

**ZOOPLANKTON ABUNDANCE, BIOVOLUME AND
COMPOSITION IN THE UTHUKELA PELAGIC ZONE,
KWAZULU-NATAL (KZN)**

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As the candidate's Supervisor and Co-supervisor, I (We) agree to the submission of this thesis.

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Declaration

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Acronyms:

African Coelacanth Ecosystem Programme (ACEP)
Average abundance (Av. Abund.)
Average similarity (Av. Sim.)
Critical Biodiversity Areas (CBAs)
Convention on Biological Diversity (CBD)
Conductivity, temperature, and depth instrument (CTD)
Cumulative percentage (Cum.%)
Dissolved oxygen (DO)
Distance-based linear model (DistLM)
Distance-based redundancy analysis (dbRDA)
Exclusive Economic Zones (EEZs)
Cluster Analysis (CLUSTER)
KwaZulu-Natal (KZN)
Marine Protected Areas (MPAs)
Marine Spatial Planning (MSP)
Meroplankton richness (S)
National Biodiversity Assessment (NBA)
National Protected Areas Expansion Strategy (NPAES)
Non-metric multidimensional scaling (nMDS)
Percentage contribution (%Contr.)
Pielou's evenness index (J')
Shannon diversity index (H')
Similarity percentages (SIMPER)
Similarity Profile (SIMPROF)

Abstract

The uThukela Banks is one of the three new (2019) Marine Protected Areas (MPAs) in KwaZulu-Natal (KZN) established through Operation Phakisa; a national initiative which set out to achieve 5% protection of South Africa's waters by 2018 through a representative MPA network. As part of the African Coelacanth Ecosystem Programme (ACEP) Spatial Solutions project, this study aimed to provide baseline data on zooplankton communities in the uThukela Banks pelagic zone and to assess zooplankton community structure in waters overlying reef and sand substrates as well as within and outside of the MPA. Due to their rapid turnover rates, zooplankton are essential in marine food webs and can be used as bioindicators in the pelagic region. Zooplankton samples were collected in 2016 at 18 sites in the KZN Bight area, including the uThukela Banks MPA. Zooplankton community structure was compared between locations (inside/outside the MPA) and underlying substrate types (reef/sand). The samples were analysed in terms of overall zooplankton abundance and composition as well as a more detailed analysis of meroplankton community structure. Zooplankton abundance was significantly higher over sand substrate than over reef substrate, potentially because reef substrates support a higher abundance of zooplanktivorous fish. Higher abundance was also found over sand substrates located outside the MPA, possibly because sand substrate dominated the stations outside the MPA. These sites were also usually located downstream of the Agulhas Current, suggesting the southward transportation of zooplankton. Copepoda contributed over 65% of the total zooplankton abundance inside and outside the MPA, with Appendicularia contributing 14% inside and 6% outside the MPA. Chaetognatha, Hydrozoa, and Decapoda were also among the dominant groups. Fifty-one meroplankton taxa were recorded, with Caridea being the most abundant across all stations. Inside the MPA, Portunidae, Alpheidae, and Paguridae followed in abundance, while Callianassidae dominated sand stations outside the MPA, contributing over 20% to total abundance. pH was the only environmental factor that significantly influenced both zooplankton and meroplankton abundance. Although not included in this study, currents also play an essential role due to the drifting nature of zooplankton. This study provides baseline data on the zooplankton communities in the uThukela Banks pelagic zone, contributing to systematic conservation planning for the KZN coastal waters.

CHAPTER 1: Introduction

1.1 Background and context of the study

The ocean covers 71% of the earth's surface and provides significant marine resources contributing to economic development, food security, human well-being, and employment security (Costanza et al., 1997, 2014; Turpie et al., 2003). Costanza et al. (1997) valued marine ecosystem services at US\$21 trillion globally, an estimated 70% more than land-based ecosystems provide. A recent ecosystem service assessment indicated that marine ecosystems are worth approximately US\$50 trillion (Costanza et al., 2014). There has, however, been a decrease in their overall estimated economic value due to the substantial loss of coral reef area (Costanza et al., 2014). Despite their immense value, marine ecosystems face increasing anthropogenic threats. Globally, key pressures include overfishing, habitat destruction, pollution, climate change, and invasive species, all contributing to declining biodiversity and ecosystem function (Baum & Myers, 2004; Lewison et al., 2004; Game et al., 2009).

In South Africa, economic activities in the marine environment include 22 fisheries sectors, petroleum extraction, diamond mining, ecotourism, and shipping (Findlay, 2018). However, these environments are also under growing pressure due to the extraction or consumption of natural resources (Driver et al., 2012; Harris et al., 2012). The National Biodiversity Assessment (NBA) Coastal and Marine Component has identified over-exploitation of resources, by-catch, incidental seabird mortalities, climate change, and habitat damage as major threats to marine biodiversity (Driver et al., 2012; Sink et al., 2012; Harris et al., 2012). Furthermore, anthropogenic activities such as coastal development and pollution are central pressures affecting marine ecosystems (Sink et al., 2012). To address these threats, South Africa, alongside global efforts, has increasingly turned to special management tools such as Marine Protected Areas (MPAs) (Harris et al., 2012). Marine Protected Areas are one of the primary techniques for efficiently managing the biodiversity and ecosystems of the world's oceans (Attwood et al., 1997; Robert et al., 2017). MPAs can help protect marine habitats, species, communities, and ecological systems and processes (Attwood et al., 1997). MPAs can also help to restore marine and coastal habitat productivity, minimise degradation, and buffer climate change (Roberts et al., 2017). In some cases, MPAs can also contribute to the

socioeconomic welfare of coastal communities (Badalamenti et al., 2000; Mann-Lang et al., 2021).

The uThukela Banks MPA within the KwaZulu-Natal (KZN) Bight was one of 20 MPAs declared in 2019 in South Africa (DEA, 2019). It was established to safeguard various habitats and the associated diverse wildlife and ecological processes. The habitats include offshore areas like soft sediment and reefs, undersea canyons, shelf edge ecosystems, and slope ecosystems, open water, and coastal regions like sandy beaches, rocky shores, and estuaries (RSA, 2016). The MPA protects ecologically essential features such as habitat connectivity, spawning grounds, and nursery functions. Freshwater and sediment input from the uThukela River contributes to nutrient availability, which boosts primary production, supports diverse and heterogeneous nearshore habitats, and maintains critical biogeochemical cycles (Scharler et al., 2016a; Green et al., 2022). Furthermore, the MPA aims to play a critical role in aiding fisheries recovery and increasing species abundance in adjacent areas, particularly for line fish and sharks. It actively contributes to managing marine and coastal species by protecting spawning grounds and other gatherings of marine fish species (Harris et al., 2012; RSA, 2016).

Given these objectives, the effectiveness of the MPA must be monitored over time to ensure that conservation goals are met and to improve adaptive management measures (Day et al., 2012). However, meaningful monitoring is only possible if there is an initial understanding of the ecosystem processes present prior to protection (Kareiva et al., 2014). This makes baseline studies critical. Zooplankton are ideal indicators communities due to their sensitivity to environmental changes and importance in the marine food webs (Richardson, 2008; Pretorius et al., 2016). The diversity and abundance of zooplankton can serve as indicators of the overall health and stability of marine ecosystems (Jakhar, 2013), as fluctuations in their populations can reveal shifts in environmental conditions or disturbances. Zooplankton is a crucial component of marine ecosystems, substantially impacting the food chain and ecosystem health (Pandya, 2022). This study aims to add to the existing knowledge in this ecological environment by investigating zooplankton abundance, biovolume, and composition. Furthermore, this study takes a forward-looking approach by collecting essential baseline data on zooplankton within the uThukela MPA prior to its formal protection, thereby establishing a robust baseline for evaluating future changes, trends, and potential impacts. Such data are crucial for detecting ecological change following MPA implementation and evaluating whether conservation goals are being met (Samhoury et al., 2011; Sink et al., 2019).

1.2 Marine Protected Areas (MPAs)

Establishing MPAs is one of the most effective approaches to ocean conservation (Hyrenbach et al., 2000). MPAs are crucial in conserving marine biodiversity, supporting social and economic well-being, and restoring degraded marine ecosystems (Erm et al., 2023). MPAs allow for the recovery of negatively impacted habitats and fish stocks (Sink et al., 2011b). However, it is important to acknowledge that the establishment and successful management can be financially and operationally challenging (Friedman et al., 2015). The effectiveness of MPAs relies on proper planning, management, enforcement, and monitoring (Erm et al., 2023). Fully protected MPAs, known as ‘no-take’ MPAs prohibit all fishing activities, providing the highest biodiversity protection. In contrast, partially protected areas allow for certain regulated activities, such as fishing, under specific restrictions. These areas balance conservation goals with sustainable use, helping to preserve biodiversity while still providing social and economic benefits to local communities (Blampied et al., 2022; Phillips et al., 2023). Although MPAs can yield positive biological outcomes, their effectiveness is highly context-dependant and influenced by factors such as species mobility, MPA size, enforcement, and surrounding management. the detection of their effect also requires robust monitoring framework, as highlighted by Kerr et al. (2019)

South Africa has exclusive rights and control over the waters and resources within its EEZ (covering 1.54 million km²), including fishing, resource exploration, and environmental protection, as outlined by the United Nations Convention on the Law of the Sea (Hannesson, 2013; Potgieter, 2018). Due to the poor protection level of offshore ecosystems, there has been a growing demand to expand MPAs in the South African EEZ (Attwood et al., 1997; Lombard et al., 2004; Driver et al., 2012). It has been recognised that South Africa’s ocean environment requires a more diverse network of MPAs and additional strategies to safeguard its essential ecosystem services and critical ecological infrastructure (Sink et al., 2011b). The National Department of Environmental Affairs and the South African National Biodiversity Institute (SANBI) developed a National Protected Areas Expansion Strategy (NPAES) for South Africa to address the Convention on Biological Diversity (CBD) targets and the shortcomings highlighted in the NBA (Lombard et al., 2004). This strategy aimed to expand the protected

area network cost-effectively, ensuring ecological sustainability and adaptation to climate change (DEA, 2010).

Prior to the 1994, an ad hoc and opportunistic approach was applied to implement and declare new MPAs (Kirkman et al., 2023). However, this approach was biased towards certain habitats and species (Cowling et al., 1999). There may have been a lack of comprehensive planning and understanding of the unique features of coastal areas when they were initially established, leading to a management approach not fully suited to their specific needs (Hockey and Buxton, 1991). This highlights the importance of considering the distinct characteristics of marine and coastal environments when managing and conserving these areas. Several challenges confronted MPA governance during the ad hoc period (between 1964 and 1994), including legislative deficiencies, policy inconsistencies, lack of central coordination, and an emphasis on preservation without regard for sustainable uses (Attwood et al., 1997; Glavovic, 2006; Kirkman et al., 2023). These shortcomings may have affected the effective administration and achievement of MPA goals.

Marine Spatial Planning (MSP) was developed in response to several issues and needs associated with the long-term management of marine and coastal environments (Lagabriele et al., 2018). The MSP approach was suggested to achieve the most adequately developed representative network of MPAs (Cowling et al., 1999). The MSP approach maps the biodiversity features in the environment of concern and its current uses. It then identifies the most efficient or optimal solutions for meeting biodiversity targets while trying, where possible, to avoid highly utilised areas (Balmford, 2002; Cowling et al., 2003). MSP enables the identification of priority conservation areas at various levels, from small to large and from coastal to offshore, while considering the distribution of biodiversity elements and human activities (Lagabriele et al., 2018). This strategy offers a more efficient spatial solution for achieving conservation goals within MPAs. MSP supports processes for integrated ocean governance while allocating marine and coastal resources sustainably and efficiently through space and time (Douvere, 2008; Lagabriele et al., 2018) to achieve socio-economic and ecological objectives. MSP provides a clear framework for assessing the spatial distribution of biological patterns and physical processes that sustain marine biodiversity (Douvere, 2008; Agardy et al., 2011). Integrating different ecological and social system scales has been identified as the major issue in developing MSP (Moilanen and Arponen, 2011). Hence, cross-scale dimensions have been recommended to account for the multi-scale nature of conservation

problems while considering diverse priorities at multiple spatial scales (Cumming et al., 2006; Guerrero et al., 2013).

To address the shortcomings of cross scaling, Ezemvelo KZN Wildlife, the conservation authority for South Africa's KZN Province, developed the SeaPLAN marine conservation planning project (Harris et al., 2012). This included 640 km of the KZN coastline and its provincial waters, incorporating marine habitats (coastal, estuarine, benthic, and pelagic), from the shoreline out to the offshore limits of the EEZ. In this KZN plan, the assessment of the protection status of 417 mapped features and processes (based on the biodiversity target) was set to ensure the viability, persistence, and current level of spatial protection from pressures shown by these features. Critical Biodiversity Areas (CBAs) and important areas for conservation efforts were identified (Harris et al., 2012). The focus areas (Figure 1) for biodiversity protection included Childs Bank, Cape Canyon, Protea Seamount, Browns Bank, Agulhas Bank, Southwest Indian Seamount, offshore Port Elizabeth, Protea Banks, iSimangaliso Wetland Park, and uThukela Banks (Sink et al., 2011b). Sink and Atwood (2008) also identified the uThukela Banks as one of the CBAs containing essential habitats such as rocky reefs and soft sediments. This emphasises the significance of effective conservation measures in the area to protect essential marine ecosystems. The uThukela Banks plays an important role in supporting marine biodiversity, fisheries, economies, and climate regulation. Protecting this marine ecosystem is not only an environmental imperative but also an economic, social, and cultural necessity for South Africa and the global community (Mann-Lang et al., 2021). Sustainable management and conservation efforts are essential to ensure its continued health and the well-being of those who rely on it (NBA, 2018). Results from the spatial planning process can be used to guide the placement of new MPAs or other types of marine resource management strategies (Harris et al., 2012; Lagabrielle et al., 2018).

To mitigate biodiversity loss, the Convention on Biological Diversity (CBD) has consistently pressed countries with coasts to increase the number and size of MPAs to encompass a minimum of 10% of the world's Exclusive Economic Zones (EEZs) by 2020 (CBD, 2010). Aichi objective 11 was designed to primarily focus on enhancing MPA coverage to combat biodiversity loss (CBD, 2010). This is part of a significant global effort to decrease biodiversity loss and improve marine ecosystem protection (Thomas et al., 2014; Roberts et al., 2017). In 2014, South Africa implemented Operation Phakisa to fast-track the process of unlocking the blue economic potential of South Africa's oceans and coast (Sink, 2014). In 2018, the cabinet

announced 20 additional MPAs representing South Africa's rich coastal and oceanic biodiversity, increasing the protection of South Africa's EEZ from 0.4% to 5% in alignment with global conservation targets such as United Nations CBDs 10% by 2020 and the World Perks Congress recommendation of 30% by 2030 (Sink et al., 2019; Hughes, 2023).

