive affinity) (Chevene *et al*., 1994; Bremner *et al*., 2003) for each data table. This allowed for species to exhibit multiple trait modalities to varying degrees. To avoid bias by ensuring that traits which contain more modalities were equally weighted to traits with fewer modalities when conducting the statistical analysis, fuzzy codes were transformed to proportions with sum of modalities per trait equal to one (Darr *et al*., 2014). Each trait was standardised separately using the "prep.fuzzy" function of the 'ade4' package in R (Dray & Dufour, 2007).

Table 3.1. Morphological, life history, and behavioural traits and modalities selected to compare functional diversity patterns of epifauna and infauna sampled on the west coast of South Africa. Modalities exclusive to a dataset are marked with an asterisk (*trawl epifauna dataset and **grab infauna dataset).

Trait	**Modality**	**Code**	**Trait**	**Modality**	**Code**
Morphology			Behaviour		
Maximum adult size (cm)	< 0.5	MS1**	Mobility	None	AM1
	0.5-1	MS2**		Low	AM2
	1-3	MS3		Medium	AM3
	3-6	MS4		High	AM4
	6-10	MS5	Degree of attachment	None	DA1
	> 10	MS6		Temporary	DA2
Body form	Cylindrical	BF1		Permanent	DA3*
	Dorso-ventrally flattened	BF2	Adult habitat	Sessile	AH1
	Laterally flattened	BF3		Burrower	AH2
	Globulose/Spherical	BF4		Surface crawler	AH3
	Elongate/Vermiform	BF5		Swimmer	AH4*
	Irregular	BF6		Tube dweller	AH5
	Upright/Erect	BF7*	Feeding habit	Suspension/Filter feeder	FH1
				Surface deposit feeder	FH2
Life history				Subsurface deposit feeder	FH3
Larval development	Planktotrophic	LT1		Large detritus feeder	FH4
	Lecithotrophic	LT2		Scavenger	FH5
	Direct	LT3		Carnivore/Omnivore	FH6
Adult longevity (yrs)	< 2	AL1			
	2-5	AL2			
	5-10	AL3			
	> 10	AL4			

The standardised species by trait matrix (Q-table) and the standardised, fourth root transformed station by species abundance matrix (L-table) were multiplied to obtain a station by trait matrix (QL-table) for each sampling type. Therefore, the trawl Q-table was biomass-weighted whereas the grab Q-table was count-weighted. The collinearity between traits was tested for using draftsman plots and the associated correlation matrices between all pairs of traits (Käß *et al.*, 2021). This resulted in the removal of trait DA3 (permanent attachment) from the trawl data table which was highly correlated with trait AM1 (immobile, r>0.95) and the removal of trait DA1 (unattached) from the grab data table which was highly correlated with traits AM2 (low mobility) and AH3 (surface crawler, r>0.95).

3.2.2. Statistical analysis

The statistical analysis compared the biomass-weighted trawl QL-table and the count-weighted grab QL-table to determine whether functional diversity patterns were similarly detected by the different sampling methods. The Q-tables were used to calculate distance matrices based on Gower dissimilarity (Gower, 1971) as this distance measure is best suited for fuzzy-coded data (Pavoine *et al.*, 2009).

Comparison of functional diversity indices

The species abundance L-tables were used to calculate taxonomic diversity across trawl stations and grab stations using the Shannon Index $H'_{(loge)}$. Based on the Gower distance matrix, four common functional diversity indices were calculated for each sampling type: functional richness (FRic), functional evenness (FEve) and Rao's quadratic entropy (FD RaoQ) using the 'FD' package in R (Laliberté & Legendre, 2010; Laliberté *et al.*, 2014). FRic indicates the functional space filled by a community (Villéger *et al.*, 2008; Schleuter *et al.*, 2010). FEve examines whether trait abundance is evenly distributed in functional space (Mouillot *et al.*, 2005; Villéger *et al.*, 2008). Rao's quadratic entropy (FD RaoQ) was calculated as a measure of functional diversity (FD) as it is the most commonly used metric to calculate FD since functional richness, functional evenness and functional divergence are included in the equation (Botta-Dukát, 2005; Van Der Linden *et al.*, 2012). The choice of these measures corresponded to the univariate analysis conducted in Chapter 2 to aid comparability.

Additionally, functional redundancy (FdH') was calculated as the ratio between FD RaoQ and $H'_{(log\ e)}$. This ratio is used to estimate how sensitive communities are to changes and potential species loss (Van Der Linden *et al.*, 2012). Following the process of analysis conducted in Chapter 2, the associations between indices detected by trawl and by grab were compared using

Pearson correlations. Linear regression was applied to significant correlations to visualise the associations between the functional diversity indices detected by each sampling method.

Comparison of trait assemblage patterns

Using the ‘vegan’ package in R (Oksanen *et al.,* 2020), non-metric multidimensional scaling (nMDS) ordinations were applied to each trawl and grab Gower distance matrix to visualise the dissimilarities between trawl stations and between grab stations in two-dimensional space where stress values <0.20 indicate adequate representation and accurate ordinations (Clarke & Warwick 2001). Traits with the highest significant correlation to site scores for the first two nMDS axes were determined and their abundance-weighted trait values were overlayed as bubble plots in the nMDS ordination plots to visualise changes in abundance-weighted trait values across sites and ecosystem types. This was done to determine important traits in place of a SIMPER analysis which could not be applied to the Gower’s distance matrices. A SIMPROF analysis was conducted on the trawl and grab Gower distance matrices to determine significant trait assemblages *a posteriori.* This was discussed further in Chapter 4 (Fig. 4.1).

Similarly to Chapter 2, direct comparisons between the trawl and grab samples were achieved by applying symmetric co-correspondence analysis (sCoCA; ter Braak & Schaffers, 2004) using the “cocorresp” package in R (Simpson, 2009), however, now applied to their QL-tables. The axes were produced by maximising the covariance between trawl and grab trait assemblages. The number of important axes explaining most of the co-structure between QL-tables were identified and Pearson product-moment correlations between the important axes of trawl and grab sample and trait scores were calculated. Correlations now indicate co-correspondence between trait assemblages detected by different sampling methods.

A Monte-Carlo permutation test with 9999 permutations was used to test the significance of the total covariance between the two QL-tables (Alric *et al*., 2020). In contrast to Chapter 2, the null hypothesis being tested is that compositional variation is independent between the two functional trait assemblages sampled by the different methods. Again, a null distribution was estimated from the covariance calculated for the permuted data and the covariance is recalculated for every permutation by reapplying the sCoCA. However, the row samples of the trawl QL-table were randomised for each permutation, preserving the abundance-weighted trait values of the trait columns, while the grab QL-table was held constant. The null distribution of the permutated covariance was compared to the observed covariance to obtain a significance measure.

Following the analyses conducted in Chapter 2, ordination triplots were constructed from the sCoCA by plotting the trait and sample scores computed from each sampling method's QL-table for the first two axes (ter Braak & Schaffers, 2004) using the package 'compositions' in R (van den Boogaart *et al.*, 2022). Samples were plotted at the centre of the traits they contain, and traits were plotted in the centre of the samples they were recorded in. Significant environmental vectors were plotted to have maximum correlation with corresponding sample points.

3.3. Results

3.3.1. Functional structure of the benthic community

A total of 60 epifaunal taxa exhibiting 34 trait modalities and 101 infaunal taxa exhibiting 35 trait modalities were identified in the study area. The functional structure of the two sampling method groups differed to varying degrees depending on the trait (Fig. 3.1). Overall, trawl samples were dominated by the following traits: large sizes (>10 cm=51%), dorso-ventrally flattened body forms (44%), free-living (73%), medium mobility (40%), surface-crawling (53%), carnivorous/omnivorous feeding (46%), planktotrophic larval development (63%) and medium or long lifespans (2-5 yrs=39%, >10 yrs=36%).

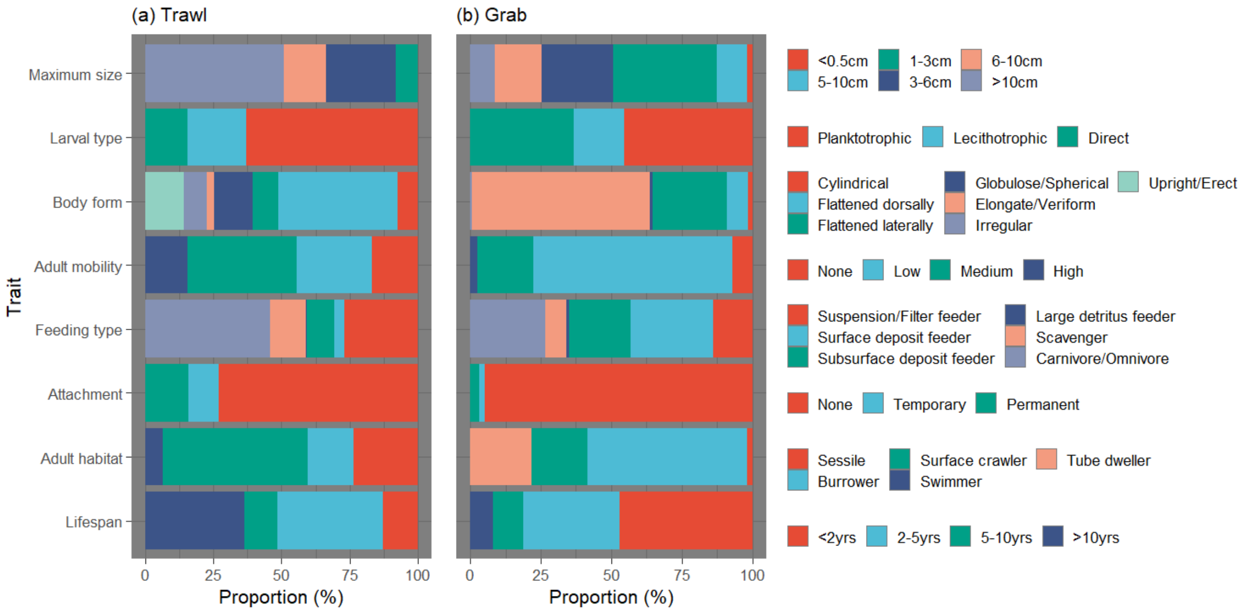


Figure 3.1. Abundance based proportions of trait modalities among two sampling types: trawl (a) and grab (b) from across the west coast of South Africa.

Grab samples were dominated the following traits: small sizes (1-3 cm=37%), vermiform/elongate body forms (63%), low mobility (71%), surface deposit feeding (30%), planktotrophic larval development (45%) and short lifespans (<2 yrs=47%).

3.3.2. Comparison of functional diversity indices

Of the four functional diversity indices compared between sampling types, functional richness (FRic) was the only index which showed a significant positive correlation between sampling types on the west coast of South Africa (Fig. 3.2; r=0.454, t=2.391, df=22, p<0.05). There was no significant relationship between trawl and grab functional evenness (FEve), functional diversity (FD RaoQ) or functional redundancy (FdH').

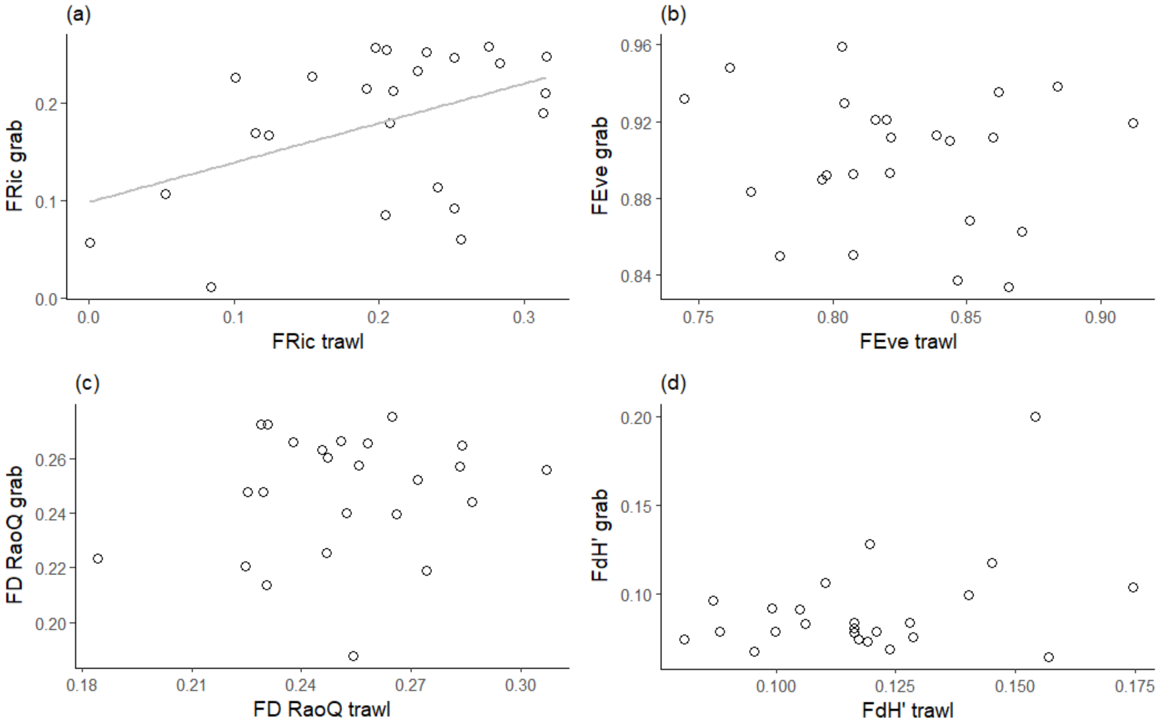


Figure 3.2. The relationships between functional richness (a), functional evenness (b), functional diversity (c) and functional redundancy (d) detected by trawl and grab on the west coast of South Africa.

3.3.3. Comparison of trait assemblage patterns

Site pairs clustered in broadly similar patterns across ordinations (Fig. 3.3). Sites 14 and 18 were the only sites exhibiting major differences in its trait composition relative to other sites when compared between the two sampling methods. The four trait modalities explaining the most variation (highest correlations) in the trait-based assemblage patterns for trawls were maximum size of >10 cm, medium adult mobility, direct larval development and planktotrophic larval development (Table 3.2).

Figure 3.3. nMDS ordination plots showing trait composition for samples collected by demersal trawl (a, c, e, g) and grabs (b, d, f, h) from the same sites on the west coast of South Africa. Bubble plots are superimposed on each ordination, scaled to represent abundance distribution of important traits (Table 3.2) at each trawl or grab station. Stress values are all <0.2. Colours represent the ecosystem type based on the national marine ecosystem classification (Sink *et al*., 2019).

Grab sample trait assemblage patterns were most explained by low adult mobility, burrowers, adult longevity of <2 yrs and planktotrophic larval development. The important trait modalities are different for each sampling method, however, they showed similar abundance-weighted gradient patterns across the west coast (Fig. 3.3). Generally, the main traits appeared less dominant (lower abundance-weighted trait values) in the shallower, muddy ecosystem types and increased in abundance with depth and sandy sediment.

Table 3.2. The four functional traits explaining the most variation (highest correlations with nMDS axes scores) in station distribution patterns among sampling types trawl and grab on the west coast of South Africa (*p<0.05, **p<0.01, and ***p<0.001).

Trawl				Grab			
Trait	**Modality**	**Code**	**R^2**	**Trait**	**Modality**	**Code**	**R^2**
Maximum size	>10cm	MS6	0.82***	Adult mobility	Low	AM2	0.96***
Adult mobility	Medium	AM3	0.81***	Adult habitat	Burrower	AH2	0.93***
Larval type	Direct	LT3	0.75***	Adult longevity	<2yrs	AL1	0.91***
Larval type	Planktotrophic	LT1	0.74***	Larval type	Planktotrophic	LT1	0.91***

The common variance between the two sampling group datasets explained 38.93% of the total variation of grab trait data and 58.80% of the total variation of trawl trait data. Of the common variance, 88.13% was accounted for by the first three axes of the sCoCA (sCoCA axis 1: 52.67%, axis 2: 27.23%, axis 3: 8.23%). The first three ordination axes of the trawl abundance-weighted trait values were significantly ($p<0.05$) and highly correlated with the first three axes of the grab abundance-weighted trait values: $r=0.76$, 0.83 and 0.78. This demonstrated a high degree of similarity in how trait assemblages sampled by trawl and grab changed in structure along environmental gradients on the west coast. The test for trait assemblage independence was significant for both the first constrained axis ($p=0.003$) and all constrained axes ($p=0.002$). Therefore, there was evidence supporting the dependence between the trait assemblages sampled by demersal trawl and grab based on the results of the Monte-Carlo permutation tests.

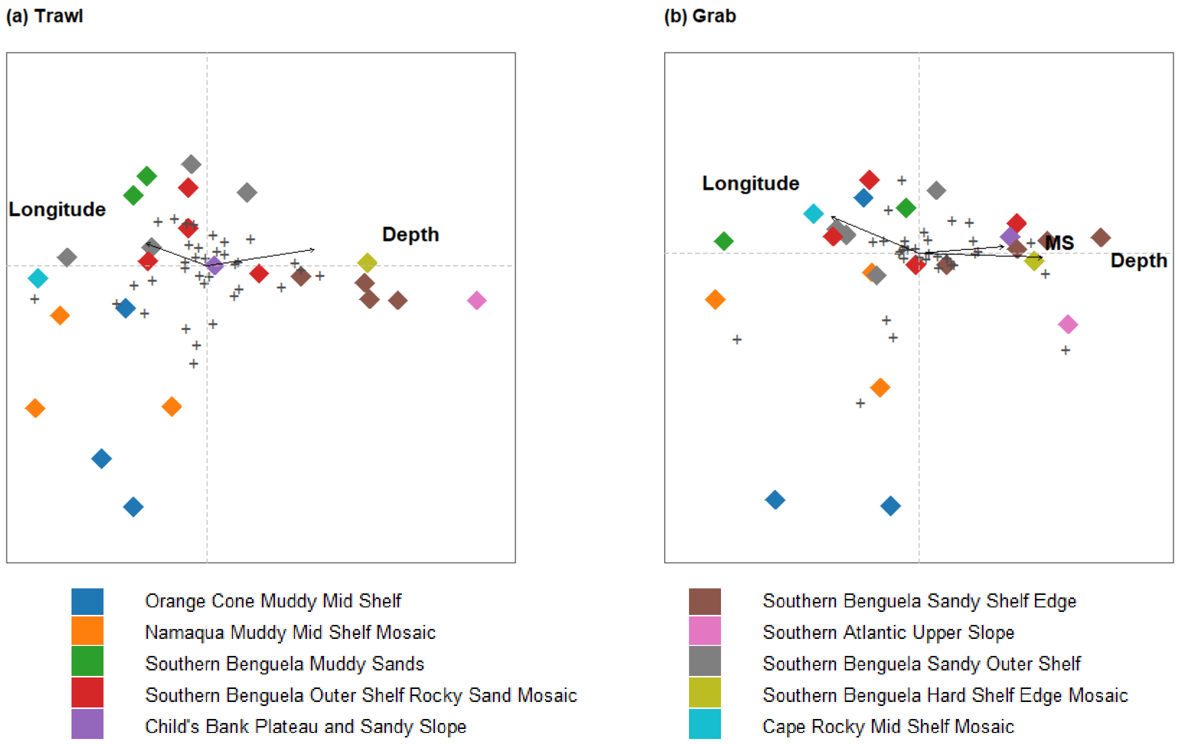


Figure 3.4. Ordination triplots representing the position of sites (numbers) and abundance-weighted trait values (grey crosses) on the first two axes of the symmetric co-correspondence analysis for (a) data collected by demersal trawl and (b) data collected by grab on the west coast of South Africa. Arrows are significantly correlated environmental variables. Colours represent the ecosystem type based on the national marine ecosystem classification (Sink *et al*., 2019).

Epifaunal trait assemblages detected by trawls and infaunal trait assemblages detected by grabs co-varied along environmental gradients (Fig. 3.4). Depth (R^2=0.87, $p<0.05$) and longitude (R^2=0.33, $p<0.05$) were significantly correlated with the trawl site axes scores (Fig. 3.4.a). Depth (R^2=0.66, $p<0.05$), longitude (R^2=0.43, $p<0.05$), and percentage medium sand (R^2=0.31, $p<0.05$) were significantly correlated with grab site axes scores (Fig. 3.4.b). The similarities in trait assemblage patterns detected by both sampling methods and shown in the sCoCA can once again be linked to the same environmental gradients experienced by both suites of benthic fauna (epifauna and infauna) operating at the scale sampled (i.e. ecoregion scale).

3.4. Discussion

Demersal trawl and grab estimates of benthic communities on the west coast of South Africa shared both similarities and differences. The functional structure of the benthic community was collected complementarily by the two sampling methods which generally sample different components of the marine benthos. Functional diversity indices gave inconsistent results when compared between sampling methods, although functional richness showed evidence of some significant linear association between trawl and grab samples across the west coast. Despite differences in the functional structure and functional diversity indices, trawl and grab sampling detected similarities in multivariate benthic community trait assemblage patterns at the ecoregion scale.

3.4.1. Functional structure and important biological traits

Th morphological traits tended to reflect the traits of organisms best observed by the sampling methods. The morphological traits of taxa dominating trawl samples were large, dorso-ventrally flattened animals. Since traits were species abundance weighted, the functional structure was proportionate to taxonomic diversity. These morphological traits are consistent with crab and starfish taxa which dominate the epibenthic invertebrate megafauna (Schiaparelli *et al*., 2016; Clark *et al*., 2016). These traits were also likely more easily sampled by demersal trawl. Smaller sized epifaunal invertebrate taxa (<40 mm in size as the codend mesh liner is 40mm when stretched; Axelsen & Johansen, 2015) passed through the trawl net and those retained were more easily missed during the collection of animals from the net (Clark *et al*., 2016). Typically, large, firm-bodied epifauna were efficiently sampled whereas the destructive sweep by the trawl net damaged soft-bodied, stalked or fragile epifauna (Schiaparelli *et al*., 2016; Clark *et al*., 2016). This potentially led to the under-representation of these functional groups in the samples.

Furthermore, maximum adult size >10 cm explained the largest amount of variation in trawl trait assemblage patterns. Body size is a fundamental trait for predicting species' behaviour and ecology. It tends to be linked to many other traits and plays a lead role in determining the structure of food webs, the abundance of species (Blanchard *et al*., 2009) and their distribution across relatively large spatial scales (Webb *et al*., 2009). Body size determines responses to fishing effort in both marine fish (Jennings *et al*., 1998, 1999) and invertebrates (Bremner *et al*., 2003; Tillin et al., 2006). This trait has been correlated to various environmental drivers, such as depth, temperature and disturbance, and other physiological traits, such as metabolic rate (Brown *et al*., 2002; Murillo *et al*., 2020).

In contrast to trawls, the dominant morphological traits of animals sampled by grab were small sizes, and vermiform/elongate or laterally flattened body forms. These traits are consistent with taxa typical of infaunal communities which are generally dominated by polychaete worms, amphipods and bivalves (Schiaparelli *et al*., 2016; Narayanaswamy *et al* 2016). Small size, elongation and flexibility are morphological adaptations to interstitial, narrow spaces (Giere, 1993). In addition, the small size class sampled by grab is a product of infaunal species adaptation to living in soft sediment where a particular size class optimizes feeding mechanisms and life history (Warwick & Clarke, 1984; Edgar *et al*., 1994; Warwick *et al*., 2006), but also indicative of the characteristics of the sampling gear (Bett, 2013). The grabs sampled a small area and volume thus missing large, mobile species. The depth of penetration was limited by the size and weight of the grab (McIntyre, 1956), so large, deep-burrowing infauna were potentially under-sampled or missed entirely since large infauna burrow deeper than small infauna (Zaklan & Ydenberg, 1997; Watling, 2019).

Behavioural traits were similarly represented except for degree of mobility and feeding type. The behavioural traits of taxa which dominated trawl samples were free-living, low/medium mobility, surface-crawling, and predatory. These traits are once again consistent with the animals which dominate epibenthos, such as crabs and starfish. These are mobile animals that pursue and feed on individual prey species (Kingston, 2001). Other abundant behavioural traits included being sessile, attached, and suspension-feeding. Being sessile, attached and suspension-feeding were highly correlated behavioural traits and are consistent with sponge, coral, bryozoan, and hydroid taxa. Hard substrata found in steep areas and slopes where sediment cannot accumulate, provide a base for the attachment of sessile animals (Kingston, 2001). Areas on the west coast likely vary in their dominant behavioral traits between hard substratum habitats with high water movement consisting of attached, suspension-feeding animals, and sedimentary habitats dominated by motile, burrowing, predatory animals. Notably, demersal trawling detected these different functional components as these traits were abundant in samples.

Similarly, the behavioural traits of infaunal taxa which dominated grab samples were free-living, burrowing, low/short-ranged mobility and deposit-feeding. Deposit feeders form the largest feeding group of benthic infauna in most environments but the proportion is greatly influenced by the nature of the sediment (e.g. fine silts and muds have increased proportions of deposit feeders (Kingston, 2001). For most benthic species, the main energy/food source is derived from above and, as a result, competition between benthic animals is usually for space (Kingston, 2001). Benthic infauna demonstrate vertical distribution by burrowing. This is related to the competition for space, but burrowing also serves a variety of functions, including avoiding predation, protection from environmental stress and disturbance, access to more deposit-feeding food resources and the protection of eggs (Butler, 1995).