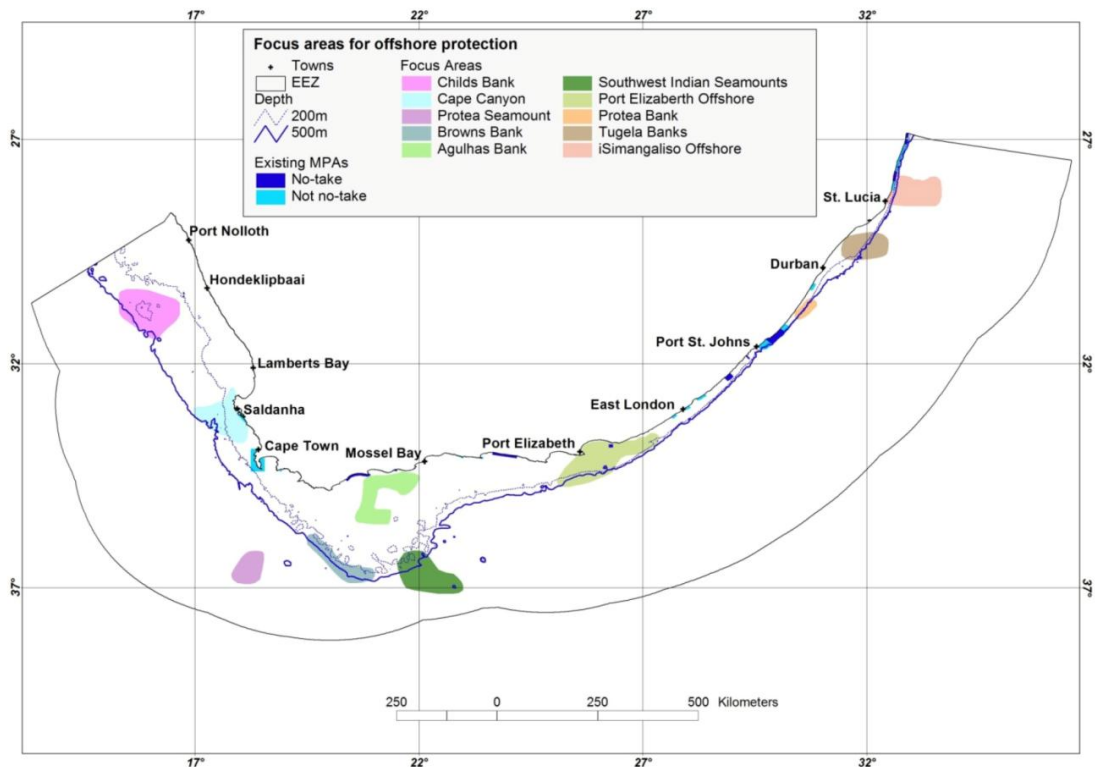


Figure 1. The ten key regions for safeguarding offshore biodiversity through MPAs or other forms of spatial management (Sink et al., 2011b).

1.3 The pelagic zone

The pelagic ecosystem is characterised by the physical, chemical, and biological properties of the open ocean's marine water column (Game et al., 2009), constituting the largest and most ecologically important biological realm on earth (Gubbay, 2006). This ecosystem also provides critical habitats for species, plays an essential role in global climate regulation, and supports sustainable fisheries (Hyrenbach et al., 2000; Game et al., 2009; Wedding et al., 2013). The pelagic environment comprises two main groups of marine life: floating organisms (plankton) and active-swimming organisms (nekton). The pelagic zone is highly dynamic, with physical (temperature, salinity) and biological (productivity) factors fluctuating across different spatial

and temporal scales (Gubbay, 2006). In order to adjust to these changes, animals migrate to take advantage of favourable conditions in various regions, migrate to locations with an abundance of prey, and drift with ocean currents as larvae or juveniles (Gubbay, 2006).

Although pressures on marine ecosystems have been well documented, the pelagic environment, the most significant marine realm in supporting biodiversity and sustaining marine food webs, faces distinct vulnerabilities. Human-induced impacts such as overfishing, pollution, climate change, eutrophication, mining, and species introductions have led to the decline of many species (Baum and Myers, 2004; Lewison et al., 2004; Crawford et al., 2007; Game et al., 2009). Species abundance and diversity face further pressure as a result of bycatch or incidental catch (Gubbay, 2006). Individually or collectively, these pressures degrade ecosystem functioning, modify habitats, and reduce habitat availability and species diversity, which then degrade ecosystem services (Gubbay, 2006). This decline calls for more protection for biodiversity and ecosystems.

In contrast to other environments, such as coastal and benthic areas, pelagic regions are globally underrepresented in the network of MPAs (Krüger et al., 2017). The uThukela Banks has been recognised as a critical area of focus in two separate systematic biodiversity plans: one at the national level aimed at pinpointing offshore protection areas (Sink et al., 2012) and another at a more detailed provincial level specifically for the province of KZN (Harris et al., 2012).

1.4 Oceanography of the KZN coastline

The KZN province is on the South African east coast, covering 640 km of the coastline and 233, 747 km² of the EEZ waters (Lagabrielle et al., 2018). The northern KZN seafloor has a distinctly narrow continental shelf and a steep slope, incised by canyons running down to the abyssal plain (Lagabrielle et al., 2018). Due to the steepness of the slope, the Agulhas Current follows a stable trajectory parallel to the coast; the shelf widens from Richards Bay to the south of Durban (close to the KZN Bight), which creates disturbances in the current, leading to localised topographically-induced upwelling (Figure 2) in some places. The Agulhas Current

flows southwards on the east coast of KZN and forms the western boundary current of the Indian Ocean Gyre (Lutjeharms, 2006; Lamont et al., 2016; Roberts et al., 2016). The Agulhas Current contributes significantly to the distribution of species and southwards larval distribution in the KZN region by transporting warm, salty tropical waters southwards along the KZN coastline (Lutjeharms and Ansorge, 2001). Rocky reefs on the continental shelf are a characteristic feature of the province, and the northern part of KZN has an increased distribution of coral reefs (Schleyer et al., 2008; Lagabriele et al., 2018).

The KZN Bight occurs between Richards Bay and Durban, bordering the oligotrophic Agulhas Current, but is considered one of the most productive areas of the Subtropical South African east coast (Pretorius et al., 2016; Roberts et al., 2016; Scharler et al., 2016b). It stretches from about 400 meters south of the uSeteni Estuary to about 4 km north of the uMlalazi Estuary, including a portion of the uThukela Estuary. The KZN Bight exhibits tropical and subtropical characteristics due to processes moving the Agulhas Current into the shelf (Schumann and van Heerden, 1988; Lutjeharms, 2006). Fluvial input of organic matter is dominant in the KZN Bight due to the outflow of the uThukela River (Bosman et al., 2007). The results of studies by Lutjeharms (2006) and Scharler et al. (2016a) suggest that riverine input has a significant role in the biology of the uThukela Banks and the KZN Bight. Turpie and Lamberth (2010) discovered that during the periods of lower freshwater flow from the uThukela River, prawn-trawl catches declined by up to 11%, demonstrating that nutrients play an important role in driving changes in secondary production in this region and influence fisheries yields. The turbid, nutrient-rich conditions contribute significantly to crustaceans' life-history phases (breeding, nursery, and feeding), demersal species, migratory fish, turtles, and sharks (Sink et al., 2011b). A large commercial prawn fishery operated in the uThukela Banks in the past, and the area serves as a nursery area for many species (Sink et al., 2011b; Scharler et al., 2016b).

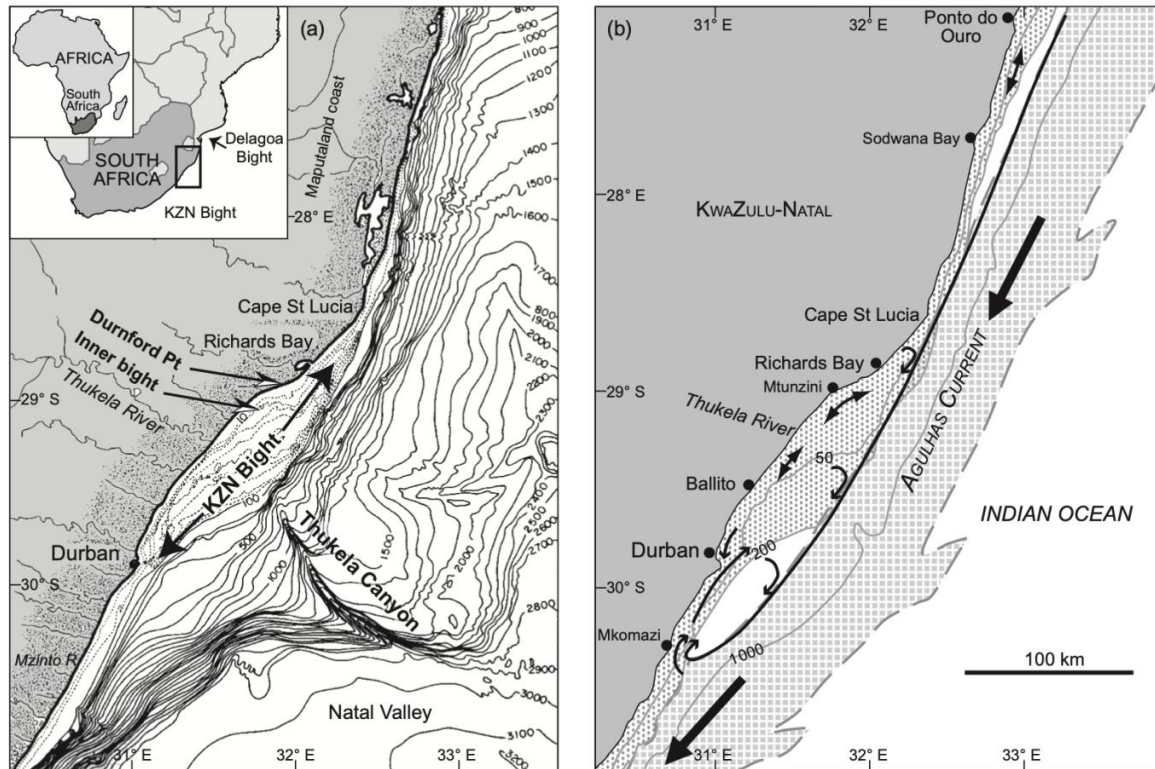


Figure 2. (a) Bathymetry map (in meters) of the KwaZulu-Natal (KZN) coast in South Africa (adapted from Martin and Flemming 1988). The raised terrace on the slope off Durban, located between 300 m and 500 m, plays a significant role in the creation of the cyclonic, semi-permanent Durban Eddy. (b) Schematic from Schumann (1987) that highlights significant circulation within the KZN Bight as visualised by Robert et al. (2016).

1.5 Zooplankton

Zooplankton play a significant role in the food webs of marine ecosystems, as they constitute a large part of the diet of mid-trophic level fishes (Gibbons and Hutchings, 1996). Furthermore, these organisms contribute significantly to benthopelagic coupling through nitrogen excretion, sinking carcasses, and exuviae to the seabed, diel vertical migration and ontogenesis (Schnack-Schiel and Isla, 2005). This functional importance emphasises the need to understand zooplankton distribution, dynamics, and biodiversity, particularly considering the various anthropogenic pressures on marine ecosystems. Marine zooplankton distribution is influenced by the physical dynamics and features of the water masses in which they reside. This is shown in the adaptation of various animal taxa to relatively narrow ranges in temperature and salinity (Sabatés et al., 1989). Based on developmental stages, zooplankton can be divided into two

main groups, holoplankton and meroplankton. Meroplankton includes larval stages of fish and invertebrates, which spend part of their life in the water column. In contrast, holoplankton spend their whole life in the water column, these include copepods and euphausiids (Richardson et al., 2019).

For the past 20 years in South Africa, zooplankton studies have been concentrated on the West and South Coasts, regions known for the presence of commercially important pelagic fish species, as highlighted by Pretorius et al. (2016). Zooplankton studies conducted on the KZN East Coast include some surveys completed in the 1960s and gelatinous zooplankton studies (Carter and Schleyer, 1988; Thibault-Botha et al., 2004; Buecher et al., 2005). Pretorius et al. (2016) assessed the copepod biomass distribution of the KZN Bight. Lastly, a study on chaetognaths along a transect from Durban to 100 km offshore was described by (Schleyer, 1985). These studies concentrate on specific taxa or locations, and while they are valuable, they provide only a limited understanding of the broader role of zooplankton in South African marine ecosystems. The African Coelacanth Ecosystem Programme (ACEP) studies that have been conducted include a survey that examined zooplankton biomass, distribution, and size composition in the KZN Bight during a wet and dry season in 2010 (Pretorius et al., 2016) and zooplankton trophic linkages using isotope methodologies (de Lecea et al., 2015). However, due to the emphasis on specific species and seasons, there is still much to learn about the year-round dynamics of zooplankton in the KZN Bight and surrounding waters. The pelagic environment is faced with multiple anthropogenic activities, therefore, a clear understanding of the existing zooplankton biodiversity is crucial for its protection (Gubbay, 2006). Furthermore, despite the growing understanding of anthropogenic constraints on the pelagic environment, there is still a need for a more comprehensive review that links these pressures to their direct impact on zooplankton diversity.

1.6 Research aims, objectives, questions and hypotheses

This study forms part of the African Coelacanth Ecosystem Programme (ACEP) Spatial Solutions project, which aims to build on the systematic approach of the conservation project formed by SeaPLAN, which identified five CBAs and proposed three new MPAs on the South African East coasts (Harris et al., 2012). The overall aim of the ACEP Spatial Solutions Project was to elucidate the biological, geological, and oceanographic features that characterise the five CBAs and the areas between them. This study examines zooplankton communities prior to the establishment of the uThukela Banks MPA. The study investigates overall zooplankton abundance, biovolume and composition (broad taxonomic groups) as well as a more detailed analysis of meroplankton abundance, diversity and taxonomic composition. The study includes a more detailed focus on meroplankton due to their important function in benthic-pelagic coupling and potential as ecosystem indicators, particularly in MPAs such as the uThukela Bank. Meroplankton, which includes the larval stages of benthic organisms, are closely linked to specific habitats and can provide valuable insights into connectivity between benthic and pelagic ecosystems. This baseline data will contribute to the monitoring of the functioning of the uThukela Banks MPAs after its establishment and validate existing CBAs and MPAs and proposed expansions of those areas.

In summary, the main objectives of the study were as follows:

- To examine the overall zooplankton abundance, biovolume and taxonomic composition inside and outside the MPA, and over different substrates (reef and sand).
- To examine meroplankton abundance, diversity and taxonomic composition inside and outside the declared MPA and over different substrates (reef and sand).
- To examine the influence of the environmental/oceanographic variables on zooplankton and meroplankton community structure.

Given that the study was conducted at uThukela Bank prior to the establishment of the MPA, it was hypothesised that there would be no significant difference in zooplankton/meroplankton abundance inside and outside the MPA, but that abundance and community structure would differ depending on location and substrate type. Furthermore, it was hypothesised that environmental factors (temperature, turbidity, chlorophyll-a, salinity, pH and dissolved oxygen) would have a structuring role on zooplankton/meroplankton communities.

CHAPTER 2: Materials and Methods

2.1 Study area

The KwaZulu-Natal (KZN) coast bridges the subtropical Natal and tropical Delagoa bioregions on the east of South Africa (Livingstone et al., 2018). It has a narrow (average of 11 km) continental shelf with a steep slope that supports a stable trajectory of the northern Agulhas Current (de Ruijter et al., 1999). The KZN Bight, which extends approximately 160 km from Cape St Lucia in the north to Durban in the south, reaches its widest point (about 50 km) near the mouth of the uThukela River (Lutjeharms, 2006; Fennessy et al., 2016). This study focuses on the uThukela Bank, the widest section of the Bight, located between Durban (29.8587°S; 31.0213°E) and Richards Bay (28.5151°S; 32.3983°E) (Figure 3). Eighteen sites were sampled, including sampled stations (SS) SS1–SS20 (excluding SS13 and SS15) (Figure 3, Table 1). The sites were selected to include different substrate types (reef and sand) as well as locations inside and outside of the MPA (Table 1). Samples were collected onboard the *Angra Pequena* from May to June of 2016.

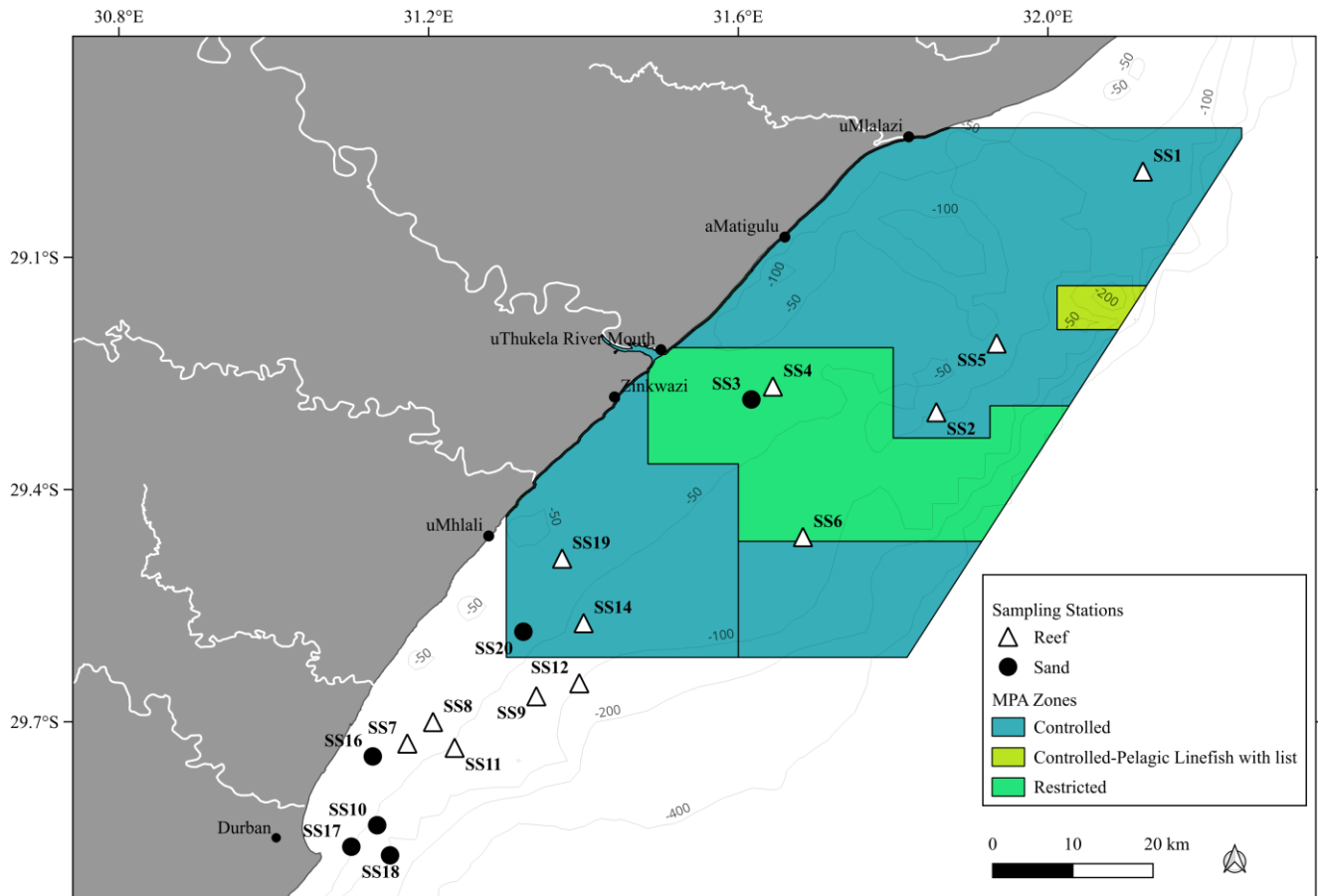


Figure 3. The study area between Durban and Richards Bay in the KZN Bight showing the Marine Protected Area (uThukela Banks) and the locations of the sampling sites.

Table 1. Distribution of sampling stations by locations (inside/ outside MPA) and underlying substrate types (reef/ sand).

Stations	Location	Underlying substrate
SS1	Inside MPA	Reef
SS2	Inside MPA	Reef
SS3	Inside MPA	Sand
SS4	Inside MPA	Reef
SS5	Inside MPA	Reef
SS6	Inside MPA	Reef
SS7	Outside MPA	Reef
SS8	Outside MPA	Reef
SS9	Outside MPA	Reef
SS10	Outside MPA	Sand
SS11	Outside MPA	Reef
SS12	Outside MPA	Reef
SS16	Outside MPA	Sand
SS17	Outside MPA	Sand
SS18	Outside MPA	Sand
SS20	Inside MPA	Sand

2.2 Physio-chemical variables

To collect environmental data, a conductivity, temperature, and depth instrument (CTD) (Seabird SBE19 plus v2) was deployed just above the seafloor and then retrieved at a speed of 1 m/s. The CTD was equipped with auxiliary sensors to measure additional parameters, including the concentration of dissolved oxygen (DO) (mg/L), pH, salinity (PSU), turbidity (NTU), fluorescence (chlorophyll-a (mg/m³), and temperature (°C). The CTD deployment was done once at each station before the plankton tows, and the measured values were averaged across the entire water column.

2.3 Zooplankton sampling

Triplicate plankton tows were carried out at each site using a plankton net (500 µm mesh, 2.5 m long, 57 cm mouth diameter) equipped with a General Oceanic Model 2030R propeller-driven flowmeter mounted at the mouth of the net. The net was deployed from the side of the boat by lowering it to the seafloor and then towed obliquely up through the water column for

approximately 10–20 minutes at a retrieval of approximately 4–8 m per minute (depending on the sampling depth) with a ship towing speed of 2.5 knots. The samples were collected between the 40 m and 80 m depth contour (Figure 3). The winch speed, number of weights, and floats determined the length of the rope and the depth of the net. The flow meter reading and time were taken before and after each tow to calculate the volume (m³) of water passing through the net. After each tow, each sample was washed from the cod-end bucket of the net into a 500 mL labelled sample jar. All the samples were preserved in 4% buffered formaldehyde in seawater aboard the ship and were transported to the laboratory for further analysis. Fish larvae were separated and removed before analysis as they were to be used for a separate study.

2.4 Zooplankton abundance, biovolume and community structure

To determine biovolume, preserved samples were poured into a graduated cylinder in the laboratory and left to settle; readings were taken after 48 h to ensure settlement (Harris et al., 2000). The biovolume (mL/m³) was then calculated by dividing the settled volume by the volume filtered (1) through the net. The following formulae (2) was used to determine the volume of water filtered and towing distance (rotor constant=26873) respectively

$$\text{Volume filtered} = \frac{3.14 \times (\text{net diameter})^2 \times \text{tow distance}}{4} \dots\dots\dots (1)$$

$$\text{Towing distance} = \frac{\text{Difference in Counts} \times 26873}{999999} \dots\dots\dots (2)$$

To determine zooplankton abundance, each sample was decanted into a beaker, the formalin carefully removed, and the sample diluted to a final volume of 5 L. The contents were thoroughly stirred with a rod to ensure a homogeneous suspension. Three subsamples were then extracted using a 20 mL vial attached to a metal rod (Perissinotto and Wooldridge, 1989; Carrasco et al., 2010) and poured into a counting tray for enumeration. Identification of major taxonomic groups (to Phylum, Class, and Order level) was conducted under a dissecting microscope at 40× magnification using relevant zooplankton guides (Boltovskoy, 1999; Conway et al., 2003). To account for variability among subsamples, these triplicates were used to estimate density per sample. Abundance was expressed as individuals per cubic meter (ind/m³), and three replicate samples per site were used in all subsequent analyses.

To determine meroplankton abundance, all meroplanktonic organisms were separated from each entire sample and stored in 20 mL vials prior to taxonomic identification and counting under a dissecting microscope using Boltovskoy, (1999) and Al-Yamani et al. (2011) guides. All individuals in each sample were counted and identified to the lowest possible taxonomic level. Abundance was again calculated by dividing the number of individuals in the sample by the volume of water filtered by the plankton net, as above.

2.5 Statistical analysis

2.5.1 Univariate Statistical Analysis

Univariate statistical analyses were conducted using IBM SPSS 25 for Windows. A one-way ANOVA was used to compare biovolume and abundance (zooplankton and meroplankton) between stations. A two-way ANOVA was performed to determine whether there were significant differences in environmental variables between substrate types (reef and sand) and locations (inside and outside the MPA). Additionally, a two-way ANOVA was applied to test for differences in biovolume, zooplankton abundance, and meroplankton abundance between substrates (sand and reef) and locations inside and outside the MPA. The normality and equality of variances for residuals were tested using the One-Sample Kolmogorov-Smirnov test and Levene's test, respectively. All the variables (zooplankton biovolume, zooplankton abundance and meroplankton abundance) that did not meet the test assumptions were log-transformed prior to parametric testing and then re-tested.

All meroplankton was identified to the Family level and data was used to calculate diversity indices. The meroplankton richness (S), Shannon diversity index (H'), and Pielou's evenness index (J') were calculated using DIVERSE on PRIMER v7 (Clark and Gorley, 2015). Richness (S) reflects the number of meroplankton families detected in this study. H' is calculated as (3), where p_i is the proportion that the i^{th} taxa contributed to the total abundance in a sample. H' represents the alpha diversity (diversity between sites) while considering abundance. J' is defined as H'/H'_{max} , where H'_{max} is the highest possible H' . J' represents how each family's individuals are dispersed evenly at the site. A two-way ANOVA was utilised to see if there was a difference in the diversity indices between locations (within and outside the MPA) and substrates (reef and sand). The assumptions of residual normality were evaluated using a One-Sample Kolmogorov-Smirnov test, and the equality of residual variance was tested using

Levene's test. The assumptions of residual normality and variance equality were met for all variables ($p > 0.05$)

$$-\sum_i p_i \log(p_i) \dots \dots \dots (3)$$

2.5.2 Multivariate analysis of zooplankton abundance and biomass.

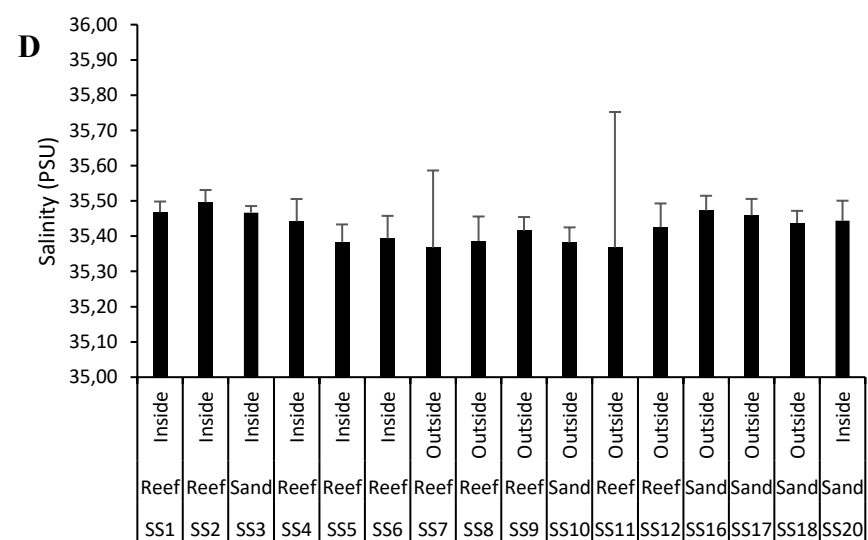
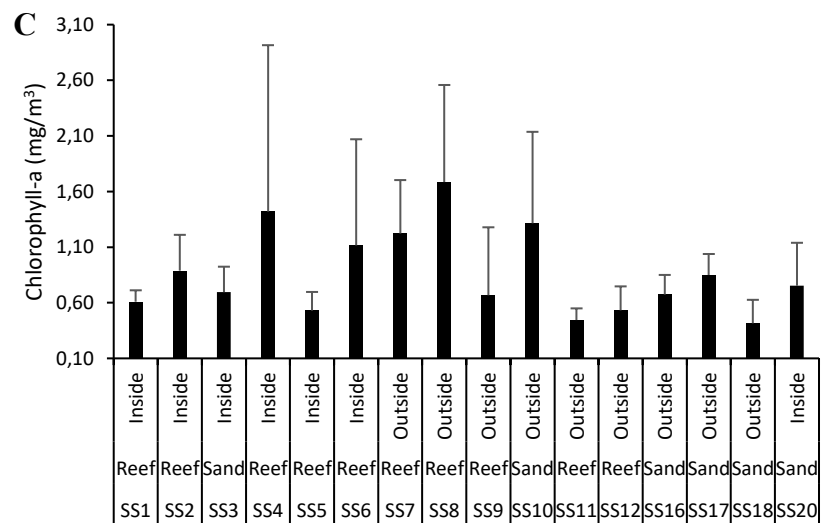
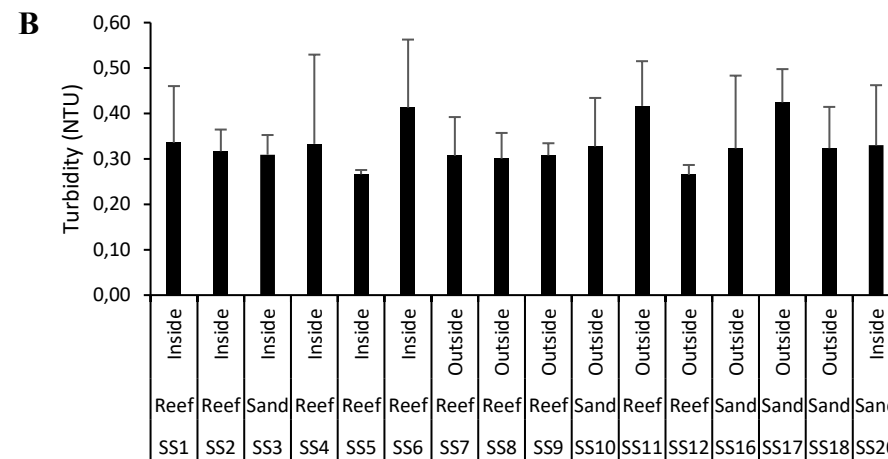
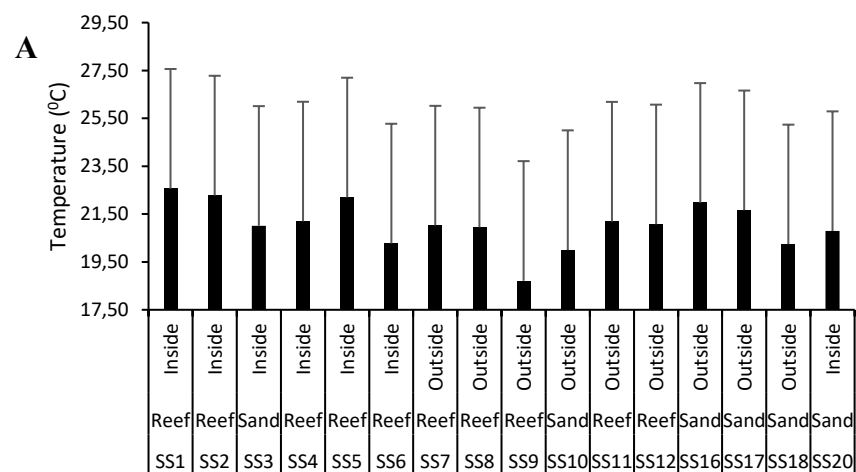
Multivariate analyses were performed using PRIMER V7 with PERMANOVA software (Anderson, 2008; Clarke and Gorley, 2015). The zooplankton and meroplankton abundance data were square-root transformed to reduce the effects of very abundant taxa and take the less common taxa into account. A similarity matrix was then constructed using the Bray-Curtis dissimilarity index to assess the similarities between samples. A PERMANOVA was run to test whether the zooplankton and meroplankton community structures differed between locations (fixed: 2 levels. "inside vs outside" and between the substrates (fixed: 2 levels. "sand vs reef"). A Hierarchical Cluster Analysis (CLUSTER) using group average linkage method was performed on the resemblance matrix to determine sample group structure in zooplankton data. Additionally, a Similarity Profile (SIMPROF) test was used to test for significant clustering patterns between the samples (Clarke and Gorley, 2015). Similarity percentages (SIMPER) analysis determined which zooplankton taxon contributed most to the location and substrate type variability.

To quantify the extent to which environmental variables explain the distribution patterns of meroplankton and zooplankton abundance, multivariate patterns were explored using the distance-based linear model (DistLM) (Anderson, 2008). Forward selection with adjusted R^2 criteria was used as the selection procedure. The distance-based redundancy analysis (dbRDA) was used as a visualisation tool to model the DistLM in a multidimensional space using vector overlays and eigen analysis of the fitted data cloud (Anderson, 2008). The length of each vector in the dbRDA figure represents the strength of its contribution to data variance, with longer vectors signifying variables with the strongest influence on the direction and grouping of sites.