Predatory infauna were also abundant in grab samples, however far less common than in trawl samples representing the epifaunal community. The proportion of predators varies less across different sediment types (Kingston, 2001). More active predatory infauna have also adapted to accessing prey species within the sediment matrix and attack prey *in situ*. Polychaete families such as Glyceridae, Eunicidae and Onuphidae are active predators and were also abundant in grab samples. Biases in sampling may have arisen if the large, mobile polychaete species avoided the grab, thus potentially reducing the representation of this feeding mode in infaunal samples.

Mobility was an important predictor of variation for trawl (medium mobility) and grab (low mobility) trait assemblage patterns. Mobility has been linked to predation, disturbance, and the building of biological structures (Hinchey *et al*., 2006; Murillo *et al*., 2020) and is likely linked to a number of other biological traits. Mobility is important to ecosystem functioning: mobility within sediments and tubes enhances sediment oxygenation and influences nutrient cycling (Aller, 1982; Mermillod-Blondin *et al*., 2004; Kristensen & Kostka, 2005), sediment stabilization, transport and burial (Aller, 1982), and metabolic requirements and thus influences production and trophic support (Brown *et al*., 2002).

Trawl samples were dominated by taxa with the following life history traits: planktotrophic larval development and medium/long lifespans. Life history traits which dominated grab samples included planktotrophic or direct larval development and short lifespans. Planktotrophic larval development was also an important predictor of trait assemblage patterns for both trawls and grabs. The majority of the benthic species experience a pelagic phase in their larval development (Kingston, 2001). This offers sessile species or species with restricted movement the ability to colonise and expand their spatial distribution (Kingston, 2001). The high productivity and upwelling of the Southern Benguela Shelf ecoregion could support the long pelagic phase of larvae as they need to reach surface waters to feed on phytoplankton. The existence of a planktotrophic larval stage may be the strongest predictor of genetic differentiation between populations (Teske *et al*., 2007) and can also shape species distributions (e.g. the relationship between abundance and occupancy).

Direct larval development also explained a large proportion of variation for trawls, but the pattern appeared to be inversely correlated to planktotrophic larval development. The results show that for trawls, direct development may have been more prominent in the deeper shelf edge/upper slope sites whereas planktotrophic species were abundant in mid shelf sites.

Therefore, depth could be a strong predictor of patterns in this trait on the west coast. Greater depths affect planktotrophic larvae's ability to disperse and reach surface waters and limits the availability of energy required to produce enough eggs to survive until settlement (Kingston, 2001). Larval development strategies are also dependent on variables such as productivity, latitude and disturbance (Thorson, 1950; Kingston, 2001; Murillo *et al.*, 2020).

Direct larval development was an abundant trait category for infauna. Direct development is more common in species which need to resettle in the same environment as the adults (e.g. intertidal conditions; Kingston, 2001) or in habitats which have scarce food resources/phytoplankton for larvae to exploit (e.g. artic regions and the deep-sea benthos; Kingston, 2001). However, since trawl and grab samples were taken from the same site locations, the greater abundance of infaunal species exhibiting direct development compared to epifaunal species was likely linked to other factors. Infauna were largely burrowing or tube-dwelling which potentially provides a safe environment for eggs to hatch into miniature adults and grow *in situ* (Butler, 1995). Scarcer food resources below the sediment may prohibit the energy expenditure required to produce massive amounts of eggs necessary for planktotrophic larval development and releasing them above the sediment surface and into the water column.

A lifespan of <2 years explained a large proportion of variation in grab trait assemblage patterns. Generally, smaller animals have shorter lifespans and larger animals tend to live longer (Speakman, 2005). This observation has been explained by the metabolic theory of ecology (Brown *et al*., 2004) which links metabolism to macroecological and physiological processes. Growth rate and life history traits tend to scale with body size and temperature (Charnov & Gillooly, 2004; Moss *et al*., 2016). Lifespan is correlated with temperature and therefore depth and latitude (Munch & Salinas, 2009). Depth is an important driver of community patterns on the west coast (Lange and Griffiths, 2014; Steffani *et al*., 2015; Karenyi, 2016) which could explain the importance of lifespan in structuring trait assemblage patterns. Previous studies have found that depth predicts lifespan variation in marine benthic communities (Murillo *et al*., 2020). Disturbance has also been found to predict patterns in longevity since disturbance affects life history strategies (Juan *et al*., 2007; Murillo *et al*., 2020).

3.4.2. Functional diversity

Despite having sampled complementary functional components of the benthic community, the communities sampled by trawl and grab had similar functional richness patterns. Functional richness can be understood as the volume of functional space occupied by a community with species distributed in a multidimensional functional space (Villéger *et al*., 2008). Although no studies to date have directly compared the functional diversity indices detected by trawls and grabs, some studies have looked at drivers of functional richness for epifauna and infauna. Environmental gradients operating on the west coast were likely the reason for the similarity in functional richness patterns detected by the two sampling methods.

Functional evenness is independent of functional richness and unlike functional richness, is proportional to species relative abundance (Villéger *et al*., 2008). Although epifaunal and infaunal communities may have presented similar changes in the volume of functional space occupied across sites, the regularity of the distribution of abundance in this volume (i.e., functional evenness) was dissimilar. Change in the volume of functional-trait space filled by a community does not have the same value as a shift in the distribution of abundance within that volume (Villager *et al*., 2008) which is why patterns in functional richness and functional evenness were detected differently. Changes in functional richness can indicate shifts in environmental conditions (Cornwell *et al*., 2006), whereas changes in functional evenness have been attributed to alterations in the intensity of competitive interactions (Mason *et al*., 2008).

The functional diversity index used incorporated both the relative abundances of species and a measure of the pairwise functional differences between species, thus it incorporated all facets of functional diversity into the equation (Botta-Dukát, 2005). No significant linear relationship was detected between functional diversity patterns across sites between the sampling methods. Functional redundancy measures the sensitivity of communities to change and potential species loss and was detected differently by trawls and grabs on the west coast. There was also no relationship in the relative changes in functional redundancy patterns detected by the different methods across sites so patterns in relative functional redundancy values also differed between the two communities or sampling methods. Previous studies have not found similar functional redundancy responses between infauna and epifauna. Epifauna and infauna have been found to exhibit inverse functional redundancy relationships, for example in response to disturbance by trawling (Muntadas *et al*, 2016).

Habitat is the main driver of biodiversity and infauna and epifauna occupy different benthic habitats and are therefore likely to have different intrinsic biodiversity patterns. Epifaunal communities could have had less regular abundance distributions of biological traits because they were exposed to greater environmental variation and more potential habitat types than infaunal communities (Kingston, 2001). Level sediment habitats are more uniform, stable environments than hard substratum. Stronger environmental gradients or exposure to disturbance can alter the community functional structure. For example, infauna exhibit very little latitude variation compared to epifauna which show a marked increase in species number with a decrease in latitude (Fischer, 1960). Infauna therefore escape the same environmental effects that epifauna are exposed to (e.g., temperature, salinity, and water movement).

The differences between functional evenness, diversity and redundancy detected by trawls and grabs were due in part to the intrinsic biodiversity patterns of epifaunal and infauna communities but were likely also a product of the biases associated with each sampling method. Trawls and grabs sampled at very different spatial scales. Trawling covered a broad spatial scale in a single sweep (~80 000 m^2), potentially traversing and including data from different habitats in a sample. This homogenised samples to varying degrees depending on the habitats the trawl covered. This could have maximised the detection of functional richness as more traits tended to be sampled across broader areas but present decreased evenness as the heterogeneity of habitats sampled in a sweep likely varied across tows. The efficiency of grab sampling was greater than that achieved by trawling because the volume of sediment collected was relatively constant between grabs. The quantitative nature of grab sampling may have allowed for the detection of more regular trait abundance distribution patterns.

The detection of functional redundancy may have also been skewed by the sampling method employed. Trawls detected different patterns in functional redundancy than grabs. This could be a result of trawls having over- or under-sampled certain traits of the epifaunal community as discussed earlier. For example, starfish and crabs dominated epifaunal communities but share similar categories of the selected traits. Both groups are often dorso-ventrally flattened, mobile, and predatory and more efficiently sampled by trawls than other taxon/functional groups. The oversampling of certain functional groups by trawl could have increased the detection of functional redundancy as species with similar biological traits were targeted.

Alternatively, the different functional diversity patterns detected by grabs and trawls could be explained in part by limitations of the sampling design and statistical analyses. Not all stations pairs were at the exact same location due to the nature of opportunistically sampled stations and therefore variations in the habitats will have caused some biodiversity differences. The number of samples were also limited as few locations on the west coast had both a grab and trawl sample available within proximity to each other. Increased sample pairs may have provided evidence of stronger relationships between trawl and grab functional diversity. There are also limitations to the functional diversity metrics when condensing multivariate trait assemblage structure into a single statistic for each sample. Analytical decisions, such as the selection of important trait or the choice of distance matrix, could have some effect on the findings of the study. FD RaoQ is also sensitive to the correlation between traits (Botta-Dukát, 2005). Although highly correlated traits were removed from each dataset, remaining traits were still closely associated. Using ordination axes in calculating functional diversity obscured these correlations and offered insight into multivariate trait assemblage congruence.

3.4.3. Trait assemblage patterns and drivers

The ‘quality’ of FD was dependent on the ability of the traits in explaining the distribution of the community (Botta-Dukát, 2005; Petchey & Gaston, 2006). The selected traits explained large amounts of variation in trait assemblage patterns increasing the reliability of the results. These results validate the importance of morphology, behaviour and life history and their relevance to macroecology (Tyler *et al*., 2012). These traits were likely correlated with strong environmental drivers on the west coast and were thus responsible for explaining large proportions in trait assemblage structure. The reasons for these traits being important in structuring assemblage patterns has already been discussed, although it should be noted that all selected traits were significant and explained large proportions of the variation in trait assemblage structure.

Trawl and grab trait assemblages were not independent and evidence of strong co-correspondence between trait assemblage patterns was found on the west coast at the ecoregion scale. Despite sampling different habitats, functional structure, traits, functional evenness, diversity and redundancy patterns; the multivariate trait assemblage structure at the ecoregion scale presented very similar patterns. This was not predicted based on previous research exploring the biological traits of epifauna and infauna (Muntadas *et al*., 2014; Muntadas *et al*., 2016; Trannum *et al*., 2019; Tiano *et al*., 2020), studies directly comparing patterns detected by different gear types (Jørgensen *et al*., 2011), the difference in community composition between sampling methods, and the differences in spatial, temporal and thematic scale between the sampling methods (Brown *et al*., 2011; Lecours *et al*., 2015).

Trannum *et al.* (2019) found some consistencies of functional diversity responses to impact across both epifaunal and infaunal communities. Epifauna and infauna experienced a decrease in sessile, tube-dwelling animals whereas burrowing, motile surface-crawling carnivore and omnivores increased in relation to deposition from mining. In this study, depth was a highly correlated variable with trait assemblage scores for both epifauna and infauna and explained large proportions in the trait assemblage variability detected by trawls and grabs. As discussed previously, depth is a predictor variable related to many of the biological traits included in this study.

3.4.4. Conclusion

The results of this chapter suggest that at the broad scale on the west coast, demersal trawling and grab sampling similarly represent ecosystem functioning based on multivariate trait assemblage patterns. This is likely due to the strong environmental gradients operating in the ecoregion, including depth and sediment type. However, due to large differences in univariate functional diversity measurements and the complementary functional structure sampled by each method, employing both trawls and grabs is needed to comprehensively represent the entire functioning of the benthic ecosystem since both methods have their own biases towards certain animal morphology, behaviour and life history traits. Correlating environmental drivers with specific traits would aid the interpretation of these results and advance knowledge in the specific environmental variables structuring ecosystem functioning based on important biological traits.

Chapter 4

Synthesis

4.1. Summary of Findings

From the same 24 sites on the west coast, grabs sampled almost three times the number of species sampled by trawls despite trawls covering an area approximately 340 000 times greater than grabs. This finding suggests that the diversity of epibenthic invertebrate communities was vastly underrepresented by demersal trawl sampling (Elefhteriou & Moore, 2013). Quantitative grab sampling detected up to three times more species but rarefraction curves are needed to determine whether the number of species sampled is an adequate reflection of the true species diversity. Replicate grab samples are almost always essential to efficiently sample an area (Eleftheriou & Moore, 2013). However, for consistency this study used single grab samples as these data have previously been used in the ecosystem classification process (Sink *et al.*, 2019). Trawls likely efficiently sampled certain taxa of the epibenthic invertebrate community thus overrepresenting these members while other groups were under-sampled. This led to low species numbers, community homogenisation, and loss of fine scale detail, but high abundances sampled across sites

4.1.1. Benthic structure

Demersal trawl and grab sampling collected different taxonomic and functional components of the marine benthos. Although both methods sampled 16 Classes and similar numbers of biological traits (34 epifaunal and 35 infaunal), trawl and grab samples were dominated by different taxa and traits. Trawl samples were dominated by large, dorso-ventrally flattened, free-living, moderately mobile, surface-crawling, predatory epifauna with planktotrophic larvae and medium-long lifespans, such as Asteroidea and Malacostraca (specifically, Decapoda) species. Anthozoa and Gastropoda were also abundant in trawl samples. Grab samples were dominated by small, vermiform or laterally flattened, slow-moving, surface deposit-feeding infauna with planktotrophic larvae and short lifespans, such as Polychaeta, Malacostraca (specifically, Amphipoda) and Bivalvia.