CHAPTER 3: RESULTS

3.1 Environmental variables

The depth-averaged temperature ranged from $18.71^{\circ}\text{C} \pm 1.95$ at SS9 off Ballito to $22.56^{\circ}\text{C} \pm 0.70$ at SS1, which lies offshore of the uMlalazi region (Figure 4A). There was no significant difference in temperature between locations (inside/outside MPA) ($df=1$, $F=1.04$, $p=0.33$) and substrates ($df=1$, $F=0.17$, $p=0.70$ Figure 5A). Average turbidity ranged from 0.26 ± 0.02 NTU at SS12 off Ballito to 0.42 ± 0.07 NTU at SS17 near Durban Harbour (Figure 4B). There was no significant difference in turbidity location (inside/outside MPA) ($df=1$, $F=0.09$, $p=0.77$) and between reef and sand substrate ($df=1$, $F=0.09$, $p=0.77$). The chlorophyll-a concentration ranged between 0.42 ± 0.21 mg/m³ at SS18 to 1.69 ± 0.87 mg/m³ at SS8 off the Durban (Figure 4C). Chlorophyll-a had no significant difference between the substrate (reef/sand) ($df=1$, $F=0.41$, $p=0.54$) and locations (inside/ outside the MPA) ($df=1$, $F=0.038$, $p=0.85$, Figure 5C). Salinity ranged from 35.37 ± 0.22 at SS7 to 35.50 ± 0.04 at SS2 in the northern mid-shelf off the uThukela River mouth (Figure 4D). There was no significant difference in salinity between locations (inside/outside the MPA) ($df=1$, $F=2.37$, $p=0.15$) and between the substrate (reef and sand) ($df=1$, $F=0.25$, $p=0.14$, Figure 5D). The pH ranged from 8.29 ± 0.02 at SS1 to 8.54 ± 0.04 and 0.02 at SS16 and 17 located off Durban (Figure 4E). The pH also varied significantly between substrates (reef and sand) ($df=1$, $F=6.42$, $p=0.03$) but had no significant difference between locations ($df=1$, $F=2.60$, $p=0.13$) and pH was higher in stations over sand than reef substrate (Figure 5E). Dissolved oxygen (DO) ranged from 4.09 ± 0.39 mg/L to 4.68 ± 0.37 mg/L, with SS9 located northeast of Durban, closer to the shore, reflecting the lowest concentration and SS2 the highest (Figure 4F). DO did not differ significantly between the locations ($df=1$, $F=1.19$, $p=0.30$) and substrate ($df=1$, $F=0.19$, $p=0.67$, Figure 5F).



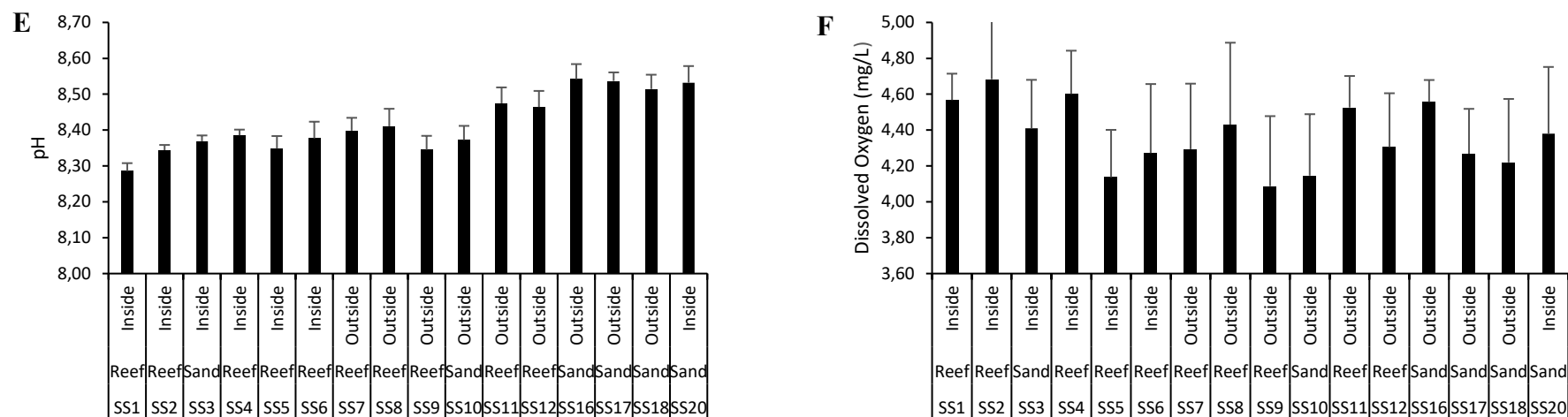


Figure 4. Environmental variables for each station in the study area. Error bars represent Standard Deviation ($\pm$ SD) of depth-integrated values.

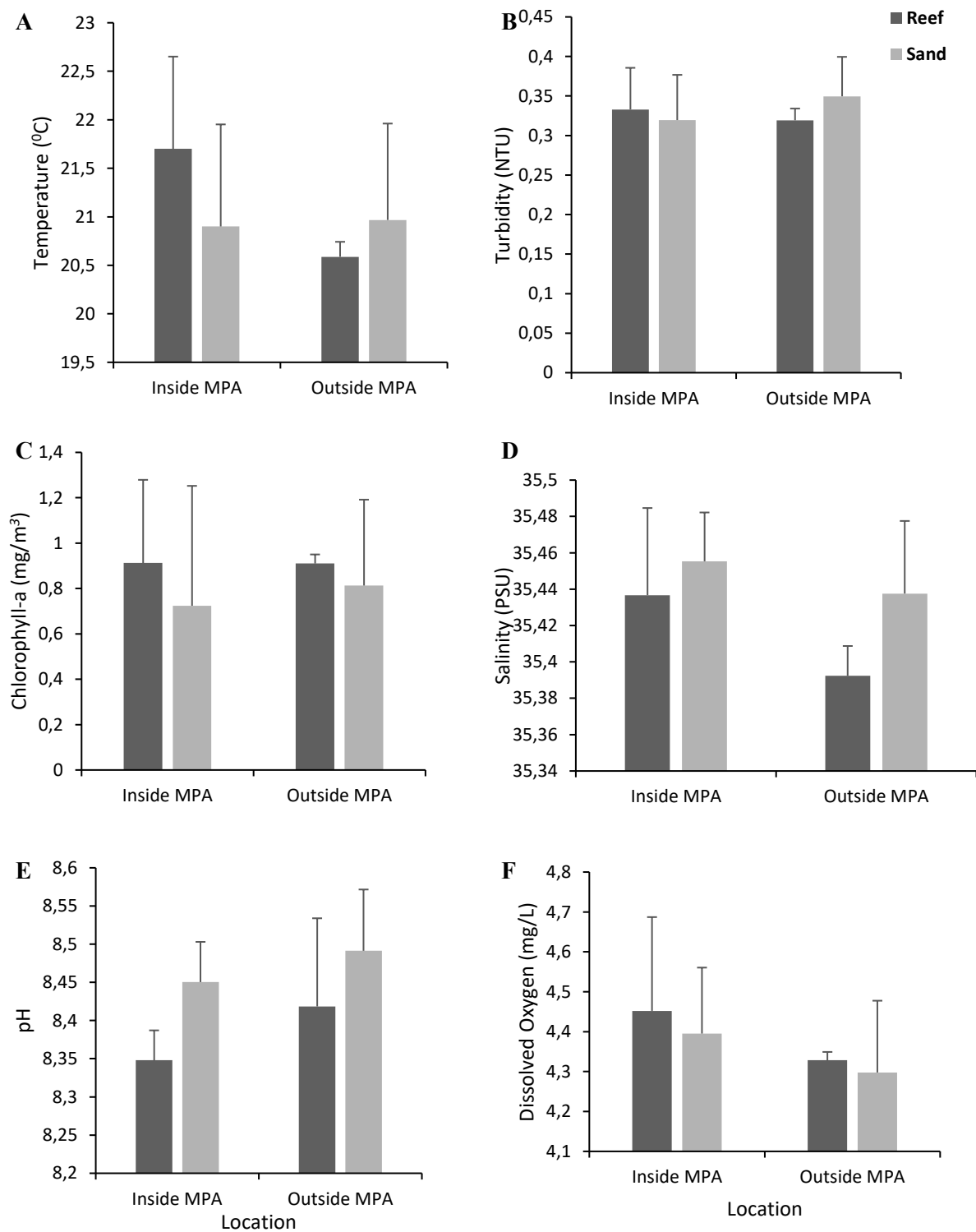


Figure 5. Environmental variables for inside and outside the MPA and between the substrate types (sand and reef). Error bars represent $\pm$ SD.

3.2 Zooplankton biovolume

There was a significant difference in zooplankton biovolume among sampled stations ($df=15$, $F=7.93$, $p<0.001$). The maximum biovolume was found at Station SS8 ($2.38 \text{ mL/m}^3 \pm 0.59$) while SS12 ($0.37 \text{ mL/m}^3 \pm 0.08$) had the lowest biovolume (Figure 6A). Biovolume was significantly different between substrate types ($df=1$, $F=17.59$, $p=0.01$) but had no significant difference between the locations ($df=1$, $F=0.37$, $p=0.54$) (Figure 6B). Higher biovolume was observed over sand substrates compared to reefs (6B).

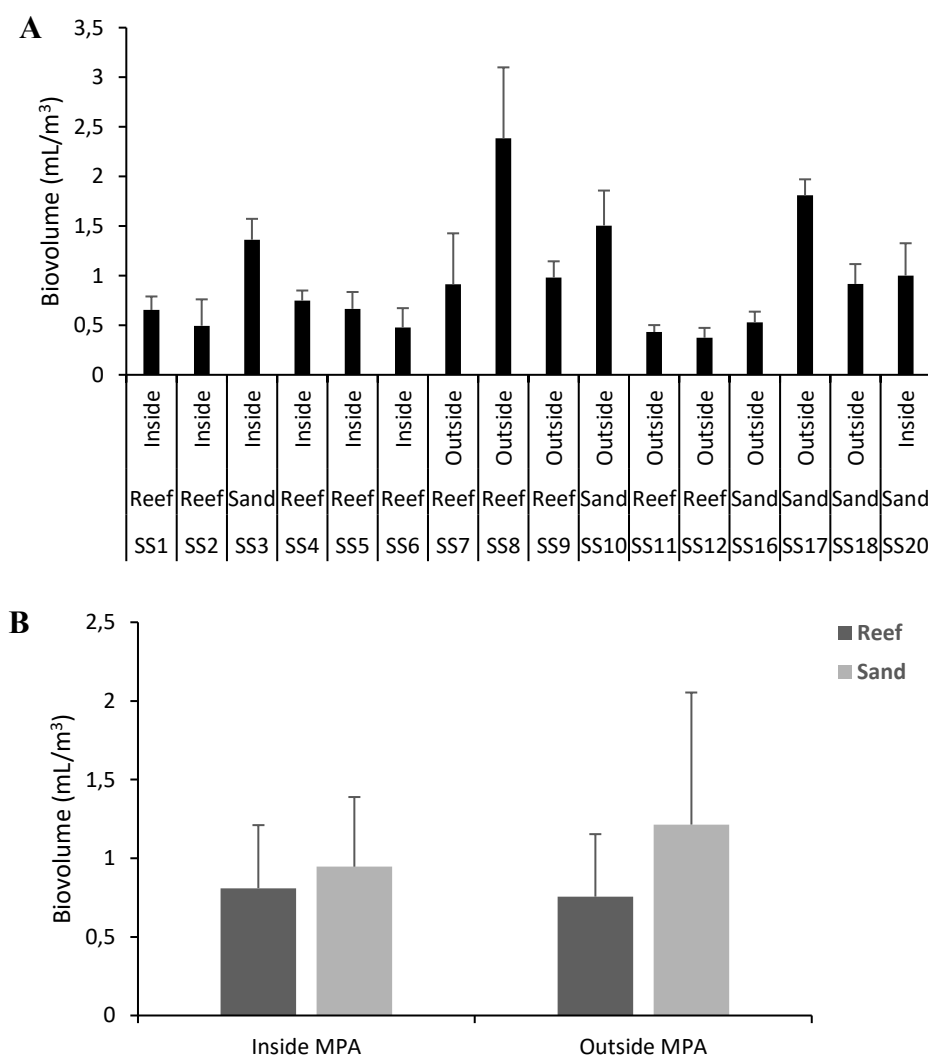


Figure 6. Zooplankton biovolume among stations (A), and (B) between locations (inside/outside the MPA) and substrates. Error bars indicate $\pm$ SD.

3.3 Zooplankton abundance

There was a significant difference in zooplankton abundance among the sampled stations ($F=7.64$, $df=15$, $p<0.001$). Station SS17 had the highest zooplankton abundance relative to all the other sampled stations (Figure 7A). Zooplankton abundance was significantly different between substrate types ($F=16.91$, $df=1$, $p<0.001$) but had no significant difference between sampled locations ($F=1.250$, $df=1$, $p=0.27$). Higher abundance was found over sand substrates (320.32 ± 248.69 ind/m³) compared to that of the reef substrates (118.83 ± 89.62 ind/m³) (Figure 7B).

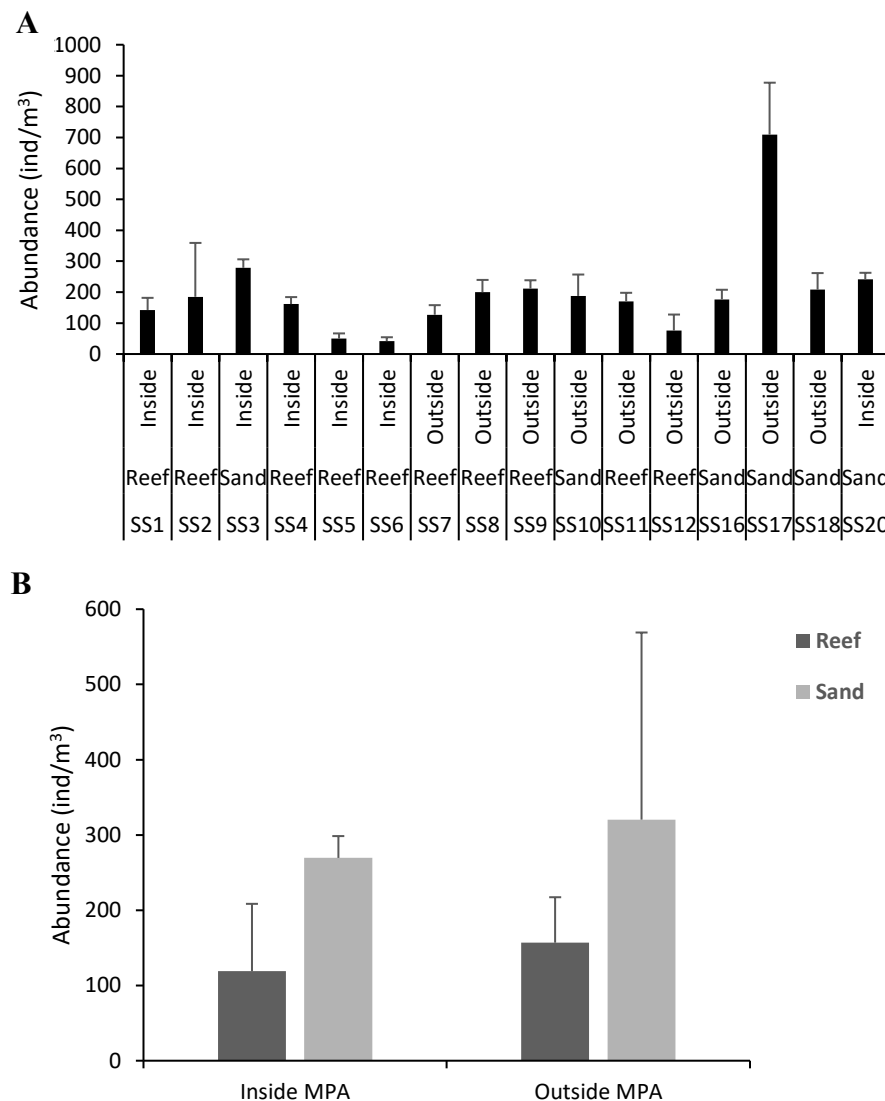


Figure 7. Zooplankton abundance among stations (A) and (B) between locations (inside/outside the MPA) and substrate. Error bars indicate $\pm$ SD.

3.4 Zooplankton composition

A total of eleven zooplankton taxa were identified across all stations (Table 2). Copepoda contributed the highest proportion, exceeding 65% within and outside the MPA. Inside the MPA, Appendicularia accounted for 14%, making it the second most abundant Class, followed by Hydrozoa and Chaetognatha at 7% and 5% respectively. In contrast, outside the MPA, Chaetognatha (6%) was the second most abundant Class, followed by Appendicularia (6%) and Decapoda (3%) (Table 2). Copepoda comprised over 70% of the zooplankton community in the sandy substrate stations, with Appendicularia contributing 5%. Conversely, Copepoda accounted for 69% of the zooplankton community in the reef substrate stations, followed by Appendicularia at 12% (Table 2).

Table 2. Summary of zooplankton abundance (ind/m³) presented as mean $\pm$ SD and percentage contribution to the total abundance (%). Inside and outside MPA and over reef and sand. Abbreviations: %Contr., Percentage contribution.

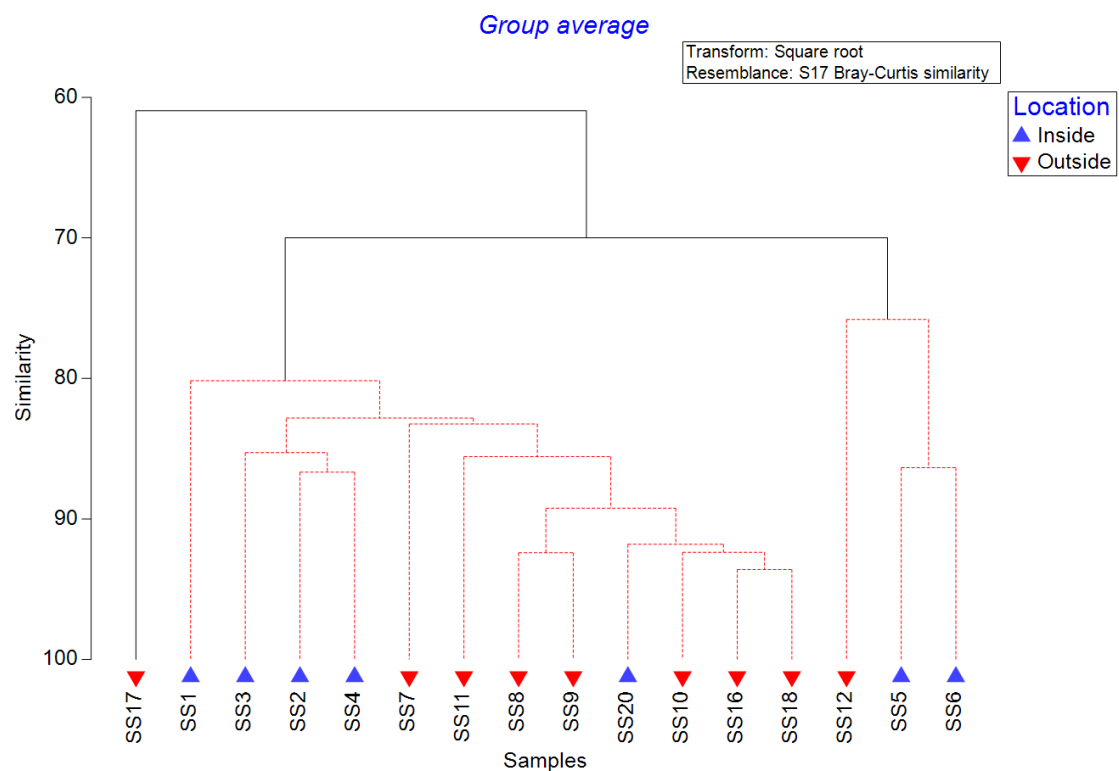
Class	Inside MPA		Outside MPA		Reef		Sand	
	Abundance $\pm$ SD	%Contr.	Abundance $\pm$ SD	%Contr.	Abundance $\pm$ SD	%Contr.	Abundance $\pm$ SD	%Contr.
Chaetognatha	5.30 $\pm$ 2.66	4.78	1.99 $\pm$ 2.76	5.54	6.52 $\pm$ 3.01	5.98	9.00 $\pm$ 3.37	4.17
Hydrozoa	10.69 $\pm$ 8.38	6.74	2.33 $\pm$ 2.70	2.95	7.05 $\pm$ 7.34	5.18	8.76 $\pm$ 4.38	3.86
Doliolida	5.56 $\pm$ 4.94	3.28	0.90 $\pm$ 1.16	0.88	3.22 $\pm$ 4.28	2.23	3.27 $\pm$ 3.47	1.41
Pteropoda	0.91 $\pm$ 0.61	0.70	0.85 $\pm$ 1.04	0.70	0.82 $\pm$ 0.49	0.67	1.60 $\pm$ 1.18	0.79
Decapoda	3.97 $\pm$ 2.24	3.16	3.54 $\pm$ 5.14	3.15	3.96 $\pm$ 1.82	3.17	9.18 $\pm$ 5.60	3.39
Amphipoda	0.79 $\pm$ 0.43	0.83	0.75 $\pm$ 0.89	0.64	1.03 $\pm$ 0.81	0.94	0.91 $\pm$ 0.61	0.43
Copepoda	110.87 $\pm$ 75.06	65.81	106.86 $\pm$ 184.08	79.95	99.54 $\pm$ 54.52	69.28	251.54 $\pm$ 208.54	80.35
Polychaeta	0.24 $\pm$ 0.24	0.23	0.13 $\pm$ 0.16	0.11	0.18 $\pm$ 0.15	0.19	0.32 $\pm$ 0.25	0.14
Appendicularia	16.29 $\pm$ 11.40	14.14	5.64 $\pm$ 7.41	5.50	13.34 $\pm$ 9.66	11.92	11.75 $\pm$ 10.26	4.96
Ostracoda	0.29 $\pm$ 0.27	0.17	0.91 $\pm$ 1.56	0.37	0.27 $\pm$ 0.21	0.19	1.47 $\pm$ 1.81	0.42
Cladocera	0.29 $\pm$ 0.41	0.15	0.44 $\pm$ 0.60	0.21	0.57 $\pm$ 0.61	0.26	0.49 $\pm$ 0.03	0.10

The PERMANOVA analysis of the zooplankton abundance data indicated a significant effect of substrate and no significant effect of location or the combination of location and substrate on community structure (Table 3). The dendrogram indicates that all the stations for both location and substrate are at least 60% similar. Three significant clusters were identified by the SIMPROF test, with reef sites SS5, 6 and 12 being similar, while station SS17 was the outlier. All other stations grouped together at 80% similarity (Figure 8).

Table 3. Full model output of PERMANOVA analyses on zooplankton abundance data based on the square-root Bray-Curtis resemblance matrix. The bold value indicates a significant difference ($p < 0.05$). Abbreviations: df, degrees of freedom; SS, sum of squares; MS, mean squares; Pseudo-F, F-ratios; and P (perm), probability level based on permutations.

Source	df	SS	MS	Pseudo-F	P(perm)
Location	1	362.88	362.88	1.39	0.23
Substrate	1	840.37	840.37	3.22	0.03
Location * Substrate	1	183.69	183.69	0.70	0.62
Total	15	4719.7			

A



B

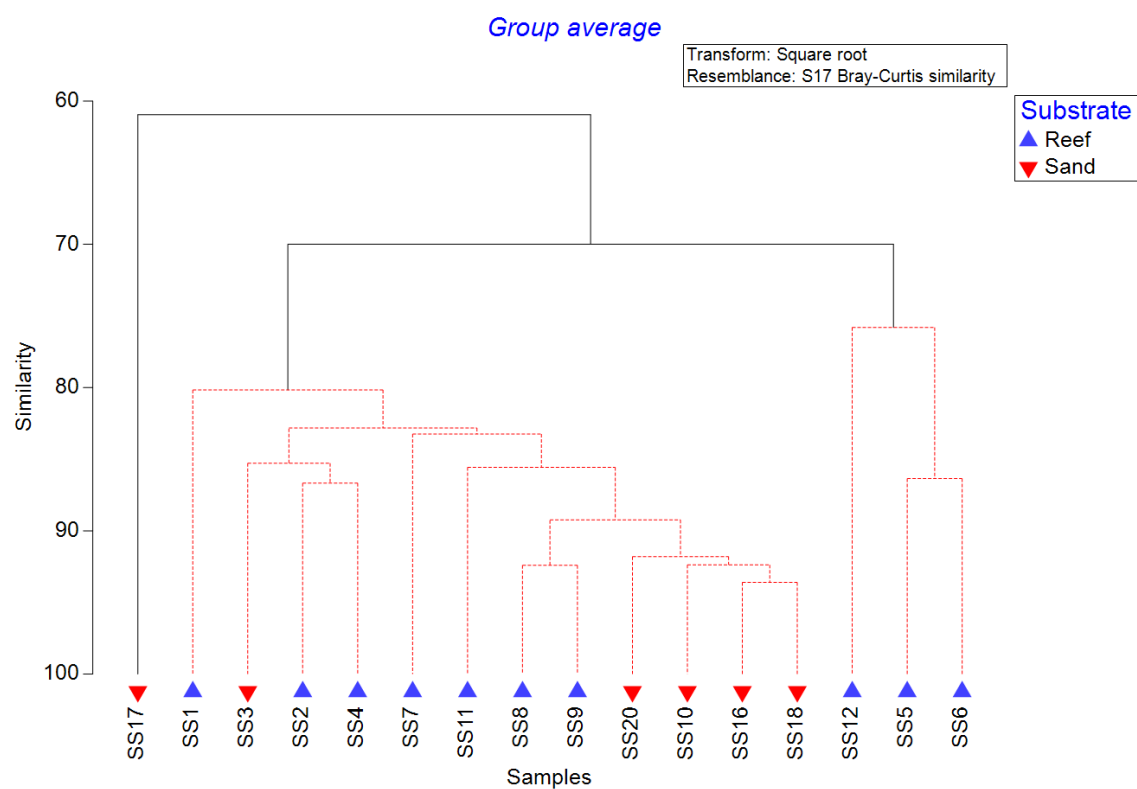


Figure 8. Dendrogram for hierarchical clustering (group-average linking) of zooplankton abundance between (A) locations (within/outside the MPA) and (B) substrate (sand/reef) based on the Bray-Curtis matrix.

The SIMPER analysis showed low dissimilarity between substrate types (reef and sand), attributed to Copepoda, Appendicularia, Decapoda, Doliolida and Hydrozoa (Table 4).

The average dissimilarity of the zooplankton between the reef and the sand was 23.99 %

(Table 4). In order of importance, the contributions to dissimilarity were as follows:

Copepods, 42.10%; Appendicularia, 10.56%; Decapoda, 8.17%; Doliolida, 7.93%; and

Hydrozoa, 7.69%. Average zooplankton abundance was greater inside the MPA than outside, except for Copepoda and Decapoda (Table 4).

Table 4. SIMPER analysis of zooplankton abundance dissimilarity between locations (within/outside the MPA). Abbreviations: Av. Abund= Average abundance; Av. Diss= Average dissimilarity; Diss/SD= Dissimilarity divided by the standard deviation; %Contr= Percentage contribution; Cum.%= Cumulative percentage (only up to $\pm 70\%$).

Groups Reef & Sand						
Average dissimilarity = 23.99						
	Group Reef	Group Sand				
Species	Av. Abund.	Av. Abund.	Av. Diss.	Diss/SD	Contr.%	Cum.%
Copepoda	9.55	15.06	10.1	1.08	42.1	42.1
Appendicularia	3.4	3.22	2.53	1.4	10.56	52.65
Decapoda	1.94	2.91	1.96	1.47	8.17	60.83
Doliolida	1.47	1.6	1.9	1.43	7.93	68.75
Hydrozoa	2.66	3.03	1.85	1.51	7.69	76.44

3.4 Effects of environmental variables on zooplankton abundance

From the DISTLM marginal test, pH was the only environmental variable affecting variability in zooplankton abundance, with a contribution of 18% (pseudo-F=3.10, $p=0.02$ respectively (Table 5). Temperature, salinity, turbidity, chlorophyll-a, and dissolved oxygen had no significant contribution, explaining little variability in the abundance of the zooplankton groups, with each contributing 3%, 15%, 12%, 3% and 8% (Table 5). The DistLM sequential test indicated that the cumulative contribution of five environmental variables to the variability in zooplankton abundance was 51%, indicating that they explained a fair amount of variation (Table 6). pH, salinity and turbidity explained the most variability when added to the model, each contributing 18, 14 and 7% of the variation (Table 6). The model was visualised on the

dbRDA plot with all environmental variables, the first axis, which captures 55.9% of the fitted variability, and the second axis, 31.2% of the total variation (Figure 9). SS17 was associated with higher pH and turbidity levels, while SS2 corresponds to higher dissolved oxygen concentration (Figure 9).

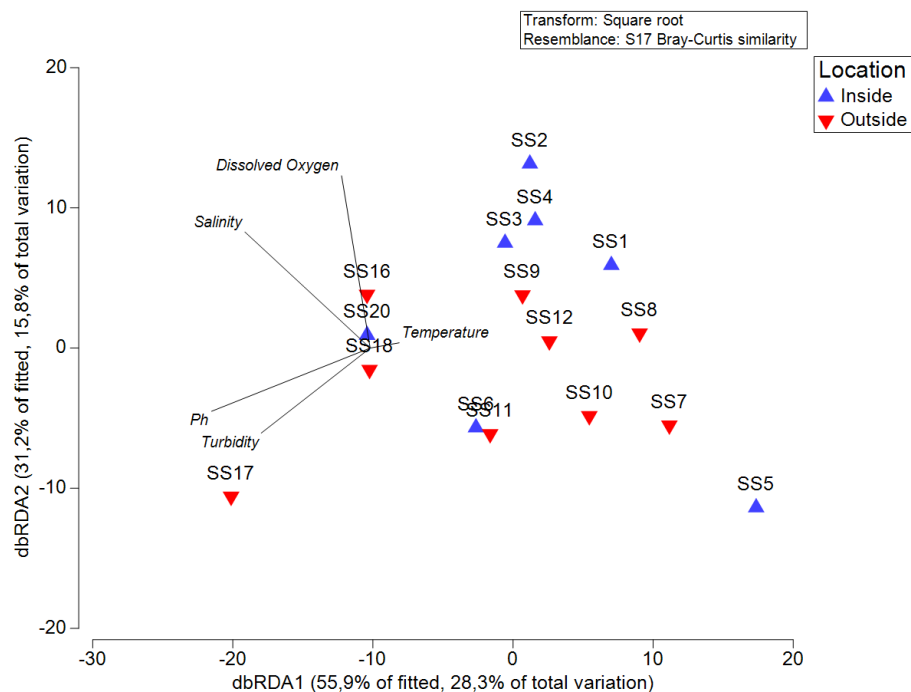
Table 5. DistLM results for the marginal test showing the relationship between zooplankton abundance and each environmental variable.

Variable	SS (trace)	Pseudo-F	P	Prop.
Temperature	132.51	0.40	0.82	0.03
Salinity	697.12	2.43	0.05	0.15
Turbidity	554.33	1.86	0.13	0.12
Chlorophyll a	140.15	0.43	0.82	0.03
pH	855.07	3.10	0.02	0.18
Dissolved oxygen	381.08	1.23	0.29	0.08

Table 6. DistLM results for the sequential test showing the relationship between zooplankton abundance and a combination of environmental variables. Forward selection with adjusted R^2 criteria was used as the selection procedure.