These findings have implications for biodiversity patterns detected by the different sampling methods because different taxon and functional groups are expected to respond differently to environmental gradients or disturbance (Jørgensen *et al.*, 2011; Flannery & Przeslawski, 2015). It is also important to employ both sampling methods to collect all faunal groups for taxonomic descriptions, species inventories and biodiversity discovery as each method samples almost completely different suites of fauna. In South Africa, offshore samples are scarce and many invertebrate species and taxa groups remain understudied or undescribed (Gibbons, 1999; Griffiths *et al.*, 2010). Accurate species description and identification provide the foundation to establishing robust biological datasets which are used in ecosystem classification (Foley *et al.*, 2010). Furthermore, quantifying the extent of our biodiversity can lead to necessary conservation planning and protection at appropriate scales (Agardy *et al.*, 2011; Collie *et al.*, 2013).

4.1.2. Diversity indices

Demersal trawl and grab sampling detected significantly similar patterns in species abundance, species richness, species diversity and functional richness values across the west coast. These measures of biodiversity had moderately positive linear relationships when sampled from the same locations, however, these relationships were not strong enough for one sampling method to replace the other as a surrogate for these measures of biodiversity. Furthermore, species evenness, functional evenness, functional diversity, and functional redundancy gave no evidence of a linear relationship between the two sampling methods. Similar patterns in species richness detected by trawls and grabs across the same biotopes have been found previously (Buhl-Mortensen *et al.*, 2012). Similarly to the findings of this thesis, species evenness and functional redundancy values have reported inconsistent responses to environmental gradients and disturbance when sampled by trawl and grab (Buhl-Mortensen *et al.*, 2012; Muntadas *et al.*, 2016).

Maintaining native species diversity has been outlined as a guiding ecological principle of Marine Spatial Planning (Foley *et al.*, 2010). Species diversity affects ecosystem functions such as productivity, resilience, capacity to maintain functional redundancy and stable food web dynamics (Stachowicz *et al.*, 2007; Palumbi *et al.*, 2009). Operationally, diversity measures (including functional diversity) need to be measured to assess these ecosystem functions (Foley *et al.*, 2010). There are a variety of diversity metrics (only some were measured in this thesis) and all should be monitored at multiple spatial and temporal scales (Foley *et al.*, 2010; Morris *et al.*, 2014).

Trawls and grabs sample most effectively at different scales (Table 1.1), and therefore their datasets should be prioritised and weighted according to the scale of assessment (Naeem, 2006). To do this, diversity indices should be quantified and compared between sampling methods and scale using rarefaction curves to account for the disparity in unit sizes. Once the ideal number of samples required by each method is determined, diversity indices can be compared to assess whether grabs or trawls detect greater diversity values at different scales. From this, diversity datasets can be prioritised and weighted and potentially incorporated into ecosystem classification as these indices represent important components of ecosystem functioning and services (Palumbi *et al.*, 2009). Diversity indices should also be related to environmental variables and disturbance to determine the drivers of diversity at multiple scales and whether these overlap for datasets collected by different methods.

4.1.3. Assemblage patterns

Demersal trawling and grab sampling detected significantly similar community and trait assemblage patterns across the west coast. The similarities in assemblage patterns are likely a result of strong environmental gradients operating at the ecoregion scale on the west coast. Studies which have detected similar community patterns between epifauna and infauna, detected these similarities at broad scales and attributed them to hydrography (Reiss *et al.*, 2010; Silberberger *et al.*, 2019). Hydrodynamic variables were not tested in this thesis but have been found to be important drivers of infaunal and epifaunal community patterns on the west coast (Karenyi, 2014; Lange & Griffiths, 2014; Karenyi *et al.*, 2016). Hydrodynamic variables should be important physical monitoring variables for top-down approaches to ecosystem classification at the broad ecoregion scale as these variables are clearly key to structuring community patterns for both epifauna and infauna at this operating scale (Strong *et al.*, 2019).

When community assemblage datasets sampled by trawls and grabs are used to define ecosystems at the ecoregion scale, they could be prioritised or weighted similarly. Grabs, however, sampled far greater variation than trawls as evident by grab samples being less similar based on average species abundance than trawls. Furthermore, grab samples delineated into a greater number of significant SIMPROF clusters than trawls when a taxonomic-based approach was used (Fig. 4.1.b). Trawls did detect variation in communities within the ecoregion and these appeared to correspond to major shelf depth boundaries (Fig. 4.1.a), but this detection in epifauna variation is strongly contrasted to the infauna variation detected by grabs (Fig. 4.1.b). Therefore, grab data may need to increase in priority/weighting with a decrease in scale when delineating ecosystems.

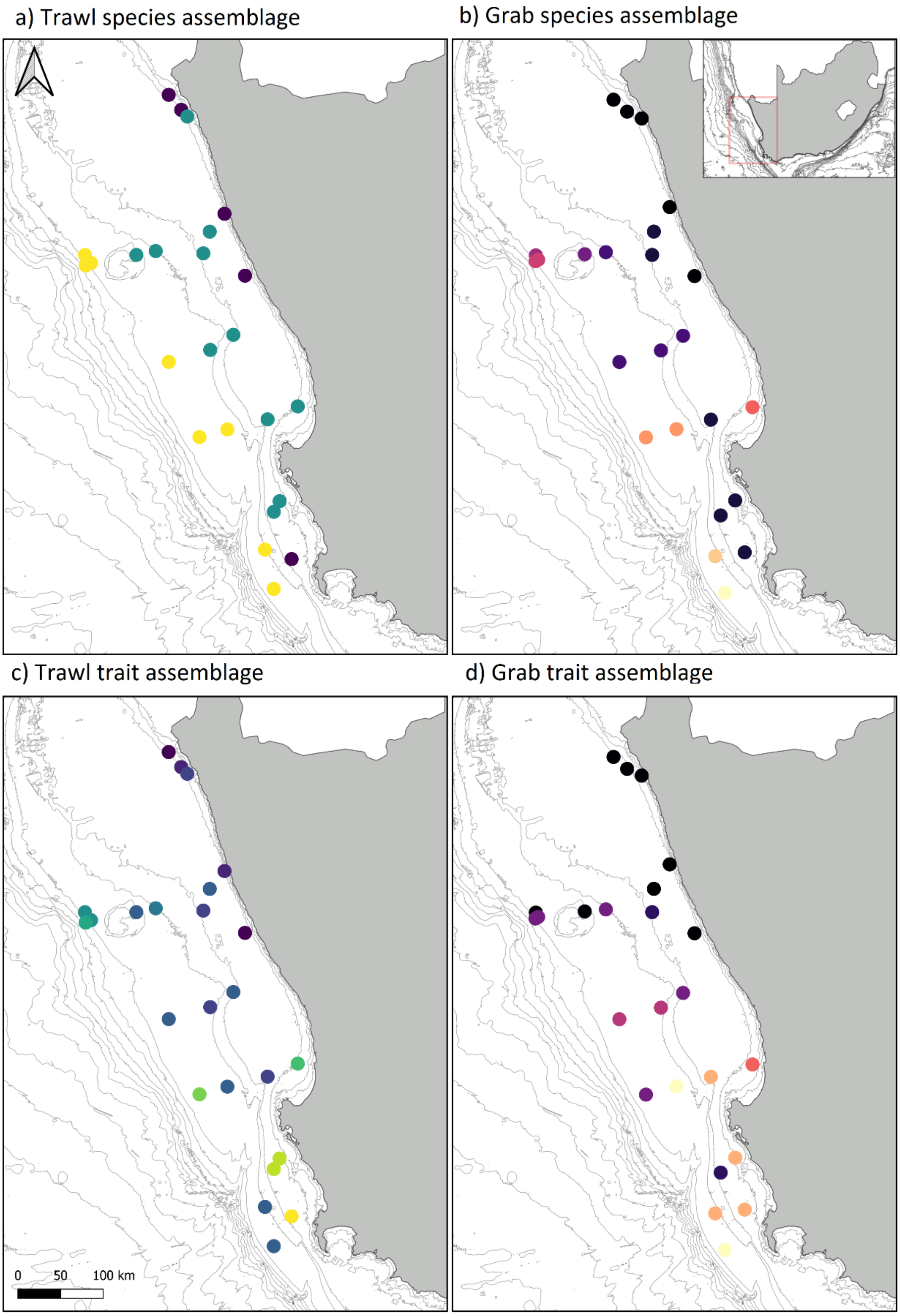


Figure 4.1. Significant groups of trawl (a, c) and grab (b, d) stations sampled from 24 offshore sites on the west coast of South Africa based on species abundance (a, b) and functional traits (c, d). The plots show 3, 10, 11, and 7 significant SIMPROF groups, respectively, represented by the colour of the points.

Whereas trawl samples may become less meaningful for delineating community boundaries within broad depth zones or substratum types in the ecoregion (Sink *et al*., 2019). The nested, hierarchical nature of the marine classification scheme used in South Africa allows data to be incorporated at different levels relevant to management (Sink *et al*., 2019; Strong *et al*., 2019; Harris & Baker, 2020).

Similarly for environmental variables, fine scale sediment data could be more heavily weighted than broad scale spatial variables as scale decreases. Depth and longitude were found to be significant environmental predictors of both demersal trawl and grab species and trait assemblage patterns. These are indirect gradient drivers and likely have many other environmental correlates, for which data were not available for this study (e.g., hydrodynamic variables). Sediment variables were available from grab samples and percentage medium sand is a significant driver of grab species and trait assemblages. Percentage mud was only correlated with grab species assemblage patterns and not trait assemblage patterns. The importance of these drivers is likely to vary according to the scale of assessment. Depth and longitude (and likely hydrography) should be prioritised at broad scales whereas *in situ* sediment characteristics may be prioritised at fine scales to distinguish ecosystem types.

4.2. The Utilisation of Co-correspondence Analysis (CoCA)

Multi-method biodiversity studies which acquired data using different sampling methods resulted in separate taxa being recorded in more than one species by site dataset, and therefore analysed a pair of data tables (e.g., species/site matrix of abundance data). To analyse a pair of tables, the common practice is to merge the two tables into a single table by standardising the data and then applying the ordination methods (e.g., Jørgensen *et al*., 2011). However, considering the disparities in data collected by different sampling methods, standardisation is often unsuitable. Alternatively, the species tables can be analysed separately by explaining the community composition using a table of environmental predictors (e.g., Flannery & Przeslawski, 2015). These ordination methods, such as canonical correspondence analysis (CCA) or redundancy analysis (RDA), require fewer predictor variables than samples and are therefore inappropriate for high-dimensional species matrix comparisons (Dray *et al*., 2002; Alric *et al*., 2020). Ideally, techniques allowing for the analysis of a pair of tables while preserving the original data structure should be used (Alric *et al*., 2020), such as co-

correspondence analysis (CoCA), a relatively recent statistical method (ter Braak & Schaffers, 2004).

Jørgensen *et al*. (2011) standardised their data and Flannery and Przeslawski (2015) compared datasets separately by relating them to environmental variables – both studies attempted to account for the inability to directly compare the data collected by different methods. CoCA addressed the methodological limitations seen in previous studies as it allowed for the direct comparison of multivariate assemblage data from different sampling methods without needing to standardise across gear types. It encompassed the unavoidable data differences between two methods instead attempting to account for them (which creates avenues for skewed results). Rather than comparing taxonomic or trait similarities it enabled a comparison of structural variability between two assemblages across the same sites in one statistical step.

Using symmetric co-correspondence analysis (sCoCA) to compare the assemblage patterns detected by trawls and grabs and to compare functional trait matrices was unique to this study and has not previously been done. This method allowed for trawl and grab datasets to be compared in the same statistical analysis in contrast to previous studies which have standardised trawl and grab datasets (Jørgensen *et al*., 2013) or analysed their datasets separately by relating assemblage patterns to environmental predictors (Flannery & Przeslawski, 2015). Therefore, the main finding that trawls and grabs detected similar assemblage patterns could also be attributed to using an analysis which preserved the original data structure but still allowed for direct comparisons and significance testing (ter Braak & Schaffers, 2004; Alric *et al*., 2020).