Variable	R^2	SS (trace)	Pseudo-F	P	Prop.	Cumul.
+pH	0.12	855.07	3.10	0.02	0.18	0.18
+Salinity	0.22	653.48	2.65	0.05	0.14	0.32
+Turbidity	0.23	316.18	1.31	0.26	0.07	0.39
+Dissolved oxygen	0.24	247.26	1.03	0.38	0.05	0.44
+Temperature	0.26	315.03	1.35	0.25	0.07	0.51

A



B

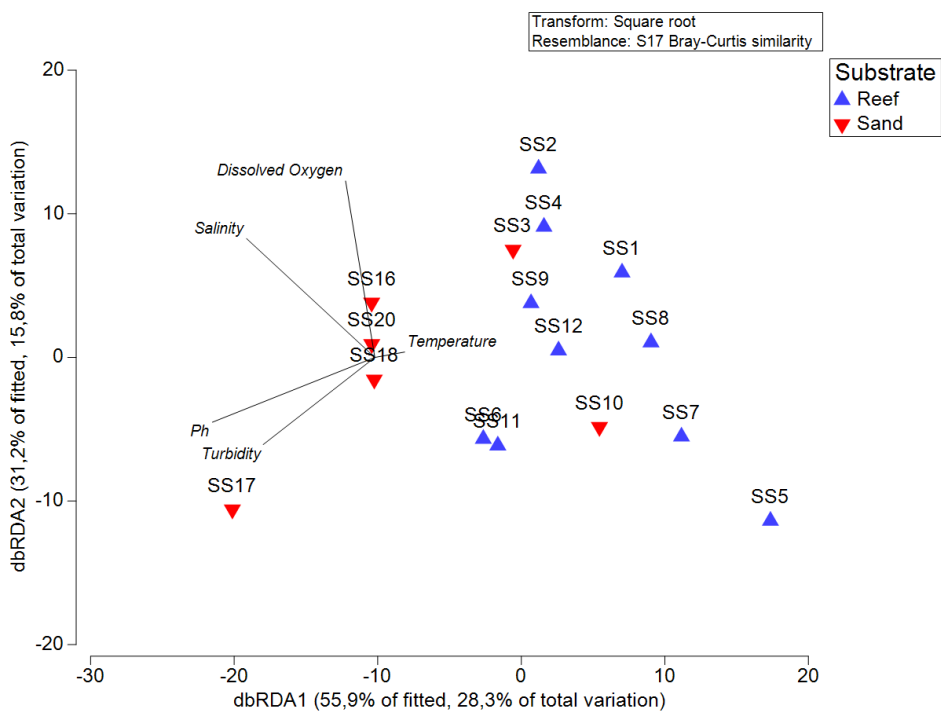


Figure 9. dbRDA plot of zooplankton group abundance overlaid with environmental variables, (A) locations (within/outside the MPA) and (B) substrate (sand/reef).

3.5 Meroplankton abundance and diversity

There was a significant difference in meroplankton abundance among the sampled stations ($df=15$, $F=15.05$, $p<0.001$). Station SS17 had higher meroplankton abundance relative to all the other sampled stations (Figure 10A). Meroplankton abundance differed significantly between substrate types ($df=1$, $F=36.53$, $p<0.001$) and sampled locations ($df=1$, $F=9.14$, $p<0.001$). Higher abundance was found over sand substrates (average: 4.95 ± 3.88 ind/m³) than over reef (average: 0.65 ± 0.27 ind/m³) and outside (1.76 ± 1.26 ind/m³) compared to inside the MPA (Figure 10B).

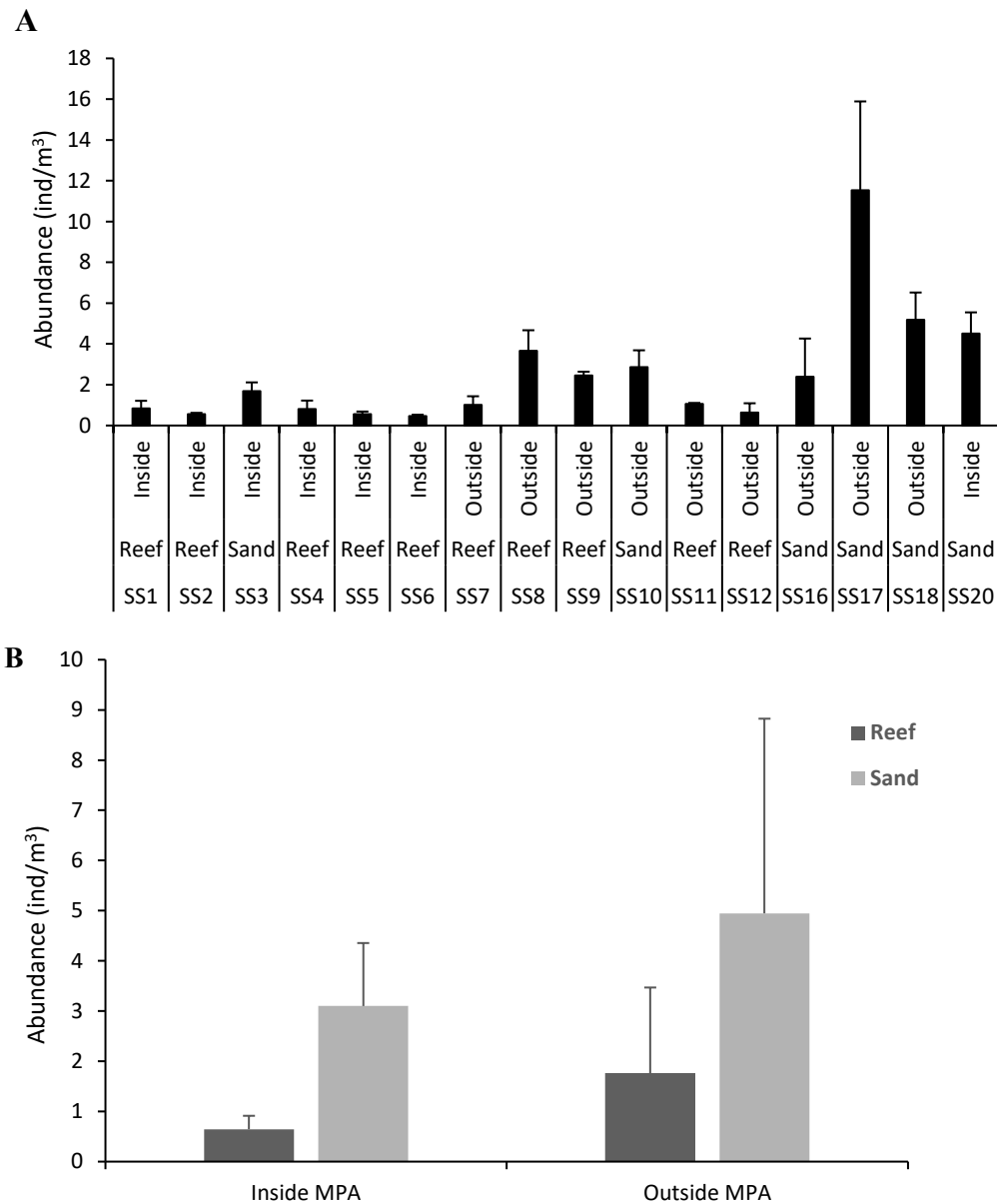


Figure 10. Meroplankton abundance among stations (A) and between locations (within/outside the MPA) and substrate (B). Error bars indicate $\pm$ SD.

There was no significant difference in the Shannon diversity index between locations ($df = 1$, $F=0.26$, $p = 0.61$) and substrate types ($df = 1$, $F =0.73$, $p = 0.40$) (Figure 11A). The meroplankton richness (S) differed significantly between substrate ($df = 1$, $F = 17.43$, $p < 0.001$) and between locations ($df = 1$, $F =10.97$, $p = 0.002$). S ranged from 29.29 ± 4.39 over sand substrate to 15.93 ± 6.50 over reef substrate, and from 29.29 ± 4.39 outside the MPA to 15.93 ± 6.50 inside the MPA (Figure 11B). The evenness (J') of meroplankton did not differ significantly between locations ($df =1$, $F =1.89$, $p =0.18$) and between substrate types ($df =1$, $F =1.34$, $p=0.25$) (Figure 11C). Margalef's richness index (d') was significantly different

between substrate types ($df = 1$, $F=5.52$, $p = 0.02$), and between locations ($df = 1$, $F=7.05$, $p=0.01$) (Figure 11D).

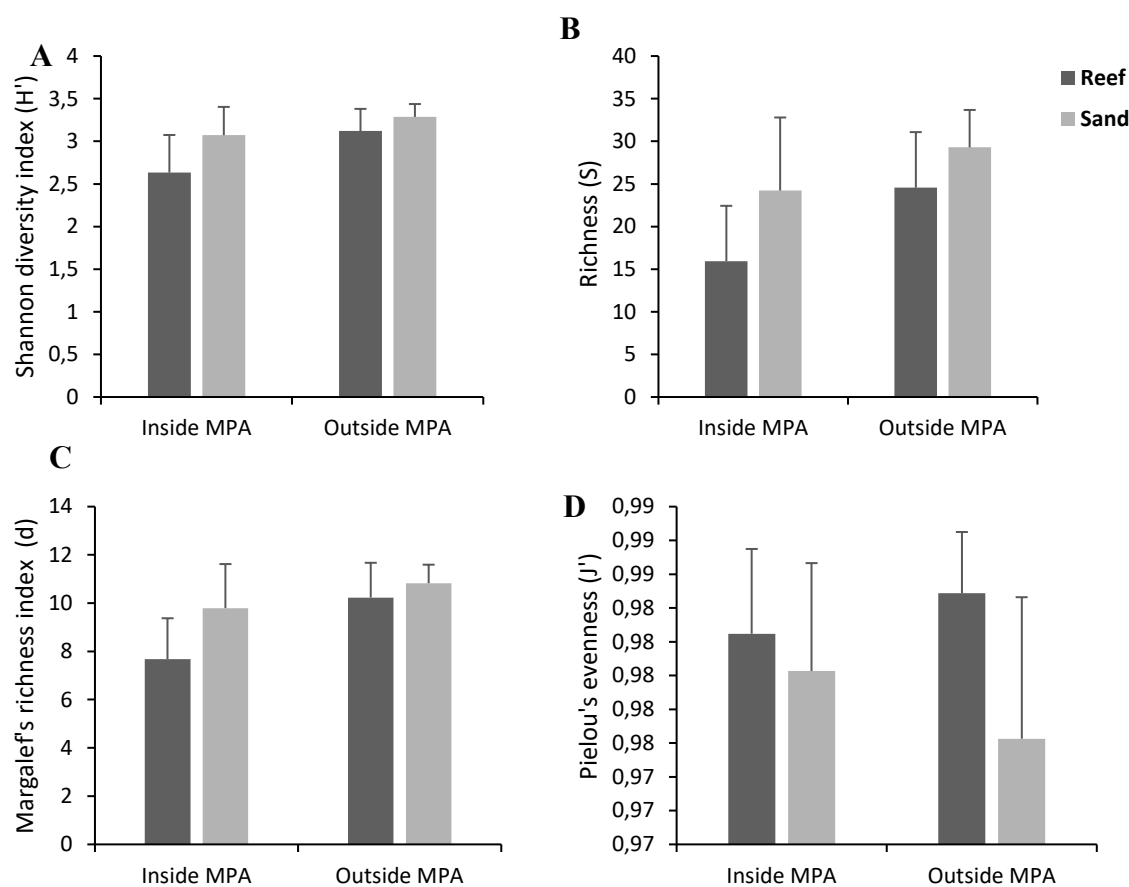


Figure 11. Average diversity indices of Meroplankton abundance. Error bars indicate $\pm$ SD.

3.6 Meroplankton composition

A total of fifty-one meroplankton taxa were recorded, with Caridea being the most abundant taxon across all stations. Inside the MPA, Portunidae contributed the second highest contribution to total abundance (14.43%), followed by Alpheidae (5.92%) and Paguridae (5.70%) (Table 7). In contrast, outside the MPA, Callianassidae was the second most abundant (16.53%), followed by Portunidae (7.43%) and Gastropoda larvae (6%) (Table 7). Portunidae (13.44%) was the second most dominant taxon after Caridea on the reef substrate, with Alpheidae (5.91%) and Gastropoda larvae (5.49%) also contributing notably. Conversely, on the sand substrate, Callianassidae contributed the highest meroplankton abundance (24.80%), followed by Caridea (22.66%), and Paguridae (6.90%) (Table 7).

Table 7. Summary of meroplankton taxa abundance (ind/m³) presented as mean $\pm$ SD and percentage contribution (%Contr.) to the total abundance (%). Only taxa that cumulatively contributed to 90% of the total abundance are listed.

Taxa	Inside MPA		Outside MPA		Reef		Sand	
	Abundance $\pm$ SD	%Contr.	Abundance $\pm$ SD	%Contr.	Abundance $\pm$ SD	%Contr.	Abundance $\pm$ SD	%Contr.
Caridea	0.37 $\pm$ 0.37	35.73	0.68 $\pm$ 0.49	29.87	0.38 $\pm$ 0.27	38.30	0.83 $\pm$ 0.59	22.66
Alpheidae	0.06 $\pm$ 0.04	5.92	0.13 $\pm$ 0.10	5.08	0.07 $\pm$ 0.09	5.91	0.14 $\pm$ 0.08	4.67
Palaemonidae	0.04 $\pm$ 0.08	2.15			0.02 $\pm$ 0.03	0.97	0.05 $\pm$ 0.08	1.95
Oplophoridae							0.05 $\pm$ 0.08	1.07
Hippolytidae			0.02 $\pm$ 0.02	1.04	0.01 $\pm$ 0.01	1.05		
Pandalidae	0.05 $\pm$ 0.09	3.77	0.10 $\pm$ 0.11	3.50	0.05 $\pm$ 0.10	2.62	0.13 $\pm$ 0.09	5.29
Paguridae	0.13 $\pm$ 0.27	5.70	0.12 $\pm$ 0.10	3.97	0.04 $\pm$ 0.05	3.42	0.26 $\pm$ 0.25	6.90
Hippidae			0.03 $\pm$ 0.01	1.04				
Callianassidae			1.29 $\pm$ 3.17	16.53			1.95 $\pm$ 3.81	24.80
Sergestidae	0.08 $\pm$ 0.21	1.97	0.10 $\pm$ 0.15	3.84	0.03 $\pm$ 0.05	1.72	0.20 $\pm$ 0.25	5.19
Penaeoidea	0.01 $\pm$ 0.01	1.34			0.01 $\pm$ 0.02	1.47		
Goneplacidae	0.03 $\pm$ 0.03	2.37			0.01 $\pm$ 0.01	1.40	0.05 $\pm$ 0.03	1.53
Leucosiidae					0.02 $\pm$ 0.01	1.58		
Portunidae	0.13 $\pm$ 0.11	14.43	0.16 $\pm$ 0.21	7.43	0.16 $\pm$ 0.20	13.44	0.13 $\pm$ 0.10	5.57
Ovalipidae	0.02 $\pm$ 0.02	3.11	0.02 $\pm$ 0.03	1.03	0.03 $\pm$ 0.03	3.02		
Dotillidae			0.03 $\pm$ 0.03	1.29	0.02 $\pm$ 0.03	1.11		
Majidae							0.08 $\pm$ 0.09	1.41
Panopeidae								
Squilloidea	0.04 $\pm$ 0.02	4.41	0.07 $\pm$ 0.06	3.68	0.06 $\pm$ 0.06	5.41	0.04 $\pm$ 0.02	1.65
Lysiosquilloidea	0.04 $\pm$ 0.07	2.06	0.08 $\pm$ 0.06	3.10	0.04 $\pm$ 0.05	2.48	0.10 $\pm$ 0.07	2.91
Gastropoda larvae	0.05 $\pm$ 0.06	4.54	0.13 $\pm$ 0.11	6.00	0.05 $\pm$ 0.03	5.49	0.18 $\pm$ 0.12	5.15
Cephalopoda	0.01 $\pm$ 0.02	1.56	0.03 $\pm$ 0.03	2.51	0.02 $\pm$ 0.03	300		

The results from the PERMANOVA analysis of meroplankton abundance indicated a significant effect of location and substrate, but no significant interaction effect between the two (Table 8). There was no clear separation of sampling sites based on location or substrate type (Figure 12A and B). However, the SIMPROF test identified four significant clusters based on location and substrate type (Figure 12A and B). Reef associated sites formed one cluster, including stations 6, 11, 12, 2, and 5, while another cluster was composed of sand substrate stations 20,16, and 18 (Figure 12B).