4.3. Taxonomic versus Trait-based Approaches

4.3.1. Representation of the benthic structure

Although trawls and grabs both sampled different taxonomic and functional components of the benthos, sampling different taxonomic components did not always translate to sampling differences in functional components. For example, the trawl and grab dataset shared only three species in common but shared the majority of biological traits in common. Taxon groups were vastly different between sampling types; however, some trait modalities were similarly represented between trawl and grab samples. Having planktotrophic larval development, being free-living, and having a longevity of 2-5 years were trait modalities that were equally represented across both epifaunal and infaunal communities. Therefore, with regards to some specific traits, taxonomic differences would not accurately predict the degree of functional difference, which overlaps to some extent.

4.3.2. Estimations of univariate indices of diversity

Trawl and grab richness was correlated using both taxonomic and trait-based approaches with similar, moderately positive linear relationships on the west coast. Benthic invertebrate species richness has been found to have strong linear associations to functional diversity (Wong & Dowd, 2015). Therefore, species richness may be an adequate surrogate for estimating functional richness at the ecoregion scale; however, correlations between these two indices should be explored for both infauna and epifauna, and across different spatial and temporal scales.

Where a significant relationship between species diversity was detected between trawls and grabs, functional diversity was not correlated across sites. This difference in diversity response indicates that taxonomic diversity may not be an adequate surrogate for functional diversity on the west coast shelf, although further regression analyses should be conducted to compare these two metrics. Studies which have directly compared benthic invertebrate taxonomic and functional diversity have found evidence of strong linear relationships (Wong & Dowd, 2015; Liu *et al*., 2019). Taxonomic and functional diversity indices should be directly compared between different faunal groups and across different scales as taxonomic and functional diversity change is dependent on scale (Edie *et al*., 2018; Jarzyna & Jetz, 2018). Taxonomic and functional diversity indices may then be weighted or prioritised differently according to faunal group and their divergence at different scales of assessment relevant to ecosystem classification.

4.3.3. Estimations of multivariate assemblage patterns

Assemblage patterns detected by trawl and grabs were found to be similar on the west coast at the ecoregion scale using both taxonomic and trait-based approaches. Although, significant clusters of sites differed when using the different approaches. With regards to demersal trawling, far more distinct clusters were detected using functional traits (11 clusters; Fig. 4.1.c) in contrast to species abundance data (3 clusters; Fig. 4.1.a). Therefore, more unique functional groups were identified than community groups based on species abundance. In contrast, grabs detected more distinct communities (10 cluster; Fig. 4.1.b) than functional groups (7 cluster; Fig. 4.1.d). Greater functional diversity than taxonomic diversity is an indicator of functional redundancy (Van Der Linden *et al*., 2012); therefore, trawls may detect greater functional redundancy than grabs (Fig. 4.1). This has implications for disturbance impacts and protection level (Henseler *et al*., 2019; Larson *et al*., 2021).

Although trawl communities separate across broad environmental gradients, functional traits may represent greater habitat variability as unique assemblages of traits respond to the fine-scale environmental drivers. Comparisons between the species assemblages and trait assemblages should be made for both datasets to determine whether multivariate species abundance data is an adequate surrogate for ecosystem functioning. Studies which have compared benthic invertebrate taxonomic and trait assemblage patterns have found trait-based approaches to be no more powerful than the taxonomic-based approach for distinguishing assemblages (Alves *et al*., 2014), or have found functional trait-based approaches to show greater similarity in assemblage patterns *(Rand et al*., 2018; Henseler *et al*., 2019), particularly at the broad scale of analysis (Edie *et al*., 2018; Jarzyna & Jetz, 2018). This implies that functional diversity patterns are likely more variable at meso- and fine scale spatial scales and these data should be prioritised accordingly.

If biological assemblages defined using both taxonomic and trait-based approaches are to be incorporated into future ecosystem classification schemes, they would need to be prioritised or weighted differently as they delineate assemblages differently (Fig. 4.1). Trawl and grab assemblages may not need to be weighted differently at the ecoregion scale as there is evidence that their datasets present similar patterns; however, within gear types or faunal groups, taxonomic and functional trait assemblage datasets may need to be prioritised differently. For example, for trawls, as scale decreases, functional diversity may detect greater variation than taxonomic diversity. Whereas for grabs, as scale decreased, taxonomic diversity may detect more variation than functional diversity. This should be analysed further by directly comparing community and trait assemblages within faunal groups and across varying scales. This could be achieved by applying predictive co-correspondence analysis (pCoCA; ter Braak & Schaffers, 2004) to taxonomic and trait datasets to determine whether taxonomic diversity is an adequate surrogate for functional diversity in the marine benthos.

Species and traits assemblages shared the same significant drivers for both datasets. Percentage mud was also significant in driving grab species assemblage patterns. This - in addition to grab samples resulting in more distinct species assemblage clusters than functional groups - may be evidence for the taxonomic-based approach detecting greater variability in grab sampling data from which to estimate biodiversity. Evidence for this needs to be explored further as previous research generally finds trait-based approaches detect greater variability (Fleddum *et al*., 2013; Wong & Dowd, 2015).

4.4. Study Limitations

Many of the major limitations of this study are based on the opportunistic nature of the sampling design. Firstly, since both trawl and grab data points needed to be available within one grid block (25’x25’) to be viable for the analysis, this limited the sample size available. Small sample sizes may affect the accuracy and reliability of the observed relationships. For example, the relationships detected between univariate diversity indices as detected by each method may have been stronger with a greater sample size.

Secondly, trawl and grab samples were not collected from identical locations in space and time. The assumption that offshore marine benthic communities are stable may be an oversimplification (Tyler, 1988; Clark *et al*., 2016). Benthic habitats are also known to be patchy (Eleftheriou, 2013; Harris & Baker, 2020) and as no replication was used, the grabs are particularly prone to this patchiness. These sampling limitations may have created greater disparities between the two datasets where differences detected are unlikely to only be due to inherent biodiversity differences or sampling gear differences, but also data limitations. In this study a trade-off was made between an increased number of samples and a less balanced design. Correlograms would offer insight into the presence of spatial autocorrelation in this study and should be investigated (Getis, 2010; Lecours *et al*., 2015).

Another limitation was the low number of environmental variables included in the study. As the trait and species assemblage patterns showed strong evidence of being highly correlated with the west coast environmental gradients, a more comprehensive suite of environmental variables potentially influencing these patterns would have been ideal to include in the analyses. Variables such as oxygen concentration, temperature, salinity, and variables related to biogeochemistry are collected during the annual demersal trawl research surveys. These data were not available in time for the inclusion in this thesis but would aid the interpretation of the results when similarities in biodiversity patterns were detected by the sampling methods. There are global databases from which these environmental data are potentially available for this region, however, the scale of resolution was not considered sufficiently accurate, and these variables were therefore not included in this study.

4.5. Thesis Conclusions

Trawls and grabs sampled different habitats and faunal groups; therefore, neither method can replace the other entirely as a surrogate (Jørgensen *et al.*, 2011; Flannery & Przeslawski, 2015). Species datasets from both sampling methods were complementary and are most valuable when used in combination (Jørgensen *et al.*, 2011). Yet, the epifaunal and infaunal communities and functional trait assemblages detected at the broad scale were structurally similar which alluded to strong environmental gradients operating on the continental shelf of the South African west coast. Similarly, taxonomic and functional diversity are both important components of measuring biodiversity and should be used in conjunction (Van Der Linden *et al.*, 2012; Alves *et al.*, 2014; Wong & Dowd, 2015; Henseler *et al.*, 2019). The relationships between species biological traits and environmental variables needs to be explored further. Functional trait datasets should be compiled and built upon (Tyler *et al.*, 2012), and this layer of information should be considered for inclusion in ecosystem classification as the trait-based approach yielded distinct assemblages from the taxonomic-based approach (Fig. 4.1).

The results of this study demonstrated how biological datasets from trawl and grab surveys could be prioritised or weighted and these findings should be taken into consideration in the marine ecosystem classification and mapping component of the next National Biodiversity Assessment (NBA: Sink *et al.*, 2019) when data driven approaches become more prominent. Understanding the degree to which the choice of sampling method affects the data obtained is crucial to the incorporation of different biological datasets into the ecosystem classification and mapping process (Flannery & Przeslawski, 2015). Currently, benthic invertebrate data are collected by grab, trawl, and remotely operated vehicle surveys, submersible, tow camera and baited underwater video, and these data are used to inform the marine ecosystem classification and map (Sink *et al.*, 2019). A nested hierarchical approach is followed to create a map of 150 ecosystem types allowing for the incorporation of different kinds of ecological data at a range of spatial scales (Misiuk *et al.*, 2018; Sink *et al.*, 2019; Harris & Baker, 2020).

One of the key research priorities for the marine ecosystem classification and map are integrative approaches to advance mapping towards a data driven, expert informed approach (Sink *et al.*, 2019). Further data driven approaches that can integrate large datasets covering various ecosystem components collected by multiple methods have been encouraged (Sink *et al.*, 2019), potentially making use of multivariate statistical techniques to define ecosystems (Shephard *et al.*, 2015; Harris & Baker, 2020). Advancement towards a statistical tool or model which updates the ecosystem classification and map with additional datasets is the motivation behind research conducted in this thesis. Prioritisation and weighting of datasets can be accomplished as modelling the marine system allows for parameterisation. Parameters are independent quantities of a system and could potentially vary for sampling type, biodiversity metric, and across different scales of the hierarchical classification to delineate ecosystem boundaries.

Before different biological datasets (e.g., trawl and grab) can be prioritised and weighted, the first step is to answer the following research question: does demersal trawling and grab sampling detect different benthic biodiversity patterns? This thesis aimed to address this research question by accomplishing the following objectives: i) determining the differences in benthic structure detected by each method, ii) comparing the measures of biodiversity estimated by each method and iii) comparing assemblages sampled by each method. These objectives were undertaken at the ecoregion scale using both taxonomic and trait-based approaches as surrogates for biodiversity. The next steps are to determine the extent to which taxonomic diversity can predict functional diversity and at which ecological scales different datasets should be prioritised. The findings from this thesis can be used towards increasing the accuracy of South Africa’s marine ecosystem classification and map in future iterations and in this way, contribute towards improved ocean management.

References

Agardy, T., di Sciara, G.N. & Christie, P. 2011. Mind the gap: Addressing the shortcomings of marine protected areas through large scale marine spatial planning. *Marine Policy*. 35(2):226–232.

Aller, R.C. 1982. The effects of macrobenthos on chemical properties of marine sediment and overlying water. In *Animal-sediment relations*. Springer. 53–102.

Alric, B., ter Braak, C.J.F., Desdevises, Y., Lebredonchel, H. & Dray, S. 2020. Investigating microbial associations from sequencing survey data with co-correspondence analysis. *Molecular Ecology Resources*. 20(2):468–480.

Alves, A.S., Veríssimo, H., Costa, M.J. & Marques, J.C. 2014. Taxonomic resolution and Biological Traits Analysis (BTA) approaches in estuarine free-living nematodes. *Estuarine, Coastal and Shelf Science*. 138:69–78.

Atkinson, L.J. & Sink, K.J. 2018. *Field guide to the offshore marine invertebrates of South Africa*.

Atkinson, L.J., Leslie, R.W., Field, J.G. & Jarre, A. 2011. Changes in demersal fish assemblages on the west coast of South Africa, 1986–2009. *African Journal of Marine Science*. 33(1):157–170.

Axelsen, B.E. & Johnsen, E. 2015. An evaluation of the bottom trawl surveys in the Benguela Current Large Marine Ecosystem. *Fisheries Oceanography*. 24(S1):74–87.

Basford, D., Eleftheriou, A. & Raffaelli, D. 1990. The infauna and epifauna of the northern North Sea. *Netherlands Journal of Sea Research*. 25(1–2):165–173.

Bett, B.J. 2013. Characteristic benthic size spectra: potential sampling artefacts. *Marine Ecology Progress Series*. 487:1–6.

Blanchard, J.L., Jennings, S., Law, R., Castle, M.D., McCloghrie, P., Rochet, M. & Benoît, E. 2009. How does abundance scale with body size in coupled size-structured food webs? *Journal of Animal Ecology*. 78(1):270–280.

Blomqvist, S. 1991. Quantitative sampling of soft-bottom sediments: problems and solutions. *Marine Ecology Progress Series*. 72(3):295–304.

van den Boogaart, K.G., Tolosana, R., Bren, M. and van den Boogaart, M.K.G., 2013. Package ‘compositions’. *Compositional data analysis. Ver,* pp.1-40.

Botta-Dukát, Z. 2005. Rao’s quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*. 16(5):533.

ter Braak, C.J.F. & Schaffers, A.P. 2004. Co-correspondence analysis: A new ordination method to relate two community compositions. *Ecology*. 85(3):834–846.

Bremner, J., Rogers, S.I. & Frid, C.L.J. 2003. Assessing functional diversity in marine benthic ecosystems. *Marine Ecology Progress Series*. 254:11–25.

Bremner, J., Rogers, S.I. & Frid, C.L.J. 2006. Matching biological traits to environmental conditions in marine benthic ecosystems. *Journal of Marine Systems*. 60(3–4):302–316.

Brown, C.J., Cooper, K.M., Meadows, W.J., Limpenny, D.S. and Rees, H.L., 2002. Small-scale mapping of sea-bed assemblages in the eastern English Channel using sidescan sonar and remote sampling techniques. *Estuarine, Coastal and Shelf Science*, *54*(2), pp.263-278.

Brown, C.J., Smith, S.J., Lawton, P. & Anderson, J.T. 2011a. Estuarine , Coastal and Shelf Science Benthic habitat mapping : A review of progress towards improved understanding of the spatial ecology of the sea fl oor using acoustic techniques. *Estuarine, Coastal and Shelf Science*. 92(3):502–520.

Brown, C.J., Smith, S.J., Lawton, P. & Anderson, J.T. 2011b. Benthic habitat mapping: A review of progress towards improved understanding of the spatial ecology of the seafloor using acoustic techniques. *Estuarine, Coastal and Shelf Science*. 92(3):502–520.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. 2004. Toward a metabolic theory of ecology. *Ecology*. 85(7):1771–1789.

Buhl-Mortensen, L., Buhl-Mortensen, P., Dolan, M.F.J., Dannheim, J., Bellec, V. & Holte, B. 2012. Habitat complexity and bottom fauna composition at different scales on the continental shelf and slope of northern Norway. *Hydrobiologia*. 685(1):191–219.

Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S.W. 2009. The merging of community ecology and phylogenetic biology. *Ecology letters*. 12(7):693–715.

Charnov, E.L. & Gillooly, J.F. 2004. Size and temperature in the evolution of fish life histories. *Integrative and Comparative Biology*. 44(6):494–497.

Chevene, F., Doleadec, S. & Chessel, D. 1994. A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater biology*. 31(3):295–309.

Clark, M.R., Consalvey, M. & Rowden, A.A. 2016. *Biological Sampling in the Deep Sea*.

Clarke, K.R. & Warwick, R.M. 2001. Change in marine communities. *An approach to statistical analysis and interpretation*. 2:1–168.

Collie, J.S., Vic Adamowicz, W.L., Beck, M.W., Craig, B., Essington, T.E., Fluharty, D., Rice, J. & Sanchirico, J.N. 2013. Marine spatial planning in practice. *Estuarine, Coastal and Shelf Science*. 117:1–11.

Cornwell, W.K., Schwilk, D.W. & Ackerly, D.D. 2006. A trait-based test for habitat filtering: convex hull volume. *Ecology*. 87(6):1465–1471.

Corte, G.N., Checon, H.H., Fonseca, G., Vieira, D.C., Gallucci, F., Domenico, M. Di & Amaral, A.C.Z. 2017. Cross-taxon congruence in benthic communities: Searching for surrogates in marine sediments. *Ecological Indicators*. 78:173–182.

Costello, M.J., Coll, M., Danovaro, R., Halpin, P., Ojaveer, H. & Miloslavich, P. 2010. A census of marine biodiversity knowledge, resources, and future challenges. *PLoS ONE*. 5(8).

Costello, M.J., Basher, Z., Mcleod, L., Asaad, I., Claus, S., Vandepitte, L., Yasuhara, M., Gislason, H., et al. 2017. Methods for the Study of Marine Biodiversity. In *The GEO Handbook on Biodiversity Observation Networks*. 129–163.

Currie, D.R., Sorokin, S.J. & Ward, T.M. 2009. Infaunal macroinvertebrate assemblages of the eastern Great Australian Bight: effectiveness of a marine protected area in representing the region’s benthic biodiversity. *Marine and Freshwater Research*. 60(5):459–474.

Darr, A., Gogina, M. & Zettler, M.L. 2014. Functional changes in benthic communities along a salinity gradient–a western Baltic case study. *Journal of Sea Research*. 85:315–324.

Day, J.H. (1967). *A Monograph on the Polychaeta of Southern Africa. Pt 1, Errantia & Pt 2, Sedentaria*. London: Trustees of the British Museum (Natural History).

Day, G.F. (1978) The Day grab – a simple sea-bed sampler. Report of the Institute of *Oceanographic Sciences*, *52*

Degen, R., Aune, M., Bluhm, B.A., Cassidy, C., Kędra, M., Kraan, C., Vandepitte, L., Włodarska-Kowalczuk, M., et al. 2018. Trait-based approaches in rapidly changing ecosystems: A roadmap to the future polar oceans. *Ecological Indicators*. 91:722–736.

Degen R & Faulwetter S (2019) The Arctic Traits Database – a repository of Arctic benthic invertebrate traits, Earth System Science Data 11: 301-322.

Díaz, S. & Cabido, M. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in ecology & evolution*. 16(11):646–655.

Douvere, F. and Ehler, C.N., 2009. New perspectives on sea use management: initial findings from European experience with marine spatial planning. *Journal of environmental management*, *90*(1), pp.77-88.

Dray, S. & Dufour, A.-B. 2007. The ade4 package: implementing the duality diagram for ecologists. *Journal of statistical software*. 22(4):1–20.

Dray, S., Pettorelli, N. & Chessel, D. 2002. Matching data sets from two different spatial samples. *Journal of Vegetation Science*. 13(6):867.

Edgar, G.J., Shaw, C., Watsona, G.F. & Hammond, L.S. 1994. Comparisons of species richness, size-structure and production of benthos in vegetated and unvegetated habitats in Western Port, Victoria. *Journal of Experimental Marine Biology and Ecology*. 176(2):201–226.

Edie, S.M., Jablonski, D. & Valentine, J.W. 2018. Contrasting responses of functional diversity to major losses in taxonomic diversity. *Proceedings of the National Academy of Sciences of the United States of America*. 115(4):732–737.

Elefttheriou, A. and Moore, D. 2013. Macrofauna Techniques. *Methods for the Study of Marine Benthos, Fourth Edition*. Eds. Eleftheriou, A. 177-253.

Faulwetter S, Markantonatou V, Pavloudi C, Papageorgiou N, Keklikoglou K, Chatzinikolaou E, Pafilis E, Chatzigeorgiou G, Vasileiadou K, Dailianis T, Fanini L, Koulouri P, Arvanitidis C (2014) *Polytraits*: A database on biological traits of marine polychaetes. *Biodiversity Data Journal* 2: e1024.

Field, J.G. & Shillington, F.A. 2006. Variability of the Benguela Current system. *The sea*. 14:833–861.

Fischer, A.G. 1960. Latitudinal variations in organic diversity. *Evolution*. 14(1):64–81.

Flannery, E. & Przeslawski, R. 2015. *Comparison of sampling methods to assess benthic marine biodiversity: Are spatial and ecological relationships consistent among sampling gear?*

Fleddum, A., Atkinson, L.J., Field, J.G. & Shin, P. 2013. Changes in biological traits of macro-benthic communities subjected to different intensities of demersal trawling along the west coast of southern Africa. *Journal of the Marine Biological Association of the United Kingdom*. 93(8):2027–2038.

Foley, M.M., Halpern, B.S., Micheli, F., Armsby, M.H., Caldwell, M.R., Crain, C.M., Prahler, E., Rohr, N., et al. 2010. Guiding ecological principles for marine spatial planning. *Marine Policy*. 34(5):955–966.

Ganesh, T. & Raman, A. V. 2007. Macrobenthic community structure of the northeast Indian shelf, Bay of Bengal. *Marine Ecology Progress Series*. 341:59–73.

Getis, A., 2010. Spatial autocorrelation. In *Handbook of applied spatial analysis* (pp. 255-278). Springer, Berlin, Heidelberg.

Gibbons, M.J. 1999. The taxonomic richness of South Africa's marine fauna: a crisis at hand. *South African Journal of Science*. 95(1):8–12.

Giere, O. 1993. The Distribution of Meiofauna. In *Meiobenthology*. Springer. 185–196.

Gioria, M., Schaffers, A., Bacaro, G. & Feehan, J. 2010. The conservation value of farmland ponds: Predicting water beetle assemblages using vascular plants as a surrogate group. *Biological Conservation*. 143(5):1125–1133.

Gower, J.C. 1971. A general coefficient of similarity and some of its properties. *Biometrics*. 857–871.

Gray, J.S. 1974. Animal-sediment relationships. Oceanogr. *Mar. Biol. Ann. Rev.* 12:223–261.

Gray, J.S. & Elliott, M. 2009. *Ecology of marine sediments: from science to management*. Oxford university press.

Griffiths, C.L. 1976. *Guide to the benthic marine amphipods of Southern Africa*. Trustees of the South African Museum.

Griffiths, C.L., Robinson, T.B., Lange, L. & Mead, A. 2010. Marine biodiversity in south africa: An evaluation of current states of knowledge. *PLoS ONE*. 5(8).

Hanson, M.A., Buelt, C.A., Zimmer, K.D., Herwig, B.R., Bowe, S. & Maurer, K. 2015. Co-correspondence among aquatic invertebrates, fish, and submerged aquatic plants in shallow lakes. *Freshwater Science*. 34(3):953–964.

Harris, P.T. & Baker, E. 2020. *Seafloor geomorphology as benthic habitat*. Second ed.

Hemery, L.G., Politano, K.K. & Henkel, S.K. (2017). Assessing differences in macrofaunal assemblages as a factor of sieve mesh size, distance between samples, and time of sampling. *Environ Monit Assess*, 189:413.

Henseler, C., Nordström, M.C., Törnroos, A., Snickars, M., Pecuchet, L., Lindegren, M. & Bonsdorff, E. 2019. Coastal habitats and their importance for the diversity of benthic communities: A species- and trait-based approach. *Estuarine, Coastal and Shelf Science*. 226(June).

Hessler, R.R. & Sanders, H.L. 1967. Faunal diversity in the deep-sea. In *Deep Sea Research and Oceanographic Abstracts*. V. 14. Elsevier. 65–78.

Hinchey, E.K., Schaffner, L.C., Hoar, C.C., Vogt, B.W. & Batte, L.P. 2006. Responses of estuarine benthic invertebrates to sediment burial: the importance of mobility and adaptation. *Hydrobiologia*. 556(1):85–98.

Jackson, D.A. & Harvey, H.H. 1993. Fish and benthic invertebrates: community concordance and community–environment relationships. *Canadian Journal of Fisheries and Aquatic Sciences*. 50(12):2641–2651.

Jarre, A., Hutchings, L., Crichton, M., Wieland, K., Lamont, T., Blamey, L.K., Illert, C., Hill, E., et al. 2015. Oxygen-depleted bottom waters along the west coast of S outh A frica, 1950–2011. *Fisheries Oceanography*. 24:56–73.

Jarzyna, M.A. & Jetz, W. 2018. Taxonomic and functional diversity change is scale dependent. *Nature Communications*. 9(1).

Jennings, S., Reynolds, J.D. & Mills, S.C. 1998. Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society of London. Series B: Biological Sciences*. 265(1393):333–339.

Jennings, S., Greenstreet, S.P.R. & Reynolds, J.D. 1999. Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *Journal of animal ecology*. 68(3):617–627.

Jørgensen, L.L., Renaud, P.E. & Cochrane, S.K.J. 2011. Improving benthic monitoring by combining trawl and grab surveys. *Marine Pollution Bulletin*. 62(6):1183–1190.

Josefson, A.B., Blomqvist, M., Hansen, J.L.S., Rosenberg, R. & Rygg, B. 2009. Assessment of marine benthic quality change in gradients of disturbance: comparison of different Scandinavian multi-metric indices. *Marine Pollution Bulletin*. 58(9):1263–1277.

Juan, S. De, Thrush, S.F. & Demestre, M. 2007. Functional changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea). 334:117–129.

Karenyi, N. 2014. Patterns and drivers of benthic macrofauna to support systematic conservation planning for marine unconsolidated sediments. (January).

Karenyi, N., Sink, K. & Nel, R. 2016. Defining seascapes for marine unconsolidated shelf sediments in an eastern boundary upwelling region: The southern Benguela as a case study. *Estuarine, Coastal and Shelf Science*. 169:195–206.

Kenny, A.J., Jenkins, C., Wood, D., Bolam, S.G., Mitchell, P., Scougal, C. & Judd, A. 2018. Assessing cumulative human activities, pressures, and impacts on North Sea benthic habitats using a biological traits approach. *ICES Journal of Marine Science*. 75(3):1080–1092.

Kensley, B.F. 1978. Guide to the marine isopods of southern Africa.

Kingston, P.F. 2001. *Benthic organisms overview*. 3rd ed. Elsevier Ltd.

Kirkman, S.P., Atkinson, L.J., Singh, L. & Axelsen, B.E. 2015. Regime shifts in demersal assemblages of the Benguela Current Large Marine Ecosystem : a comparative assessment. 24:15–30.

Koslow, J.A., Lowry, J.K., Hara, T.O., Poore, G.C.B. & Williams, A. 2001. Seamount benthic macrofauna off southern Tasmania : community structure and impacts of trawling. 213:111–125.