Table 8. Full model output of PERMANOVA analysis on meroplankton data based on the square-root Bray-Curtis **resemblance** matrix. Bold values indicate a significant difference ($p < 0.05$).

Source	df	SS	MS	Pseudo-F	P(perm)	perms
Location	1	1769.2	1769.2	2.04	0.03	994
Substrate	1	3714.7	3714.9	4.28	<0.01	992
Location Substrate*	1	951.15	951.15	1.10	0.35	994
Total	15	17764				

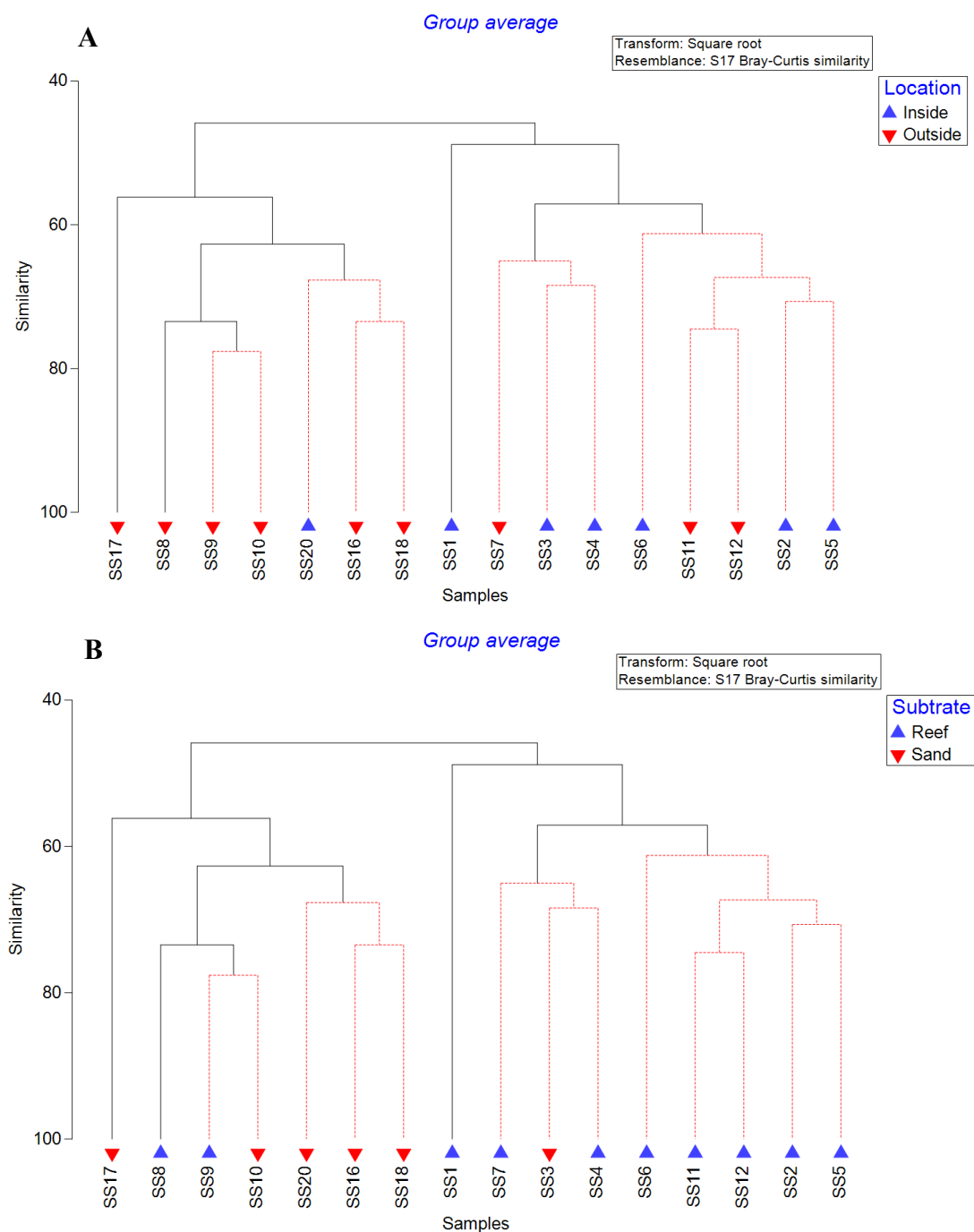


Figure 12. Dendrogram for hierarchical clustering (group-average linking) of meroplankton abundance between (A) locations (within/outside the MPA) and (B) substrate (sand/reef) based on the Bray-Curtis matrix.

From the SIMPER analysis, the average dissimilarity between substrates and their location in the MPA due to meroplankton composition was 45.12% and 48.12% (Table 9).

Meroplankton families that contributed most to the dissimilarity between the stations inside

and outside the MPA included Caridea, Callianassidae, Portunidae, Sergestidae, Pandalidae, Paguridae, and Cephalopoda (Table 9A). The differences between reef and sand stations were mainly due to Callianassidae, Caridea, Paguridae, Sergestidae, Portunidae, and Palaemonidae (Table 9B).

Table 9. SIMPER analysis of meroplankton abundance dissimilarity **a)** locations (within/outside the MPA) and **b)** substrate (reef/sand). Abbreviations: Av. Abund= Average abundance; Av. Diss= Average dissimilarity; Diss/SD= Dissimilarity divided by the standard deviation, %Contr= Percentage contribution, Cum.%= Cumulative percentage (only up to $\pm 50\%$).

A

Groups Inside & Outside						
Average dissimilarity = 45.12						
	Group Inside		Group Outside			
Species	Av. Abund	Av. Abund	Av. Diss	Diss/SD	Contr%	Cum.%
Caridea	0.56	0.79	3.02	1.96	6.69	6.69
Callianassidae	0.04	0.61	2.51	0.53	5.55	12.25
Portunidae	0.33	0.35	2.38	1.42	5.28	17.52
Sergestidae	0.12	0.27	2.24	1.65	4.95	22.48
Pandalidae	0.16	0.27	1.83	1.27	4.05	26.52
Paguridae	0.24	0.32	1.82	1.66	4.03	30.55
Lysiosquilloidea	0.14	0.25	1.72	1.62	3.82	34.37
Cephalopoda	0.08	0.16	1.57	1.14	3.47	37.84
Squilloidea	0.19	0.24	1.55	1.63	3.44	41.28
Gastropoda larvae	0.19	0.34	1.53	1.1	3.4	44.68
Alpheidae	0.22	0.33	1.52	1.23	3.37	48.05
Dotillidae	0.03	0.14	1.52	1.51	3.37	51.42

Groups Reef & Sand

Average dissimilarity = 48.12

	Group Reef	Group Sand				
Species	Av. Abund	Av. Abund	Av. Diss	Diss/SD	Contr%	Cum.%
Callianassidae	0.03	0.91	6.59	0.85	13.69	13.69
Caridea	0.58	0.86	2.61	1.26	5.43	19.11
Paguridae	0.17	0.47	2.6	1.26	5.41	24.52
Pandalidae	0.15	0.34	2.36	1.32	4.91	29.44
Sergestidae	0.11	0.36	2.18	0.93	4.54	33.97
Portunidae	0.35	0.32	1.92	1.25	3.99	37.96
Palaemonidae	0.08	0.16	1.67	1.23	3.48	41.44
Majidae	0.05	0.23	1.64	1.61	3.41	44.85
Alpheidae	0.23	0.36	1.57	1.54	3.26	48.11
Gastropoda larvae	0.21	0.39	1.56	1.55	3.24	51.35

The DistLM model marginal test exploring the influence of environmental variables on the meroplankton abundance indicated that only pH had a significant influence (Table 10). Temperature, salinity, turbidity, chlorophyll-a, and DO have no significant contribution, explaining little variability in the abundance of zooplankton in the group ($p > 0.05$; Table 10). A DistLM sequential test exploring the combination of environmental variables affecting meroplankton abundance indicated that the combination of pH, temperature, salinity, and chlorophyll-a contributed the most to the variation of meroplankton abundance, with pH and temperature contributing significant variation (Table 11). The DistLM model was visualised on the dbRDA plot with all environmental variables. The first axis captured 57.4% of the fitted variability and 24.4 % of the total variation (Figure 13A and B). Salinity and pH separated SS16, 17, 18, and 20 from most stations, but other environmental conditions did not strongly contribute to structuring the meroplankton community based on the substrate (Figure 13B).

Table 10. DistLM results (marginal test) for the relationship between the meroplankton abundance and environmental variables. Abbreviations: Prop., proportion.

Variable	SS (trace)	Pseudo-F	P	Prop.
Temperature	2386.8	2.17	0.05	0.13
Salinity	1295.1	1.10	0.32	0.073
Turbidity	777.37	0.64	0.72	0.04
Chlorophyll a	1321.8	1.13	0.31	0.07
pH	3541.1	3.49	0.01	0.20
Dissolved Oxygen	1363.2	1.16	0.29	0.08

Table 11. DistLM results (sequential test) showing the relationship between meroplankton abundance and a combination of environmental variables. Forward selection with adjusted R^2 criteria was used as the selection procedure.

Variable	Adj R^2	SS (trace)	Pseudo-F	P	Prop.	Cumul.
+pH	0.14	3541.1	3.49	0.01	0.20	0.20
+Temperature	0.23	2303.8	2.51	0.02	0.13	0.33
+Salinity	0.24	1082.7	1.20	0.28	0.06	0.39
+Chlorophyll-a	0.26	1133.1	1.29	0.24	0.06	0.45

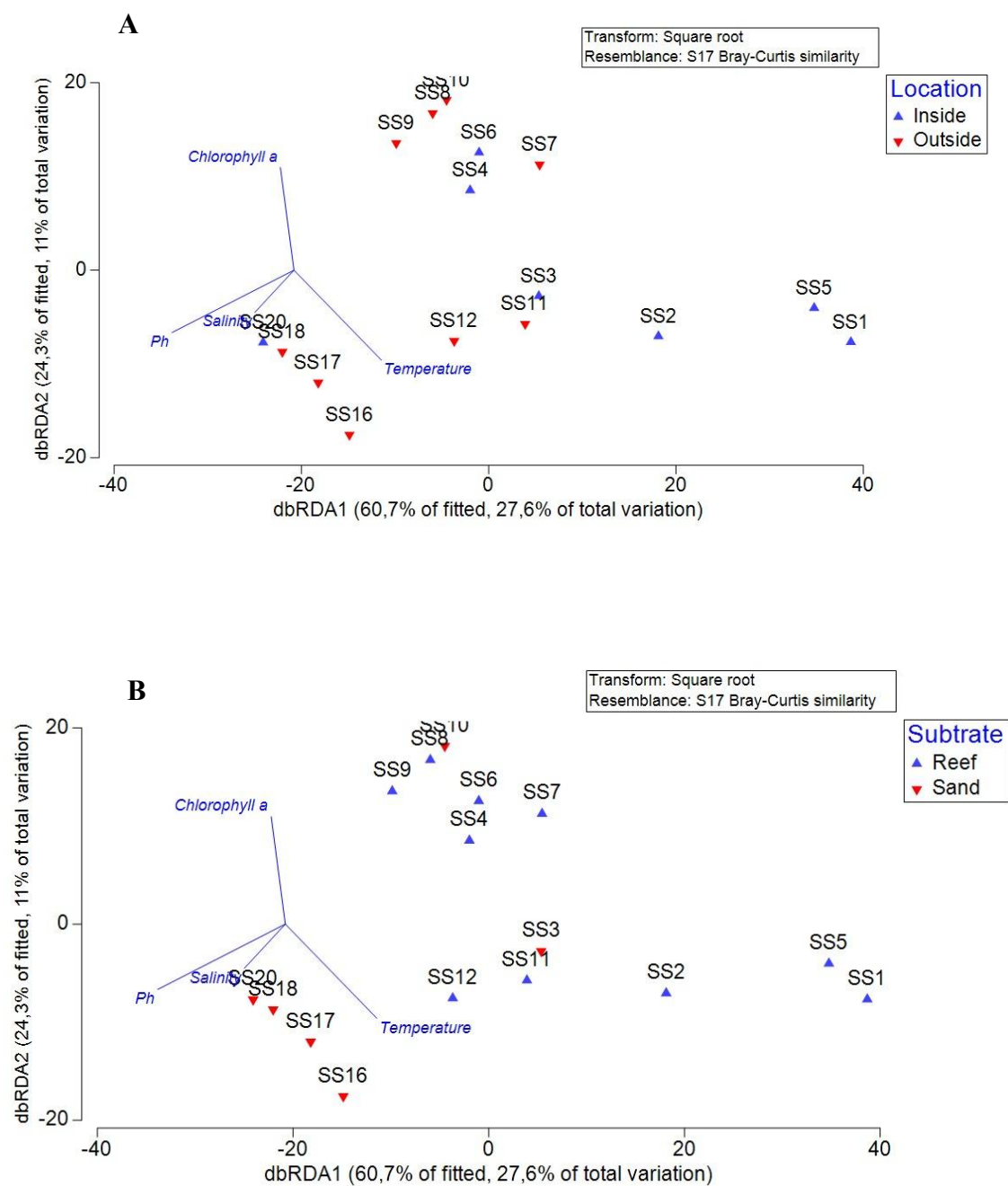


Figure 13. dbRDA plot of zooplankton group abundance overlaid with environmental variables, (A) locations (within/outside the MPA) and (B) substrate (sand/ reef).

CHAPTER 4: Discussion

This study aimed to examine the zooplankton biovolume, abundance, and composition (broad taxonomic groups) as well as a more detailed analysis of meroplankton abundance, diversity and taxonomic composition inside and outside the recently declared uThukela Banks MPA and over different substrates from samples collected prior to the establishment of the MPA. The study found that environmental factors, substrate types, and locality influence zooplankton communities.

4.1 Environmental conditions in the uThukela Banks

Overall, environmental variables were relatively consistent across sites, with minimal spatial variation. Temperature, turbidity, chlorophyll-a, salinity, and dissolved oxygen showed no significant difference between location (inside/ outside MPA) or between reef and sand substrates. However, pH was significantly higher over sand substrates compared to reefs. Reef substrates are normally associated with higher biological productivity, including respiration and microbial decomposition processes that elevate localised CO₂ concentration, thereby reducing pH (Anthony et al., 2011; Duarte et al., 2013). On the contrary, sandy substrates may support lower biological activity and permit greater water exchange, leading to more efficient CO₂ diffusion and consequently higher pH values (Hofmann et al., 2011). These substrate-specific variations are ecologically significant, particularly for calcifying species and pelagic zooplankton, given the growing concern over ocean acidification (Fabry et al., 2008). The benthic-pelagic coupling and local hydrodynamics, which can cause short-term fluctuation in carbon chemistry, may also have an impact on the geographic scale of pH variability observed in this study (Hofmann et al., 2010).

4.2 Zooplankton biovolume and abundance

The mean zooplankton biovolume in this study ranged from 0.37 ± 0.08 mL/m³ (SS12) to 2.38 ± 0.59 mL/m³ (SS8) and aligns with findings from the east coast (Huggett, 2014; Noyon et al., 2019). Huggett (2014) found that mesoscale oceanographic features have a major influence on zooplankton biovolume in the Mozambique Channel, with higher biovolume reported in the

cyclonic eddies due to nutrient-rich upwelling and lower biovolume in anticyclonic eddies where downwelling occurs. Similarly, Noyon et al. (2019) found that zooplankton biovolume in a young cyclonic eddy off southern Madagascar was higher in its centre, where upwelling increased primary productivity. The uThukela Banks forms the centre of the KZN Bight, which is considered more productive along the east coast of South Africa, mainly due to localised upwelling, riverine input from the uThukela River and transient cyclonic eddies (Lamont et al., 2016). Biovolume was significantly higher at stations over sand substrate than reef substrates. Most sand stations in this study, such as SS8, SS10, SS17, and SS18, were located closer to urban and estuarine-influenced areas like Durban Harbour, where higher chlorophyll-a and turbidity were observed. While this study did not evaluate the relationship between primary productivity and zooplankton biovolume, the co-occurrence of elevated chlorophyll-a and higher zooplankton biovolume at these stations suggests a potential link between localised productivity and zooplankton biomass. This pattern aligns with ecological understanding that areas influenced by terrestrial runoffs or upwelling support higher primary productivity and, as a result, secondary production (Longhurst & Harrison, 1989). In this study, turbidity ranged from 0.26 to 0.42 NTU, and chlorophyll-a ranged from 0.42 to 1.69 mg/m³, peaking at nearshore sand-dominated stations, consistent with higher biovolume patterns. In contrast, reefs dominate the northern and central shelf (SS3, SS4, SS6), which were located further offshore in clearer, and oligotrophic waters (Lamont et al., 2016). Similarly, stations located further offshore (SS1 and SS2) showed lower biovolume and lower chlorophyll-a concentration in this study. Although proximity to shore was not examined, the observed spatial gradient is consistent with previous studies along the KZN coast (Pretorius et al., 2016; Huggett, 2014), which have found nutrient and biomass decreases as distance from land-based sources or upwelling zones increases. Pretorius et al. (2016), found that zooplankton biomass dropped offshore due to lower concentrations of nutrients and chlorophyll-a. Huggett (2014) discovered a similar trend in the Delagoa Bight (mean 0.33 mL/m³, with a maximum of 1.9 mL/m³), where low zooplankton biovolume was linked to lower integrated chlorophyll-a levels offshore. Oliff (1973), also discovered that nutrient concentrations decrease with increasing distance from the shore.