Kristensen, E. & Kostka, J.E. 2005. Macrofaunal burrows and irrigation in marine sediment: microbiological and biogeochemical interactions. *Interactions between macro-and microorganisms in marine sediments. American Geophysical Union, Washington, DC*. 125–

157.

Käß, M., Chikina, M., Vedenin, A., Pineda-metz, S.E.A. & Soltwedel, T. 2021. Traits and drivers : Functioning of macrobenthic communities across the deep Fram Strait (Arctic Ocean). 123:107324.

Laliberté, E. & Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology*. 91(1):299–305.

Laliberté, E., Legendre, P., Shipley, B. & Laliberté, M.E. 2014. Package 'FD'. *Measuring functional diversity from multiple traits, and other tools for functional ecology*.

Lange, L. & Griffiths, C.L. 2014. Large-scale spatial patterns within soft-bottom epibenthic invertebrate assemblages along the west coast of South Africa, based on the Nansen trawl survey. *African Journal of Marine Science*. 36(1):111–124.

Larson, E.I., Poff, N.L.R., Funk, W.C., Harrington, R.A., Kondratieff, B.C., Morton, S.G. & Flecker, A.S. 2021. A unifying framework for analyzing temporal changes in functional and taxonomic diversity along disturbance gradients. *Ecology*. 0(0):1–12.

Lechner, A.M., Langford, W.T., Jones, S.D., Bekessy, S.A. & Gordon, A. 2012. Investigating species–environment relationships at multiple scales: Differentiating between intrinsic scale and the modifiable areal unit problem. *Ecological Complexity*. 11:91–102.

Lecours, V., Devillers, R., Schneider, D.C., Lucieer, V.L., Brown, C.J. and Edinger, E.N., 2015. Spatial scale and geographic context in benthic habitat mapping: review and future directions. *Marine Ecology Progress Series*, *535*, pp.259-284.

Van Der Linden, P., Patrício, J., Marchini, A., Cid, N., Neto, J.M. & Marques, J.C. 2012. A biological trait approach to assess the functional composition of subtidal benthic communities in an estuarine ecosystem. *Ecological Indicators*. 20(September):121–133.

Liu, K., Lin, H., He, X., Huang, Y., Li, Z., Lin, J., Mou, J., Zhang, S., et al. 2019. Functional trait composition and diversity patterns of marine macrobenthos across the Arctic Bering Sea. *Ecological Indicators*. 102(December 2018):673–685.

Lombard, A.T., Strauss, T., Harris, J., Sink, K., Attwood, C. & Hutchings, L. 2004. South African national spatial biodiversity assessment 2004. In *Marine Component*. V. 4. South African National Biodiversity Institute Pretoria.

Long, B.G. & Wang, Y.G. 1994. Method for comparing the capture efficiency of benthic sampling devices. *Marine Biology*. 121(2):397–399.

Magierowski, R.H. & Johnson, C.R. 2006. Robustness of surrogates of biodiversity in marine benthic communities. *Ecological Applications*. 16(6):2264–2275.

Magurran, A.E. 1988. *Ecological diversity and its measurement*. Princeton university press.

Margalef, R. 1958. Information theory in biology. *General Systems Yearbook*. 3:36–71.

Marine Ecological Surveys Limited. 2008. Marine Macrofauna Genus Trait Handbook. Marine Ecological Surveys Limited, 24a Monmouth Place, BATH, BA1 2AY. 184pp. ISBN 978-0-9506920- 2-9.

MarLIN, 2006. *BIOTIC - Biological Traits Information Catalogue.* Marine Life Information Network. Plymouth: Marine Biological Association of the United Kingdom. [2021] Available from <www.marlin.ac.uk/biotic>

Mason, N.W.H., Lanoiselée, C., Mouillot, D., Wilson, J.B. & Argillier, C. 2008. Does niche overlap control relative abundance in French lacustrine fish communities? A new method incorporating functional traits. *Journal of Animal Ecology*. 77(4):661–669.

McArthur, M.A., Brooke, B.P., Przeslawski, R., Ryan, D.A., Lucieer, V.L., Nichol, S., McCallum, A.W., Mellin, C., et al. 2010. On the use of abiotic surrogates to describe marine benthic biodiversity. *Estuarine, Coastal and Shelf Science*. 88(1):21–32. DOI: 10.1016/j.ecss.2010.03.003.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. 2006. Rebuilding community ecology from functional traits. *Trends in ecology & evolution*. 21(4):178–185.

McIntyre, A.D. 1956. The use of trawl, grab and camera in estimating marine benthos. *Journal of the Marine Biological Association of the United Kingdom*. 35(2):419–429.

Meadows, P.S., Meadows, A. & Murray, J.M.H. 2012. Biological modifiers of marine benthic seascapes: Their role as ecosystem engineers. *Geomorphology*. 157–158:31–48.

Mellin, C., Delean, S., Caley, J., Edgar, G., Meekan, M., Pitcher, R., Przeslawski, R., Williams, A., et al. 2011. Effectiveness of biological surrogates for predicting patterns of marine biodiversity: A global meta-analysis. *PLoS ONE*. 6(6).

Mermillod-Blondin, F. & Rosenberg, R. 2006. Ecosystem engineering: the impact of bioturbation on biogeochemical processes in marine and freshwater benthic habitats. *Aquatic sciences*. 68(4):434–442.

Mermillod-Blondin, F., Rosenberg, R., François-Carcaillet, F., Norling, K. & Mauclaire, L. 2004. Influence of bioturbation by three benthic infaunal species on microbial communities and biogeochemical processes in marine sediment. *Aquatic Microbial Ecology*. 36(3):271–284.

Mermillod-Blondin, F., Gaudet, J., Gérino, M., Desrosiers, G. & Creuzé des Châtelliers, M. 2003. Influence of macroinvertebrates on physico-chemical and microbial processes in hyporheic sediments. *Hydrological Processes*. 17(4):779–794.

Misiuk, B., Lecours, V. and Bell, T., 2018. A multiscale approach to mapping seabed sediments. *PLoS One*, *13*(2), p.e0193647.

Mitchell, R.J., Hester, A.J., Campbell, C.D., Chapman, S.J., Cameron, C.M., Hewison, R.L. & Potts, J.M. 2010. Is vegetation composition or soil chemistry the best predictor of the soil microbial community? *Plant and Soil*. 333(1):417–430.

Morris, E.K., Caruso, T., Buscot, F., Fischer, M., Hancock, C., Maier, T.S., Meiners, T., Müller, C., et al. 2014. Choosing and using diversity indices: Insights for ecological applications from the German Biodiversity Exploratories. *Ecology and Evolution*. 4(18):3514–3524.

Moss, D.K., Ivany, L.C., Judd, E.J., Cummings, P.W., Bearden, C.E., Kim, W.J., Artruc, E.G. & Driscoll, J.R. 2016. Lifespan, growth rate, and body size across latitude in marine bivalvia, with implications for phanerozoic evolution. *Proceedings of the Royal Society B: Biological Sciences*. 283(1836).

Mouillot, D., Mason, W.H.N., Dumay, O. & Wilson, J.B. 2005. Functional regularity: a neglected aspect of functional diversity. *Oecologia*. 142(3):353–359.

Munch, S.B. & Salinas, S. 2009. Latitudinal variation in lifespan within species is explained by the metabolic theory of ecology. *Proceedings of the National Academy of Sciences*. 106(33):13860–13864.

Muntadas, A., Demestre, M., De Juan, S. & Frid, C.L.J. 2014. Trawling disturbance on benthic ecosystems and consequences on commercial species: a northwestern Mediterranean case study. *Scientia Marina*. 78(S1):53–65.

Muntadas, A., De Juan, S. & Demestre, M. 2016. Assessing functional redundancy in chronically trawled benthic communities. *Ecological Indicators*. 61:882–892.

Murillo, F.J., Weigel, B., Bouchard Marmen, M. & Kenchington, E. 2020a. Marine epibenthic functional diversity on Flemish Cap (north-west Atlantic)—Identifying trait responses to the environment and mapping ecosystem functions. *Diversity and Distributions*. 26(4):460–478.

Murillo, F.J., Weigel, B., Bouchard Marmen, M. & Kenchington, E. 2020b. Marine epibenthic functional diversity on Flemish Cap (north-west Atlantic)—Identifying trait responses to the environment and mapping ecosystem functions. *Diversity and Distributions*. 26(4):460–478.

Naeem, S. 2006. Expanding scales in biodiversity-based research: challenges and solutions for marine systems. *Marine Ecology Progress Series*. 311:273–283.

Narayanaswamy, B., Bett, B., Lamont, P., Rowden, A., Bell, E. and Menot, L. 2016. Corers and Grabs. *Biological Sampling in the Deep Sea*. Eds. Clark, M. R., Consalvey, M. and Rowden A. 207-228.

Paavola, R., Muotka, T., Virtanen, R., Heino, J., Jackson, D. & Mäki-Petäys, A. 2006. Spatial scale affects community concordance among fishes, benthic macroinvertebrates, and bryophytes in streams. *Ecological Applications*. 16(1):368–379.

Palumbi, S.R., Sandifer, P.A., Allan, J.D., Beck, M.W., Fautin, D.G., Fogarty, M.J., Halpern, B.S., Incze, L.S., et al. 2009. Managing for ocean biodiversity to sustain marine ecosystem services. *Frontiers in Ecology and the Environment*. 7(4):204–211.

Parr, C. S., N. Wilson, P. Leary, K. S. Schulz, K. Lans, L. Walley, J. A. Hammock, A. Goddard, J. Rice, M. Studer, J. T. G. Holmes, and R. J. Corrigan, Jr. 2014. The Encyclopedia of Life v2: Providing Global Access to Knowledge About Life on Earth. Biodiversity Data Journal 2: e1079.

Pavoine, S., Vallet, J., Dufour, A., Gachet, S. & Daniel, H. 2009. On the challenge of treating various types of variables: application for improving the measurement of functional diversity. *Oikos*. 118(3):391–402.

Pecuchet, L., Reygondeau, G., Cheung, W.W.L., Licandro, P., van Denderen, P.D., Payne, M.R. & Lindegren, M. 2018. Spatial distribution of life-history traits and their response to environmental gradients across multiple marine taxa. *Ecosphere*. 9(10).

Petchey, O.L. & Gaston, K.J. 2006. Functional diversity: back to basics and looking forward. *Ecology letters*. 9(6):741–758.

Pielou, E.C. 1966. The measurement of diversity in different types of biological collections. *Journal of theoretical biology*. 13:131–144.

Poiani, K.A., Richter, B.D., Anderson, M.G. & Richter, H.E. 2000. Biodiversity conservation at multiple scales: functional sites, landscapes, and networks. *BioScience*. 50(2):133–146.

Rand, K., Logerwell, E., Bluhm, B., Chenelot, H., Danielson, S., Iken, K. & Sousa, L. 2018. Using biological traits and environmental variables to characterize two Arctic epibenthic invertebrate communities in and adjacent to Barrow Canyon. *Deep-Sea Research Part II: Topical Studies in Oceanography*. 152(July 2017):154–169.

Rees, H.L., Pendle, M.A., Waldock, R., Limpenny, D.S. & Boyd, S.E. 1999. A comparison of benthic biodiversity in the North Sea, English Channel, and Celtic Seas. In *ICES Journal of Marine Science*. V. 56. 228–246.

Reiss, H., Degraer, S., Duineveld, G.C.A., Kröncke, I., Aldridge, J., Craeymeersch, J.A., Eggleton, J.D., Hillewaert, H., et al. 2010. Spatial patterns of infauna, epifauna, and demersal fish communities in the North Sea. *ICES Journal of Marine Science*. 67(2):278–293.

Robinson, C.L. & Levings, C.D. 1996. *An overview of habitat classification systems, ecological models, and geographic information systems applied to shallow foreshore marine habitats*.

Rodrigues, A.S.L. & Brooks, T.M. 2007. Shortcuts for Biodiversity Conservation Planning: The Effectiveness of Surrogates. *Annual Review of Ecology, Evolution, and Systematics*. 38(1):713–737.

Salas, F., Marcos, C., Neto, J.M., Patrício, J., Pérez-Ruzafa, A. & Marques, J.C. 2006. User-friendly guide for using benthic ecological indicators in coastal and marine quality assessment. *Ocean & Coastal Management*. 49(5–6):308–331.

Schaffers, A.P., Raemakers, I.P., Sýkora, K. V & Ter Braak, C.J.F. 2008. Arthropod assemblages are best predicted by plant species composition. *Ecology*. 89(3):782–794.

Schleuter, D., Daufresne, M., Massol, F. & Argillier, C. 2010. A user’s guide to functional diversity indices. *Ecological monographs*. 80(3):469–484.

Schneider, D.C. 1994. *Quantitative ecology: spatial and temporal scaling*. Elsevier.