In the KZN Bight, upwelling processes are driven by the interaction of the Agulhas Current with the shelf topography. However, nutrient inputs from rivers, such as the uThukela River, also play a role (Pretorius et al., 2016; Scharler et al., 2016a). This study found no significant difference in zooplankton biovolume between locations within and outside the MPA,

suggesting that the proposed MPA had yet to influence biovolume patterns. Attwood and Moloney (2001) suggested that establishing an MPA may affect zooplankton biovolume over time by increasing diversity, abundance and stability through reduced anthropogenic pressures and improving trophic interactions.

Zooplankton and meroplankton abundance differed significantly across sampled stations, with station SS17 having the highest abundance. The high abundance found at SS17, located outside the MPA near Durban, could be attributed to increased nutrient input from urban runoff and nearby river mouths, promoting primary production and supporting plankton growth (Froneman, 2011). Furthermore, the sandy substrate may promote the presence of certain benthic invertebrate larvae, contributing to increased meroplankton abundance (Beckley and van Ballegooyen, 1992). Zooplankton abundance also showed a significant difference between substrate with higher abundance observed over sand substrates than reef substrates. These results are consistent with the studies from South African coastal regions, such as those in the KZN Bight, where sand habitats tend to support greater planktonic productivity (Pretorius et al., 2016; Untiedt and MacKay, 2016). This is most likely due to sand substrates providing better foraging circumstances and lower predation pressures than reef ecosystems (Porter and Porter, 1977; Scharler et al., 2016). Sand substrates have a higher abundance of zooplankton (320.32 ± 248.69 ind/m³) than reef substrates (118.83 ± 89.62 ind/m³). This further supports this pattern, suggesting that sand environments provide more stable and nutrient-rich conditions, leading to higher zooplankton populations.

Meroplankton, which includes the early life stage of many marine species, showed a similar pattern, with significantly higher abundance over sand substrate (4.95 ± 3.88 ind/m³) than reef substrates (0.65 ± 0.27 ind/m³) (Figure 10B). These findings support the findings of Hutchings et al. (2002), who discovered that sand habitats in the Agulhas Current region provide essential resources for juvenile marine organisms, particularly those in their larval stage. Meroplankton larvae are often released from benthic invertebrates, many of which live in sandy substrate. Hence, sand habitats serve as a “nursery ground” with high larval supply (Stamhuis and Videler, 1988). In contrast, reef environments have dense aggregations of planktivorous fish, which significantly reduce larval survival through predation (Hixon and Beets, 1993). Furthermore, meroplankton abundance was significantly higher outside than inside the MPA, most likely reflecting underlying habitat conditions and historical patterns of human use rather than the effect of formal protection (Lester et al., 2009; Sink et al., 2011b). This pattern is closely

related to the higher abundance of sandy substrate outside the MPA, highlighting substrate type as an important driver of meroplankton distribution in the study area. In contrast, zooplankton abundance did not show significant variation between locations inside and outside the MPA, indicating that their distribution is strongly related to local habitat characteristics, such as substrate type, nutrient availability, and proximity to riverine input, rather than by protection status alone (Pretorius et al., 2016). Although meroplankton are a subset of zooplankton, their distribution appears more closely related to benthic habitat quality. This distinction emphasizes the importance of habitat-driven processes in shaping larval distributions, regardless of formal protection.

4.3 Community structure

The findings of this study provide important insights into the overall zooplankton and meroplankton community structure across different stations within and outside the MPA, as well as on various substrate types. Eleven zooplankton groups were identified, with Copepoda dominating the community, constituting more than 65% of the total zooplankton abundance (Table 2). This pattern was consistent inside and outside the MPA, highlighting the important role of Copepoda in the ecosystem, as they serve as key components in nutrient cycling and energy transfer within marine food webs (Turner, 2004). While Copepoda was the most abundant across all locations and substrates, there were some notable differences between the inside and outside of the MPA. Inside the MPA, Appendicularia accounted for 14% of the community, suggesting that the protected environment may favour species with specific feeding strategies, such as filter-feeding, which rely on the availability of planktonic particles (Gorsky & Fenaux, 1998). On the other hand, outside the MPA, Chaetognatha was the second-most abundant, contributing 6% to the total zooplankton abundance, possibly reflecting differences in food availability or predation pressures between these areas.

Substrate type had a clear influence on the zooplankton community structure. In the sandy substrate stations, Copepoda accounted for over 70% of the zooplankton community, which is consistent with previous studies by Melo et al. (2010), which discovered that sandy habitats generally support high Copepoda abundance due to less complexity in the substrate and fewer predators. In contrast, reef substrate stations supported a more diverse zooplankton community. Copepoda comprised 69% of the total community, and Appendicularia contributed 12%,

reflecting the greater complexity and resource availability in these habitats. This highlights the importance of substrate complexity in shaping zooplankton community composition (Scharler et al., 2016). The work of Roberts et al. (2016) also emphasised the importance of substrate type in structuring planktonic communities in coastal ecosystems. Location did not appear to have a substantial impact. This suggests that although zooplankton may find similar environmental conditions inside and outside the MPA, the physical characteristics of the substrate had a greater impact on community structure, supporting this finding.

There were fifty-one meroplankton taxa recorded, with Caridea being the most abundant group across all stations. While many taxa occurred in both locations (inside and outside MPA) their relative abundance varied notably. Inside the MPA, Portunidae (13.26%) contributed the second highest to the total community, followed by Alpheidae (5.46%) and Paguridae (5.44%). These findings indicate that the MPA may provide a more favourable environment for these meroplanktonic groups. Conversely, Callianassidae was the most abundant group outside the MPA, accounting for 16.35% of total meroplankton abundance.. These taxa are also recognised for their sediment-sorting activity (Stamhuis and Videler, 1998; Stapleton et al., 2001) and play an essential role in the mixing of organic-rich surface layers into subsurface sediments, emphasising their ecological value. The SIMPER analysis reflects the variations in meroplankton composition within and outside the MPA, with Caridea, Callianassidae, Portunidae, and Sergestidae contributing considerably to the dissimilarity between these areas. This is consistent with the findings of Brandão et al. (2015) and Landeira et al. (2010), who observed similar meroplanktonic taxa in different regions and suggested that both environmental and human impacts can influence meroplankton distributions.

The results from the PERMANOVA and SIMPROF analyses of meroplankton indicated that both location and substrate type had significant effects on meroplankton abundance. This suggests that the distinct differences in meroplankton composition between reef and sandy substrates, as well as location (inside/ outside the MPA), influence community structure in a meaningful way. However, the SIMPROF test revealed four significant clusters in the meroplankton data, with one cluster composed of reef stations outside the MPA. This suggests that while meroplankton community structure is primarily influenced by substrate type, there may also be small location-related differences that require further exploration.

The SIMPER analysis revealed that Callianassidae, Caridea, Paguridae, Pandalidae, Sergestidae, Portunidae, and Palaemonidae were the main contributors to dissimilarity between reef and sand stations in meroplankton composition, highlighting the different ecological roles these families play in different substrates (Table 9). In sandy habitats, Callianassidae was the dominant group, contributing 24.80% to the total meroplankton abundance, which may be related to their burrowing activity and role in sediment mixing, as noted by Stamhuis and Videler (1998) and Stapleton et al. (2001). In contrast, Portunidae was the second abundant on reef substrates, suggesting that the reef environment may provide different types of shelter and food resources, benefiting this group more than in sandy habitats (Stoner & Acevedo, 1990).

In this study, the observed pattern in meroplankton diversity metrics indicates that substrate type plays an important role in shaping community richness than geographical location. Specifically, the significant difference in species richness (S) and Margalef's richness index (d') between sand and reef substrates indicates that habitat heterogeneity strongly influences meroplankton diversity. Sand substrate supported higher richness values, likely due to increased organic input and sediment conditions that promote larval recruitment and settlement opportunities (Stamhuis & Videler, 1998; Melo et al., 2010). The insignificant differences in Shannon diversity and Pielou's evenness (J') across location and substrate suggests that while species numbers fluctuate, the relative abundance distribution remains stable, indicating a consistent community structure despite environmental variability (Magurran, 2004). These findings emphasise the significance of substrate complexity and sediment-associated processes in shaping meroplankton communities, supporting previous research on how benthic-pelagic coupling influences larval distribution patterns in coastal systems (Morgan et al., 2009; Brandão et al., 2015).

4.4 Environmental factors affecting zooplankton and meroplankton

Zooplankton are sensitive to environmental changes and respond quickly to disturbances in physio-chemical conditions (Pace, 1986; Joseph and Yamakanamardi, 2011; Jose et al., 2015). These variations are essential in shaping the diversity and abundance of aquatic species, emphasising the ecological significance of physio-chemical parameters. Environmental factors such as pH, chlorophyll-a, salinity, dissolved oxygen, and turbidity were identified as key

contributors to the observed pattern in zooplankton and meroplankton distribution. The DISTLM marginal test revealed that pH was the only environmental variable significantly influencing zooplankton abundance, accounting for 18% of the variance. This finding implies that pH influences zooplankton abundance, possibly due to its direct impact on physiological processes such as metabolism, reproduction, and survival (Pace, 1986).

Other variables such as temperature, salinity, turbidity, chlorophyll-a, and dissolved oxygen (DO) were found to contribute minimally and were not statistically significant in influencing zooplankton abundance. This suggests that, at least in the context of this study, the influence of these variables on zooplankton populations may be less pronounced compared to pH. It is possible that other, unmeasured environmental factors or interactions between variables could be influencing zooplankton distribution in ways not captured by the model.

The DistLM sequential test showed that pH, salinity, and turbidity were the main environmental factors influencing zooplankton abundance, explaining 18%, 14%, and 7% of the variation respectively, while the full model accounted for 51% of the variability (Table 6). These results reinforce the conclusion that physio-chemical conditions, particularly pH, play a substantial role in shaping zooplankton communities, likely due to their influence on metabolic and reproductive processes (Pace, 1986; Jose et al., 2015).

The dbRDA plot confirmed these findings, demonstrating that SS17, near Durban Harbour, was associated with higher pH and turbidity, whereas SS2 was associated with increased dissolved oxygen (Figure 9), indicating site-specific environmental impacts. Although the model described a moderate fraction of the variance, approximately half remained unexplained, indicating that other factors such as biological interactions or nutritional dynamics may also play a role (Roman et al., 2000; Moreno et al., 2012).

For meroplankton, the DISTLM marginal test identified pH as the only environmental variable significantly influencing abundance (Table 10), highlighting its pivotal role in shaping early life stages of benthic invertebrates. This aligns with previous findings that show how pH can directly impact larval development, survival, and physiological stress responses (Kurihara, 2008; Dupont and Thorndyke, 2009). The DistLM sequential test revealed that pH, temperature, salinity, and chlorophyll-a explained most of the variation in meroplankton abundance, with pH and temperature exerting the greatest influence (Table 11). This is

consistent with studies showing the vulnerability of early larval stages to pH and temperature fluctuations, which affect survival and development (Kurihara, 2008; Byrne, 2011). The dbRDA plot showed that salinity and pH distinguished stations SS16, SS17, SS18, and SS20, suggesting localized environmental influences on community structure (Figure 13B). However, other variables and substrate type had minimal impact, implying that physiochemical gradients rather than habitat type primarily drive meroplankton patterns (Pechenik, 2006; Qiu et al., 2020).

4.5 Conclusion

This study provides essential baseline data on zooplankton communities in the Thukela Bank pelagic zone, offering a crucial reference for systematic conservation planning along the KZN coast. Baseline data are important because they serve as a reference point against which future environmental changes and anthropogenic impacts can be measured, allowing for more informed and adaptive management decisions. By defining the zooplankton composition in the uThukela Bight, these findings can help to identify regions that need to be protected, thus contributing to the larger goal of conserving marine biodiversity in the region.

The study revealed significant differences in zooplankton and meroplankton abundance across stations and substrates (sand vs. reef), but no differences between locations inside and outside the MPA. Sand environments consistently exhibited higher zooplankton abundance than reef substrates, likely due to lower predation pressure and more stable, nutrient-rich conditions. These sites were also located downstream of the Agulhas Current, suggesting southward transport of zooplankton.

Among the environmental variables, pH was the primary driver of zooplankton community structure, explaining a significant portion of variability in abundance. Other factors, such as chlorophyll-a, dissolved oxygen, and salinity, had minimal impact on zooplankton dynamics. These findings highlight the complexity of the zooplankton community in the uThukela Banks, shaped by pH and substrate type.

This complexity underscores the need for conservation efforts that consider both habitat-specific dynamics and environmental drivers, particularly as ocean acidification may affect pH levels.

4.6 Limitations and suggestions for future research

This study had several limitations, which should be addressed in future research. Currents that were not accounted for are likely to have considerably impacted zooplankton distribution since they influence transport and spatial variability. Moreover, the overall fluidity of zooplankton communities, driven by ocean currents and biological turnover, means that community composition can change over a short period (days to months), and this study covered only a single sampling period. As a once-off survey, these results provide only a snapshot; therefore, long-term, high-frequency monitoring is required to capture seasonal and interannual variability and improve our understanding of plankton dynamics. The omission of fish larvae prior to analysis impacted abundance and biovolume data, leaving out an essential component of the zooplankton ecosystem. The lack of detailed identification guides for our region restricted identification of some taxonomic groups to lower levels. Key environmental factors such as nutrient fluxes and current dynamics were not assessed, reducing the explained variability of zooplankton community structure. Additionally, sampling sites inside and outside the MPA, and between reef and sand substrates, were not evenly distributed, potentially introducing bias into comparative analyses. However, some of the less represented categories still contributed significantly to other analyses, indicating that meaningful ecological patterns were detected despite the imbalance.

Furthermore, the limited sample size and spatial coverage restrict the generalisability of our findings and may affect how well these results can inform broader marine spatial planning efforts. The MPA studied was primarily designed around reef habitats, yet our results show that sandy substrates support higher zooplankton abundance, suggesting that protection measures may need to better incorporate these soft-bottom habitats to ensure comprehensive ecological representation. Routine, long-term sampling within and adjacent to MPAs is therefore essential to track changes in zooplankton communities over time, enabling improved evaluation of MPA effectiveness and more informed adaptive management.

Future research should include the current dynamics, finer mesh sizes, and DNA-based identification to improve taxonomic resolution and expand geographical and temporal scopes to compare sites within and outside MPAs along the KZN coast. Including fish larvae in analyses will provide a more complete picture of community dynamics, and MPA design should emphasise sand and mud habitats, which support significant zooplankton abundance. Finally, integrating additional environmental variables, including nutrient availability and sedimentation rates, will provide more insight into the ecological drivers of zooplankton dispersal and support conservation planning. Sedimentation influences habitat quality and plankton distribution, highlighting human impacts on soft-bottom habitats often underrepresented in current MPA designs.

CHAPTER 5: References:

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