Shephard, S., van Hal, R., de Boois, I., Birchenough, S.N.R., Foden, J., O’Connor, J., Geelhoed, S.C.V., Van Hoey, G., et al. 2015. Making progress towards integration of existing sampling activities to establish Joint Monitoring Programmes in support of the MSFD. *Marine Policy*. 59(2015):105–111.

Shiaparelli, S., Rowden, A. and Clark, M. 2016. *Deep Sea Fauna. Biological Sampling in the Deep Sea*. Eds. Clark, M. R., Consalvey, M. and Rowden A. 782-794.

Shojaei, M. G., Gutow, L., Dannheim, J., Pehlke, H., & Brey, T. (2015). Functional diversity and traits assembly patterns of benthic macrofaunal communities in the southern North Sea. In Towards an Interdisciplinary Approach in Earth System Science (pp. 183-195). Springer International Publishing.

Silberberger, M.J., Renaud, P.E., Buhl-Mortensen, L., Ellingsen, I.H. & Reiss, H. 2019. Spatial patterns in sub-Arctic benthos: multiscale analysis reveals structural differences between community components. *Ecological Monographs*. 89(1):1–24.

Simpson, G.L., 2009. cocorresp: co-correspondence analysis ordination methods. R package version 0.1-9.

Sink, K., Holness, S., Harris, L., Majiedt, P., Atkinson, L., Robinson, T., Kirkman, S., Hutchings, L., et al. 2012. National Biodiversity Assessment 2011: Technical Report. Volume 4: Marine and Coastal Component. Pretoria: South African National Biodiversity Institute.

Volume. 4:325.

Sink, K., Harris, L., Skowno, A., Livingstone, T., Franken, M., Porter, S., Atkinson, L., Bernard, A., et al. 2019. *Chapter 3: Marine Ecosystem Classification and Mapping*.

Smith, L., 1995. Sieve mesh-size and taxonomic resolution needed to describe natural spatial variation of marine macrofauna. *Marine Ecology Progress Series,* 118:187-198.

Speakman, J.R. 2005. Body size, energy metabolism and lifespan. *Journal of Experimental Biology*. 208(9):1717–1730.

Stachowicz, J.J., Bruno, J.F. & Duffy, J.E. 2007. Understanding the effects of marine biodiversity on communities and ecosystems. *Annu. Rev. Ecol. Evol. Syst.* 38:739–766.

Steffani, N., Sedick, S., Rogers, J. & Gibbons, M.J. 2015. Infaunal benthic communities from the inner shelf off southwestern Africa are characterised by generalist species. *PLoS ONE*. 10(11):1–20.

Strong, J.A., Clements, A., Lillis, H., Galparsoro, I., Bildstein, T. & Pesch, R. 2019. A review of the influence of marine habitat classification schemes on mapping studies: Inherent assumptions, influence on end products, and suggestions for future developments. *ICES Journal of Marine Science*. 76(1):10–22.

Teske, P.R., Papadopoulos, I., Zardi, G.I., McQuaid, C.D., Edkins, M.T., Griffiths, C.L. & Barker, N.P. 2007. Implications of life history for genetic structure and migration rates of southern African coastal invertebrates: planktonic, abbreviated and direct development. *Marine Biology*. 152(3):697–711.

Thomaz, S.M., Bini, L.M. & Bozelli, R.L. 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia*. 579(1):1–13.

Tiano, J.C., van der Reijden, K.J., O'Flynn, S., Beauchard, O., van der Ree, S., van der Wees, J., Ysebaert, T. & Soetaert, K. 2020. Experimental bottom trawling finds resilience in large-bodied infauna but vulnerability for epifauna and juveniles in the Frisian Front. *Marine Environmental Research*. 159(March):104964.

Tillin, H.M., Hiddink, J.G., Jennings, S. & Kaiser, M.J. 2006. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Marine Ecology Progress Series*. 318:31–45.

Trannum, H.C., Borgersen, G., Oug, E., Glette, T., Brooks, L. & Ramirez-Llodra, E. 2019. Epifaunal and infaunal responses to submarine mine tailings in a Norwegian fjord. *Marine Pollution Bulletin*. 149(0349):110560.

Tribot, A.S., Mouquet, N., Villéger, S., Raymond, M., Hoff, F., Boissery, P., Holon, F. & Deter, J. 2016. Taxonomic and functional diversity increase the aesthetic value of coralligenous reefs. *Scientific Reports*. 6(August):1–12.

Tyler, P.A. 1988. Seasonality in the deep sea. *Oceanogr Mar Biol Annu Rev*. 26:227–258.

Tyler, E.H.M., Somerfield, P.J., Berghe, E. Vanden, Bremner, J., Jackson, E., Langmead, O., Palomares, M.L.D. & Webb, T.J. 2012. Extensive gaps and biases in our knowledge of a well-known fauna: Implications for integrating biological traits into macroecology. *Global Ecology and Biogeography*. 21(9):922–934.

Underwood, A.J. & Chapman, M.G. 2013. Design and analysis in benthic surveys in environmental sampling. *Methods for the study of Marine Benthos*. 4:1–45.

Villéger, S., Mason, N.W.H. & Mouillot, D. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*. 89(8):2290–2301.

Warwick, R.M. 1993. Environmental impact studies on marine communities: pragmatical considerations. *Australian Journal of Ecology*. 18(1):63–80.

Warwick, R.M. & Clarke, K.R. 1984. Species size distributions in marine benthic communities. *Oecologia*. 61(1):32–41.

Warwick, R.M., Dashfield, S.L. & Somerfield, P.J. 2006. The integral structure of a benthic infaunal assemblage. *Journal of Experimental Marine Biology and Ecology*. 330(1):12–18.

Webb, T.J., Tyler, E.H.M. & Somerfield, P.J. 2009. Life history mediates large-scale population ecology in marine benthic taxa. *Marine Ecology Progress Series*. 396:293–306.

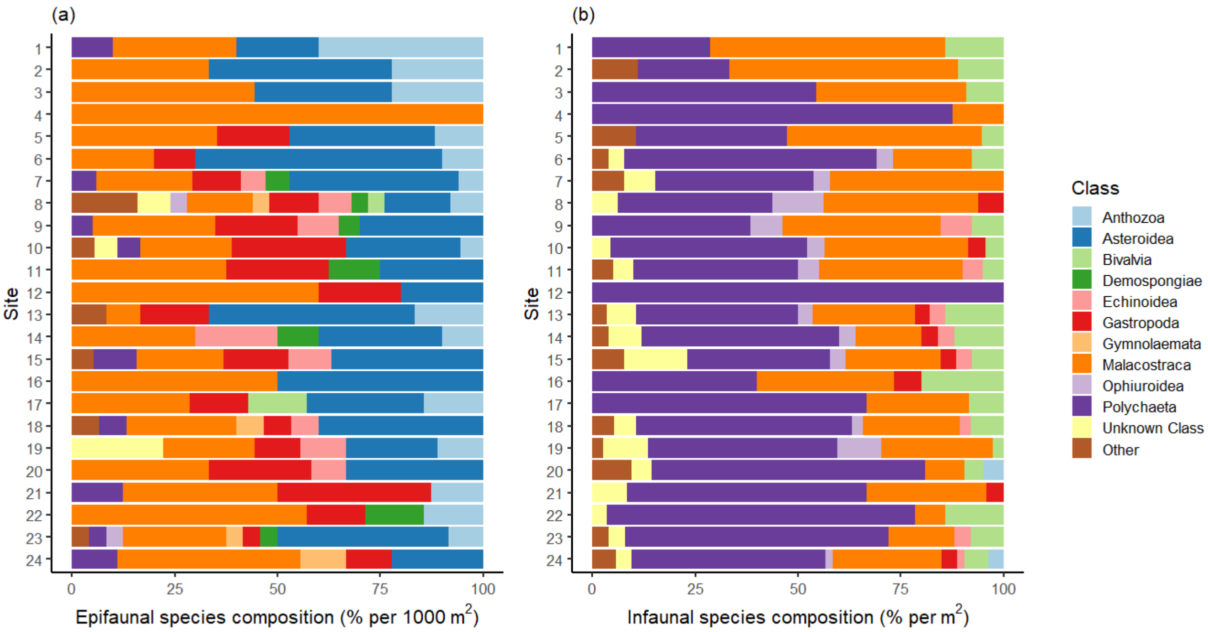
Wong, M.C. & Dowd, M. 2015. Patterns in Taxonomic and Functional Diversity of Macrobenthic Invertebrates Across Seagrass Habitats: a Case Study in Atlantic Canada. *Estuaries and Coasts*. 38(6):2323–2336.

WoRMS Editorial Board (2022). World Register of Marine Species. Available from https://www.marinespecies.org at VLIZ. Accessed 2022-02-14.

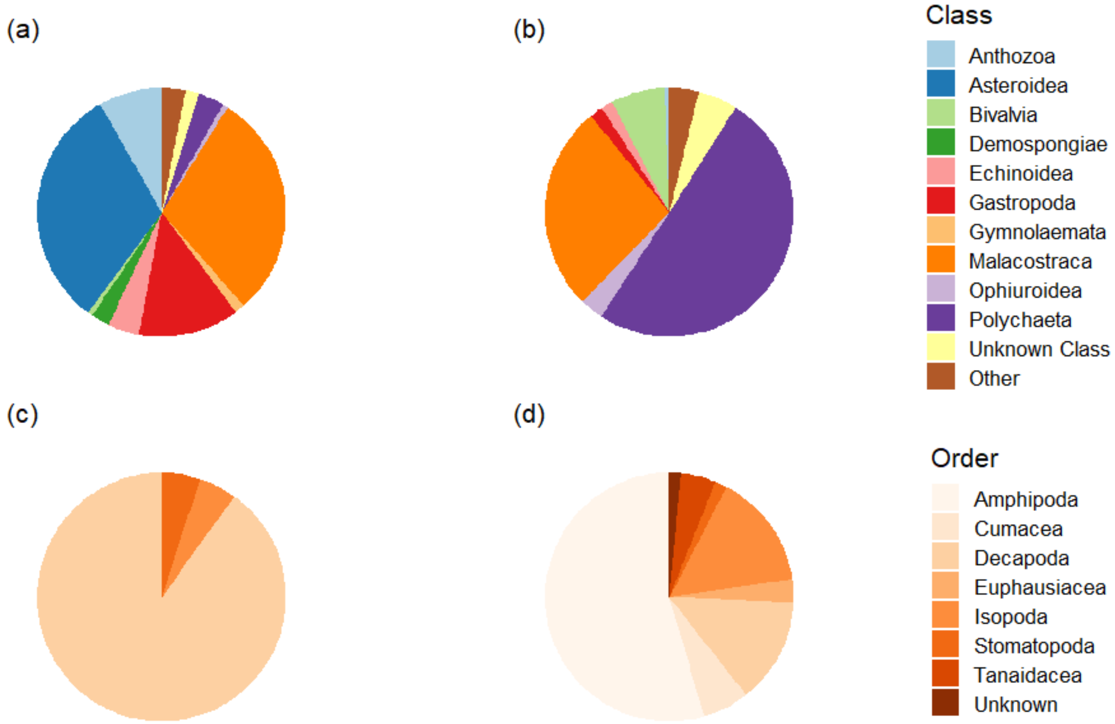
Zaklan, S.D. & Ydenberg, R. 1997. The body size–burial depth relationship in the infaunal clam Mya arenaria. *Journal of Experimental Marine Biology and Ecology*. 215(1):1–17.

Zhang, Y.J., Duo, L., Pang, Y.Z., Felde, V.A., Birks, H.H. & Birks, H.J.B. 2018. Modern pollen assemblages and their relationships to vegetation and climate in the Lhasa Valley, Tibetan Plateau, China. *Quaternary International*. 467:210–221.

Appendices



Appendix A: Species presence-based proportions of invertebrate taxa Classes sampled by two gear types: trawl (a) and grab (b) from 24 offshore sites on the west coast of South Africa.



Appendix B: Species presence-based proportions of invertebrate taxa Classes (a; b) and Malacostraca Orders (c; d) sampled by two gear types: trawl (a; c) and grab (b; d) pooled from 24 offshore sites on the west coast of South Africa.

Appendix C: The main resources frequently utilised to compile biological trait information for the Biological Traits Analysis (BTA) conducted in Chapter 3 of this thesis.

Web databases	**Books and publications**
Arctic Traits Database – a repository of Arctic benthic invertebrate traits (2019)	Atkinson and Sink (2018)
BIOTIC - Biological Traits Information Catalogue (2006)	Day (1967)
The Encyclopedia of Life v2: Providing Global Access to Knowledge About Life on Earth (2014)	Marine Macrofauna Genus Trait Handbook (2008)
Polytraits: A database on biological traits of marine polychaetes (2014)	North Sea Benthic Macrofauna Biological Traits (2015)
World Register of Marine Species (2022)	